



Modélisation systémique des performances des femelles de ruminants. Application au cas de la vache laitière.

Olivier Martin

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Olivier Martin. Modélisation systémique des performances des femelles de ruminants. Application au cas de la vache laitière.. Alimentation et Nutrition. AgroParisTech, 2009. Français. NNT : 2009AGPT0050 . pastel-00625801

HAL Id: pastel-00625801

<https://pastel.hal.science/pastel-00625801>

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N° / / / / / / / / / / / / /

THÈSE

pour obtenir le grade de

Docteur

de

**l'Institut des Sciences et Industries du Vivant et de l'Environnement
(Agro Paris Tech)**

Spécialité : Sciences Animales

*présentée et soutenue publiquement
par*

Olivier Martin

le 30 septembre 2009

MODELISATION SYSTÉMIQUE DES PERFORMANCES DES FEMELLES DE RUMINANTS

APPLICATION AU CAS DE LA VACHE LAITIÈRE

Directeur de thèse : Daniel SAUVANT



*Travail réalisé à l'UMR INRA-AgroParisTech Physiologie de la Nutrition et Alimentation
16 rue Claude Bernard 75231 Paris cedex 05, France*

Devant le jury composé de :

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Examineur
Examineur

*...à François, qui n'est plus là,
à Betty qui l'a toujours été,
à Gaïa qui va, qui court, qui s'envole...*

Remerciements

« Was mich nicht umbringt, macht mich stärker »

Friedrich Nietzsche

Je remercie Daniel Sauvant pour l'étincelle, la flamme et la lumière.

Je remercie tous ceux qui, de près ou de loin, pour un instant en passant ou assidûment depuis les premiers, ont porté un intérêt à ce travail ou à sa conduite.

Je remercie également, car je ne suis pas rancunier, tous ceux qui depuis longtemps ont substitué l'anodin « *Salut, comment ça va ?* » par le moins anodin « *Alors, cette thèse ?* ».

Je remercie surtout ma fille pour sa délicieuse ignorance du sens du mot thèse.

Résumé

Le travail de thèse décrit dans ce document s'articule autour de la construction d'un modèle de la vache laitière. Ce modèle consiste en trois modèles dynamiques, mécanistes et déterministes correspondant à des niveaux de représentation différents de la vache et présentant une fonctionnalité spécifique. Ces modèles, respectivement **téléonomique**, **énergétique** et **métabolique** s'agencent entre eux de façon hiérarchique et sont interdépendants (Figure 1).

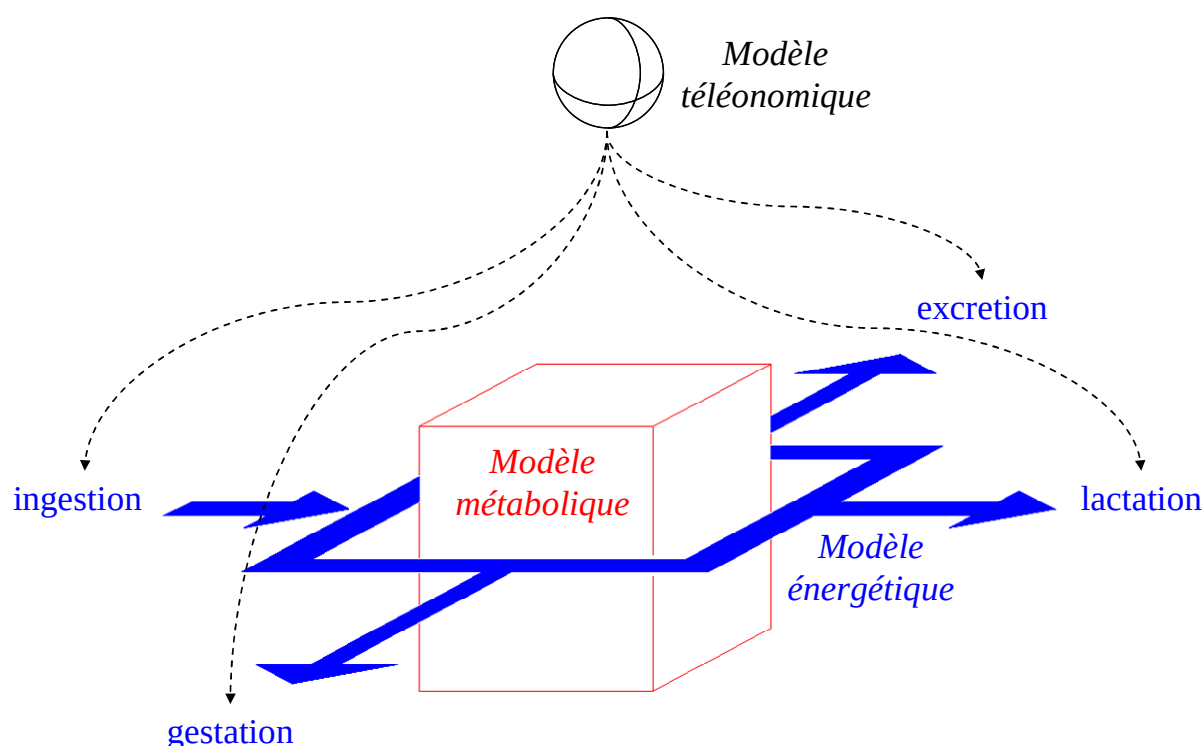


Figure 1 Agencement hiérarchique et connexion des modèles téléonomique, énergétique et métabolique,

Le modèle téléonomique (cf. Partie II.1) se situe au niveau de l'animal en tant qu'organisme vivant assurant sa survie et la pérennité de son espèce et possède une fonction de pilotage du modèle énergétique. Il s'agit d'un modèle de la **dynamique des priorités** d'une femelle entre les fonctions de croissance, de gestion des réserves corporelles et de reproduction au cours de sa vie rythmée par la succession de cycles de reproduction. Ce

modèle produit une trajectoire de référence et contrôle le modèle énergétique à travers deux voies traduisant l'homéorhèse et l'homéostasie.

Le modèle énergétique (*cf.* Partie II.2) se situe au niveau du métabolisme énergétique de l'animal et possède une fonction de prédiction des performances. Il s'agit d'un modèle de la **dynamique de partition de l'énergie** ingérée entre les flux de croissance, d'entretien, de gestation, de lactation et de mobilisation et stockage des réserves corporelles. Ce modèle simule la production et la composition laitière, la croissance fœtale et le poids du veau à la naissance, l'ingestion, et les variations de masse et de composition corporelle de la vache au cours de sa vie et durant les cycles gestation/lactation.

Le modèle métabolique (*cf.* Partie II.3) se situe au niveau du métabolisme inter-organes et possède une fonction d'interprétation métabolique des flux de matière du modèle énergétique. Il s'agit d'un modèle de la **dynamique des flux** de glucose, d'acides aminés, d'acétate/butyrate, de propionate, de triglycérides et d'acides gras non-estérifiés conditionnés par les flux de matière du modèle énergétique au cours de la lactation (production de lait, ingestion, variations de réserves). Ce modèle simule les teneurs en triglycérides du foie et des métabolites circulants dans le plasma au cours de la lactation.

Si l'implémentation de la connexion entre les modèles téléonomique et énergétique est effective, celle entre les modèles énergétique et métabolique n'est pas formellement réalisée. Elle est ici uniquement mise en perspective dans la mesure où ces modèles sont techniquement compatibles. L'agencement hiérarchique des trois modèles forme un ensemble conceptuel cohérent présenté comme une étape de travail dans un projet global.

L'introduction de ce document positionne le contexte et les objectifs de ce travail. La première partie de ce document présente le projet de modélisation qui fonde ce travail à travers ses enjeux (*cf.* Partie I.1), les points de vue adoptés pour la représentation du « système vache laitière » (*cf.* Partie I.2) et les éléments de connaissances mobilisés (*cf.* Partie I.3). La deuxième partie de ce document concerne la description du modèle proposé à travers celle des trois sous-modèles qui le composent : modèle téléonomique des priorités, modèle énergétique prédictif des performances zootechniques et modèle métabolique explicatif des flux de métabolites. La conclusion de ce document contient des propositions d'amélioration, d'extension et d'utilisation du modèle ainsi que des perspectives de travail.

Abstract

The work described in this document is centred on the building of a dairy cow model. The whole model is composed of three dynamic, mechanistic and deterministic models corresponding to three different levels of representation of the cow. Each model has a specific functionality. These models, respectively denoted **teleonomic**, **energetic** and **metabolic** are linked through a hierarchical structure and are interdependent (Figure 1bis).

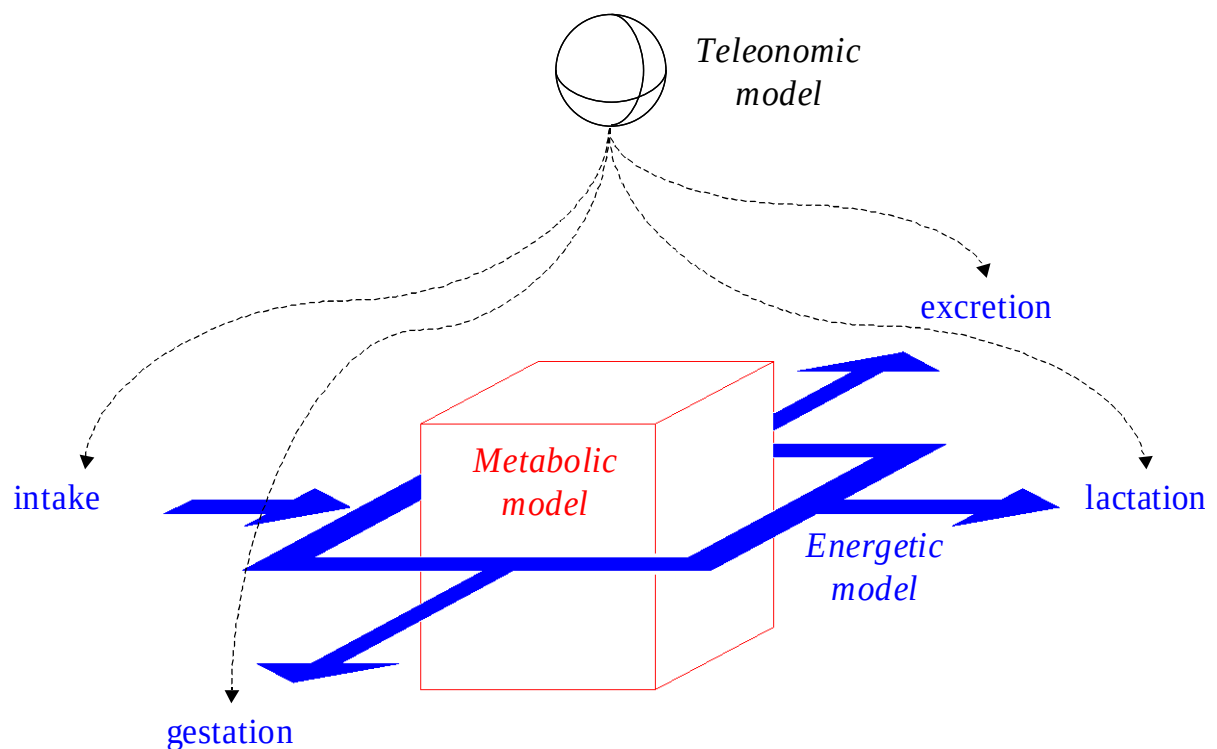


Figure 1bis Hierarchical layout and connection of the teleonomic, energetic and metabolic models,

The teleonomic model (*cf.* II.1) consists in a representation of the animal seen as a living organism ensuring its own survival and the continuation of its species. This model is aimed at driving the energetic model. The model describes the **dynamic of the priorities** of a female mammal between functions of growth, body reserve monitoring and reproduction along its lifetime punctuated by successive reproductive cycles. This model produces a reference trajectory used to control the energetic model through two paths corresponding to homeorhesis and homeostasis.

The energetic model (*cf.* II.2) consists in a representation of the animal energetic metabolism and is aimed at predicting performance. The model describes the **dynamic partitioning of energy** between flows for growth, maintenance, gestation, lactation and body reserves mobilization and storage. The model simulates milk yield and composition, foetal growth and calf birth weight, intake and changes in body mass and composition of a dairy cow throughout lifetime and during reproductive cycles.

The metabolic model (*cf.* II.3) consists in a representation of the animal metabolism at the inter-organ level and is aimed at interpreting performance predicted by the energetic model as metabolites flows. The model describes the **dynamic of flows** of glucose, amino acids, acetate + butyrate, triacylglycerides and non-esterified fatty acids associated with material flows of the energetic model during lactation (milk yield, intake, body weight changes). The model simulates liver triacylglycerides and plasma metabolites contents during lactation.

The connexion between the teleonomic and energetic models is effective, but that between the energetic and metabolic models has not been formally done but only put into perspective since these two models are technically compatible. The hierarchical layout of the three models forms a consistent set proposed as a stage of work in a whole modelling project.

The introductive part of this document presents the context and the objectives. The first part of this document presents the modelling project through its stakes (*cf.* I.1), the view points adopted for the representation of the “*dairy cow system*” (*cf.* I.2) and the mobilized elements of knowledge (*cf.* I.3). The second part of this document concerns the presentation of the proposed whole model through the description of the three sub models: teleonomic model of priorities, energetic model of animal performance and metabolic model of metabolites pathways. The conclusive part of this document contains perspectives of improvement, extension and use of the model as well as outlooks of work.

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Introduction

« Il n'y a de réel que dans une relation toujours locale et précaire entre un observateur (plus exactement sa conscience), des observés et des instruments d'observation »

Jean-Paul Baquias

Contexte

Ce travail s'inscrit dans un contexte de profondes mutations de l'élevage des animaux domestiques et en particulier des **bovins laitiers**. L'élaboration de produits animaux destinés à être utilisés par l'homme n'est plus aujourd'hui la seule composante de l'activité d'élevage. Son enracinement à un territoire fait d'hommes et de paysages ; le statut de l'animal comme être sensible, organisme génétiquement modifiable et produit traçable ; les enjeux de compétitivité à l'échelle mondiale et de durabilité des systèmes d'élevage et des filières ; l'évolution des paysans devenus techniciens, entrepreneurs ou encore gestionnaires d'écosystèmes ; les obligations de respect des attentes sociétales, des demandes des consommateurs et des normes sanitaires et environnementales ; les objectifs de maîtrise de la qualité des produits et des pratiques. Ces aspects sont autant de contraintes à intégrer par la Recherche, dans la mise au point raisonnée, l'évaluation et la promotion de techniques et de systèmes d'élevage innovants.

Une conséquence fondamentale de cette multiplication des dimensions à mettre en perspective est le **changement de paradigme** de la nutrition animale ayant émergé à la fin du XX^{ème} siècle. L'objectif central, inscrit dans un schéma productiviste, de couverture des besoins nutritionnels pour l'expression maximale par l'animal d'un potentiel génétique n'est plus qu'une composante de l'objectif global de compréhension et de **prédiction des réponses multiples** des animaux aux régimes et pratiques alimentaires (Sauvant, 1992¹). Les dimensions de production, d'efficacité, de rejets, de qualité des produits, de santé et de bien-être sont ainsi considérées comme une résultante globale du fonctionnement de l'animal (Dormont *et al.*, 2000²). Cette approche s'inscrit dans la problématique scientifique de flexibilité des réponses animales avec pour orientation pratique l'idée de leur pilotage par l'alimentation. Ce changement de paradigme traduit une modification essentielle de la représentation de l'animal d'élevage dont le statut évolue dans un premier temps de celui d'« *unité de production* » dont on optimise les performances à celui d'« *entité de gestion* » dont on maîtrise le fonctionnement. Les travaux scientifiques actuellement en essor autour des

¹Sauvant, D., 1992. Systemic modeling in nutrition. *Reproduction Nutrition Development* 32, 217-230.

²Dormont, D. et le groupe de travail « Alimentation animale et sécurité sanitaire des aliments ». *Rapport du groupe de travail « alimentation animale et sécurité sanitaire des aliments »*. [en ligne], Maisons-Alfort : AFSSA, 27 juillet 2000, [référence du 8 janvier 2008]. <http://www.afssa.fr/>

capacités d'adaptation des animaux aux évolutions des conduites, autour du bien-être animal, mais aussi en génomique, en protéomique, en métabolomique et globalement autour de la biologie intégrative tendent à prolonger cette évolution du schéma de représentation de l'animal d'élevage. Du point de vue zootechnique, l'animal redevient « *organisme vivant* » à part entière, être sensible, hautement régulé, génétiquement déterminé, élaborant des phénotypes et des produits par des processus physiologiques s'articulant de façon intégrée depuis les gènes jusqu'aux fonctions. Du point de vue conceptuel, cette évolution se traduit par une représentation de l'**animal en tant que système complexe**. D'une manière générale, les orientations de recherches agronomiques s'organisent aujourd'hui autour d'un enjeu central et fédérateur : convoler avec la complexité du vivant.

Approche

La prise de conscience de la complexité (*e.g.*, du cosmos, des organismes vivants, des sociétés humaines, des systèmes artificiels de facture humaine) s'est accompagnée au XX^{ème} siècle du développement de l'**approche systémique** (De Rosnay, 1975³). Les objets complexes sont réfractaires à l'approche cartésienne classique reposant sur un schéma de causalité linéaire et par laquelle la complexité est réduite à ses composants élémentaires. L'approche systémique propose un schéma de représentation du réel qui permet l'étude du fonctionnement des systèmes dans leur ensemble. Elle consiste en une démarche globale et interdisciplinaire qui s'attache aux échanges entre les parties du système et qui raisonne par rapport à l'objectif du système.

La systémique est une discipline différenciée avec différents niveaux d'analyse s'attachant à l'ontologie des systèmes (en tant que représentation de la connaissance), à leur technologie (cybernétique, théorie de l'information, théorie des jeux, etc.) et à la science des systèmes dans le cadre d'une théorie générale des systèmes (Von Bertalanffy, 1968⁴) ou de l'étude de systèmes particuliers, comme les systèmes biologiques. Ses domaines d'applications sont extrêmement variés en biologie, mais aussi en sciences humaines, sociales et économiques et en informatique.

³ De Rosnay, Joël, 1975. *Le Macroscopie. Vers une vision globale*. Paris : Le Seuil (col. Points), 305 p.

⁴ Von Bertalanffy, Ludwig, 1968. *General System Theory : Foundations, Development, Applications*. New York: Georges Braziller (traduction française : *Théorie Générale des systèmes*. Paris : Dunod, 1973, 295 p.

Le concept moderne de système sur lequel repose les développements de la Systémique s'est forgé principalement à travers les travaux de Ludwig Von Bertalanffy (biologiste, fondateur de la Théorie Générale des Systèmes dès 1937), de John Von Neumann (mathématicien, fondateur de la Théorie des jeux en 1944), de Norbert Wiener (mathématicien, fondateur de la Théorie de la communication ou Cybernétique en 1947), mais aussi de Claude Elwood Shannon (ingénieur électricien, fondateur de la Théorie de l'information en 1948), de Warren Sturgis McCulloch (neurophysiologiste, inventeur de la bionique), et de Jay Wright Forrester (ingénieur électricien, fondateur de la Théorie de la Dynamique des Systèmes dans les années 50).

Le découpage systémique peut se révéler arbitraire et non-univoque. Sa réalisation relève du principe de pertinence selon lequel : « *Toute description sera acceptable à condition qu'elle soit cohérente, c'est-à-dire qu'elle soit faite d'un point de vue déterminé. Une fois ce point de vue adopté, certains traits, dits pertinents, sont à retenir : les autres, non pertinents, doivent être écartés résolument* » (Martinet, 1967⁵).

La démarche systémique est mise en œuvre à travers le processus technique de **modélisation** qui dans son sens général correspond à la transcription abstraite d'une réalité concrète. Ce processus est une démarche itérative et heuristique d'agrégation de connaissances dans un formalisme mathématique, appliquée à un objet d'étude aux contours définis et associée à un objectif fixé qui prescrit la nature et l'ampleur de la tâche.

L'approche systémique et la modélisation, en tant que filtres d'analyse pour extraire, synthétiser et diffuser de la connaissance, permettent de mener une action qui s'inscrit parfaitement dans les missions de l'INRA (Goffinet *et al.*, 2004⁶). La modélisation en sciences animales a déjà fait ses preuves depuis une trentaine d'années et constitue indiscutablement un levier de progrès.

La philosophie générale et la méthodologie de la Systémique sont adoptées pour la réalisation de ce travail focalisé sur une représentation de l'animal en tant que système.

⁵ Martinet, André, 1967. *Éléments de linguistique générale*. Paris : Librairie Armand Colin, 217 p.

⁶ Goffinet, B. et le groupe de réflexion Modélisation. *La modélisation à l'INRA*. [en ligne], Paris : INRA, 2006, [référence du 25 avril 2007]. http://www.inra.fr/mia/doc/rapport_modelisation_VO.pdf

Objectif

L'objectif central de ce travail de thèse est le développement d'un **modèle mathématique de la femelle en lactation**, en se focalisant sur la **vache laitière** pour des raisons de disponibilité de données et d'importance pratique. Cet objectif se décline à trois niveaux : la représentation des mécanismes de régulation, la prédiction des performances zootechniques et l'intégration des principaux flux métaboliques.

L'attention est centrée sur l'animal dans son ensemble considéré comme l'unité productive du système d'élevage et modélisé en tant qu'entité biologique active (Friggens and Newbold, 2007)⁷, exprimant au cours de sa vie un potentiel génétique dans un environnement fluctuant, défini dans son milieu d'élevage par le système d'alimentation.

Un des enjeux de ce travail est d'intégrer des mécanismes clefs de régulations à l'origine des **capacités adaptatives** des bovins femelles. Ces régulations sont en particulier envisagées comme le déterminant de la flexibilité des réponses productives aux variations du régime alimentaire (Bocquier *et al.*, 2004⁸). Un autre enjeu concerne l'incorporation de paramètres dont les variations sont destinées à simuler la **variabilité génétique** entre les animaux. Ces clefs de modulation du fonctionnement du modèle doivent permettre d'ouvrir la porte à des connections avec les travaux de généticiens (Doeschl-Wilson *et al.*, 2007)⁹ et de développer un modèle à l'échelle du troupeau composé d'une collection de modèles présentant des spécificités individuelles. Enfin, ce travail propose une exploration de différents niveaux de représentation de l'animal conduisant à différentes approches de modélisation complémentaires.

Le modèle est envisagé à la fois comme un outil d'intégration des connaissances sur les processus biologiques déterminant l'élaboration des produits animaux et un outil de simulation des réponses productives à différents scénarii de conduite d'élevage. Ces finalités sont en parfaite cohérence avec les enjeux et missions du département PHASE de compréhension du fonctionnement animal et d'évaluation des pratiques.

⁷ Friggens, N.C. and Newbold, J.R., 2007. Towards a biological basis for predicting nutrient partitioning: the dairy cow as an example. *Animal* 1, 87-97.

⁸ Bocquier, F., Blanc, F., Agabriel, J. and Chilliard, Y. Régulations biologiques de la composante animale des systèmes d'élevage. In : Chia, E., Dedieu, B., Moulin, C. H. & Tichit, M. (éd.), *Transformation des pratiques techniques et flexibilité des systèmes d'élevage*, Montpellier, France, 15-16 mars 2004. Montpellier : INRA SAD TRAPEUR, Agro M., 2004.

⁹ Doeschl-Wilson, A.B., Knap, P.W., Kinghorn, B.P. and Van der Steen, H.A.M., 2007. Using mechanistic animal growth models to estimate genetic parameters of biological traits. *Animal* 1, 489-499.

Partie I Projet de modélisation

« Quand un bon sculpteur modèle des corps humains, il ne représente pas seulement la musculature, mais aussi la vie qui les réchauffe »

Auguste Rodin

1 Enjeux

Ce chapitre présente les enjeux de ce travail et introduit les idées clefs qui structurent la démarche.

Le principal objectif de la construction d'un **modèle de la vache** est de produire un **outil de simulation des performances** d'un animal évoluant au cours de sa vie dans un environnement d'élevage.

Cet objectif positionne la problématique de modélisation des performances au niveau de la **prédiction** de la dynamique des variables d'intérêt zootechniques, principalement la quantité de lait produit et sa composition, la quantité d'aliments ingérés mais aussi la taille et la composition de sa masse corporelle. D'autres variables peuvent être considérées telles que celles relatives à la reproduction de l'animal (fertilité, durée de gestation, poids du veau, ...), à ses rejets (émission de gaz et excrétion d'excréments), à sa consommation d'eau, ses échanges de chaleur, son état sanitaire, etc.

Cet objectif de modélisation s'attache à répondre à la question « **combien ?** ».

Il existe différentes voies possibles pour produire une réponse à cette question. Une approche, dite mécaniste s'attache à modéliser les phénomènes biologiques sous-jacents à l'élaboration des performances. Cette voie interroge la question du « **comment ?** » et la performance est considérée par agrégation de modèles à des niveaux sous-jacents. Le corpus des connaissances actuelles sur le fonctionnement biologique de l'animal est probablement encore insuffisant pour y parvenir. Une autre approche, dite empirique propose une reproduction du fonctionnement global de l'animal. Cette voie propose directement une mise en équation du « **combien ?** ». La performance est alors envisagée comme une sortie en réponse à une entrée, qu'il s'agisse par exemple de la quantité de lait produit en fonction de la quantité d'aliments ingérée (dans une perspective de simulation) ou à l'inverse de la quantité d'aliments ingérée en fonction de la quantité de lait produit (dans une perspective de recommandation). Ces questions du « **combien ?** » et du « **comment ?** » opposent la reproduction du fonctionnement global d'un système objet d'étude à la représentation des

déterminants de son fonctionnement. Une autre approche possible s'attache à appréhender la finalité du système à travers la question du « ***pourquoi ?*** » (Friggens and Newbold, 2007).

Un enjeu de ce travail de thèse est d'explorer et de mettre en relation ces différentes voies à travers un montage original formant un modèle à l'échelle de l'animal composé de trois modèles connectés, chacun étant spécialisé pour un objectif : gouverner, prédire et expliquer. Dans ce modèle hybride, le « ***pourquoi ?*** » permet de construire la réponse à la question « ***combien ?*** » et le « ***combien ?*** » fonde l'examen de la question du « ***comment ?*** ».

La problématique de construction d'un modèle de prédiction des performances au niveau animal peut se réduire à la celle de la modélisation de la **partition des nutriments** entre les fonctions physiologiques. Cette question mobilise des efforts de recherche en sciences animales depuis plus d'un demi-siècle. La figure ancienne reportée par Kerth (2005) propose un schéma générique décrivant la modulation des quantités de tissus adipeux, musculaire et osseux par le niveau d'alimentation. Ce schéma est explicitement présenté comme un modèle de **priorité** pour les nutriments (Figure 2). L'idée d'ordre de priorité entre les tissus apparaît ici comme une composante du mécanisme de régulation assurant la survie de l'individu dans une situation de restriction alimentaire.

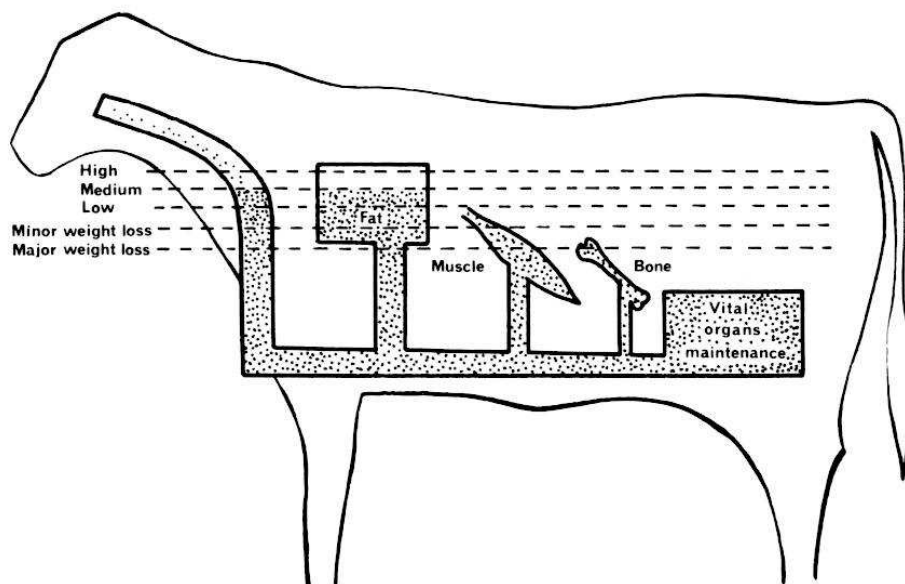


Figure 2 Cité par Kerth (2005): *Fig. 2.18 A model of priorities for nutrients during growth at any rate or during body weight loss.*

Le schéma de Owen (1978) décrit le principe de la partition des nutriments chez la vache sous un angle mécanique (Figure 3) à l'aide d'une valve de partition qui représente les

chemins possibles de l'apport alimentaire vers le lait ou les réserves, et la contribution éventuelle des réserves pour assurer la sortie vers le lait. Cette valve représente l'opération de régulation à même d'être réalisée, selon la priorité pour les chemins.

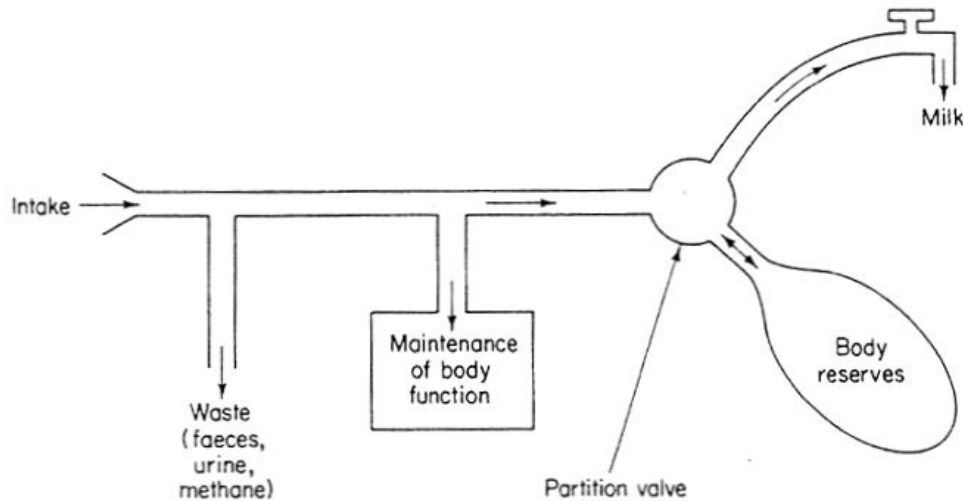


Figure 3 Owen (1978): Figure 11.1 Model cow.

Ces représentations illustrent la problématique centrale en nutrition animale de la partition des nutriments entre fonctions physiologiques : comment cette partition est-elle modulée selon l'alimentation ? comment évolue-t-elle au cours de la vie de l'animal, selon son état physiologique, son génotype ?

Un enjeu de ce travail de thèse est de proposer une approche globale pour tenter de répondre à ces questions à travers laquelle la partition des nutriments déterminant les performances correspond à la **trajectoire de vie d'un génotype à travers un environnement alimentaire**.

La production d'un modèle de prédiction des performances implique une exigence de fiabilité. Un modèle doit être capable de reproduire des situations observées et capable de prédire des situations inexplorées. Ce second point est fondamental. La démarche classique de construction d'un modèle repose sur sa calibration, c'est-à-dire sa mise en conformité avec des observations, puis sa validation, c'est-à-dire sa confrontation à d'autres observations pour évaluer l'étendue de son domaine de validité. Des exemples typiques concernent le type d'aliment, le stade physiologique, la race, etc. D'une manière générale, l'objectif est de produire un **modèle générique** qui demeure valable quelque soit le génotype de l'animal, quelque soit l'environnement dans lequel il évolue et quelque soit son état physiologique. Une

solution souvent mise en œuvre consiste à produire une structure générale du modèle et à proposer des paramétrages spécifiques selon le contexte (modèle de croissance selon la race, coefficient d'efficacité énergétique selon la fonction, etc.). Une autre option consiste à se focaliser sur les déterminants du fonctionnement biologique de l'animal. Plutôt que de représenter les réponses associées à une série de contextes, l'idée est de représenter directement les mécanismes de modulation de la réponse à des variations du contexte, c'est-à-dire les **régulations**. L'ambition d'étendre le domaine de validité des modèles et la volonté de reproduire au mieux le fonctionnement des organismes vivants, systèmes complexes hautement régulés, ont naturellement conduit différents auteurs à proposer des modèles de régulations.

Dans sa définition la plus large, le concept de régulation renvoie aux notions d'interaction entre éléments instables, de critère ou de repère, et de comparateur. C'est Lavoisier qui importe le mot « *régulateur* » de la mécanique vers la physiologie animale au XIX^{ème} siècle avant que le mot « *régulation* » ne soit par la suite proposé. Dans le Premier Mémoire sur la Respiration des Animaux (Lavoisier et Seguin, 1789), Lavoisier écrit : « *la machine animale est principalement gouvernée par trois régulateurs principaux* », (respiration, transpiration, digestion) empruntant clairement au domaine de la mécanique le concept de fonction d'équilibre dans le vivant. Claude Bernard utilise lui aussi des métaphores d'inspiration mécanique lorsqu'il évoque le mode de « *vie oscillante* » des animaux supérieurs ou lorsqu'il développe le concept de constance du milieu intérieur: l'animal est en relation avec son milieu « *de façon telle que son équilibre résulte d'une continuelle et délicate compensation établie comme par la plus sensible des balances* » (Bernard, 1878). Il est aujourd'hui acquis que la régulation est le *fait biologique* par excellence, impliquée dans le fonctionnement du vivant depuis la morphogénèse jusqu'à l'adaptation aux conditions du milieu. Le principe de régulation repose sur l'existence d'une norme, la détection des déviations par rapport à la norme et l'activation des mécanismes de rétablissement de la norme. L'étude interdisciplinaire de la structure des systèmes de régulation est le principal objet de la **cybernétique**. Cette science se focalise sur les interactions entre systèmes gouvernant et gouverné, au niveau desquelles s'organisent des boucles de circulation d'information. L'angle d'attaque scientifique de la question des régulations se situe à un niveau biomoléculaire impliquant la description du comportement de récepteurs, les transports d'ions, l'activation d'enzymes, etc. Les connaissances actuelles sur ces mécanismes sont insuffisantes pour être agrégées au niveau d'un modèle à l'échelle de l'animal entier. Classiquement, les travaux de

modélisation de l'animal ont ainsi eut recours à des approches théoriques pour injecter dans des modèles des fonctions de régulations ajustant leur comportement à des contextes variables. Dans la définition de la fonction de régulation comme fonction de préservation de l'intégrité d'un tout, ou encore fonction de maintien d'un bon fonctionnement, d'une constance, d'un équilibre, la notion de **norme** est centrale. Les mots « *intégrité* », « *bon* », « *constance* », « *équilibre* » évoquent la même idée d'une norme sous-jacente. Pour Cannon (1932), cette norme est un état et l'**homéostase** est la propriété régulatrice associée à son rétablissement. Pour Waddington (1957), cette norme est une trajectoire et l'**homéorhèse** est l'extension dynamique de l'homéostase. Waddington utilise le terme « **chreod** » pour nommer cette trajectoire qui représente la norme comme le déroulement d'un ensemble de phénomènes. Le terme « *chreod* » fixe ainsi le concept déterministe de norme, support des régulations. Cette trajectoire est par ailleurs envisagée comme une composante génétique de l'individu.

Un enjeu de ce travail de thèse est de proposer une approche qui incorpore une représentation des propriétés d'homéorhèse et d'homéostase et la représentation du concept de norme comme trajectoire de référence des performances. Cette notion de référence exprimant l'idée d'une trajectoire dans un environnement sans contraintes. Cette approche propose de faire évoluer la mise en équation des performances (P) à travers la somme d'un effet du **génotype** (G), de l'**environnement** (E) et de leur interaction ($P = G + E + G * E$) vers une fonction globale de la forme $P = f(G, E)$.

La prédiction des performances de l'animal est classiquement envisagée de façon cloisonnée en se focalisant sur une fonction : croissance, lactation, gestation, ingestion. Un enjeu de ce travail est de proposer une approche holistique qui appréhende les interactions entre ces fonctions en envisageant leur signification en tant que composantes d'un processus unique de **survie de l'organisme pour la pérennité de son espèce**.

Un autre cloisonnement classiquement effectué dans les approches de modélisation concerne la race (laitière ou bouchère) ou l'espèce (bovin, ovin, caprin, etc.). Un enjeu de ce travail est de proposer une approche générique concernant une femelle de mammifère. L'adoption d'un point de vue générique et la focalisation sur les mécanismes moteurs de régulation est envisagée comme une option à même d'étendre la validité du modèle développé.

Ce travail propose enfin de faire coexister des considérations théoriques pour l'élaboration des modèles avec le recours à de nombreuses données bibliographiques pour en garantir la fiabilité. L'enjeu étant de mettre en conformité la plage de variation des sorties des modèles avec celle émergeant de la compilation de bases de données.

L'enjeu clef de ce travail est de tendre non plus à la réalisation d'un autre modèle compilant une série d'équations mais vers la réalisation du prototype d'un **animal virtuel**, défini comme un modèle de l'animal dans son ensemble, contenant sa propre norme de fonctionnement, ses propres mécanismes d'adaptation aux contraintes alimentaires et ses propres traits d'expression d'une variabilité individuelle.

2 Système objet d'étude

Ce chapitre présente les points de vue adoptés dans de ce travail pour la représentation de l'animal et qui fondent la construction des modèles. La représentation procède par des décompositions dont les lignes de coupe relèvent dans certains cas de l'arbitraire et d'un point de vue personnel envisagé comme une alternative aux positions classiques.

L'organisme dans son ensemble est envisagé à travers trois niveaux de représentation reposant sur une conception de l'animal en tant que processus finalisé, en tant qu'interface physique et en tant que machine biologique. Cette décomposition permet de considérer les trois composantes essentielles qui instituent la représentation de l'animal sous forme d'un système: la coordination de son fonctionnement pour la réalisation d'un but, la subordination de son fonctionnement à des échanges avec le milieu de vie et l'organisation de son fonctionnement à travers différents niveaux hiérarchiques constitués d'éléments en interaction.

Conceptuellement, cette démarche de représentation chemine depuis un point de vue en « *boîte noire* »¹⁰ pour lequel l'animal est une entité fonctionnelle vers un point de vue en « *boîte blanche* » au sein de laquelle s'organise sa fonctionnalité.

2.1 L'animal en tant que processus

Une caractéristique fondamentale du vivant est sa disposition à se multiplier dans l'espace et se perpétuer dans le temps. Cet énoncé trivial contient la base à partir de laquelle est élaboré le premier niveau de représentation de l'animal. Dans cette perspective, un organisme est envisagé comme un processus par lequel la continuité du vivant est assurée. Son existence replacée aux échelles de la population et de la génération joue le rôle d'un relais. Cette représentation donne un sens au fonctionnement biologique de l'individu dans sa dimension de véhicule de la forme de vie dont il est un représentant. Son existence individuelle est

¹⁰ Termes utilisés par Norbert Wiener : un point de vue « black box » s'intéresse aux entrées et aux sorties du système vu comme un élément dans son environnement ; un point de vue « white box » s'intéresse aux éléments internes du système et aux déterminants de son fonctionnement.

aliénée à une condition de vecteur de la pérennité de ce qu'il est, et sa survie est un moyen d'assurer la survie d'une substance dont il n'est que porteur, de la vie dont il n'est qu'une expression. Cette vision de l'organisme réduit à un processus de continuation est l'angle classique des travaux sur l'évolution des espèces. L'individu est le vecteur de transmission du patrimoine génétique de l'espèce d'une génération à l'autre. Au sein d'une population, il représente une variante particulière soumise à la sélection naturelle et ouvre un chemin possible pour l'évolution de l'espèce à laquelle il appartient.

La considération de l'individu en tant que matériau d'expression et de propagation d'une information permet de concevoir le fonctionnement biologique de l'individu à travers un but. L'animal est vu comme un processus finalisé et ce point de vue place la reproduction comme une finalité principale. Le terme téléonomie (du grec *telos* : fin et *nomos* : loi) désigne le concept scientifique de finalité. Cette notion repose sur un postulat d'objectivité qui reconnaît le caractère téléonomique des êtres vivants et admet que « *dans leurs structures et performances, ils réalisent et poursuivent un projet* » (Monod, 1970).

La conception téléonomique du vivant ouvre la perspective d'une vision globale de l'organisation biologique, nécessité soulignée par Cornish-Bowden (2007) face à l'accumulation de données expérimentales issues de la protéomique et à la quasi-absence d'un cadre général interrogeant la nature même de la vie pour organiser cette connaissance. Cet auteur rappelle que la question « *qu'est-ce que la vie ?* » posée par Erwin Schrödinger en 1944 n'a mobilisé au cours de la seconde moitié du XX^{ème} siècle que peu d'intérêt scientifique, la question du « *comment ?* » accaparant les esprits et sollicitant les avancées technologiques.

La notion de finalité est par ailleurs fondamentale en systémique. Dans ses origines communes avec la cybernétique, la systémique est définie comme la science des organisations finalisées (Wiener, 1948) et la définition de système proposée par Joël de Rosnay (1975)¹¹ incorpore explicitement la notion fondamentale de but en fonction duquel s'organisent les éléments du système. Dès Aristote (330 av. J.C.), la « *cause finale* » est identifiée comme une des composantes de la compréhension méthodique des objets du monde.

¹¹ Un système est défini par Joël de Rosnay (1975) comme « *un ensemble d'éléments en interaction dynamique, organisé en fonction d'un but* ».

L'idée centrale de la représentation de l'animal en tant que processus est d'assumer l'existence d'une finalité et d'en proposer une formalisation à travers un ensemble de forces motrices pilotant le fonctionnement de l'organisme dans son ensemble. L'utilisation du terme processus permet d'agréger différentes composantes clefs : celle d'une suite continue d'opérations élémentaires, celle de mode opératoire, de façon de faire et celle de résultat déterminé.

L'animal en tant que processus est vu à travers un enchaînement de phénomènes biologiques selon un schéma dynamique qui organise la réalisation d'un but. L'animal-processus est ainsi résumé en la trajectoire d'un génotype à travers un environnement potentiellement contraignant. Cette trajectoire constitue un chemin nécessaire, référence qui tend à être privilégiée dans la mesure du possible et constitue un chemin optimal, équilibre qui tend à être retrouvé lorsque des déviations sont imposées par le milieu. Dans le domaine de la biologie du développement, le terme « *chreod* » a été proposé par Waddington (1957) pour définir ce concept de trajectoire et introduire la propriété d'homéorhèse qui désigne les mécanismes de retour à cette trajectoire. Près d'un siècle après l'intuition de Claude Bernard (1865) qui identifie le maintien d'un état d'équilibre physiologique interne comme une composante fondamentale du vivant, Waddington établit un cadre conceptuel pour décrire les systèmes vivants. L'homéorhèse est ainsi définie comme une extension de la propriété d'homéostasie proposée par Cannon (1929 ; 1932) et désignant les mécanismes de retour à un état d'équilibre physiologique. Waddington capture l'idée que les organismes ne tendent pas simplement à maintenir un état mais un enchaînement dynamique d'états, c'est à dire une trajectoire. En sciences animales, la notion de finalité est mobilisée pour formaliser les mécanismes de régulation (Sauvant, 1994), classiquement décomposés en termes d'homéostasie et d'homéorhèse (Bauman and Currie, 1980).

La représentation de l'animal en tant que processus finalisé repose sur ce concept de trajectoire. La finalité est traduite en une trame pour y aboutir et cette trame est utilisée pour diriger le fonctionnement physiologique de l'animal. Elle incarne un pilotage, un contrôle biologique centralisé, rationalisé et finalisé. Ce pilotage, placé à un niveau d'organisation supérieur est ensuite différencié pour moduler son effet à des niveaux d'organisation inférieurs et représenter des contributions indirectes à la finalité globale de survie de l'espèce.

La formalisation de cette trame repose sur la définition de priorités associées à des phénomènes biologiques élémentaires. Chacune de ces priorités est orientée en fonction d'un

but qui correspond à une composante du processus de reproduction. La finalité globale de l'animal en tant que processus est ainsi décomposée en priorités qui constituent des opérations élémentaires organisant sa réalisation. Cette formalisation repose sur l'interprétation de l'animal-processus en une potentialité phénoménologique globale ventilée entre les phénomènes élémentaires pour traduire leur importance relative au cours du cycle de vie de l'animal.

Les phénomènes élémentaires sont représentés sous forme de compartiments et le concept de priorité d'un phénomène élémentaire est capturé par l'intermédiaire d'une substance immatérielle contenue dans un compartiment à un instant donné. La quantité de cette substance traduit l'importance relative du phénomène élémentaire et la circulation d'une quantité totale unitaire de cette substance entre les compartiments traduit le déroulement du processus en termes d'enchaînement ordonné de phénomènes élémentaires. L'animal-processus est ainsi représenté par une dynamique de priorités qui formalise sa finalité, organise son accomplissement et en régit l'aboutissement. L'animal en tant que processus est ainsi réduit à un programme, une procédure, une trame, un scénario, une trajectoire dont le but est de « *survivre pour se survivre* » (Bricage, 2002).

Les transitions entre les stades physiologiques de la vie de l'animal, moments du cycle de vie et étapes du processus, sont interprétés en tant que transfert de priorités entre phénomènes élémentaires. A l'échelle de la vie de l'individu, la priorité est transférée depuis « *croître* » vers « *équilibrer ses réserves* » à mesure que l'individu se développe et devient mature, puis de « *équilibrer ses réserves* » vers « *vieillir* » à mesure que la vitalité de l'individu décline et qu'il perd son statut d'adulte en état de procréer. La priorité « *croître* » concerne la construction biologique de l'individu. La priorité « *vieillir* » traduit le déclin de la priorité « *équilibrer ses réserves* ». La priorité « *équilibrer ses réserves* » concerne l'établissement d'un état physiologique maternel propice à investir dans un cycle de reproduction. Cette priorité, orientée vers l'individu, exprime un potentiel reproductif dans la mesure où cette priorité est potentiellement transférable vers celle de survie de la descendance et effectivement transférée lorsqu'un cycle de reproduction démarre au moment de la conception. Au cours d'un cycle de reproduction, la priorité est transférée depuis « *équilibrer ses réserves* » à travers un enchaînement de phénomènes élémentaires qui constituent des étapes de procréation et des aspects de la priorité globale de survie de la descendance: « *assurer la survie du fœtus* », « *assurer la survie du nouveau-né* » et « *assurer la survie du*

jeune ». A mesure que le jeune acquiert son autonomie la priorité est transférée vers « *équilibrer ses réserves* » traduisant un désinvestissement maternel dans le cycle reproductif en cours au profit d'un réinvestissement maternel pour le cycle suivant. Ce transfert de priorité en boucle représente un arbitrage entre « *se survivre* » (survie de l'espèce) et « *survivre pour se survivre* » (survie de l'individu) (Bricage, 2002). La priorité « *assurer la survie du fœtus* » concerne l'investissement maternel dans la reproduction au cours de la période de vie intra-utérine du fœtus, jeune en devenir. La priorité « *assurer la survie du nouveau-né* » concerne la transition au moment de la parturition, de l'investissement maternel dans la reproduction entre les phases intra- et extra-utérines du cycle. La priorité « *assurer la survie du jeune* » concerne l'investissement maternel dans la reproduction au cours de la vie extra-utérine du jeune, adulte en devenir.

Cette représentation se positionne à un niveau général et générique et l'animal en tant que processus est réduit à son statut essentiel de femelle de mammifère. Elle permet de concevoir une trame de fonctionnement de l'organisme en tant que processus, délibérément déconnectée des processus biologiques et dont elle décrit la finalité. Cette trame est une partition au sens de la ventilation d'une potentialité phénoménologique globale entre des phénomènes élémentaires dont elle quantifie la dynamique de priorité au cours du temps et également une partition dans son statut d'écriture du fonctionnement global de l'organisme dont elle orchestre les fonctions physiologiques.

Le modèle téléonomique décrit dans la partie II.1 est une formalisation mathématique de cette partition dynamique des priorités. Le modèle énergétique décrit dans la partie II.2 consiste en une transcription de la partition dynamique des priorités en une partition dynamique de l'énergie. Le modèle métabolique décrit dans la partie II.3 consiste en une interprétation en termes de flux de métabolites, des flux de matières déduits de la partition dynamique de l'énergie.

2.2 L'animal en tant qu'interface

L'animal dans son milieu de vie est un site d'échanges de matière, d'information et d'énergie. Ces échanges impliquent des entrées, des sorties et un stockage transitoire. L'animal en tant qu'interface est le siège de transformations des flux de matière, d'information et d'énergie qui transitent en son sein et de conversions de ces flux entre eux. Dans une représentation en « *boîte noire* » l'animal est un système ouvert dont le

fonctionnement et la survie repose sur ces échanges. L'animal en tant qu'interface est une frontière entre son milieu physiologique interne et son milieu physique externe.

Les principaux échanges se produisant au niveau de l'animal-interface sont ceux impliquant de la matière sous forme de molécules organiques pouvant de par leur nature être des sources d'énergie chimique. Les échanges d'énergie de l'animal avec son environnement sont de nature thermique ou mécanique, sa fonction de motion produisant un travail, source d'énergie. La représentation de l'animal en tant qu'interface est le support des approches de modélisation empirique de l'animal, perçu comme une boîte noire (Figure 4). Ces modèles s'attachent à relier quantitativement entre eux les entrées et sorties de l'animal. Ce point de vue est l'approche classique de la zootechnie qui s'intéresse aux productions de l'animal en réponse à des pratiques s'exprimant principalement par des modulations qualitative et quantitative des entrées du système animal.

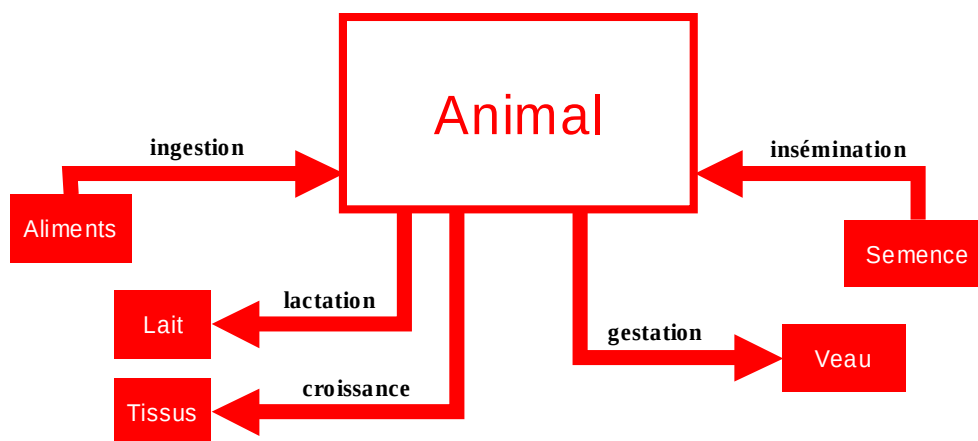


Figure 4 Représentation de l'animal en tant qu'interface.

Cette représentation de l'animal en tant qu'interface est le niveau d'approche du modèle énergétique décrit en Partie II.2. Ce modèle représente une partition « statique » de l'énergie métabolisable ingérée entre les fonctions de croissance, d'entretien, de lactation, de gestation et de gestion des réserves corporelles. A ce niveau d'interface, des coefficients d'efficacité sont utilisés pour convertir les flux d'énergie en flux de matières.

2.3 L'animal en tant que machine

La représentation de l'animal en tant que machine s'attache à décortiquer de façon plus ou moins élaborée les mécanismes sous-jacents déterminant l'élaboration des réponses agrégées

au niveau de l'animal-interface. Les traits fondamentaux qui caractérisent un organisme vivant sont son organisation structurelle et la capacité fonctionnelle qui s'y élabore. Ces champs de compréhension du vivant focalisés sur les structures et les fonctions sont les objets d'études de l'anatomie et de la physiologie. La représentation de l'animal en tant que machine repose sur la description de l'agencement de ses parties constitutives et des processus dont elles supportent le déroulement. L'utilisation du terme « *machine* » fait implicitement référence aux notions de fonction, d'assemblage d'appareils, de capacité mais aussi de pilotage. Les développements de la cybernétique se sont nourris d'aller-retour entre systèmes artificiel et systèmes biologiques, édifiant ainsi le terme de machine en un concept générique « *qui permet de concevoir les divers types ou classes d'organisations actives [d'une] extrême diversité, des machines purement physiques [...] aux machines biologiques et sociales* » (Morin, 1977). En tant que concept et dans son interprétation cybernétique le concept de machine incarne une représentation du fonctionnement global d'un système finalisé à travers son fonctionnement intime au niveau de ses structures, elles-mêmes envisagées en tant que systèmes. Pour Morin (1977), le système est la complexité de base, l'« *unitas multiplex* » : unité elle-même composée d'unités. L'animal en tant que machine est ainsi une entité dont l'organisation s'exprime à travers des niveaux hiérarchiques présentant une unité à différentes échelles :

Atome	Élément chimique de base
Molécule	Assemblage d'atomes
Cellule	Unité vivante de base
Tissu	Ensemble de cellules semblables participant à une même fonction
Organe	Association de tissus
Système	Regroupement d'organes
Organisme	Être vivant dans son ensemble

Les processus à ces niveaux systémiques, depuis l'infra- vers le supra- s'agrègent en fonctions émergeant à l'échelle de l'organisme dans son ensemble. La vue d'ensemble des structures et des fonctions qui composent le schéma général de représentation de la vache en tant que machine biologique est abordée à travers ces niveaux, depuis le niveau atomique

jusqu'à l'organisme. Cette démarche suit le chemin par lequel une représentation complète de l'animal peut se concevoir.

Cette démarche permet de mettre en lumière les simplifications extrêmes de la représentation sur laquelle repose ce travail dans la perspective générale de modélisation d'un animal ambitionnée au sein du département PHASE de l'INRA, depuis les gènes jusqu'aux fonctions.

2.3.1 Niveau atome

Le niveau atomique relève de la traduction de l'organisme sous la forme d'une formule chimique pouvant approximativement s'écrire : $(C_{185}H_{95}O_{650}N_{33}Ca_{15}P_{10}K_4S_3Na_2Cl_2Mg)_n$ (Campbell *et al.*, 2006). Ce niveau de représentation n'est pas pertinent : il donne sous cette forme une formulation statique et indifférenciée du vivant. Le seul aspect de ce travail relevant du niveau atomique se limite aux considérations d'équilibre dans la stœchiométrie du carbone dans modèle métabolique.

2.3.2 Niveau molécule

Au niveau moléculaire, le vivant est constitué d'eau, d'ions minéraux, de glucides, d'acides aminés, de lipides et de leurs précurseurs, de nucléotides et de macromolécules (protéines, acides nucléiques et de polysaccharides). La structure de l'organisme et les processus biologiques qui s'y déroulent reposent intimement sur des transports, des interactions et des transformations de ces molécules.

La composition chimique d'un organisme fournit une mesure de la quantité des principales classes de molécules qui constitue sa masse corporelle. Classiquement, elle correspond à la partition de cette masse en lipides, protéines, eau et minéraux (*cf.* revue historique en Annexe 1 et revue méthodologique en Annexe 2). Cette partition s'établit sur l'animal vide, c'est-à-dire après vidange des contenus des tractus digestif (digestas du reticulo-rumen et des intestins) et uro-génital (contenu vésical, fœtus, fluides et annexes fœtales). Cette partition relève conceptuellement et techniquement d'une destruction des niveaux d'organisations supérieurs pour ne retenir qu'une description de la structure chimique globale de l'organisme. L'évolution de cette partition au cours de la vie de l'animal permet d'identifier et de quantifier la balance entre les phénomènes d'anabolisme et de catabolisme de ces constituants chimiques. Ces flux d'échanges résultent du métabolisme global de l'organisme, à l'interface

entre un milieu actif, siège de transactions moléculaires et un milieu passif, site de stockage de molécules.

La structure du modèle métabolique repose sur une représentation de l'organisme en des compartiments de molécules sous des formes stockées induisant une masse corporelle et des formes libres impliquées dans des processus.

La masse corporelle est ainsi définie dans ce modèle par la somme de masses homogènes composées de lipides réduit à un compartiment de triglycérides, de protéines réduit à un compartiment d'acides aminés polymérisés, de minéraux et d'eau.

Une base de données sur la composition corporelle chimique des bovins a été réalisée en amont de ce travail. Ces données ont permis d'une part de fournir des repères quantitatifs et d'autre part de développer un modèle empirique de la composition corporelle de la vache intégrant notamment la note d'état corporel comme prédicteur de la quantité de lipides corporels, permettant ainsi de relier des mesures au niveau de l'animal entier avec des estimations au niveau chimique. Ce travail (Martin and Sauvant, 2005) est présenté en Annexe 3.

Les métabolites circulants sous une forme libre représentés dans le modèle métabolique sont les acides gras, le glycerol, les triglycérides, un pool formé de l'acétate et du butyrate, le propionate, le glucose, les acides aminés sous forme libre ou désaminée et le lactate. Outre les transferts de ces métabolites entre des zones anatomiques, les principales transactions entre eux sont détaillées dans la partie II.3

2.3.3 Niveau cellule

Ce travail n'incorpore pas de représentation explicite au niveau cellulaire. En particulier, il n'invoque pas d'identification de type cellulaires (adipocytes, hépatocytes, lactocytes, etc.). Les transactions métaboliques considérées dans le modèle métabolique sont en effet représentées de façon globale sans aucune connexion avec un fonctionnement à l'échelle de la cellule. L'idée d'approcher le fonctionnement de tissus ou d'organes à travers une représentation générique du métabolisme du type cellulaire constituant son unité de base est conceptuellement séduisante. C'est probablement le chemin à suivre pour envisager l'élaboration des performances d'un animal dans une démarche intégrative depuis les gènes

jusqu'aux fonctions. L'opérationnalité de cette approche reste aujourd'hui à démontrer mais des avancées significatives allant dans ce sens ont déjà été produites (Van Milgen, 2002).

2.3.4 Niveaux tissu et organe

L'architecture du modèle métabolique est organisée à travers trois sites anatomiques correspondant à des tissus (tissus protéique, tissus adipeux et sang¹²), et cinq sites anatomiques correspondant à des organes (rumen, intestins, utérus, foie et mamelle). Cette représentation est utilisée pour qualifier des pools de métabolites à ces niveaux anatomiques. Le modèle métabolique n'incorpore pas en tant que tel une représentation détaillée du fonctionnement de ces tissus et organes, mais propose une architecture minimale impliquant ces structures au titre des transactions métaboliques clefs qui s'y exécutent.

L'appareil digestif est en soi un système objet d'étude dont la représentation peut s'établir à plusieurs niveaux : en tant que processus dédié à l'approvisionnement de l'organisme en éléments nutritifs absorbables, en tant qu'interface entre le milieu extérieur à l'animal (cédant un flux de matière alimentaire et recevant un flux de matière fécale) et son milieu interne (recevant des flux de métabolites) et en tant que machine composée d'une séquence d'organes réalisant les fonctions élémentaires (buvée, ingestion, mastication, salivation, rumination, fermentation microbienne, expulsion de gaz, digestion chimique, transport péristaltique, déshydratation et défécation) participant à la fonction globale de nutrition de l'organisme.

La glande mammaire est en soi un système objet d'étude dont la représentation peut se concevoir à plusieurs niveaux : en tant que processus dédié à l'approvisionnement du jeune en éléments nutritifs, en tant qu'interface entre le milieu interne de l'animal au sein duquel sont prélevés les précurseurs des constituants du lait et les citernes de la mamelle au sein desquelles est sécrétée le lait et en tant que machine composée d'unités sécrétrices réalisant les étapes élémentaires participant à l'élaboration du lait.

2.3.5 Niveau système

Le niveau système fournit un prisme d'analyse focalisé sur les fonctions physiologiques. Un organisme animal peut ainsi être décrit à travers 11 systèmes vitaux présentant une unité fonctionnelle physiologique (Tableau 1). Ces systèmes sont indissociables, présentent des

¹²Le sang est un tissu conjonctif liquide, c'est à dire un ensemble de cellules de même origine, regroupées en ensemble fonctionnel, séparées par une matrice extracellulaire liquide, le plasma.

recouvrements anatomiques et fonctionnent de façon coordonnée. Ils constituent un découpage artificiel de l'organisme, propre à en faciliter l'étude.

Les systèmes respiratoire, cardiovasculaire, urinaire, lymphatique et tégumentaire sont des systèmes supportant les fonctions vitales essentielles de l'animal. Elles participent à cet égard au maintien de l'animal dans un état physiologique stable autorisant la réalisation des autres fonctions physiologiques. Les systèmes squelettique, musculaire et la majeure partie du système nerveux forment l'appareil locomoteur. La physiologie associée à ces systèmes relève principalement des sciences vétérinaires.

Les systèmes pertinents pour la représentation minimale d'une vache laitière sont les systèmes digestif, reproducteur et métabolique. Ces systèmes et les fonctions physiologiques qu'ils supportent sont en effet directement impliqués dans l'élaboration d'une des principales productions animales d'intérêt zootechnique : le lait. C'est au niveau de ces systèmes que se jouent les mécanismes clefs à l'origine de la variabilité des réponses productives.

Le système endocrinien forme un ensemble complexe. Son action est différenciée en de multiples régulations spécifiques agissant au niveau des autres systèmes et les connaissances sur son fonctionnement global sont aujourd'hui encore parcellaires. Sa fonction de coordination globale de l'ensemble des fonctions physiologiques n'est pas considérée ici en tant que tel. Ce système est envisagé à travers les fonctions physiologiques (nutrition, reproduction, métabolisme) dont il module le fonctionnement. A ces niveaux, les réseaux d'actions hormonales ne sont pas considérés dans le détail mais sous l'angle fonctionnel de leur action régulatrice globale en réponse à une perturbation. Il s'agit d'une représentation empirique en « *boîte noire* » qui s'attache aux principaux effets de modulation du fonctionnement des autres systèmes, en établissant directement un lien entre l'effet et sa finalité. Cette représentation est réductrice du point de vue endocrinologique mais opérationnelle pour intégrer des mécanismes de régulation, c'est-à-dire une coordination réaliste des fonctions physiologiques d'intérêt zootechnique et donner au système animal dans son ensemble une cohérence de fonctionnement. Le modèle téléonomique est à ce titre un modèle de la régulation hormonale, fonction centrale du système endocrinien et le modèle énergétique un modèle du système métabolique.

2.3.6 Niveau organisme

L'imbrication des modèles téléonomique, énergétique et métabolique relève d'une représentation de l'« *animal vache* » dans son ensemble. Cette construction ne procède pas par agrégation de tous les niveaux d'organisation hiérarchiques constitutifs mais recherche un squelette minimal à même d'aboutir à une représentation opérationnelle et évolutive de l'animal. Cette représentation repose sur l'idée clef de découplage des fonctions d'un modèle global par l'intermédiaire de sous modèles : la fonction de pilotage est centralisée au niveau du modèle téléonomique, la fonction de prédiction est assignée au modèle énergétique et la fonction explicative est assignée au modèle métabolique.

Tableau 1 Systèmes biologiques.

Système	Structures anatomiques principales	Fonction
Respiratoire	Narines, pharynx, larynx, trachée, poumons, diaphragme.	RESPIRATION Échanges gazeux avec l'air atmosphérique (fourniture d'O ₂ et élimination du CO ₂)
Digestif	Bouche (langue, dents, glandes salivaires [†]), œsophage, reticulo-rumen, omasum, abomasum, intestin grêle (duodénum, jéjunum, iléon), pancréas [†] , gros intestin (cæcum, colon rectum), anus.	NUTRITION Buvée, ingestion et digestion des aliments, absorption des produits et expulsion des gaz issus de la digestion, échanges hydriques et excrétion des matières fécales.
Reproducteur	Appareil génital (vulve, vagin, cervix, utérus, ovaire [†]) et glande mammaire [†] .	REPRODUCTION Insémination, fécondation, gestation et parturition.
Cardiovasculaire	Cœur, artères, veines, capillaires, sang.	IRRIGATION Circulation du sang (transport des nutriments, des gaz, des déchets, des hormones).
Urinaire	Reins, uretères, vessie, urètre.	ÉPURATION Filtration du sang (épuration des toxines et des déchets du métabolisme et régulation de l'équilibre hydroélectrolytique), sécrétion de l'urine et miction.

Métabolique	Foie, vésicule biliaire, tissu adipeux	ÉNERGÉTIQUE Transformations moléculaires, stockage et transferts d'énergie (anabolisme et catabolisme)
Lymphatique	Vaisseaux et ganglions lymphatiques, moelle osseuse, rate, thymus, lymphé.	DÉFENSE Renouvellement et circulation de la lymphé (transport des éléments du système immunitaire, anticorps et macrophages)
Endocrinien	Glandes endocrines : épiphyse, hypothalamus, hypophyse, thyroïde, thymus, surrénales, pancréas endocrine, ovaires.	RÉGULATION HORMONALE Sécrétion dans le milieu interne (sang et lymphé) des hormones et coordination des fonctions physiologiques.
Nerveux	Organes sensoriels (œil, oreille, naseaux), système nerveux central (cerveau, moelle épinière), nerfs et ganglions nerveux des systèmes nerveux périphérique et autonome (sympathique et parasympathique), liquide céphalo-rachidien ;	PERCEPTION & COORDINATION Détection et traitement des stimuli, intégration et émission des messages nerveux, et coordination des activités végétatives et motrices.
Musculaire	Muscles	MOTION Mouvement des parties du corps et de substances à l'intérieur du corps.
Squelettique	Os, tendons, ligaments, cartilage.	SUPPORT Structuration physique du système corporel et protection des organes internes
Tégumentaire	Peau, phanères, glandes sudoripares et sébacées.	INTERFACE Interface avec le milieu externe: protection mécanique, perception sensorielle, thermorégulation.

[†]organe du « système exocrine » présentant une unité fonctionnelle biologique de sécrétion dans le milieu extérieur de substances (suc, sueur, salive, sébum, lait) par l'intermédiaire d'un canal mais ne présentant pas d'unité fonctionnelle physiologique.

3 Connaissances

*Ce chapitre relève d'une revue de la littérature et s'attache à passer en revue les éléments de connaissance clefs de la biologie de la vache qui nourrissent le travail de modélisation. Cette partie est structurée par **fonctions physiologiques** : croissance, gestation, lactation et ingestion. Les graphiques inclus dans cette partie présentent des compilations de données de la littérature.*

*L'étude de la **variabilité des cinétiques** des principales variables d'intérêt zootechniques (aliment ingéré, quantité de lait produit et poids vif de l'animal) au cours de la lactation a fait l'objet d'une étude par méta-analyse (Martin and Sauvant, 2002) présentée en Annexe 4.*

*En complément de cette revue des **éléments de biologie**, une revue des **travaux de modélisation** réalisés à différents niveaux systémiques impliquant une modélisation de la vache est présentée en Annexe 5. Cette revue est structurée à travers une grille de lecture systémique proposée comme alternative aux typologies classiques.*

3.1 Croissance

La croissance consiste en un flux d'accumulation de tissus constitutifs de la masse corporelle. C'est la fonction biologique qui assure l'augmentation de la taille et de la masse corporelle d'un individu conduisant à l'acquisition d'un format adulte. L'externalisation des tissus par l'animal intervient au moment de la mort de l'animal (réforme dans un contexte d'élevage) : formellement le système animal cède une carcasse qui constitue potentiellement un produit pour la filière de commercialisation de viande bovine.

La masse corporelle de l'animal intervient dans cette représentation comme un compartiment de stockage sous forme de tissus d'une fraction des ressources alimentaires ingérées au cours de sa vie. Cette représentation au niveau de l'animal-interface définit la croissance de façon agrégée, en tant que processus d'élaboration d'un poids vif. De façon synthétique, cette représentation formalise simplement l'idée que l'animal produit un ensemble de tissus dont la masse augmente au cours de sa vie. Le pattern globalement

curvilinéaire de la dynamique du poids vif d'un animal à l'échelle de sa vie est présenté en Figure 5.

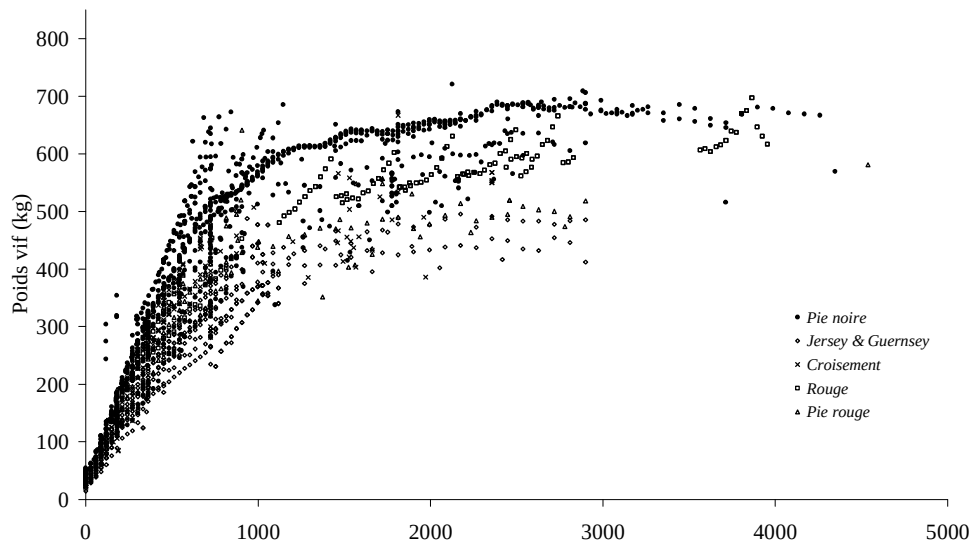


Figure 5 Evolution du poids vif avec l'âge de vaches laitières : Données de la littérature¹³ pour différentes races (Pie Noire, Jersey & Guernsey, Croisement, Rouge, Pie Rouge) à différents stades physiologiques (croissance, entretien, lactation, gestation, stades *pre-* ou *postpartum*).

Les tissus constitutifs de l'animal sont au cours de son existence le site d'exécution des fonctions vitales de l'organisme qui font intervenir de façon continue et simultanée des processus d'anabolisme et de catabolisme. De plus, la croissance, résulte d'une succession de phases de croissance différentielles à l'échelle des compartiments anatomiques et d'une succession de phases de stockage et de déstockage à l'échelle des cycles de reproduction. Le cours de la lactation est ainsi associé à un pattern dynamique du poids vif illustré en Figure 6 à travers un faisceau de cinétiques collectées dans la littérature (Martin and Sauvant, 2002). Le pattern de la dynamique du poids vif au cours de la transition entre les phases de gestation et de lactation est présenté en Figure 7 à travers une compilation de cinétiques collectées dans

¹³ Eckles, 1920 ; McCandlish, 1922 ; Bartlett, 1926a ; Bartlett, 1926b ; Espe *et al.*, 1932 ; Ragsdale, 1934 ; Hilder and Fohrman, 1949 ; Ellenberger *et al.*, 1950 ; Reid *et al.*, 1951 ; Campbell and Flux, 1952 ; Matthews and Fohrman, 1954 ; Davis and Hathaway, 1956 ; Morrison, 1956 ; Burt, 1957 ; Davis, 1957 ; Crichton *et al.*, 1959 ; Crichton *et al.*, 1960 ; Swanson, 1960 ; Martin *et al.*, 1962 ; Wickersham and Schultz, 1963 ; Swanson and Hinton, 1964 ; Bath *et al.*, 1965 ; McDaniel and Legates, 1965 ; Miller *et al.*, 1967 ; Swanson, 1967 ; Hollon *et al.*, 1972 ; Rakes and Davenport, 1972 ; Lamb and Barker, 1975 ; Grieve *et al.*, 1976 ; Berglund *et al.*, 1980 ; Herland and Wiktorsson, 1982 ; Lee *et al.*, 1982 ; Fisher *et al.*, 1983 ; Lebengarts *et al.*, 1984 ; Butler-Hogg *et al.*, 1985 ; Lin *et al.*, 1985 ; Reddy and Basu, 1986 ; Ribas and Ponce de Leon, 1986 ; Heinrichs and Hargrove, 1987 ; Johnson *et al.*, 1987 ; Pikina, 1987 ; Polyakov *et al.*, 1987 ; Singh and Bath, 1987 ; Hocking *et al.*, 1988 ; Moore *et al.*, 1990 ; Akbulut *et al.*, 1993 ; Berg and Ekern, 1993 ; Grabowski *et al.*, 1993 ; Peri *et al.*, 1993 ; Andrew *et al.*, 1994 ; Dhour *et al.*, 1995 ; Groen and Vos, 1995 ; Hoffman *et al.*, 1996 ; Koenen and Groen, 1996 ; Kunzi *et al.*, 1996 ; Colburn *et al.*, 1997 ; Hoffman, 1997 ; Kertz *et al.*, 1998 ; Vacek *et al.*, 1999 ; Freely *et al.*, 2000.

la littérature. A l'échelle du nycthémère, des variations de poids vif reflètent des variations de la quantité d'aliments ingérés transitant dans le tractus digestif (Paquay *et al.*, 1971 ; Maltz *et al.*, 1997).

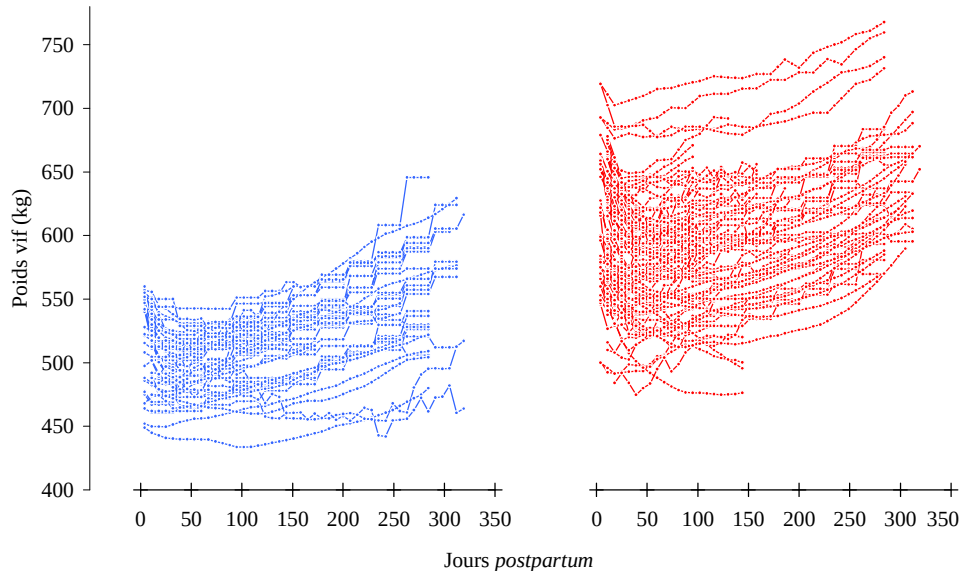


Figure 6 Évolution du poids vif *postpartum* de vaches laitières : Données de la littérature¹⁴ pour des animaux primipares (*en pointillés bleus*) et multipares (*en rouge*).

Une représentation simplifiée de l'animal en tant qu'interface n'est ainsi pas suffisante pour appréhender de façon complète les variations de son poids vif. Et c'est à un niveau de représentation de l'animal en tant que machine biologique qu'elles peuvent se concevoir, en s'appuyant notamment sur une décomposition de la masse corporelle en compartiments différenciés et en représentant *a minima* leur spécificités fonctionnelles.

La vitesse de croissance n'est en effet pas la même pour tous les constituants anatomiques de l'organisme et il existe globalement un gradient depuis la tête jusqu'à l'arrière train (Owens *et al.*, 1993), la maturité du cerveau étant par exemple atteinte avant celle du squelette, des muscles et des dépôts adipeux intramusculaires. Ce phénomène de croissance différentielle par vagues est connu sous le nom d'allométrie et induit une modification

¹⁴ Rook and Campling, 1965 ; Mohrenweiser and Donker, 1967 ; Swanson, 1967 ; Broster *et al.*, 1969 ; Cowan, 1970 ; Decaen, 1970 ; Wiktorsson, 1971 ; Wiktorsson, 1973 ; Broster *et al.*, 1975 ; Lodge *et al.*, 1975 ; Everson *et al.*, 1976 ; Johnson, 1977 ; Vérité and Jourmet, 1977 ; Wohlt and Clark, 1978 ; Johnson, 1979 ; Kronfeld *et al.*, 1980 ; Garnsworthy and Topps, 1982 ; Holter *et al.*, 1982 ; Pinchasov *et al.*, 1982 ; Donker, 1983 ; Johnson, 1983 ; Krohn *et al.*, 1983 ; Llahr *et al.*, 1983 ; Holter *et al.*, 1984 ; Taylor and Leaver, 1984a ; 1984b ; DePeters, 1985 ; DePeters, 1989 ; Staples *et al.*, 1990 ; Kertz *et al.*, 1991 ; Wohlt *et al.*, 1991 ; Holter and Hayes, 1992 ; Holter *et al.*, 1993 ; Ostensen *et al.*, 1997 ; Tolcamp *et al.*, 1998 ; Soder and Holden, 1999.

morphologique au cours de la croissance, les dépôts structurels osseux et protéiques intervenant avant les dépôts fonctionnels de gras.

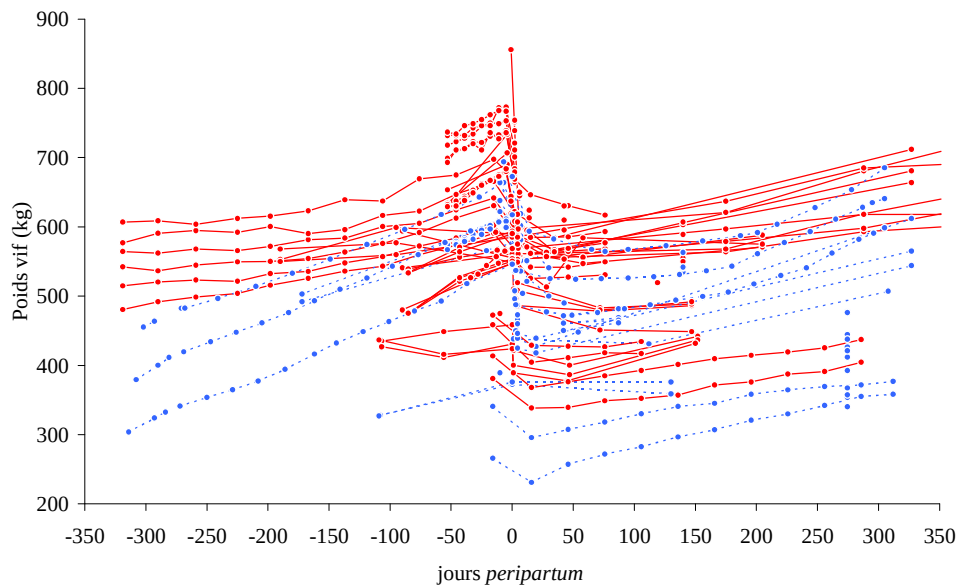


Figure 7 Évolution du poids vif *peripartum* de vaches laitières : Données de la littérature¹⁵ pour des animaux primipares (en pointillés bleus) et multipares (en rouge).

Dans le modèle énergétique, le poids vif est décomposé en une masse non-labile structurelle déterminant le format global de l'animal, une masse non-labile fonctionnelle jouant le rôle d'un compartiment de réserve d'énergie, un compartiment utérin dont les variations de masse reflètent la croissance du fœtus au cours de la gestation et un compartiment digestif dont les variations de masse reflètent les variations de contenus digestifs induits par l'ingestion d'aliment. Dans le modèle métabolique, la décomposition du poids vif de l'animal procède d'une compartimentation du poids vif vide en ses constituants chimiques (lipides, protéines, eau et minéraux) et en un compartiment de contenus digestifs.

La croissance est considérée au niveau du modèle téléonomique en tant que priorité de réalisation d'une masse non-labile mature, fixée *a priori* et envisagée comme la formalisation d'un déterminisme génétique. Cette priorité impose une partition de l'énergie au niveau du

¹⁵ Bartlett, 1926b ; Blaxter, 1944 ; Burt, 1957 ; Broster *et al.*, 1958 ; Swanson, 1960 ; Castle and Watson, 1961 ; Wickersham and Schultz, 1963 ; Swanson and Hinton, 1964 ; Hight, 1968 ; Schmidt *et al.*, 1971 ; Rakes and Davenport, 1972 ; Lamb and Barker, 1975 ; Smith *et al.*, 1978 ; Strickland and Broster, 1981 ; Bellows *et al.*, 1982 ; Macleod *et al.*, 1983 ; Gordon, 1984 ; Butler-Hogg *et al.*, 1985 ; Boisclair *et al.*, 1986 ; Taylor and leaver, 1986 ; Hocking *et al.*, 1988 ; Sieber *et al.*, 1988 ; Goehring *et al.*, 1989 ; VanSaun *et al.*, 1993 ; Berg and Ekern, 1993 ; Devir *et al.*, 1995 ; Groen and Vos, 1995 ; Grummer *et al.*, 1995a ; Peyraud *et al.*, 1996 ; Hoffman *et al.*, 1996 ; Kertz *et al.*, 1997 ; Hoffman, 1997 ; Morrison *et al.*, 1999 ; Weder *et al.*, 1999 ; Freetly *et al.*, 2000.

modèle énergétique qui provisionne et oriente le métabolisme dans le sens d'une accréation de masse non-labile. A mesure que cette masse s'approche de son niveau mature la priorité à la croissance décroît. Cette coordination entre les modèles téléonomique et énergétique permet de formaliser une représentation de nature homéorhéticque de la croissance mais aussi homéostatique dans la mesure où le niveau d'apport énergétique conditionne la vitesse de croissance. Cette approche reliant le niveau de maturité à la proportion d'énergie dédiée à la croissance est une application du modèle de développement ontogénétique proposé par West *et al.* (2001). Cette partition est par ailleurs considérée comme sensible à l'équilibre entre les masses labile et non-labile avec l'hypothèse que la proportion d'énergie dédiée à la croissance est accrue lorsque le niveau de la masse labile est en dessous d'un seuil critique. Cette priorité temporairement exacerbée induit notamment une croissance accélérée de la masse non labile après une phase de restriction énergétique. Cette représentation permet de reproduire la croissance compensatrice à travers une augmentation du besoin énergétique et donc de l'ingestion, et une augmentation du gain de masse non-labile, structurellement plus riche en protéines. Cette construction est cohérente avec les connaissances actuelles sur ce phénomène.

Les variations de la masse labile résultent également du couplage entre les modèles téléonomique et énergétique. Au niveau du modèle énergétique, anabolisme et catabolisme de la masse labile sont dépendants de l'écart entre son niveau courant et un niveau qualifié d'optimal, fixé *a priori* et envisagé au même titre que la masse non-labile mature comme la formalisation d'un déterminisme génétique. Ces processus d'anabolisme et de catabolisme ont ainsi un fonctionnement qui tend à maintenir la masse labile à un niveau d'équilibre. L'expression de ce fonctionnement basal est modulée par le modèle téléonomique qui prescrit des séquences physiologiques au cours desquelles il peut être inhibé, laissant ainsi se produire des déviations du niveau d'équilibre. Il existe ainsi des phases durant lesquelles des réserves corporelles peuvent être mobilisées ou accumulées en fonction des orientations pilotées par le modèle téléonomique et du niveau d'apport énergétique. Inversement, des phases accordent une priorité maximale au rétablissement du niveau d'équilibre de la masse labile. La priorité à la croissance a un effet inhibiteur sur cette force de rappel, de telle sorte que la construction d'une masse non-labile précède la constitution de la masse labile. Cette représentation permet de rendre compte indirectement du gradient d'allométrie entre dépôts musculaire et adipeux.

Les modifications de composition corporelle au cours de la croissance sont classiquement représentées globalement ou partiellement à travers le formalisme allométrique de Huxley

(1932). La croissance d'un constituant chimique ou anatomique est ainsi envisagée relativement à la croissance d'un autre élément ou de l'ensemble dont il est constitutif, qu'il s'agisse par exemple du poids vif vide par rapport au poids vif (Robelin, 1990 ; Hoch *et al.*, 2004), de la masse délipidée par rapport au poids vif vide (Keele *et al.*, 1992) ou à la masse protéique (Hoch *et al.*, 2004), de la masse protéique par rapport à la masse délipidée (Robelin, 1990) ou de la masse lipidique par rapport au poids vif vide (Keele *et al.*, 1992 ; Robelin, 1990). Le modèle de Robelin (1990) repose sur cette approche à travers laquelle la croissance des différents tissus est déduite de la croissance globale de l'animal.

La croissance différentielle des masses labile et non-labile n'est pas explicitement établie dans le modèle énergétique par un formalisme allométrique mais résulte d'une évolution des priorités au cours de la croissance de l'animal. C'est ainsi au niveau du modèle téléonomique que se jouent les déterminants de l'allométrie de croissance. Ces notions de priorités décroissantes et de contrôle en amont sont déjà formalisées dans le modèle de Oltjen *et al.* (1986) qui hiérarchise les anabolismes protéique et lipidique, et utilise la dynamique d'accrétion d'ADN comme force motrice de la croissance. Dans les approches focalisées sur le besoin énergétique de la croissance, la force motrice est résumée dans une courbe de référence calibrée pour un type d'animal. La composition corporelle est déduite par allométrie (INRA, 1989 ; AFRC, 1993) ou par analogie avec celle d'une composition de référence (NRC, 1989 ; SCA, 1990). Ces approches fournissent des formules de calcul de l'énergie associée à la composition d'un gain de poids et fondent les systèmes de recommandations alimentaires des bovins en croissance. Dans le modèle de Hoch et Agabriel (2004a ; b), il n'y a pas de partition a priori de l'énergie et la force motrice de la croissance est l'énergie ingérée par l'animal. Des affinités différentes pour cette énergie induisent l'accrétion différentielle des constituants chimique de la carcasse et du 5^{ème} quartier. Dans le modèle de France *et al.* (1987), la croissance est considérée au niveau métabolique et ce sont les pools de métabolites qui pilotent la croissance. Les priorités d'utilisations des métabolites sont ainsi régulées par le jeu de constantes d'affinités des compartiments d'accumulation.

La dynamique du poids vif à l'échelle de la vie de l'animal implique une diminution progressive de la vitesse de croissance avec l'âge et l'existence d'une asymptote associée à l'idée de déterminisme génétique du poids à maturité. Cette dynamique présente une allure sigmoïde lorsqu'elle incorpore la croissance fœtale depuis la conception. Le point d'inflexion de cette courbe, qui correspond à la transition entre les phases de croissance auto-accélérée et

auto-inhibée (Brody, 1945) est classiquement interprété comme le moment de la puberté et localisé aux alentours de 60% du poids à maturité.

La représentation adoptée dans ce travail intègre explicitement deux composantes du poids mature : un niveau mature de masse non-labile et un niveau d'équilibre de la masse labile.

L'idée d'un poids à maturité et d'un déterminisme génétique à sa réalisation présuppose une relative invariance de la masse corporelle adulte. La relative constance de la composition chimique de la masse corporelle délipidée d'un individu adulte (Figure 8 et Figure 9) est cohérente avec ce point de vue dans la mesure où elle constitue un critère satisfaisant pour la détection d'un stade mature. La maturité de la masse corporelle délipidée est ainsi envisagée par le biais de la stabilisation de sa composition chimique. En revanche, l'élasticité des réserves corporelles, principalement constituées de lipides dans les tissus adipeux et liée à leur rôle de réservoir d'énergie, impose d'affiner le poids vif à maturité à travers un indicateur d'état d'engraissement à maturité. Cette distinction entre format et état corporel est appliquée par Cundiff (2003) qui utilise pour caractériser les races bovines un indicateur de rapport entre masses corporelles maigre et grasse (« *lean to fat ratio* ») en complément de l'indicateur de format à maturité. Il existe par ailleurs un faisceau d'évidences autour de l'existence d'un niveau « *normal* » de réserves adipeuses envisagé comme l'expression d'un déterminisme génétique (Friggens *et al.*, 2004) et dont l'équilibre est supposé mettre en œuvre des mécanismes de régulation de la prise alimentaire et du métabolisme (théorie lipostatique, Kennedy, 1953).

La représentation de la croissance en tant que réalisation d'un état mature est un point de vue classique et la plupart des fonctions mathématiques du temps utilisées pour simuler la croissance pondérale des animaux incorpore explicitement un paramètre d'asymptote. La question de la nature biologiquement factuelle ou mathématiquement artefactuelle de cette asymptote a été posée par certains auteurs (Knight, 1968 ; Ricker, 1979) et d'autres ont proposé des formalismes mathématiques pour une croissance indéterminée (Tanaka, 1982 ; 1988) ou dont l'asymptote est à même de varier au cours de la croissance selon les conditions du milieu (Thornley and France, 2005 ; Thornley *et al.*, 2007).

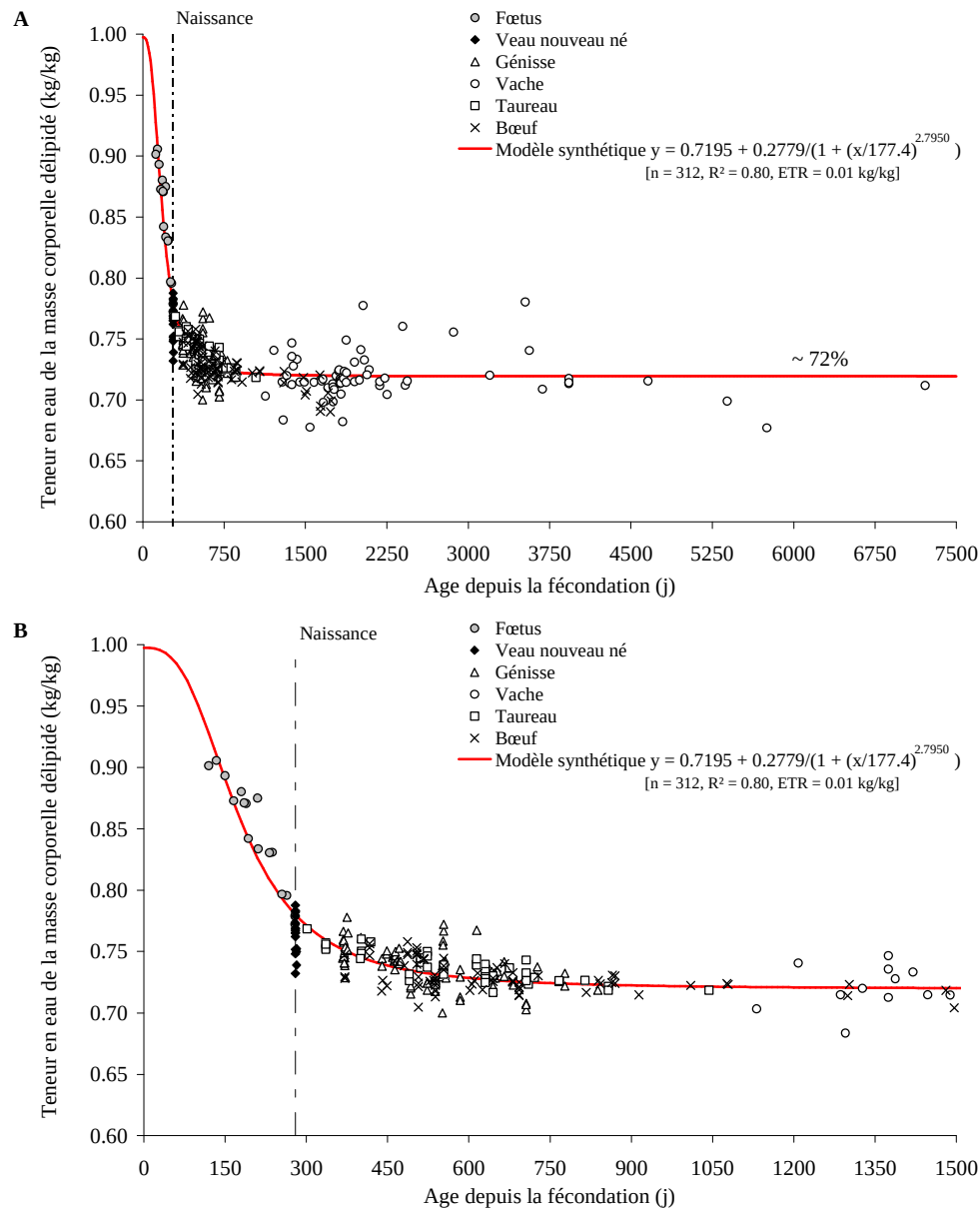


Figure 8 Évolution de la teneur en eau de la masse corporelle délipidée en fonction de l'âge depuis la fécondation (âge depuis la naissance + durée de gestation, 280 jours). Données bibliographiques¹⁶ et modèle synthétique. A : ensemble des données sur 7500 jours. B : zoom sur 1500 jours.

¹⁶ Haigh *et al.*, 1920 ; Moulton *et al.*, 1922 ; Moulton *et al.*, 1923a ; Esskuchen, 1931 ; Meigs *et al.*, 1935 ; Hopper, 1944 ; Paloheimo, 1944 ; Ellenberger *et al.*, 1950 ; Henseler and Jentsch, 1973 ; Ferrell *et al.*, 1976a ; Lonsdale, 1976 ; Foot and Tulloh, 1977 ; Robelin and Geay, 1978a ; Robelin *et al.*, 1979 ; Fortin *et al.*, 1980 ; Thompson *et al.*, 1981 ; Bird *et al.*, 1982 ; Chigaru and Holness, 1983 ; Tyrrell and Haaland, 1983 ; Odwongo *et al.*, 1984 ; Wright and Russel, 1984 ; Arnold *et al.*, 1985 ; Robelin, 1986 ; Gibb and Baker, 1987 ; Bailey and Lawson, 1989 ; Gibb and Baker, 1989 ; Buckley *et al.*, 1990 ; Gibb and Baker, 1991 ; Gibb and Baker, 1992b ; Andrew *et al.*, 1994 ; Blome *et al.*, 2000.

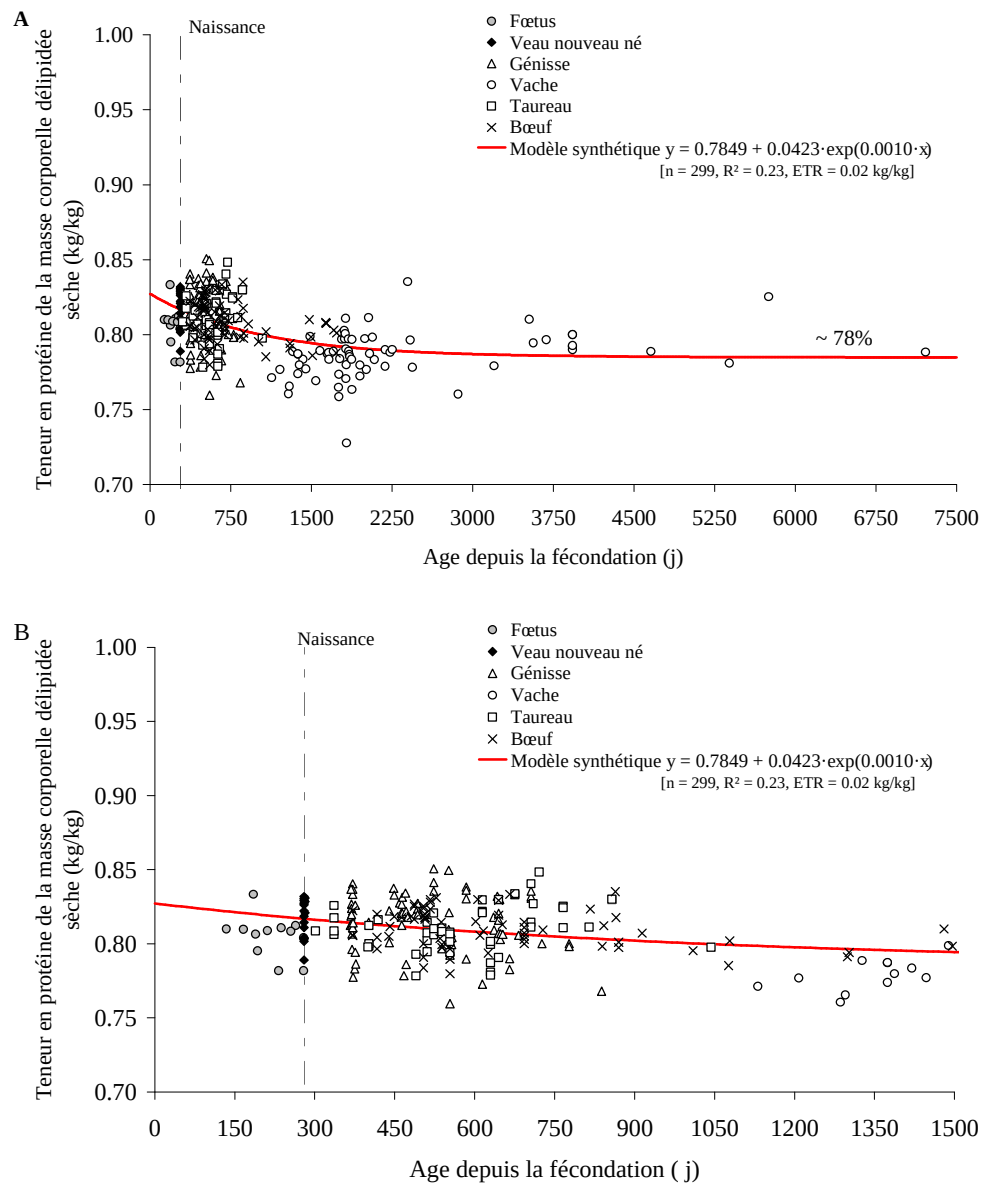


Figure 9 Évolution de la teneur en protéine de la masse corporelle délipidée sèche en fonction de l'âge depuis la fécondation (âge depuis la naissance + durée de gestation, 280 jours). Données bibliographiques¹⁷ et modèle synthétique. A : ensemble des données sur 7500 jours. B : zoom sur 1500 jours.

¹⁷ Haigh *et al.*, 1920 ; Moulton *et al.*, 1922 ; Moulton *et al.*, 1923a ; Meigs *et al.*, 1935 ; Hopper, 1944 ; Paloheimo, 1944 ; Ellenberger *et al.*, 1950 ; Henseler and Jentsch, 1973 ; Ferrell *et al.*, 1976a ; Lonsdale, 1976 ; Foot and Tulloh, 1977 ; Robelin and Geay, 1978a ; Robelin *et al.*, 1979 ; Fortin *et al.*, 1980 ; Thompson *et al.*, 1981 ; Bird *et al.*, 1982 ; Chigaru and Holness, 1983 ; Tyrrell and Haaland, 1983 ; Odwongo *et al.*, 1984 ; Wright and Russel, 1984 ; Arnold *et al.*, 1985 ; Robelin, 1986 ; Gibb and Baker, 1987 ; Bailey and Lawson, 1989 ; Gibb and Baker, 1989 ; Buckley *et al.*, 1990 ; Gibb and Baker, 1991 ; Gibb and Baker, 1992b ; Andrew *et al.*, 1994 ; Blome *et al.*, 2000.

Toutes les approches de modélisation de la croissance des bovins intègrent l'existence a priori d'un niveau mature éventuellement variable entre races et individus, soit explicitement par l'intermédiaire d'un poids vif maximal (Robelin, 1990) ou de tailles maximales de compartiments corporels (Hoch *et al.*, 2004 ; Keele *et al.*, 1992) soit implicitement par l'intermédiaire de la saturation d'une variable de pilotage (Oltjen *et al.*, 1986) ou de la diminution programmée du taux de croissance (Danfaer, 1991). Le concept même de maturité n'est par ailleurs pas complètement standardisé (Arnold and Bennett, 1991).

L'approche adoptée ici consiste à proposer un modèle de la force motrice qui représente explicitement une dynamique de priorités à un niveau générique et l'utilise pour réguler la répartition des flux d'énergie entre les tissus. Ce contrôle s'opère à la fois à travers l'expression d'un besoin énergétique pour la réalisation d'une croissance génétiquement programmée et l'adaptation de cette croissance à l'énergie disponible. Dans le modèle téléonomique, croissance et mobilisation/reconstitution des réserves sont des priorités. Dans le modèle énergétique, ces processus sont des flux d'énergie. Dans le modèle métabolique, seuls sont interprétés les flux d'anabolisme et de catabolisme des lipides et de protéines au cours de la lactation.

3.2 Insémination et gestation

L'insémination correspond à l'introduction de sperme dans l'appareil génital de la vache, réalisée quasi-systématiquement aujourd'hui de façon artificielle. La nature de ce flux est déterminée par le programme d'amélioration génétique du troupeau et son occurrence par la politique de mise à la reproduction des animaux (période d'attente volontaire après parturition, programme de détection des chaleurs, traitement de synchronisation des chaleurs, etc.). Ce flux est un transfert discret (acte vétérinaire) et son efficacité se traduit par son succès, c'est-à-dire la fécondation de la vache.

La parturition correspond à l'expulsion d'un veau au terme de la gestation. Formellement, le processus de gestation consiste en un flux continu d'accumulation d'un ensemble de tissus (le fœtus et les annexes fœtales) au sein d'un compartiment de stockage transitoire (l'utérus de l'animal) et s'achève par un transfert discret du contenu de ce compartiment vers le milieu extérieur. L'efficacité de ce flux se traduit par la viabilité du veau. Conception et parturition correspondent à des événements au cours du cycle reproductif. Ils sont considérés en tant que tels au niveau du modèle téléonomique dont ils rythment le fonctionnement cyclique et au niveau du modèle énergétique dont ils bornent l'intervalle de temps de gestation durant lequel

la croissance du fœtus et des annexes fœtales génèrent un besoin. Le cycle reproductif est ainsi considéré de façon très simplifiée, les déterminants biologiques de la fertilité étant ignorés. Cette représentation intègre uniquement une date de conception pour chaque cycle de reproduction (âge de la vache pour le premier cycle et intervalle après parturition pour les cycles suivants) et une courbe de croissance pondérale de l'utérus gravide au cours de la gestation. Cette courbe est déterminée *a priori* par le poids du veau à la naissance (Figure 10), lui même déterminé *a priori* par le poids de la vache à maturité (Figure 11).

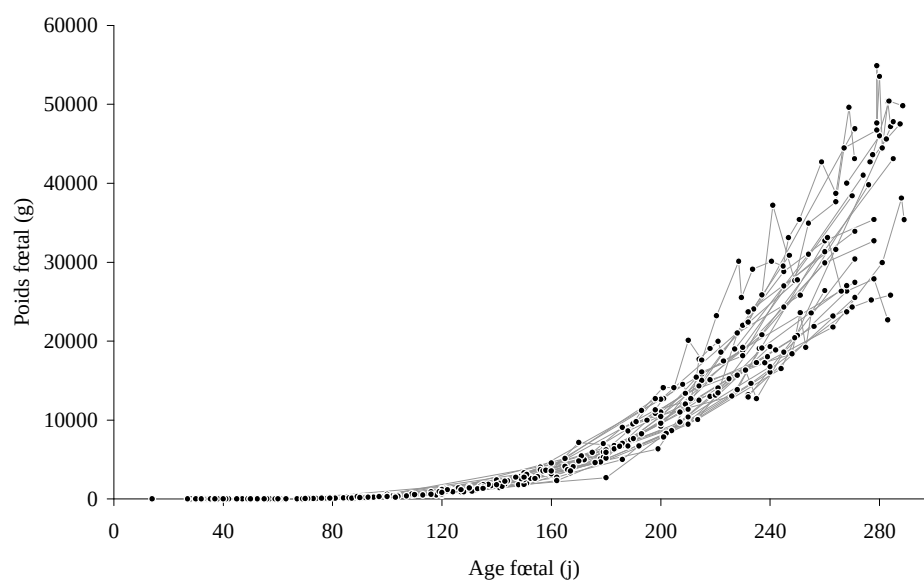


Figure 10 Croissance fœtale du veau au cours de la gestation : Données de la littérature¹⁸.

La durée de gestation est gouvernée par l'intermédiaire du modèle téléonomique, le moment du vêlage étant celui de l'investissement maternel maximal dans le développement intra-utérin du veau. Cette approche génère implicitement une relation entre durée de gestation et poids du veau à la naissance (Figure 12), liée au numéro du cycle de reproduction.

¹⁸ Buchem, 1909 ; Bergmann, 1921 ; Hammond, 1927 ; Esskuchen, 1931 ; Swett *et al.*, 1937 ; Hatch *et al.*, 1941 ; Winters *et al.*, 1942 ; Nichols, 1944 ; Swett *et al.*, 1948 ; Ellenberger *et al.*, 1950 ; Becker *et al.*, 1951 ; Melton *et al.*, 1951 ; Mäkelä, 1956 ; Joubert et Van Marle, 1959 ; Lyne, 1960 ; Hubbert *et al.*, 1972 ; Ferrell *et al.*, 1976 ; Eley *et al.*, 1977 ; Chew *et al.*, 1979 ; Anthony *et al.*, 1986 ; Sultan *et al.*, 1987 ; Bellows *et al.*, 1990 ; Reynolds *et al.*, 1990 ; Ferrell, 1991 ; House and Bell, 1993 ; Okano, 1994 ; Zhang *et al.*, 1999.

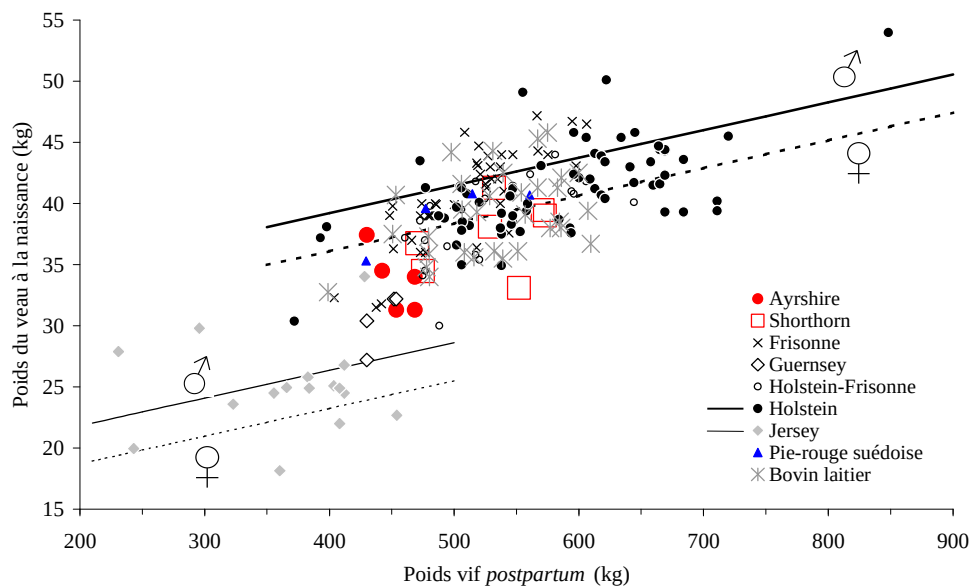


Figure 11 Relation entre poids du veau à la naissance et poids de la vache *postpartum* pour différentes races de vaches laitières : Données de la littérature¹⁹ et modèles linéaires synthétiques pour des veaux mâle (trait plein) et femelle (trait pointillé) de race Holstein et Jersey.

¹⁹ Eckles, 1916 ; Henry and Morrison, 1917 ; Eckles, 1919 ; Fitch *et al.*, 1924 ; Joubert and Van Marle, 1959 ; Ridler *et al.*, 1963 ; Wickersham and Schultz, 1963 ; Swanson and Hinton, 1964 ; Broster and Tuck, 1967 ; Gleeson, 1973 ; Lodge *et al.*, 1975 ; Yadava *et al.*, 1976 ; Gardner *et al.*, 1977 ; Heitzman *et al.*, 1979 ; Huth and Schmidt, 1979 ; Østergaard, 1979 ; Erb *et al.*, 1981 ; Laird *et al.*, 1981 ; Collier *et al.*, 1982 ; Holter *et al.*, 1986 ; Berglund and Philipsson, 1987 ; Stelwagen and Grieve, 1992 ; Kume and Bicoku, 1993 ; Lacasse *et al.*, 1993 ; Troccon, 1993 ; Moore, 1994 ; Troccon *et al.*, 1994 ; Kertz *et al.*, 1997 ; Hansen *et al.*, 1999 ; Negash, 1999 ; Keady *et al.*, 2001 ; Johanson and Berger, 2003.

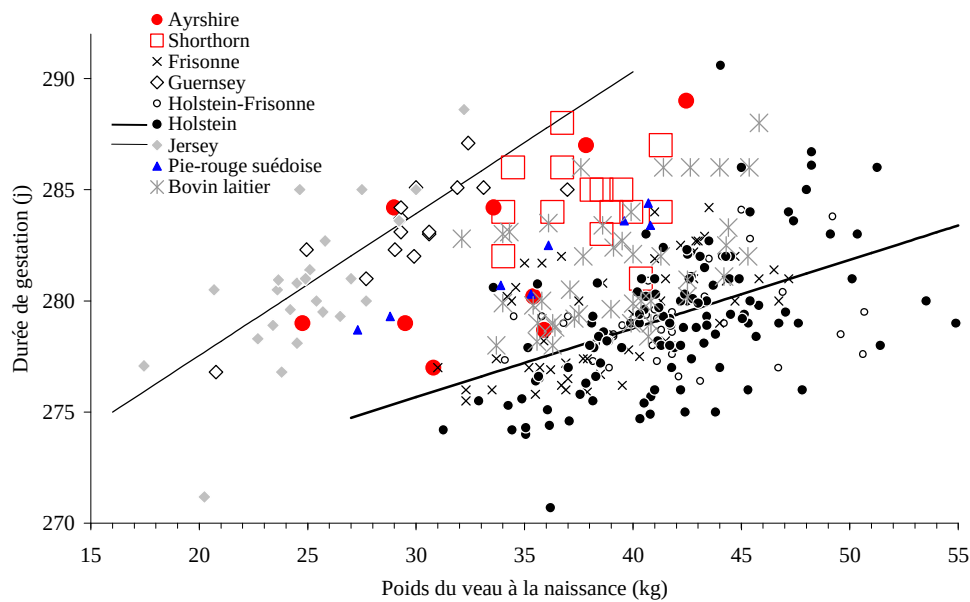


Figure 12 Relation entre durée de gestation et poids du veau à la naissance pour différentes races de vaches laitières : Données de la littérature²⁰ et modèles synthétiques (veaux ♀ et ♂, races Holstein et Jersey).

²⁰ Eckles, 1919 ; Fitch *et al.*, 1924 ; Dinkhauser *et al.*, 1944 ; Ellenberger *et al.*, 1950 ; Brakel *et al.*, 1952 ; Davis *et al.*, 1954 ; Foote *et al.*, 1959 ; Huth, 1962 ; Ridler *et al.*, 1963 ; Andersen and Plum, 1965 ; Boyd and Hafs, 1965 ; Everett and Magee, 1965 ; Touchberry and Bereskin, 1966 ; DeTena Andreu, 1973 ; Romita, 1973 ; Beardsley *et al.*, 1974 ; Gianola and Tyler, 1974 ; Hocking, 1974 ; Koubek, 1974 ; Muller and Owens, 1974 ; Oldenbroek, 1974 ; Dijkstra *et al.*, 1975 ; Beardsley *et al.*, 1976 ; Eliya and Christensen, 1976 ; Guaragna *et al.*, 1976 ; Manrique *et al.*, 1976 ; Philipsson, 1976 ; Serrano *et al.*, 1976 ; Vos *et al.*, 1976 ; Laurijsen and Oldenbroek, 1977 ; Morgan, 1977 ; Everitt *et al.*, 1978 ; Fisher and Williams, 1978 ; Gaillard, 1978 ; Martinez *et al.*, 1978 ; Veris, 1978 ; Arbaban-Ghafouri, 1980 ; Egbunike and Togun, 1980 ; Gaillard, 1980 ; Lazarevic and Novakovic, 1980 ; Meijering, 1980 ; Chew *et al.*, 1981 ; Erb *et al.*, 1981 ; Gaillard, 1981 ; Leeuwen and Zijlstra, 1981 ; Little and Harrison, 1981b ; Gaillard, 1982 ; Das *et al.*, 1984 ; Oldenbroek, 1984 ; Bhuyan and Mishra, 1985 ; Oferrall *et al.*, 1985 ; VonKorn and Langholz, 1985 ; Holter *et al.*, 1986 ; Sang *et al.*, 1986 ; Shin *et al.*, 1986 ; Berglund and Philipsson, 1987 ; Eppard *et al.*, 1987 ; Trilk *et al.*, 1988 ; Gravert *et al.*, 1990 ; Guilbault *et al.*, 1990 ; Hagger and Hofer, 1990 ; Oferrall and Ryan, 1990 ; Rooy *et al.*, 1990a ; Rooy *et al.*, 1990b ; Anonymous, 1991 ; Rémond *et al.*, 1991 ; KB-Mitteilungen, 1993 ; Troccon, 1993 ; Kojima, 1999 ; Zhang *et al.*, 1999 ; Jacobsen *et al.*, 2000 ; Perfield *et al.*, 2002 ; Johanson and Berger, 2003.

3.3 Lactation

La lactation correspond à la sécrétion de lait par la mamelle de la vache dont l'externalisation du système animal est opérée par la traite dans un contexte productif et par la succion du veau dans un contexte naturel. La nature du flux de lait produit est classiquement résumée par sa teneur en ses trois principaux composés organiques (lactose, lipides et protéines) et interprétée en énergie (Perrin, 1958 ; Tyrrel and Reid, 1965) exprimant ainsi la fonction de lactation dans une unité équivalente à celle utilisée pour résumer l'ingestion. La composition du lait est relativement constante au sein des ordres de mammifères (Oftedal, 1984) et constitue un trait caractéristique d'une espèce (Figure 13).

Les données moyennes de composition du lait de vache sur l'ensemble de la lactation reportées dans la littérature sont généralement comprises entre 3.0% et 6.0% pour les lipides, 3.0% et 4.0% pour les protéines et 4.5% et 5.0% pour le lactose. Ces différences traduisent des différences entre races bovines, entre individus d'une même race et des différences liées aux régimes alimentaires des animaux. C'est quantitativement et qualitativement la composition du lait en matière grasse qui varie le plus en réponse à des variations de régime (Grummer, 1991 ; Palmquist *et al.*, 1993).

Le processus de sécrétion de lait dans les citernes de la glande mammaire est un phénomène continu alors que l'éjection du lait produit au cours de la traite ou de l'allaitement est un phénomène discret. La représentation adoptée dans ce travail et sa modélisation au pas de temps du jour n'intègre pas de distinction entre sécrétion et éjection. La production de lait est considérée à cette échelle de temps comme un flux continu, la quantité de lait produite chaque jour étant implicitement un flux de matière sortant du système animal. Ce flux intervient au cours des périodes de lactation depuis le moment de la mise bas qui constitue un « *évènement animal* » (régie interne) jusqu'au moment du tarissement qui constitue une « *opération humaine* » (régie externe). Au cours de la lactation, la quantité et la composition du lait varient selon un pattern dynamique caractéristique illustré en Figure 14, Figure 15 et Figure 16 à travers un faisceau de cinétiques collectées dans la littérature (Martin and Sauvant, 2002). Le pattern dynamique de la courbe de production laitière au cours de la lactation est souvent décrit à l'aide du modèle de Wood (1967), dont le formalisme dérivé d'une fonction gamma permet de résumer la cinétique à travers trois critères synthétiques : un niveau de production, une date de production maximale et un taux de décroissance de cette production après le pic.

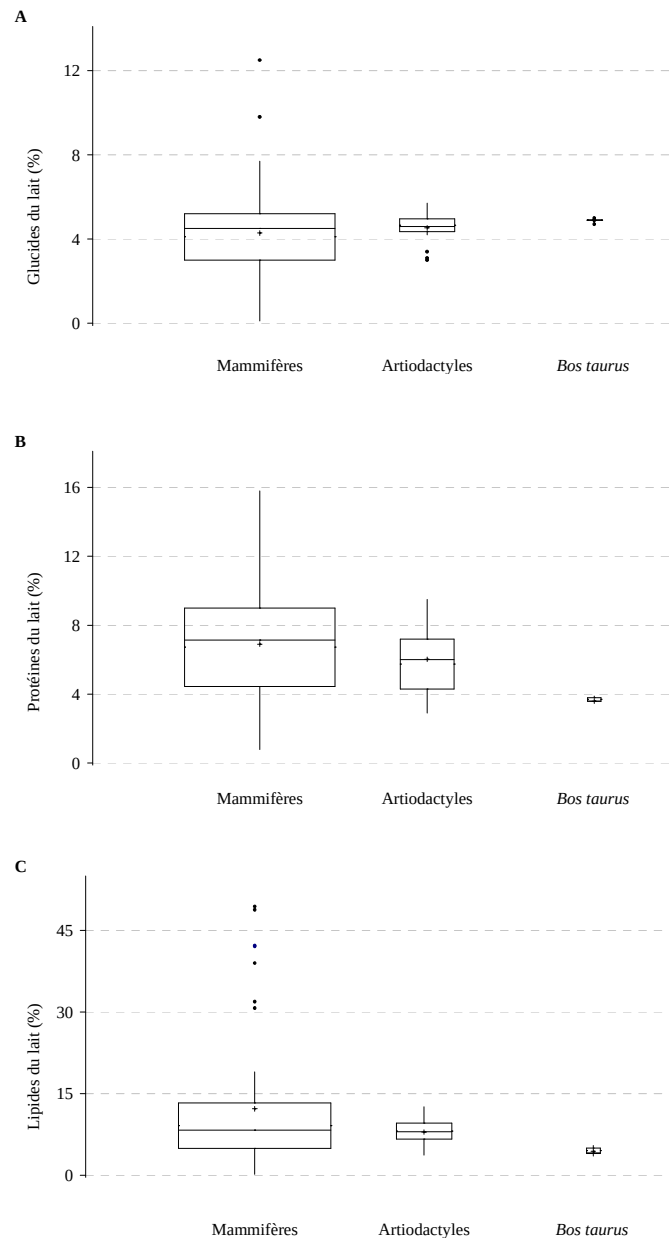


Figure 13 Composition du lait en lipides, protéines et glucides dans la classe des mammifères (56 espèces parmi 9 ordres, Oftedal, 1984), l'ordre des artiodactyles (20 espèces, Oftedal, 1984) et l'espèce *Bos taurus* (5 races, Bremel, 1995).

Dans le modèle métabolique, la glande mammaire est représentée à son niveau d'interface à travers laquelle des précurseurs prélevés dans le sang (glucose, acides aminés, glycérol, acétate+butyrate et acides gras) sont convertis en lactose, protéines et triglycérides constitués d'acides gras à chaînes courtes ou longues. Dans ce modèle à vocation explicative, la dynamique de production laitière au cours de la lactation est fixée *a priori* par l'intermédiaire du modèle de Wood dans sa version modifiée par Dhanoa (1981), et interprétée en termes de flux de ses précurseurs métaboliques. La représentation de la glande mammaire est également

limitée dans le modèle énergétique à son niveau d'interface qui convertit un faisceau de flux d'énergie orientés vers la fonction de lactation en un faisceau de flux de matières (eau, lactose, protéines et lipides). La quantité de lait produite s'élabore dans ce modèle par un compromis entre une réalisation potentielle et une réalisation effective. La réalisation potentielle est déterminée au niveau du modèle téléonomique qui formalise une priorité à la fonction de lactation dans une perspective d'accomplissement de la finalité particulière d'assurer la survie du jeune dans la finalité globale de pérennité de l'espèce. Cette formalisation agit comme une force motrice qui gouverne l'orientation du métabolisme énergétique vers la production de lait. La quantité de lait potentielle est alors régie à travers cette gouvernance dynamique sans dimension et à travers un facteur d'échelle qui quantifie un niveau propre à l'animal et capture l'idée d'une capacité génétique. La réalisation potentielle est traduite en un besoin énergétique et conditionne un équilibre de fonctionnement du métabolisme énergétique lorsque ce besoin est couvert par une ingestion qualifiée d'optimale. L'apport d'énergie effectif par l'alimentation, qui traduit les conditions environnementales, peut imposer une déviation de cet équilibre, dans le sens d'un excès ou d'un déficit d'énergie. Le modèle énergétique contient une formalisation mathématique d'une règle de partition de cette déviation : un ajustement du fonctionnement de l'organisme dans son ensemble est ainsi établi exprimant la réalisation effective de la production laitière. Le couplage des modèles téléonomique et énergétique formalise ainsi un équilibre parmi des équilibres potentiels de fonctionnement de l'organisme et les transitions entre ces états lorsque les conditions alimentaires sont plus au moins favorables à leur établissement.

La notion de pilotage élaboré de façon intime au sein de l'organisme à déjà été incorporée dans des approches de modélisation de la lactation. Elle est notamment formalisée à travers une « *hormone de lactation* » par Neal et Thornley (1983). D'autres auteurs comme Dijkstra *et al.* (1997), Friggens *et al.*, 1998, Pollot (2000) ou Vetharaniam *et al.* (2003a ; 2003b) ont également cherché à représenter la lactation en incorporant les mécanismes clefs de la biologie de la glande mammaire (différentiation cellulaire, apoptose, activité sécrétoire, etc.).

L'invocation d'un potentiel de lactation et sa connexion à un déterminisme génétique est également classique pour individualiser des profils de production laitière. Ici, le potentiel correspond à un équilibre incorporant un fonctionnement global du métabolisme énergétique et non un maximum. Dans le modèle métabolique, un paramètre de potentiel est également

utilisé pour dérouler les transactions métaboliques associées à des niveaux de production laitière variables.

La philosophie générale adoptée dans ce travail pour représenter la lactation relève d'une reconsidération de sa signification dans la fonction de reproduction. La sécrétion de lait est la fonction de la glande mammaire, glande exocrine et organe sexuel femelle, et sa finalité est la nutrition extra-utérine du jeune en relais de l'utérus qui assure cette fonction de nutrition au cours de la gestation. Ce point de vue, bien que fondamentalement évident et naturel, n'est pas celui, classique, qui envisage plus la lactation comme une fonction de transformation d'une ration alimentaire que comme une composante finalisée de la reproduction.

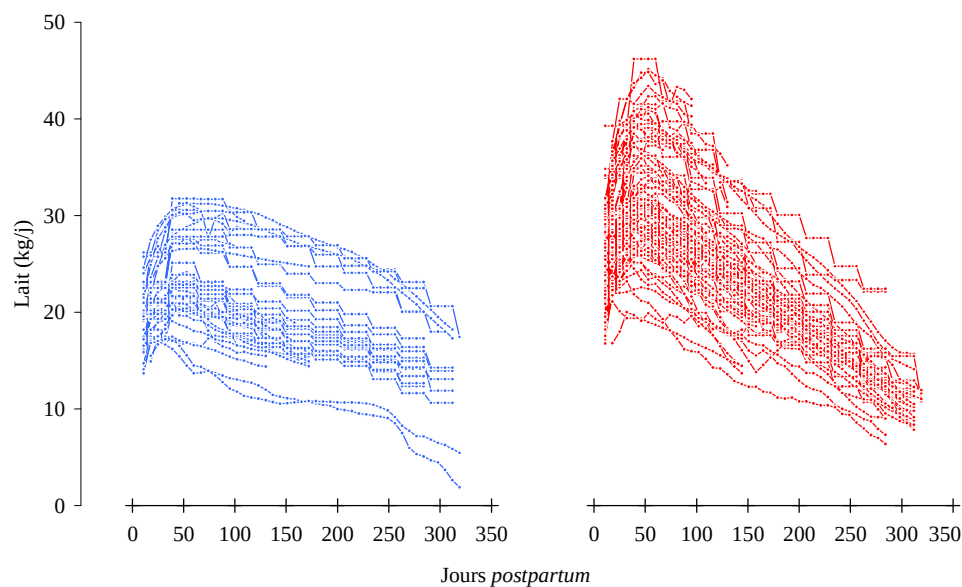


Figure 14 Évolution de la production laitière au cours de la lactation de vaches laitières : Données de la littérature²¹ pour des animaux primipares (*en bleu*) et multipares (*en rouge*).

²¹ Rook and Campling, 1965 ; Swanson, 1967 ; Broster *et al.*, 1969 ; Decaen, 1970 ; Broster *et al.*, 1975 ; Lodge *et al.*, 1975 ; Everson *et al.*, 1976 ; Johnson, 1977 ; Vérité and Journet, 1977 ; Wohlt and Clark, 1978 ; Johnson, 1979 ; Kronfeld *et al.*, 1980 ; Garnsworthy and Topps, 1982 ; Holter *et al.*, 1982 ; Pinchasov *et al.*, 1982 ; Donker, 1983 ; Johnson, 1983 ; Llahr *et al.*, 1983 ; Holter *et al.*, 1984 ; Taylor and Leaver, 1984a ; 1984b ; DePeters, 1985 ; DePeters, 1989 ; Staples *et al.*, 1990 ; Kertz *et al.*, 1991 ; Wohlt *et al.*, 1991 ; Holter and Hayes, 1992 ; Holter *et al.*, 1993 ; Ostensen *et al.*, 1997 ; Tolkamp *et al.*, 1998 ; Soder and Holden, 1999.

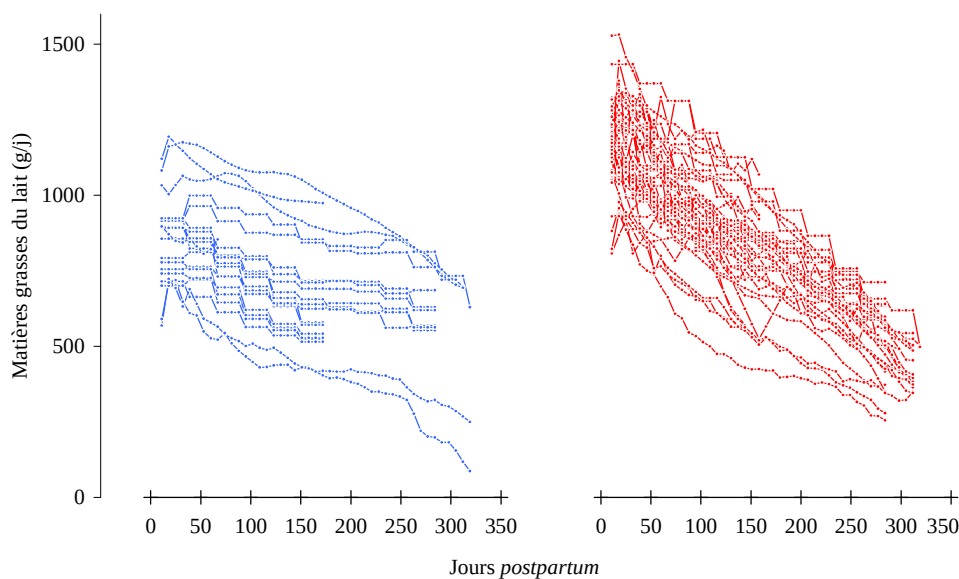


Figure 15 Évolution de la production de matières grasses du lait au cours de la lactation de vaches laitières : Données de la littérature²² pour des animaux primipares (*en bleu*) et multipares (*en rouge*).

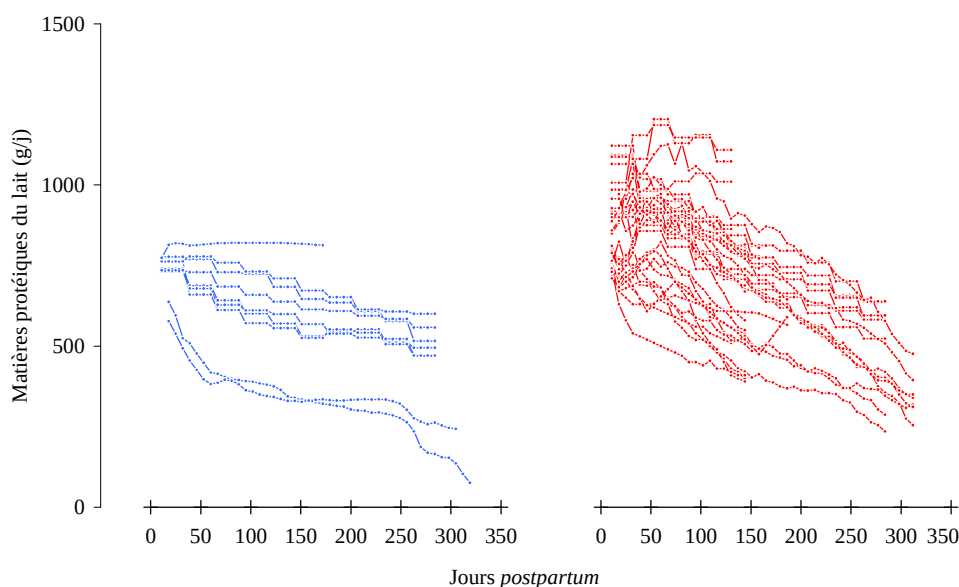


Figure 16 Évolution de la production de matières protéiques du lait au cours de la lactation de vaches laitières : Données de la littérature²³ pour des animaux primipares (*en bleu*) et multipares (*en rouge*).

²² Rook and Campling, 1965 ; Swanson, 1967 ; Decaen, 1970 ; Broster *et al.*, 1975 ; Everson *et al.*, 1976 ; Johnson, 1977 ; Wohlt and Clark, 1978 ; Johnson, 1979 ; Kronfeld *et al.*, 1980 ; Donker, 1983 ; Johnson, 1983 ; DePeters, 1985 ; Staples *et al.*, 1990 ; Kertz *et al.*, 1991 ; Wohlt *et al.*, 1991 ; Holter and Hayes, 1992 ; Ostensen *et al.*, 1997 ; Tolcamp *et al.*, 1998.

²³ Rook and Campling, 1965 ; Decaen, 1970 ; Johnson, 1977 ; Wohlt and Clark, 1978 ; Johnson, 1979 ; Kronfeld *et al.*, 1980 ; Donker, 1983 ; Johnson, 1983 ; Wohlt *et al.*, 1991 ; Ostensen *et al.*, 1997 ; Tolcamp *et al.*, 1998.

3.4 Ingestion

L'ingestion correspond à l'entrée d'aliments et d'eau de boisson dans l'appareil digestif de la vache. La nature de ce flux est déterminée par les ingrédients de la ration mise à disposition de la vache dont le choix relève des pratiques au sein de l'élevage et de la sélection par l'animal qui exprime ses préférences pour les aliments plus ingestibles et digestibles. L'ingestion n'est pas un flux continu à l'échelle du nyctémère mais intervient par phases en alternance avec les activités de rumination et de buvée (Dulphy and Faverdin, 1987). Ces phases sont constituées d'une succession de prises alimentaires regroupées au sein de repas (Tolkamp *et al.*, 1998 ; Tolkamp and Kyriazakis, 1999a ;1999b) réalisés principalement aux moments des distributions d'aliments, aux levers et couchers du soleil et dont la répartition pour un individu donné est liée à son statut social au sein du groupe. Ces aspects du comportement alimentaire mettant en jeu des mécanismes d'expression de la faim et de la satiété à court terme sont ignorés dans le modèle dont le pas de temps est le jour et dans lequel l'ingestion est en conséquence considérée comme un phénomène continu.

Dans le modèle énergétique, l'ingestion est considérée sous forme d'un flux de matière sèche converti en un flux d'énergie métabolisable qui constitue l'entrée du métabolisme énergétique et sous forme d'un flux de matière fraîche transitant au sein d'un unique compartiment digestif dont il influence la masse. Dans le modèle métabolique, le flux d'aliment ingéré est traduit en cinq flux de métabolites qui constituent l'entrée alimentaire du système animal : flux d'acides gras volatils absorbés par l'organisme à travers la paroi ruminale (acétate+butyrate et propionate) et flux d'acides aminés, de glucose et d'acides gras absorbés par l'organisme à travers la paroi intestinale.

Dans le modèle métabolique, dont l'objectif est l'interprétation des échanges intervenant au niveau du système productif en termes de transactions métaboliques, la dynamique de la quantité ingérée à l'échelle de la lactation est fixée *a priori*. Le pattern caractéristique de cette dynamique est illustré en Figure 17 à travers un faisceau de cinétiques collectées dans la littérature. Dans le modèle énergétique, la dynamique d'ingestion à l'échelle de la vie de l'animal est envisagée comme une réponse. Le modèle téléonomique gouverne des orientations physiologiques qui expriment au niveau du modèle énergétique des besoins en énergie pour assurer des processus et une capacité physique à ingérer qui traduit un encombrement tolérable du reticulo-rumen. La densité énergétique de la ration détermine ainsi une quantité d'aliments à ingérer pour couvrir ces besoins. L'ingestion est alors

représentée par une quantité requise pour couvrir un niveau de besoin énergétique et une quantité permise pour saturer un niveau de potentialité physique. La quantité effectivement ingérée consiste finalement en un compromis entre ces valeurs : elle est au plus égale à la quantité permise, au moins égale à la quantité requise et égale à une quantité qui peut excéder le besoin strict de l'animal dans la mesure où elle permet d'améliorer l'état corporel de l'animal.

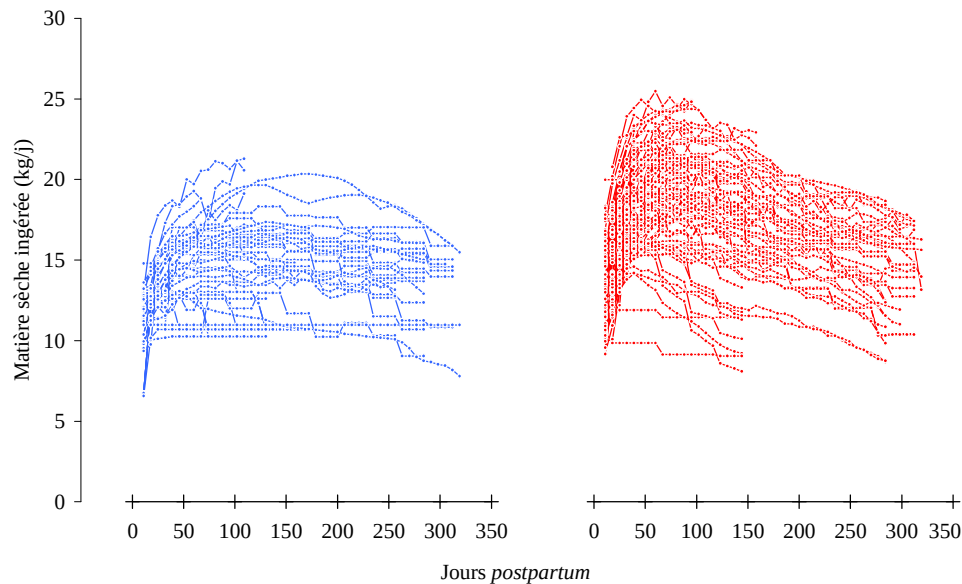


Figure 17 Évolution de la quantité de matière sèche ingérée au cours de la lactation de vaches laitières : Données de la littérature²⁴ pour des animaux primipares (*en bleu*) et multipares (*en rouge*).

La compréhension des mécanismes régulant l'ingestion et sa prédiction à partir des caractéristiques des aliments et de l'état physiologique de l'animal relèvent d'une problématique centrale en sciences animales. Depuis près de 50 ans, le lien entre des variations de niveau de production laitière et des variations de niveau d'ingestion alimente les débats et mobilise des efforts de recherche (Faverdin *et al.*, 2007). La question soulevée appelle deux points de vue alternatifs sur la force motrice dans la représentation de l'animal-interface : « *push* » (les entrées font les sorties) ou « *pull* » (les sorties font les entrées) (Drackley *et al.*, 2006).

²⁴ Broster *et al.*, 1969 ; Broster *et al.*, 1975 ; Cowan, 1970 ; Decaen, 1970 ; DePeters, 1985 ; DePeters, 1989 ; Everson *et al.*, 1976 ; Garnsworthy and Topps, 1982 ; Holter *et al.*, 1982 ; Holter *et al.*, 1984 ; Holter *et al.*, 1992 ; Holter *et al.*, 1993 ; Johnson, 1977 ; Johnson, 1979 ; Johnson, 1983 ; Kertz *et al.*, 1991 ; Kronfeld *et al.*, 1980 ; Krohn *et al.*, 1983 ; Llahr *et al.*, 1983 ; Lodge *et al.*, 1975 ; Mohrenweiser and Donker, 1967 ; Ostensen *et al.*, 1997 ; Pinchasov *et al.*, 1982 ; Rook and Campling, 1965 ; Soder and Holden, 1999 ; Staples *et al.*, 1990 ; Swanson, 1967 ; Taylor and Leaver, 1984a ; 1984b ; Tolkamp *et al.*, 1998 ; Vérité and Journet, 1977 ; Wallace, 1959 ; Wiktorsson, 1971 ; Wiktorsson, 1973 ; Wohlt and Clark, 1978 ; Wohlt *et al.*, 1991.

Classiquement, l'ingestion est envisagée à travers les concepts de capacité physique et celui de couverture énergétique d'un besoin. Les systèmes d'alimentation développés à travers le monde et de nombreux travaux de modélisation reposent sur une formalisation de ces concepts. En France notamment, l'utilisation des unités fourragères (Vermorel, 1978 ; Vermorel *et al.*, 1987) et de l'unité d'encombrement (Jarrige *et al.*, 1979) pour caractériser les aliments en sont l'illustration. A la suite des travaux de Conrad *et al.* (1964), des approches de modélisation reposant sur une double prédiction « *physique* » et « *énergétique* » ont été développées (Hyppöla and Hasunen, 1970 ; Forbes, 1977 ; Kristensen and Ingvarsen, 1986 ; Dulphy *et al.*, 1987 ; Mertens, 1987). Dans ce travail, encombrement physique et besoin énergétique interviennent dans la détermination de la quantité d'aliments ingérés. L'originalité réside dans l'introduction d'une notion de besoin énergétique « *différé* » en plus du besoin énergétique « *instantané* ». Le besoin instantané est associé à la couverture des besoins énergétiques pour la réalisation des processus physiologiques en cours (pour la croissance, l'entretien et la reproduction) ; le besoin différé correspond au stockage de l'énergie sous forme de réserves permettant la constitution d'un état corporel propice à la réalisation des processus physiologiques futurs (en particulier, les dépenses énergétiques associés au cycle de reproduction à venir). Cette représentation incorpore explicitement une régulation de l'ingestion liée au niveau des réserves corporelles dont les principes relèvent de la théorie lipostatique invoquée au début des années 50 par Kennedy (1953). Cette théorie suggère l'existence d'un état d'équilibre des réserves corporelles agissant comme une force de rappel et gouvernant la prise alimentaire dans le long terme. L'incorporation du niveau des réserves corporelles dans la prédiction des quantités ingérées par une vache a déjà été effectuée dans des approches de modélisation (Ellis *et al.*, 2006b). Dans le modèle énergétique, l'ingestion est représentée comme une fonction régulée à un niveau global par l'intermédiaire du modèle téléonomique, et implique ainsi de façon concertée les demandes associées à l'ensemble des fonctions physiologiques dont celle de gestion à long terme des réserves corporelles. En revanche, la régulation de l'ingestion liée aux caractéristiques de la ration alimentaires est limitée à la considération de sa densité énergétique. Il existe en effet de nombreux niveaux de caractérisation des aliments : espèce végétale, constituant de l'appareil végétatif, type de sous-produit, forme de présentation, classe d'aliment, composition chimique, granulométrie, digestibilité, etc. Ces niveaux permettent une sophistication de l'information relative au matériau alimentaire et fournissent potentiellement des clefs pour apprécier le déroulement du processus digestif dans son ensemble. La caractérisation des aliments et la compréhension de son influence sur la digestion s'inscrivent dans la

problématique d'interprétation des aliments en termes de nutriments assimilables par l'organisme, qui eux mêmes déterminent l'élaboration des performances animales. Les systèmes d'alimentation développés pour rationaliser l'alimentation du bétail se fondent sur l'utilisation d'une référence commune pour caractériser les aliments en termes d'apports et les fonctions biologiques de l'animal en termes de besoin. Ce principe a historiquement été introduit au XIX^{ème} siècle par Thaer (1809) qui fut vraisemblablement le premier à envisager comment évaluer des aliments en termes de production à travers cette question simple : *« Quelle quantité d'un aliment donné est nécessaire pour le substituer à un aliment de référence sans induire de modification de production ? »*.

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Partie II Proposition de modèle

« The best material model of a cat is another, or preferably the same, cat »

Norbert Wiener

1 Modèle téléonomique

La description du modèle téléonomique est présentée sous la forme d'un article soumis à la revue Animal :

Martin O and Sauvant D 2009. Modelling dairy livestock lifetime performance. 1. Teleonomic trajectories of life function priorities. Animal (submitted ²⁵).

²⁵ Accepté après la soutenance de thèse sous la forme : **Martin, O. and Sauvant, D., 2010a. A teleonomic model describing performance (body, milk and intake) during growth and over repeated reproductive cycles throughout the lifespan of dairy cattle. 1. Trajectories of life function priorities and genetic scaling. Animal (in press).**

Modelling dairy livestock lifetime performance.

1. Teleonomic trajectories of life function priorities

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This is the first paper of a short series of two accompanying papers describing a teleonomic model of lifetime performance of dairy livestock. The conceptual framework is based on the coupling of a regulating sub-model providing drives to rule the work of an operating sub-model. The regulating sub-model describes the dynamic partitioning of a mammal female's priority between life functions targeted to growth (G), ageing (A), balance of body reserves (R), and nutrient supply of the unborn (U), newborn (N) and suckling (S) generations. The so-called GARUNS dynamic pattern of priorities defines a teleonomic trajectory goal-directed to the survival of the individual for the survival of its life form. The operating sub-model describes changes in body weight and composition, fetal growth, milk yield and composition, and food intake over lifetime and during phases of gestation and lactation of repeated reproductive cycles. This dynamic pattern of performance defines a reference trajectory of a female livestock under normal husbandry conditions and feed regimen. Genetic parameters are incorporated in the model to scale individual performance and simulate differences within and between breeds. The model was calibrated in dairy cows with literature synthetic data. The model was evaluated by comparison with simulations of previously published models of body weight, body condition score, milk yield and composition, and food intake. Model simulations with varying values of genetic parameters are shown in graphs. The model allows to simulate the range of variability of dairy cattle performance.

Keywords: teleonomic model, reproductive cycle, dairy cow, lactation, body reserves

Implications

This model of lifetime performance of dairy livestock opens new perspectives in the field of modelling animal physiology and provides a prototype of an integrative whole animal model. This work involves (1) an innovative conceptual framework by focusing on priorities for physiological functions, (2) a holistic view of growth, reproduction and nutrition, (3) a combination of genotype and environmental effects in the prediction of performance, and (4) a generic formalism with scaling parameters allowing to simulate different animal genotypes.

Introduction

“Prediction of nutrient partitioning is a long-standing problem of animal nutrition that has still not been solved. Another substantial problem for nutritional science is how to incorporate genetic differences into nutritional models. These two problems are linked as their biological basis lies in the relative priorities of different life functions (growth, reproduction, health, etc.) and how they change both through time and in response to genetic selection” (Friggens and Newbold, 2007). This statement, made in the context of dairy cattle nutrition modelling, highlights the importance of being able to describe the changing priorities of an animal as it ages, through repeated reproductive cycles, and over successive generations.

Ultimately, relative priorities change to ensure the survival of the individual and to maximize the production of viable offspring. The achievement of these two major overlapping goals involves two main regulatory mechanisms: homeostasis and homeorhesis. The survival of the individual implies a continuous maintenance of a non-lethal physiological state in a fluctuating environment. Homeostasis is the

tendency to maintain such an internal physiological equilibrium (Bernard, 1865; Cannon, 1929; 1932) and refers to the reactive and appropriate changes to restore a physiological state perturbed by environmental constraints. The production of viable offspring involves a genetically driven time-based succession of physiological processes. This can be seen as a schedule of changing dominance of the following main goal-directed functions: growth to reach maturity, investment in reproduction to produce and rear offspring, and modulation of body reserves to safeguard physiological requirements for future reproduction and counter seasonal changes in food availability. Within a given species, this schedule has a characteristic pattern with variation between individuals. Homeorhesis is the tendency to home on to such a physiological dynamic process (Kennedy, 1967) and refers to the orchestrated changes in metabolism necessary to support a dominant physiological state (Bauman and Currie, 1980). In animal nutrition, homeorhesis, also coined teleorhesis (Bauman and Currie, 1980) (“directed flow”) or teleophorhesis (Chilliard, 1986) (“towards a goal”), explain the changes in partitioning of circulating nutrients during different developmental and physiological stages.

The term homeorhesis (“similar flow”) was introduced by Waddington (1957) to expand the concept of homeostasis (“similar state”) and to capture the idea that what living things really hold “*constant is not a single parameter, but a time-extended course of change, that is to say, a trajectory*”. While homeostasis is the property of a system that returns to a particular state, homeorhesis is the property of a dynamic system that returns to a trajectory. Waddington introduced the term chreod (“necessary path”) to describe the trajectory itself. From the modelling standpoint, this distinction between the end and the means-to-the-end is an essential point, and the properties of homeorhesis and homeostasis can be seen respectively as the

77 long- and short-term components of the general process that make living organisms
78 follow a trajectory in their physiology despite disturbing environmental conditions.
79 This trajectory being compatible with life, genetically determined and evolutionarily
80 targeted to ensure species continuation.

81 The problem pointed out by Friggens and Newbold (2007) concerns the integration
82 of homeorhetic and homeostatic regulations in nutrition models in which the animal
83 would be considered “*as an active biological entity with its own ‘agenda’*” (Friggens
84 and Newbold, 2007). Following this idea, the modelling of a trajectory, i.e., a
85 schedule of priority of life functions genetically designed and acting as an
86 homeorhetic driving force and an homeostatic reference state, should be the starting
87 point (Friggens *et al.*, 2004). Several nutrition models of lactating animals, mainly in
88 cattle, have been published in the last 20 years (e.g., review in Sauvant, 1992; 1996;
89 Tedeschi *et al.*, 2005; Chalupa *et al.*, 2004). Homeorhetic and homeostatic
90 regulations were generally not the main focus of these modelling approaches
91 although they contained control or retro-control components implicitly or explicitly
92 incorporated in the model core. Control mechanisms with homeostatic properties
93 have been used in models to smooth the short term failures of adjustment between
94 input and output (Sauvant, 1994). Homeorhetic type controls have been introduced in
95 a few nutritional models by the way of meta-hormones. This concept refers to the
96 empirical modelling of complex hormonal systems by a theoretical hormone used as
97 a driving variable (e.g., lactation hormone (Neal and Thornley, 1983), anabolic and
98 catabolic hormones (Sauvant and Phocas, 1992; Baldwin, 1995; Martin and Sauvant,
99 2007). In Danfaer (1990), growth hormone and insulin actions on metabolism was
100 explicitly modelled. These (meta-)hormones formalize in mechanistic animal models

101 the idea of control of the operating subsystem (involving metabolic pathways) by a
102 higher level regulating subsystem (simulating endocrine controls) (Sauvant, 1994).

103 However, none of these approaches explicitly focused on the modelling of
104 homeorhetic and homeostatic regulations by incorporating the teleonomic concept of
105 an inherent trajectory. This idea was pioneered by Friggens *et al.* (2004) in
106 developing a genetically driven pattern of body lipid change through pregnancy and
107 lactation in dairy cattle, seen as a trajectory safeguarding reproductive success
108 (Friggens, 2003), and used in a model of feed intake regulation in dairy cow (Petruzzi
109 and Danfaer, 2004). In a model of dairy goat energy metabolism, Puillet *et al.* (2008)
110 explicitly represented a regulating sub-system producing dynamic drives for gestation
111 and lactation although this model was not designed to deal with variability in nutrition
112 supply.

113 We propose in a short series of two accompanying papers a modelling approach,
114 explicitly incorporating a goal-directed trajectory of priority aimed at generating
115 homeorhetic and homeostatic regulations. This model is designed for dairy livestock
116 and applied to the dairy cow. The model consists of two sub-models. The regulating
117 sub-model describes the dynamic partitioning of relative priorities between growth,
118 reproductive functions and body reserves constitution/reconstitution during lifetime
119 punctuated by successive reproductive cycles. The concept of priority embodies the
120 idea that the coordination of physiological functions is goal-directed toward the
121 preservation of life for the reproduction of life form (Bricage, 2002). From this
122 teleonomic view, the process of living is considered as the dynamic partitioning of an
123 overall priority between priorities associated with elementary life functions. These
124 trajectories of priority are used to generate a reference pattern of physiological
125 processes, which represents a genetically driven pattern of lifetime performance and

establishes homeostatic set-points for the operating sub-model (Paper 1). In the operating sub-model, this pattern of performance is interpreted into a dynamic partition of energy required for growth of body tissues, maintenance, pregnancy and lactation, which determines a desired level of dietary energy input. Finally, in response to the actual level of energy intake, this partition is modulated by the way of an homeostatic regulation function, which apportions the difference between energetic supply and demand between physiological processes (Paper 2). Thus, the concept of priority at the regulating sub-model level provides teleonomic drives used in the operating sub-model to formalize homeorhetic regulations of lifetime performance and homeostatic regulations of energy partitioning.

The whole model allows the prediction of milk yield and composition, foetal growth, calf birth weight, intake, and body mass and composition changes in dairy cows over their lifespan and during repeated gestation/lactation cycles.

Model description

Rationale

The regulating sub-model (**Figure 1.1**) describes the partition of a mammal female's priority over lifetime t (d) between six components of the goal of maximizing the number of viable offspring:

- G : achieve *growth* of the mother to maturity by body mass accretion during the developmental stage of life;
- A : achieve *ageing* of the mother to death by reducing investment in repair processes resulting in a decline of the ability to perform vital functions;
- R : balance body *reserves* of the mother to maintain favourable reproductive conditions by storage or mobilization;

- U : complete intrauterine growth of the *unborn* generation (the embryo in the gravid mother uterus) during pregnancy;
- N : supply nutrients to the *newborn* generation (the neonate) by lactation initiation and body reserve mobilization at the transition time between gestational and lactational stages of the reproductive cycle;
- S : supply nutrients to the *suckling* generation (the nursing young substitute by the milking machine in dairy production context) by lactation persistency.

The so-called unborn, newborn and suckling generations consist physically of the same young that suckles its mother after birth. The distinction between them is made from the physiological standpoint of the maternal functions involved in their survival, *i.e.*, gestation, lactation and the transition phase between them which involves mobilization of body reserves. At parturition, there occurs the transfer of the function of supplying nutrients to the offspring from the placental uterine unit to the mammary gland.

The concept of priority is formalized as a dimensionless quantity flowing through these compartments: from G to R during growth, from R to A with ageing, and cyclically through R , U , N and S during reproductive cycles (**Figure 1.2**). An essential feature of the model is the steadiness of the overall priority the dynamic partition of which is described by the regulating sub-model.

$$G + A + R + U + N + S = 1 \quad (1)$$

Forthwith, the term priority is employed in the sense of the “quantity of relative priority” represented by each of these state variables. An important point is that, at the level of the regulating sub-model, the value of a given priority only quantifies the overall relative rank of superiority of a goal, not the intensity of the physiological

processes involved in its achievement. Thus, for instance, a priority of 1 implies a paramount importance but not necessary a maximal realisation.

Priority components

Growth. Priority G to growth represents the investment in the construction of a mature individual and is linked to the level of achievement of a mature structural body mass, assumed to be an individual genetic trait. The main component of this investment is the allocation of available energy to build tissue. In a general model for ontogenetic growth (West *et al.*, 2001), the quantity $1 - (\text{current weight} / \text{mature weight})^{1/4}$ was defined as the proportion of total available metabolic energy fuelling the production of new biomass, the remaining quantity $(\text{current weight} / \text{mature weight})^{1/4}$ being the proportion of total available metabolic energy allocated to maintenance and other functions. This partition of energy is assumed to mirror the partition at the conceptual level of priority and the differential equation for G is defined consistently with the analytical rule given by

$$G = 1 - \left(\frac{W}{W_M} \right)^{1/4}, \quad (2)$$

where W and W_M are respectively the current and mature non-labile body weights (see (22) in the operating sub-model section).

The differential equation for G is

$$\frac{dG}{dt} = -d, \quad (3)$$

with $G_{t=0} = 1 - (W_B / W_M)^{1/4}$ and where W_B is the non-labile body weight at birth (see in the model development section).

194 The flow d (development) from G to R is defined to update G according to
195 changes in W with respect to (2) and is given by

$$d = \frac{1}{4 \cdot W_M^{1/4} \cdot W^{3/4}} \cdot \frac{dW}{dt} \quad (4)$$

196 Formally, this flow represents the synchronization of the regulating sub-model with
197 the operating sub-model according to the achieved level of maturity. By this way,
198 priority to growth is updated according to its level of completion and follows a
199 curvilinear pattern ($G \rightarrow 0$ and $A + R + U + N + S \rightarrow 1$ with age as $W \rightarrow W_M$ with age).
200 Priority defined by $1 - G = A + R + U + N + S$ is the overall priority to functions of the
201 mature, fully-developed individual (**Figure 1.3**).

202

203 *Ageing.* Priority A to ageing represents the relative loss in other priorities. The
204 increase in A with time relies on the progressive decline with age of the ability to
205 perform the work of life, including survival and reproduction (Brody, 1924).

206 The differential equation for A is

$$\frac{dA}{dt} = s, \quad (5)$$

207 with $A_{t=0} = 0$.

208 The flow s (senescence) from R to A is arbitrarily formalized with a logistic function:

$$s = \sigma \cdot A \cdot (1 - A), \quad (6)$$

209 where σ (d^{-1}) is the fractional rate of senescence.

210 To initiate the flow s ($s = 0$ while $A = 0$), a discrete transfer from R to A is triggered
211 at first conception to set A to 10^{-3} (arbitrarily small quantity):

$$t = t_c(0) \Rightarrow \begin{cases} A_{t+1} = A_t + 10^{-3} \\ R_{t+1} = R_t - 10^{-3} \end{cases} \quad (7)$$

where $t_c(0)$ (d) is the age at first conception (see further).

The underlying assumption is that the senescence process starts when animal first involves in reproduction. The flow s induces a sigmoid shape for A (**Figure 1.2**) and causes the integral transfer of the sum of relative priorities to A ($A \rightarrow 1$ and $G + R + U + N + S \rightarrow 0$ with age). Thus, the flow s delimits an interval within the animal lifespan during which the regulating sub-model is functional. The asymptotic value $A=1$ represents the state of being old but not necessary dead, *i.e.*, a state of fully expression of processes of senescence leading to death. A sigmoid pattern rather than an exponential one was chosen to capture this idea and to avoid the *a priori* definition of a time at which $A=1$. Priority defined by $1 - (G + A) = R + U + N + S$ is the overall “available capital of priority” to functions of the individual in age of procreating and is maximal within a lifetime period during which $G + A$ is at nadir.

Reserves. Priority R concerns the goal of balancing body reserves assuming the existence of an optimal target level of body reserves (Friggens, 2003) maintained by physiological processes of storage and mobilization. Storage of body reserve occurs for the construction of this level during developmental stage of life and takes place for the reconstitution of this level during reproductive cycles. Mobilization occurs at parturition as part of the lactation physiological process and is targeted by N (see further) but also takes place for the deconstruction of excessive level of body reserves constituted during overfeeding periods (see paper 2). Relying on Friggens (2003), the view taken here is that the changes in body reserves are to a large extent genetically driven and follow a trajectory which is a natural component of the reproductive cycle to support the evolutionary goal of maximizing reproductive success. The body reserve reconstitution at the end of a reproductive cycle allows

the restoration of the individual mother body state and is targeted to the accomplishment of the subsequent reproductive cycle. From that standpoint, through the balance of a body condition compatible with reproduction, priority R traduces a potential maternal investment in reproduction: R is loaded during developmental stage of life (flow d), progressively unloaded by senescence (flow s) and cyclically discharge (flow p) and reloaded (flow w) during reproductive cycles.

The differential equation for R is

$$\frac{dR}{dt} = d - s - p + w, \quad (8)$$

with $R_{t=0} = 1 - G_{t=0} = (W_B/W_M)^{1/4}$.

Since $U + N + S = 0$ during non-reproductive stages of life, priority $R = 1 - (G + A)$ quantifies the level of potential investment in reproduction, i.e., a “quantity of priority” potentially conveyable from R to U , which increases during development and decreases in elderly animals. The key role of R as a source for priority to reproduction in the model reflects the crucial importance of energy storage in body tissues in reproduction of mammals. As seen in **Figure 1.2**, priority R oscillates during the reproductive stages of life defining “opportunity peaks” of body reserves reconstitution between reproductive cycles. During non reproductive stages, R shows a continuous and undisturbed pattern traducing a priority to stabilize body reserves to an optimal level.

Unborn generation. Priority U to the unborn generation represents the maternal investment to complete successfully the current pregnancy.

The differential equation for U is

$$\frac{dU}{dt} = p, \quad (9)$$

259 with $U_{t=0} = 0$.

260 The flow p (pregnancy) from R to U is derived from a model of fetal growth (Laird,
261 1966) with the assumption that priority U to pregnancy is proportional to foetal
262 growth (see Appendix A) and is given by

$$p = \begin{cases} \alpha \cdot \ln\left(\frac{Z}{U}\right) \cdot U & \text{if } \varepsilon \leq U < 1 - (G + A) - \varepsilon \\ 0 & \text{elsewhere} \end{cases}, \quad (10)$$

263 with $Z = \varepsilon \cdot \exp(-\ln(\varepsilon)/(1 - \exp(-\alpha \cdot \pi)))$ and $\varepsilon = \varpi/W_N$, where W_N is the theoretical
264 maximum neonate birth weight assumed to equal W_B , α and ϖ are parameters
265 defined in Laird (1966), and π is the theoretical maximum pregnancy length. This
266 classic and generic Gompertz-based model of embryonic growth was chosen
267 because of its generic form in which only the time and weight scales of process differ
268 among avian and mammalian species. The parameter ϖ is the initial foetus weight at
269 conception and the variable ε is thus the relative proportion of the neonate weight at
270 conception, and corresponds to the initial investment in pregnancy at the start of the
271 reproductive cycle. The flow p only occurs when the animal is pregnant, *i.e.*, $U \geq \varepsilon$,
272 and while the animal can invest in procreation, *i.e.*, $U < 1 - (G + A) - \varepsilon$. Conception is
273 defined as a periodic discrete event starting at age at first conception and repeated
274 cyclically during each reproductive cycle numbered by c (a reproductive cycle c is
275 defined from conception to the next conception with $c = 0$ at $t = 0$). To avoid the
276 unrealistic start of reproductive cycles in elderly animals the condition $A < 0.2$ is
277 required for conception. At conception times, the transfer of the small quantity ε from

278 R to U is triggered, which acts as a seed to initiate the flow p while the
279 reproductive cycle number is incremented:

$$t = t_c(c) \text{ and } A < 0.2 \Rightarrow \begin{cases} R_{t+1} = R_t - \varepsilon \\ U_{t+1} = U_t + \varepsilon, \\ c = c + 1 \end{cases} \quad (11)$$

280 where $t_c(c)$ (d) is the age at conception occurring during reproductive cycle c and is
281 given by

$$t_c(c) = t_p(c) + PCI(c), \quad (12)$$

282 where $t_p(c)$ is the age at parturition during reproductive cycle c and $PCI(c)$ (d) is an
283 input parameter of the model defining the parturition to conception interval of
284 reproductive cycle c .

285 The initial value $t_p(0)$ is set to zero and corresponds to birth which gives
286 $t_c(0) = PCI(0)$ where $PCI(0)$ corresponds to the age at first conception.

287 The equation for p is designed to yield $U = 1$ after π d of pregnancy (see Appendix
288 A) and the time of parturition is defined as the integral transfer of R to U , i.e., the
289 time of maximal investment in the current reproductive cycle (Friggens, 2003).
290 Actually, the maximal transfer from R is equal to $1 - (G + A)$ and is thus always lower
291 than one so that theoretical maximal pregnancy length is never reached. The discrete
292 event parturition triggers the transfer of U to N , which sets U to zero, updates the
293 age at parturition for the current reproductive cycle and set the boolean indicator of
294 mammary stimulation *milking* to one ($milking = 1$ when the animal is milked;
295 $milking = 0$ if not):

$$U \geq 1 - (G + A) - \varepsilon \Rightarrow \begin{cases} N_{t+1} = N_t + U_t \\ U_{t+1} = 0 \\ t_p(c) = t \\ \text{milking} = 1 \end{cases}, \quad (13)$$

296 This discrete transfer represents parturition and birth, *i.e.*, the fetus expulsion from
297 the mother uterus. At this moment, priority to survival of the unborn generation
298 becomes priority to survival of the newborn generation.

299

300 *Newborn generation.* Priority N to the newborn generation represents the maternal
301 investment in physiological functions allowing the initiation of lactation to provide
302 nutrients for the neonate's own requirements. The concrete expression of this
303 investment is mobilization of mother body reserves and lactogenesis. Structurally, N
304 can be seen as an intermediary compartment that ensures the continuity between
305 gestation and lactation within the reproductive cycle.

306 The differential equation for N is

$$\frac{dN}{dt} = -l, \quad (14)$$

307 with $N_{t=0} = 0$.

308 The flow l (lactation) from N to S describes with a simple mass action the transfer
309 of maternal investment from N (priority, inherited from U at parturition, to initiate
310 lactation) to S (priority to maintain lactation) with advancing time and is given by

$$l = \mu \cdot N, \quad (15)$$

311 where μ (d^{-1}) is the fractional rate of lactation initiation.

312 The mass action formalizes the ineluctability of the sequence gestation-lactation.

313

314 *Suckling generation.* Priority S to the suckling generation represents the maternal
315 investment in physiological functions allowing lactational persistency. As previously

mentioned, both N and S are priorities to the survival of the same physical generation (the young) by the way of the same process (the lactation) but N and S are priorities to specific components of this process, respectively its short-time establishment and its long-time course.

The differential equation for S is

$$\frac{dS}{dt} = l - w, \quad (16)$$

with $S_{t=0} = 0$.

The flow w (weaning) describes the trade-off between priorities S and R , *i.e.*, the shift between the priority to continue to invest in the lactation and carry on with the current reproductive cycle and the priority to restore body reserves to start a new reproductive cycle in favourable body conditions. The flow w is formalized with a mass action in which the fractional rate λ is designed to account for body reserve level, pregnancy effect and mammary stimulation:

$$w = \lambda \cdot S, \quad (17)$$

with

$$\lambda = \lambda_0 + \Lambda_x + \gamma \cdot U + \tau \cdot (1 - \text{milking}), \quad (18)$$

and

$$\Lambda_x = \lambda_1 / \left(1 + \left(\frac{X/W}{\chi_s} \right)^5 \right), \quad (19)$$

where X is the current body reserve mass (see (23) in the operating sub-model section), *milking* is the boolean indicator of mammary stimulation, and λ_0 , λ_1 , γ , τ (d^{-1}) and χ_s (kg/kg) are parameters governing the dynamic patterns of S and R . The parameter λ_0 is the basal fractional rate of transfer from S to R and determines

the slowest transfer from S to R . The term Λ_x is the body reserves dependent fractional rate of transfer from S to R and is a decreasing sigmoid function of the ratio X/W : it decreases asymptotically to zero when $X/W > \chi_s$, increases to λ_1 when X/W tends to zero, and is equal to $\lambda_1/2$ when $X/W = \chi_s$. The parameter χ_s corresponds to a safeguarding threshold under which the transfer of priority from S to R is enhanced. By this way, when body reserves are low, the fractional rate λ is increased, the transfer from S to R is thus accelerated and priority to maternal investment in the suckling generation is decreased to support the priority to maternal body reserves reconstitution (Wade and Schneider, 1992). In challenging contexts such as food restriction, "*homeostatic controls for survival can overwhelm homeorhetic mechanisms*" (Bauman and Currie, 1980) so that the priority of staying alive prevails. Formally, this effect represents the synchronization of the regulating sub-model with the operating sub-model according to the level of body reserves. An emerging property of this formalism is that as the level of body reserve is higher before the first reproductive cycle (shown by numerous authors through differences in body condition score at parturition between parity) the transfer of S to R is slower in the first reproductive cycle which induces a better persistency of the priority to lactation in primiparous cow which is a known feature of lactation.

The term $\gamma \cdot U$ represents the effect of the emerging of a new unborn generation, *i.e.*, the start of a new reproductive cycle, which increases λ and induces a decrease in priority to the suckling generation in aid of the next generation to be born.

The term $\tau \cdot (1 - \text{milking})$ represents the effect of mammary stimulation on S . The fractional rate λ is increased and the flow w from S to R is consequently accelerated when $\text{milking} = 0$, *i.e.*, when the young is no longer suckling after

weaning or death, or when the animal is no longer milked after drying off in dairy production context. The discrete event *drying off* sets *milking* to 0 after 320 d in milk, which induces an abrupt transfer from *S* to *R*.

Global and differential priority. State variables of the regulating sub-system are designed to quantify the relative priorities of functional goals, *i.e.*, the relative importance of a target the completion of which involves physiological functions. The connection of this purpose level to the level of performance in the operating sub-system involves two steps of interpretation through combinations of priorities and the definition of the concept of differential priority.

Combinations of priorities have been defined such as $1 - G = A + R + U + N + S$ (priority to functions of the fully-developed individual) and $1 - (G + A) = R + U + N + S$ (priority to functions of the individual in age of procreating). Other combinations of priority used afterwards are $G + A + R$, which is the overall priority to functions oriented to the individual and the complementary priority $U + N + S = 1 - (G + A + R)$ which is the overall priority to functions oriented to the offspring (**Figure 1.2**). These global priorities are used to inhibit and/or activate processes in the operating sub-model and act as taps.

The notion of differential priority traduces the idea that a given physiological process though contributing to a priority, may be partially effective according to the level of that priority. The formalism of a priority raised to the power of a given exponent is used to capture this idea. Thus, in the operating sub-model description, the differential priority $(1 - G)^y$ is used as an index of the ability to secrete milk. The shape of $(1 - G)^y$ is altered relative to that of $1 - G$ traducing a decay between specific priority to the particular physiological function of producing milk and the

overall priority to function of the fully developed individual (**Figure 1.3**). Specifically, $(1-G)^y$ represents the acquisition of maturity by the udder and is used in the operating sub-model to regulate milk secretion. To carry on with the plumbing metaphor, if the priority is the degree to which the tap is open, the differential priority is the diameter of the pipe and the physiological process is the water flow. With the same formalism the differential priority $(1-G)^x$ is used and defined as an index of the ability to balance body reserves (storage or mobilization). The shape of $(1-G)^x$ is altered relative to that of $1-G$ (**Figure 1.3**). During development, the differential priority to balance body reserves increases at a proportionally lower rate than the priority to function of the fully-developed individual. This formalism accounts for the delayed deposition of fat during growth. With the same formalism the differential priorities N^k and S^k are used and defined as indexes of the ability to secrete a particular milk constituent during lactation stages.

From a mathematical standpoint this allometric formalism ($f(x) = x^k$) gives flexibility to drive specific physiological processes at the underlying level of the operating sub-model. This formalism has nevertheless a biological sense as a given goal involves many specific physiological processes contributing to its completion at different biological levels and with a different rank of priority. The priority to growth, for instance, involves a differential increase of constitutive body tissues. Allometric functions have been widely used in this field to simulate differential growth of body constituents relative to the growth of the whole body. The same technique is used here to simulate the differential priority of physiological processes relative to the priority of the whole organism. The biological significance of these indexes is that they embody a holistic description of the complex endocrine controls of homeorhesis.

Trajectories of G , A , R , U , N and S (denoted *GARUNS* pattern) over 1500 d of life and through reproductive cycles are presented in **Figure 1.4**.

Operating sub-model

Variables of the operating sub-model concern body weight (BW , kg), body condition score (BCS , 0 to 5 scale defined by Mulvany, 1977), milk yield (MY , kd/d) and dry matter intake (DMI , kg/d). The formalism defined afterwards corresponds to a reference pattern of performance in a theoretical unchallenging feeding context. This formalism is used in the companion paper as the basis to simulate a reference pattern of energy partitioning.

Body weight (BW , kg) is given by

$$BW = EBW + GU + DT, \quad (20)$$

where EBW (kg) is the empty body weight given by

$$EBW = W + X, \quad (21)$$

where W (kg) is the non-labile body mass weight which determines the animal frame size, X (kg) is the labile body mass weight (X standing for extra-weight), DT (kg) is the digestive tract contents weight and GU (kg) is the gravid uterus weight including foetus and foetal annexes (placentome, membranes and fluids). Components W and X of the empty body weight are not associated with real anatomic parts of the body mass but are theoretical body compartments defined through their respective function of body frame and reserve.

The differential equation for W is given by

$$\frac{dW}{dt} = G \cdot (G + A + R) \cdot I/e_w, \quad (22)$$

with $W_{t=0} = W_B$ (non-labile body mass weight at birth, kg) and where e_w (Mcal/kg) is the growth *ME* requirement (for the accretion of 1 kg W , see Appendix B) and I is

the dietary *ME* input defined afterwards (see (34) in the food intake section) . Gain in *W* has priority when growth prevails (control by *G*) and the overall priority $G + A + R = 1 - (U + N + S)$ inhibits growth when gestation and lactation prevails during reproductive cycles. The term $(G + A + R) \cdot G$ defines the proportion of energy *I* inflowing from diet channelled to growth. In non-reproductive stages of life, $G + A + R = 1$ and equation (22) is consistent with the formalism proposed by West et al. (2001).

The differential equation for *X* is given by

$$\frac{dX}{dt} = bal - mob, \quad (23)$$

with $X_{t=0} = X_B$ (labile body mass weight at birth, kg) and where *bal* (kg/d) corresponds to changes in *X* associated with the balance of an equilibrium level of body fatness and *mob* (kg/d) corresponds to mobilization of body reserves.

Balance of *X* is given by

$$bal = (1 - G)^x \cdot b_0 \cdot R \cdot \left(1 - \frac{X}{\chi_M \cdot W_M} \right), \quad (24)$$

where $\chi_M \cdot W_M$ determines a target body reserves level (Friggens et al., 2004) attained and defended at the fractional rate b_0 (d⁻¹) modulated by priority *R* . The term $(1 - G)^x$ is the above defined differential priority, which represents an index of the ability to store and mobilize body reserves and modulates changes in *X* during animal lifetime. In particular, the constitution of body reserve is postponed relative to growth of the non-labile body mass in early developmental stages (Vernon et al., 1999; Owens et al., 1993). The control by *R* implies that balance of labile body reserves to an optimal level prevails during developmental stages of life (constitution of body reserves) and during the transition between lactational and gestational

stages of two successive reproductive cycles (reconstitution of body reserves by mobilizing surplus or filling deficit). The control by R also implies that balance of body reserves is inhibited at the onset of lactation ($R \approx 0$). This regulation is consistent with the fact that anabolism of body tissues is known to be hindered in early lactation (Bauman and Currie, 1980; Vernon and Flint, 1984; Chilliard and Robelin, 1985; McNamara, 1997). The construction of R (see (8), (17), (18) and (19)) implies an increase of body reserve storage when the level of X is excessively low. In the present version of the model describing a reference pattern of performance in unchallenging feeding contexts, the balance of X is always positive. In the companion paper, the balance of X can be negative when body reserves exceed the target level $\chi_M \cdot W_M$.

Mobilization of body reserves is given by

$$mob = (1 - G)^x \cdot m_0 \cdot N \cdot X \cdot \nu_X, \quad (25)$$

where m_0 (d^{-1}) is the fractional rate of mobilization modulated by priority N and ν_X (dimensionless) is a parameter scaling individual body reserve mobilization. This latter parameter, defined as a genetic parameter and set to 1 in model development steps, is used to account for individual variability in the amount body reserves mobilised in early lactation (see the model evaluation section). The control by N (maximum mobilization of body reserve at parturition when $U = R = S = 0$ and $N = 1 - (G + A)$) contributes to the supply of energy for milk secretion dedicated to the survival of the neonate which is a main feature in mammals (Pond, 1984; Oftedal, 2000). Moreover, mobilization is proportional to the level of body reserves, which is well established (Broster and Broster, 1998; Martin and Sauvant, 2002).

The differential equation for GU is given by

$$\frac{dGU}{dt} = p \cdot \frac{W_B}{\phi}, \quad (26)$$

473 with $GU_{t=0} = 0$ and $GU = 0$ at discrete event *parturition*, and where ϕ (kg/kg) is the
474 weight ratio of foetus to gravid uterus. Maternal uterus weight and uterine involution
475 are neglected for simplicity to avoid distinguishing the maternal part of gravid uterus
476 increase during gestation.

477 Developed on a daily timescale, the model is not designed to represent the diurnal
478 variations of body weight associated to changes in the digestive tract contents
479 weight. The mean retention time of solid food material in the digestive tract is
480 generally lower than three days (Hartnell and Satter, 1979; Mambrini and Peyraud,
481 1997). Therefore, the daily changes in digestive tract contents are simply described
482 with a differential equation incorporating the daily intake of fresh material and a
483 slightly delayed removal applied to contents exceeding a permanent digestive tract
484 contents weight scaled to body size.

485 The differential equation for DT is given by

$$\frac{dDT}{dt} = \frac{DMI}{DMC} - k_0 \cdot (DT - \delta \cdot W), \quad (27)$$

486 with $DT_{t=0} = \delta \cdot W_{t=0}$ and where DMC (kg/kg) is the diet DM content set to 0.60 for
487 model development, k_0 (t^{-1}) is the fractional rate of DT removal and δ (kg/kg) is a
488 parameter scaling a permanent digestive tract contents weight to body size.

489 Body condition score is calculated according to the current amount of empty body
490 fat (EBF , kg) with an empirical model proposed in a previous paper (Martin and
491 Sauvant, 2005):

$$BCS = \left(\frac{EBF}{(1 - \exp(-0.0068 \cdot (EBW - EBF)))^{3.7235}} - 17.9 \right) / 39.8, \quad (28)$$

492 with

$$EBF = \beta_w \cdot (W/W_M) \cdot W + \beta_x \cdot X, \quad (29)$$

where β_w and β_x (kg/kg) are the fat content of W at maturity and X respectively.

The daily raw milk yield (MY , kg/d) is defined as the sum of yields of milk constituents j (lactose ($j:L$), protein ($j:P$), fat ($j:F$) and water ($j:H$)) and is given by

$$MY = \sum_j MY_j, \quad (30)$$

with

$$MY_j = (1 - G)^y \cdot (k_{jn} \cdot N^{y_{jn}} + k_{js} \cdot S^{y_{js}}) \cdot W_M \cdot \nu_j \cdot \nu_Y, \quad (31)$$

where y , y_{jn} and y_{js} (dimensionless) and k_{jn} , k_{js} (kg/kg W_M) are parameters governing the kinetics of milk constituents yield and $\nu_{j:F,L,P,H}$ and ν_Y (dimensionless) are parameters scaling individual milk yield and composition. These latter parameters, defined as genetic parameters and set to 1 in model development steps, are used to account for individual variability in the amount of milk yield by the way of parameter ν_Y and in the milk fat, protein and lactose content by the way of parameters ν_F , ν_P and ν_L respectively (see the model evaluation section). Milk water yield is assumed to remain unchanged and ν_H is fixed to 1. The term W_M is used to scale milk yield to body size. The term $(1 - G)^y$ is the differential priority above defined as an index of milk secretion ability and allows representing the effect of mammary gland maturity which appears through the increase in milk yield with age (Brody et al., 1923). Terms $N^{y_{jn}}$ and $S^{y_{js}}$ are the differential priorities above defined as indexes of ability to secrete milk constituents.

Milk constituent j contents MC_j (kg/kg) are given by

$$MC_j = \begin{cases} MY_j/MY & \text{if } MY > 0 \\ 0 & \text{elsewhere} \end{cases} \quad (32)$$

Food intake, conventionally expressed in a *DM* basis, is given by

$$DMI = I/e_D, \quad (33)$$

where e_D is the diet *ME* content and I (Mcal/d) is the dietary *ME* input balancing energy requirements for maintenance, milk yield, pregnancy, growth and body reserves storage, given the energy issued from body reserves mobilization:

$$I = \frac{e_M \cdot BW^{0.75} + \sum_{j:L,P,F,H} e_j \cdot MY_j + e_U \cdot dGU/dt + e_{Xa} \cdot bal - e_{Xc} \cdot mob}{1 - G \cdot (G + A + R)}, \quad (34)$$

where e_M (Mcal/kg^{0.75}) is the maintenance *ME* requirement, e_j (Mcal/kg) is the *ME* requirement for the yield of milk constituent j , e_U (Mcal/kg) is the pregnancy *ME* requirement (for the accretion of 1 kg *GU*), e_{Xa} is the *ME* requirement for the storage of 1 kg X and e_{Xc} is the *ME* supply by the mobilization of 1 kg X (see Appendix B). The term $1 - (G + A + R) \cdot G$ defines the proportion of dietary *ME* channelled to maintenance, lactation, gestation and body reserve storage, the term $(G + A + R) \cdot G$ being the proportion of dietary *ME* fuelling growth, as previously described.

Model development

The model was implemented with Modelmaker version 3.0 software (Cherwell Scientific Ltd, 2000) using the Runge-Kutta 4 numerical integration procedure and a fixed integration step of 1 d from $t = 0$ to $t = 7300$ d.

Specific parameter settings.

Parameters of the regulating and operating sub-models are listed in **Table 1** and **Table 2** respectively. Numerical values of model parameters were either fixed as input parameters, found in appropriate literature or estimated through a global fitting procedure.

The diet *ME* content was set to the average value of $e_D = 2.7$ Mcal/kg *DM* (Martin and Sauvant, 2002) for model development, regardless of the animal physiological stage. Input parameters concerning the timing of the reproductive cycles are the age at first conception set to $PCI(0) = 450$ d and the interval from parturition to conception set to $PCI(c) = 120$ d whatever $c > 0$, the number of the reproductive cycle. These average values yield a first calving around 24 months of age, which is classically proposed as an economic and physiological optimum in Holstein cows (Gill and Allaire, 1976; Ettema and Santos, 2004) and a calving interval around 400 d which is a contemporary average. In the field, the interval from parturition to conception is the result of breeding practices, through the voluntary waiting period and the heat detection program (Caldwell, 2003) and of animal physiology, through the lengths of anovulatory anoestrus period and ovulatory cycles, and the insemination success rate. The length of the parturition to conception interval is moreover affected by the body condition score at calving and its loss in early lactation (Lopez-Gatius *et al.*, 2003). To simplify the time scaling of the model to data, the value of $PCI(c)$ was locked for model development steps consistently with the mean value of the stochastic model developed by Allore *et al.* (1998).

Parameters of the regulating sub-model are either involved in the specific scaling of the foetal growth (α , ϖ and π) or in the control of the shape of the *GARUNS* pattern (μ , σ , λ_0 , λ_1 , γ , χ_s and τ). Numerical values of α and ϖ were found in Laird

(1966) and the maximal pregnancy length parameter was derived from the review of Andersen and Plum (1965) and set to $\pi = 285$ d. The fractional rate of senescence was set to $\sigma = 0.0018$ to yield a maximum milk production in the fifth parity. The parameter χ_s defining the safeguarding threshold of body reserves and linking the operating sub-model with the regulating sub-model level was set to $\chi_s = 0.2$ which corresponds to a body condition score of 1.8 (value of 2.4 on a 1-5 scale). This value is close to the lower bound of the calving body score range recommended to safeguard from health problems (Gearhart and Curtis, 1990) and under which the risk of becoming too thin increases (Wattiaux, 1996). The fractional rate τ is involved in the decrease of priority S after drying-off and was set to $\tau = 0.1$ to yield an approximately integral transfer from S to R completed within 2 weeks after drying-off, triggered at 320 days in milk. Numerical values for parameters μ , λ_0 , λ_1 , γ were estimated through the global fitting procedure described afterwards.

Empty body weight at birth (EBW_B , kg) is estimated with the formula proposed by Taylor and Murray (1987): $EBW_B = 0.197 \cdot (W_M + X_M)^{0.83}$, leading to an average ratio EBW_B/EBW_M around 6.5 %. The chemical composition of W and X is homogeneous with the assumption that W and X contain respectively 3% at maturity and 75% of body fat (the remainder fat-free mass being composed of 73% water, 22% protein and 6% minerals consistently with Martin and Sauvant, 2005). The value of 75% for X is set consistently with the results of Tamminga *et al.* (1997) on the average composition of empty body tissue mobilization in early lactation. The value of 3% was set arbitrarily, assuming that W stands for a carcass tissue containing 30% of muscle containing 10% of muscular fat. With the assumption that X accounts for 3% of EBW at birth ($X_B = 0.03 \cdot EBW_B$ and $W_B = 0.97 \cdot EBW_B$), the

newborn calf *EBW* contains 2.5% fat, which is consistent with slaughter data on chemical composition of the bovine female neonate reported in the literature (Ellenberger *et al.*, 1950).

Parameters W_M , χ_M , ϕ , δ and k_0 of the operating sub-model are involved in body weight modelling. The mature non labile body mass is a genetic parameter governing the overall animal size. It was arbitrarily set to $W_M = 500$, which yield post calving body weights of 551 kg, 613 kg, 663 kg and 697 kg for parity 1, 2, 3 and 4 respectively and a non-pregnant non-lactating elderly cow weighing 762 kg. The parameter χ_M defining the target body reserves level at maturity was set to $\chi_M = \frac{1}{3}$, which corresponds to a body condition score at maturity of 3.4 (value of 3.7 on a 1-5 scale). This target value is close to the upper bound of the calving body condition score range recommended to safeguard from health problems (Caldwell, 2003; Wattiaux, 1996; Gearhart and Curtis, 1990). Moreover, this value is close to the calving body condition scores recognized for optimum milk production (Waltner *et al.*, 1993) and number of days to first oestrus (Friggens, 2003). This value leads to an empty body fat content of 21% for a non-pregnant non-lactating elderly cow, which is close to the average value reported by Ellenberger *et al.* (1950). The parameter giving the weight ratio foetus:gravid uterus was set to $\phi = 0.58$ consistently with findings of Ferrell *et al.*, (1976) and Huth and Smith (1979). The parameter scaling the permanent digestive tract contents weights to body size was set to $\delta = 0.17$ kg/kg and the fractional rate of digestive tract removal was set to $k_0 = 1.1$, leading to a ratio DT/BW ranging from 12% in dry cow to 16% in lactating cows consistently with average values reported in the literature (Martin and Sauvant, 2003).

Maintenance ME requirement is set to $e_M = 0.143 \text{ Mcal/kg}^{0.75}$ according to the synthesis of Agnew *et al.* (2003) and ME requirements for milk constituents yield were set derived from Dado *et al.* (1993) and set to $e_L = 6.164 \text{ Mcal/kg}$ lactose, $e_F = 13.574 \text{ Mcal/kg}$ fat, $e_P = 7.714 \text{ Mcal/kg}$ protein and $e_H = 0.144 \text{ Mcal/kg}$ water. Pregnancy ME requirement was set to $e_U = 7 \text{ Mcal/kg GU}$ daily gain, yielding average daily pregnancy ME requirements of 2.2, 3.6, 4.7 and 5.4 Mcal/d during respectively the 6th, 7th, 8th and 9th months of pregnancy, which is close to US energy systems of recommendations (NRC, 2001; Fox *et al.*, 2004) and falls in the range of recommended values of European energy systems. Assuming that 1 kg lipid and 1 kg protein contain respectively 9.5 and 5.7 Mcal net energy (Brouwer, 1965), that partial net efficiencies of metabolizable energy utilization for protein and lipid gain are respectively 0.20 and 0.75 (Geay, 1984), and that the efficiency of use of ME coming from body reserve mobilization is 82% (Agnew *et al.*, 2003), the following estimates for ME values of body weight changes were obtained with the formula used by Williams and Jenkins, 2003 (see Appendix B) : $e_W = 6.46 \text{ Mcal/kg}$, $e_{Xb} = 11.07 \text{ Mcal/kg}$ and $e_{Xm} = 6.10 \text{ Mcal/kg}$ (net energy contents of W and X are respectively 1.50 and 7.44 Mcal/kg and efficiencies of use of ME for gain in W and X are respectively 23% and 67%).

Global fitting

Numerical values of other parameters of the operating sub-model (x , b_0 , m_0 , y , and $\{k_{jn}, y_{jn}, k_{js}, y_{js}\}_{j:L,F,P,W}$) together with above mentioned parameters of the regulating sub-model (μ , λ_0 , λ_1 and γ) were simultaneously estimated through a global fitting procedure. These parameters govern the teleonomic pattern of the model, *i.e.*, body

composition, body weight changes and milk constituents yield in the reference situation of exact coverage of requirements. The fitting procedure was achieved on synthetic datasets on dairy cattle (mainly of Holstein-Friesian type) found in the literature to capture an average profile of dairy cow performance. The datasets used concerned body weight changes during growth, body condition score changes during growth and over successive gestation/lactation cycles, and milk yield and composition over successive lactations. References of datasets are detailed in **Table 3**. The least square procedure was performed with the simplex algorithm embedded in the optimization tool of Modelmaker version 3.0 software (Cherwell Scientific Ltd, 2000) with default advanced parameters value and 100 convergence steps.

Results

Parameter estimates resulting from the global fitting procedure are given in **Table 1** and **Table 2**. Model simulations of *BW*, *BCS* and *MY* dynamics from birth to 3000 d of life and milk fat, protein and lactose contents dynamic over the first three lactations are plotted with data used in the global fitting procedure in **Figure 1.5** and **Figure 1.6**. Model simulations were found to be in satisfactory agreement with classical patterns of dairy cows' body weight and condition changes during growth and reproductive cycles and milk yield and composition during lactation. The increase in peak milk yield and the associated change in milk persistency along the lactation course from the 1st to the 3rd parity are well represented. The decrease in calving *BCS* from the 1st to the 2nd reproductive cycle is consistent with observations reported in the literature (Martin, unpublished meta-analysis). The model fails to represent the *BCS* pattern of changes in early developmental stages by

systematically overestimating *BCS* from birth to 500 d of life. This result seems to indicate that empty body fat is overestimated during this period. Nevertheless, the simulated fat content in the first days of life is consistent with values reported in the literature. As the model used to calculate *BCS* was developed with a dataset mainly concerning adult cows (Martin and Sauvant, 2005), no improvement was considered assuming that the *BCS* prediction from *EBF* and *EBW* was not appropriate for young heifers.

Model evaluation

Model evaluation is aimed at presenting through graphic results the ability of the model to produce realistic patterns of lifetime performance of dairy cows under normal husbandry conditions and feeding regimens. Model simulations were generated with different values of parameters scaling individual size (W_M) and performance (ν_X , ν_Y , $\nu_{j:F,P,L}$) to produce a set of curves expressing the model variability relying on genetic diversity. These curves are shown together with curves produced with literature models on production variables and intake.

Production variables

A survey of 37 articles published between 1928 and 2007 provided parameters values of different empirical models for *BW*, *BCS*, *MY*, MC_F and MC_P fitted by authors to successive lactation data recorded worldwide on cows of various dairy cattle breeds (**Table 4**). Published models simulating the growth pattern of dairy cattle from birth to maturity without particular representation of body weight changes during reproductive cycles were also considered. Model simulations of *BW* from birth

676 to 2500 d of life were generated with three different body sizes ($W_M = \{300;450;600\}$)
677 and are shown in **Figure 1.7**. The overall simulated growth pattern is consistent with
678 previously published models. The range of variation of the scaling size parameter
679 W_M allows to simulate growth pattern differences within breeds (between animals of
680 different strains) and between breeds. The model was fitted to curves derived from
681 the models proposed by Turner (1928) and Rotz *et al.* (1999) to determine values of
682 the scaling parameter W_M to simulate growth pattern for the Jersey ($W_M = 275$) and
683 Guernsey ($W_M = 340$) breeds and for animals of small ($W_M = 440$), average
684 ($W_M = 500$) and large ($W_M = 560$) sizes within the Holstein breed. Model simulations
685 of *BCS* were generated with 3 different values of the genetic parameter scaling body
686 reserves mobilization potential ($\nu_x = \{0.2;1.0;1.8\}$). In the field, the variability of *BCS*
687 at calving results from previous feeding regimens (Garnsworthy and Topps, 1982;
688 Ruegg and Milton, 1995). The current version of the model produces an average
689 pattern of *BCS* and the parameter ν_x only governs the intensity of body reserves
690 mobilization in early lactation seen through the decrease in *BCS*. Consequently, to
691 evaluate the model simulations vs. previously modelled kinetics of *BCS* changes
692 during lactation, all curves are expressed in percentage of the 2nd parity postcalving
693 *BCS* and are shown in **Figure 1.8**. Model simulations of *MY* were generated with
694 different milk potential values ($\nu_y = \{0.5;1.0;1.5\}$ with body size set to $W_M = 450$ kg)
695 and are shown in **Figure 1.9**. The raw milk yield shape and scale changes with parity
696 are consistent with the previously published models and genetic parameters allow to
697 simulate the variability of milk production levels. For a reference 3rd parity Holstein
698 cow ($W_M = 500$) peak milk yields of 15 kg and 50 kg are generated with $\nu_y = 0.5$ and

$\nu_Y = 1.5$ respectively. These values leads to 305-d milk, milk fat, milk protein and milk lactose yields of 3215 kg, 123 kg, 106 kg, 159 kg and 10151kg, 389 kg, 338 kg, 501 kg respectively with average milk fat, protein and lactose contents remaining stable at 38 g/kg, 33 g/kg and 49 g/kg respectively. Model simulations of $MC_{j:F,P}$ were generated with three different values of milk composition genotetic parameters values ($\nu_{j:F,P} = \{0.9;1.0;1.1\}$) and are shown in **Figure 1.10** and **Figure 1.11**. This range of variation produces average milk fat contents ranging from 35 g/kg to 43 g/kg, milk protein content ranging from from 31 g/kg to 38 g/kg, and milk lactose ranging from 44 g/kg to 54 g/kg. The values of $\nu_{j:F,P,L}$ can thus be used to specify a particular genotype of a given dairy breed.

Intake

Models of *DMI* listed in **Table 5** and commented (for the most) in Faverdin (1992), Ingvarsten (1994) and Roseler *et al.* (1997a) were considered to evaluate the model simulation of *DMI* generated with the scaling size parameter set to $W_M = 500$ and genetic parameters fixed to the reference value 1. Predictors used in these empirical models are model simulated values of production variables (MY , $MY_{j:F,P}$, MC_F , $MY_4 = MY \cdot (0.4 + 15 \cdot MC_F)$, BW , dBW/dt and BCS), lactation time scales (day in milk (d_{im}) and week in milk ($wim = \text{int}((d_{im} + 6)/7)$) where $\text{int}(x)$ is the integer part of x), gestation time scales (day in pregnancy (dip) and week in pregnancy ($wip = \text{int}((dip + 6)/7)$), age at parturition of the reproductive cycle $t_p(c)$, and feed characteristics set to an average standard diet (concentrate: $DM_{CO} = 0.40$ kg/kg DM , crude fiber: $CF = 0.26$ kg/kg DM , acid detergent fiber: $ADF = 0.31$ kg/kg

DM , neutral detergent fiber: $NDF = 0.43 \text{ kg/kg } DM$), digestible energy: $DE = 3.3$
Mcal/kg DM). Model simulations of DMI are plotted together with these predictions
from birth to 2000 d of life in **Figure 1.12**. The lifetime shape of intake simulated by
the model falls in the range of predictions of these models.

Discussion

The approach adopted here to model lifetime performance of dairy livestock was to
focus on generic regulatory processes. The orchestration of life functions is
considered through a conceptual framework describing their priority. Relying on
Waddington's concept of choreod, it was assumed that from birth to death, relative
priorities of life functions follow a specific dynamic pattern of changes adapted to the
realization of the work of life. Through this model, the animal is seen as a system, *i.e.*
a set of interacting elements organized towards a goal (De Rosnay, 1975), and life is
seen as a goal-directed process involving a time-based coordination of elementary
operations. The introduction of the idea of goal-directed process as a driving force at
a high level of control referred to the teleonomy concept of Monod (1970) :
*"organisms are endowed with a purpose which is inherent in their structure and
determines their behavior"*. This deterministic point of view is formalized by focusing
on the biological signification of processes giving rise to performance elaboration,
i.e., the preservation of life for the reproduction of life form. The proposed model thus
falls into the category of "teleonomic models" according to the typology of Thornley
and France (2007). The target of species continuation through reproduction involves
growth as the acquisition of a mature reproductive status, the sequence gestation-
lactation for the production of viable offspring, and the use of body reserves to cover
physiological requirements of the reproductive cycle. The dynamic partitioning of

priorities is converted into a theoretical pattern of performance expressing a genetic potential. The notion of potential refers to an optimal equilibrium between life functions rather than a maximum possibility, which is the classical view used for instance by Faverdin *et al.* (2007) for milk production potential. This trajectory involves an optimal body condition balanced during the transition between successive reproductive cycles and safeguarded to ensure individual survival. The coupling of this generic level of representation with an operating predictive model of production variables is proposed as a framework of modelling lifetime performance of dairy cows. Compared to previously published dairy cow production models the main originality of this integrative work is to provide a conceptual framework for whole-animal and lifetime predictions.

Published models considering lifetime performance were mainly built in a herd level perspective with a simple representation of nutrient partitioning at the animal level (Blackburn and Cartwright, 1987; Sorensen *et al.*, 1992; Tess and Kolstad, 2000). This issue is considered as the main focus in the proposed model. Several models of dairy livestock have already incorporated an explicit representation of a “driving force” underlying physiological processes. The first attempt was performed by Neal and Thornley (1983) by the way of a theoretical hormone controlling the division rate of basic udder cells to provide active secretory cells in the mammary gland. Further developments were done by Dijkstra *et al.* (1997), Vetharaniam *et al.* (2003a, 2003b) and Pollott (2004). This principle of modeling was also used to direct adipose tissue anabolism and catabolism (Sauvant and Phocas, 1992, Baldwin, 1995; Martin and Sauvant, 2007) or to provide kinetics of plasma growth hormone and insulin driving exchanges between tissues and udder (Danfaer, 1990). However, none of these approaches focused on a whole regulating model. The proposed

model consist in a generalization of the approach proposed in Puillet *et al.* (2008) in which the modeling of “driving forces” was considered within a dedicated sub-model. To our knowledge, this is the first attempt to incorporate a goal-directed dimension of partitioning in a model of dairy livestock performance. This approach relies on the plan of Friggens and Newbold (2007) to tackle the question of nutrient partitioning by focusing on “*why*” rather than “*how*”. The application of this conceptual framework has led to a whole animal model predicting performance in terms of body weight and condition, milk yield and composition and intake. These predictions are performed simultaneously with the same biological basis, as components of an unique regulatory process and ultimately as an overall trajectory of performance.

The construction of an integrated regulating sub-model driving the relations between functions of nutrition, lactation, gestation, growth and balance of body reserves pertains to a systemic view of the animal. The regulating sub-model acts as a “reservoir of raw information” which is transmitted and modulated by the way of differential priorities to monitor the work of the operating sub-model. This differential formalism is used to capture the idea that functions contributing to the completion of a top-level goal may be triggered as soon as this goal has priority or progressively for increasing levels of relative priority. The regulating sub-model based on priorities of life functions is thus kept at an upper and undifferentiated level of representation. This formalism applied to drive performance is used to drive energy metabolism in the second paper of this short series and could be extended to directly drive a reference pattern of hormones kinetics and metabolites transactions in a mechanistic animal model. The ability of the *GARUNS* pattern to control underlying processes such as lipolysis and lipogeneis, neoglucogenesis, or mammary gland amino acid uptake for instance would have to be explored to do so. The generalization of this

modelling approach is based on a top integrated model of driving forces used to control down the work of operating models at underlying levels of organization. The main originality of this approach in the field of livestock nutrition modeling is to explicitly model a regulation core before modeling the metabolic piping channeling energy and/or metabolites to functions and/or organs.

The model evaluation is at present limited to an overall comparison of the model simulations with previously published models. Results are encouraging and this representation of the animal as an autonomous entity is believed to open perspectives for nutritional models. As such, the proposed whole model is regarded as a prototype. A key issue, which remains to be explored is the coupling of regulating and operating submodels. A systematic exploration of the model fitting properties should be done to estimate the model prediction accuracy and to determine keys of refinements. This work in progress will be facilitated by the fact that each parameter acts mainly on a specific feature of the model response at different levels of the model structure. In particular, input parameters have been specifically incorporated to define the timing of reproductive events, the scaling of individual performance relying on a genetically determined ability and the characterization of diet.

Input parameters timing reproductive events can be changed to simulate differences in pattern of performance. Results shown in **Figure 1.13** for different ages at first conception are consistent with known patterns of response (Wickersham and Schultz, 1963; Little and Kay, 1979; Sakaguchi et al., 2005) but no specific work of validation have yet been made. In the present version of the model, reproductive events are fixed inputs and fertility is not considered as a response. In particular, a sub-model focusing on the biological basis of the parturition to conception interval

could be appended to the model. Such a sub-model could be stochastic (Oltenacu et al., 1980) and/or empiric, using variables such as the body condition score to predict the length of the service periods (Lopez-Gatius et al., 2003), or mechanist, using the *GARUNS* pattern of priorities to drive hormonal profiles governing fertility (Blanc et al, 2001).

The incorporation of scaling parameters explicitly embodying genetic differences between animals and breeds of dairy cattle allows the simulation of the diversity of performance. These so-called genetic parameters have been conceived as command buttons allowing to use the model as a simulation tool scaled to a given animal genotype. Moreover, this feature is intended to open perspectives of connecting this approach with works focusing on genetic aspects of animal performance and their elaboration from genotypes to animal products (Bryant *et al.*, 2004; Doeschl-Wilson *et al.*, 2007). For simplicity and to preserve the generic feature of the regulating sub-model, these parameters have only been incorporated into the operating sub-model. Further work will be necessary to evaluate the need to incorporate deformations of the regulating sub-model pattern of priorities pertaining to genetics. In the future, the model could be specifically designed as a generic tool to simulate genetic selection effects on dairy livestock performance.

The present parameterisation has been conceived for dairy cows. An attempt to evaluate the model ability to simulate dairy goats performance has been performed by setting specific parameters of the model to appropriate values (pregnancy length $\pi = 150$ d, parameters of foetal growth (Laird, 1966) $\varpi = 2.4 \cdot 10^{-6}$ and $\alpha = 0.0209$, mature weight $W_M = 55$ kg, growth rate parameter $b_0 = 0.2 \text{ d}^{-1}$, milk potential $v_y = 1.6$, age at 1st conception $PCI(0) = 240$ d and parturition to calving interval $PCI(c) = 210$ d). Simulations of *BW* and *MY* are shown in **Figure 1.14** together with

individual records (INRA experimental flock). The application of the model to dairy goats has proved successful and provides a first validation step of the model's generic formalism. In the future, the ability of this representation to model lifetime performance of other domestic mammalian females will be explored. An interesting point to investigate falls in the field of ecology and concerns the validity of this overall theoretical representation to compare different reproductive strategies in mammals (Martin, 1984).

The *GARUNS* pattern of priorities can thus be considered as a postulate to be tested by experiments and subsequently refined. Several possible refinements have already been identified and concern for instance its start at conception rather than at the parturition time to formalize the initiation of the process of individual in utero growth.

Teleonomic drives of the regulating sub-model are used to control production variables of the operating sub-model, leading to a reference dynamic pattern of lifetime performance. The pattern of intake is defined as the exact coverage of associated requirements. This version of the whole model is thus limited to *ad libitum* feeding and is not designed to simulate challenging feeding contexts. In the second paper of this short series, the same formalism of control is used and the reference dynamic pattern of lifetime performance is expressed in terms of a reference dynamic pattern of energy partitioning. The operating sub-model in the companion paper is thus a model of energy metabolism governed by the priority based on the teleonomic model proposed in the present paper. Additionally, a homeostatic function is proposed to model lifetime performance when actual intake is above or below requirements. Starting from the teleonomic pattern of energy partitioning acting like a chreod, animal performance are modeled through a comprehensive combination of

homeorhetic drives (the long term tendency to home on to the chreod) and homeostatic control (the short term tendency to adapt animal responses to effective supply).

As such, the model can be used as a “virtual cow” to simulate mean performance and provide inputs to “feed” scientific models focusing on particular physiological aspects, such as the control of fertility as previously mentioned or the description of main metabolic pathways associated with performance (Martin and Sauvant, 2007). The simulation tool of lifetime performance can also be connected with works focused on profitability or sustainability of farming systems by converting performance into economic or environmental values.

Conclusion

We proposed a conceptual framework for modelling lifetime performance of dairy livestock based on the dynamic partitioning of life functions priorities. This approach formalizes performance as the realization of a goal-directed and genetically scaled trajectory. Applied to dairy cows, this framework allowed to build a whole animal and lifetime predictive tool. As such, it provides a dynamic pattern of production variables and intake in which the monitoring of body reserves is considered as a full-fledged function. The conceptual framework is proposed as a way to tackle the question of nutrient partitioning prediction in nutritional models and as a postulate to be tested in other lactating species. A refinement of the model is proposed in the companion paper, in which the proposed pattern of performance is used as a reference to simulate challenging feeding contexts.

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- 1238

1239 **Appendix A**

1240 Giving the theoretical non-labile birth weight W_B , priority U to the unborn generation

1241 is defined as the specific growth curve of the foetal weight W_F relative to W_B such as

$$\frac{dU}{dt} = \frac{1}{W_B} \cdot \frac{dW_F}{dt}, \quad (\text{A. 1})$$

1242 equivalent to

$$U = \frac{W_F}{W_B}. \quad (\text{A. 2})$$

1243 The complementary Gompertz function proposed by Laird (1966) to describe foetal

1244 growth is used and given by

$$W_F = \varpi \cdot \exp\left(\frac{A_0}{\alpha} \cdot (1 - \exp(-\alpha \cdot t))\right), \quad (\text{A. 3})$$

1245 where ϖ , A_0 and α are specific parameters governing the shape of the foetal

1246 growth curve leading to the following formalism for U and its derivative dU/dt :

$$U = \frac{\varpi}{W_B} \cdot \exp\left(\frac{A_0}{\alpha} \cdot (1 - \exp(-\alpha \cdot t))\right), \quad (\text{A. 4})$$

$$\frac{dU}{dt} = A_0 \cdot \exp(-\alpha \cdot t) \cdot U. \quad (\text{A. 5})$$

1247 By setting $\varepsilon = \varpi/W_B$ and $Z = \varepsilon \cdot \exp(A_0/\alpha)$, Eq. (A. 4) can be written

$$U = Z \cdot \exp\left(-\frac{A_0}{\alpha} \cdot \exp(-\alpha \cdot t)\right), \quad (\text{A. 6})$$

1248 which is equivalent to

$$\alpha \cdot \ln\left(\frac{Z}{U}\right) = A_0 \cdot \exp(-\alpha \cdot t), \quad (\text{A. 7})$$

1249 and leads by substitution in Eq. (A. 5) to

$$\frac{dU}{dt} = \alpha \cdot \ln\left(\frac{Z}{U}\right) \cdot U, \quad (\text{A. 8})$$

1250 which is the formalism given in text for U (see (10)).

1251 The equation of Laird (1966) is finally constrained to give $W_F = W_B$ at $t = \pi$
1252 (equivalent to $U = 1$ at $t = \pi$) where π is the theoretical maximum length of
1253 pregnancy, leading from Eq. (A. 3) to

$$W_B = \varpi \cdot \exp\left(\frac{A_0}{\alpha} \cdot (1 - \exp(-\alpha \cdot \pi))\right), \quad (\text{A. 9})$$

1254 and giving rise to

$$A_0 = \frac{-\alpha \cdot \ln(\varepsilon)}{1 - \exp(-\alpha \cdot \pi)}, \quad (\text{A. 10})$$

1255 which leads by substitution to the following formalism given in text (see (10)) for Z :

$$Z = \varepsilon \cdot \exp\left(\frac{-\ln(\varepsilon)}{1 - \exp(-\alpha \cdot \pi)}\right). \quad (\text{A. 11})$$

1256

1257 **Appendix B**

1258 Giving the net energy contents of 1 kg fat and 1 kg protein (respectively 9.5 and 5.7
1259 Mcal/kg) and the fat and protein contents of body compartments X and W
1260 ($fat_X = \beta_X$, $fat_W = \beta_W \cdot (W/W_M)$, $prot_X = 0.22 \cdot (1 - fat_X)$ and $prot_W = 0.22 \cdot (1 - fat_W)$),
1261 the energy contents of body compartments X and W are given by

$$energy_X = 9.5 \cdot fat_X + 5.7 \cdot prot_X, \quad (B. 1)$$

1262 and

$$energy_W = 9.5 \cdot fat_W + 5.7 \cdot prot_W. \quad (B. 2)$$

1263 Assuming that partial net efficiencies of metabolizable energy utilization for protein
1264 and lipid gain are respectively 0.20 and 0.75 (Geay, 1984), and using the formula
1265 described by Williams and Jenkins (2003), the metabolizable energy requirement for
1266 the storage of 1 kg W is given by

$$e_W = energy_W / k_W, \quad (B. 3)$$

1267 with

$$k_W = 0.75 / (1 + 2.75 \cdot 5.7 \cdot prot_W / energy_W), \quad (B. 4)$$

1268 the metabolizable energy requirement for the storage of 1 kg X is given by

$$e_{Xa} = energy_X / k_{Xa}, \quad (B. 5)$$

1269 with

$$k_{Xa} = 0.75 / (1 + 2.75 \cdot 5.7 \cdot prot_X / energy_X), \quad (B. 6)$$

1270 and the metabolizable energy supply by the mobilization of 1kg X is given by

$$e_{Xm} = energy_X \cdot k_{Xm}, \quad (B. 7)$$

1271 with $k_{Xm} = 0.82$.

Table 1 Parameters of the regulating sub-model.

Parameter	Description	Unit	Value	Assessment basis		
				Input	Fitting	Article
Fractional rate of transfer of priority						
μ	Transfer from N to S	d ⁻¹	0.06		•	
λ_0	Basal transfer from S to R	d ⁻¹	0.0017		•	
λ_1	X -dependant transfer from S to R	d ⁻¹	0.0063		•	
γ	Pregnancy dependant transfer from S to R	d ⁻¹	0.032		•	
τ	Milking dependant transfer from S to R	d ⁻¹	0.1			•
σ	Transfer from R to A	d ⁻¹	0.0018			•
Pregnancy specific scaling						
π	Maximal pregnancy length	d	285			•
α	Rate of decay of fetal growth rate	-	0.0111			•
ω	Initial value of fetal growth	kg	$3.5 \cdot 10^{-6}$			•
Reproductive events timing						
PCI(0)	Age at first conception	d	450	•		
PCI(c)	Parturition to calving interval of cycle $c > 0$	d	120	•		

1274 **Table 2** Parameters of the operating sub-model.

Parameter	Description	Unit	Value	Assessment basis		
				Input	Fitting	Article
Body mass compositional ratio						
δ	Digestive contents:non-labile body mass	kg/kg	0.17			•
χ_M	Mature labile:non-labile body mass	kg/kg	0.33			•
χ_S	Safeguarded labile:non-labile body mass	kg/kg	0.20			•
ϕ	Fetus:gravid uterus mass	kg/kg	0.58			•
β_X	Fat:labile body mass	kg/kg	0.75			•
β_W	Fat:non-labile body mass	kg/kg	0.03			•
Body mass change rate						
b_0	Balance	d ⁻¹	1.6		•	
m_0	Mobilization	d ⁻¹	0.03		•	
k_0	Digestive tract removal	d ⁻¹	1.1			•
Individual performance scaling						
W_M	Mature non-labile body mass	kg	500.0	•		
v_X	Labile body mass mobilization index	-	1	•		
v_Y	Milk yield	-	1	•		
v_F	Milk fat secretion	-	1	•		
v_P	Milk protein secretion	-	1	•		
v_L	Milk lactose secretion	-	1	•		
v_H	Milk water secretion	-	1	•		
Scaling exponent for differential priority						
x	Labile body mass balance ability	-	5.7		•	
y	Milk secretion ability	-	5.0		•	
Milk constituent secretion ability (N exponent)						
y_{FN}	fat	-	1.26		•	
y_{PN}	protein	-	1.59		•	
y_{LN}	lactose	-	1.13		•	
y_{HN}	water	-	1.15		•	

Milk constituent secretion ability (S exponent)

y_{FS}	fat	-	0.97	•
y_{PS}	protein	-	0.89	•
y_{LS}	lactose	-	1.27	•
y_{HS}	water	-	1.21	•

Scaling coefficient of milk constituent secretion

Coefficient of N^{y_j}

k_{FN}	fat	kg/kg	0.0035	•
k_{PN}	protein	kg/kg	0.0030	•
k_{LN}	lactose	kg/kg	0.0037	•
k_{HN}	water	kg/kg	0.0632	•

Coefficient of S^{y_j}

k_{FS}	fat	kg/kg	0.0032	•
k_{PS}	protein	kg/kg	0.0027	•
k_{LS}	lactose	kg/kg	0.0049	•
k_{HS}	water	kg/kg	0.0848	•

Metabolizable energy conversion factor

e_D	Dietary content (DM basis)	Mcal/kg	2.7	•
e_U	Pregnancy requirement	Mcal/kg	7	•
e_M	Maintenance requirement	Mcal/kg ^{0.75}	0.143	•
e_F	Milk fat secretion requirement	Mcal/kg	13.574	•
e_P	Milk protein secretion requirement	Mcal/kg	7.714	•
e_L	Milk lactose secretion requirement	Mcal/kg	6.164	•
e_Y	Milk water secretion requirement	Mcal/kg	0.144	•

1276 **Table 3** References of data used for model calibration.

Reference	Data source	Animals			Period	Variables
		Breed	Number	Parity		
Jenness, 1985	?	Dairy cattle	?	?	[1, 45] wk <i>pp</i> ^a	MC _L
O'Mahony, 1988	Ethiopia, 1984-1986	Dairy cattle	?	{2+}	[1, 320] d <i>pp</i>	MC _L
Schutz <i>et al.</i> , 1990	US, Minnesota, 1983-1984	Holstein	155527	{1, 2, 3+}	[7, 315] d <i>pp</i>	MY, MY _{F,P} , MC _{F,P}
Waltner <i>et al.</i> , 1993	US, Washington, 1988-1990	Holstein	350	{1, 2, 3, 4+}	[0, 11] mo <i>pp</i>	BCS
Hoffman, 1997	Field survey	US & Canadian Holstein	?	-	[0, 24] mo of life	BCS, BW
Kertz <i>et al.</i> , 1997	US, Missouri, 1989-1991	Holstein	728	[1 - 7]	[-8 , 7] wk <i>pp</i>	BCS, BW
Ostersen <i>et al.</i> , 1997	Denmark	Danish Holstein	39	{1}	[5, 328] d <i>pp</i>	MC _L
Van Amburgh <i>et al.</i> , 1998	US, New York	Holstein	265	{1}	[0, 50] wk <i>pp</i>	BCS
Drame <i>et al.</i> , 1999	Belgium	Holstein	926	{1, 2+}	[0, 400] d <i>pp</i>	BCS
Abeni <i>et al.</i> , 2000	Italy, 1992-1993	Italian Holstein-Friesian	31	-	[200, 600] d of life	BCS
Koenen <i>et al.</i> , 2001	The Netherlands, 1998-1999	Holstein & Dutch Friesian	108809	{1}	[1, 44] wk <i>pp</i>	BCS
Roche, 2003	New Zealand, 1995-2001	Friesian, Jersey & cross	77	{2+}	[1, 38] wk <i>pp</i>	MC _L
Mao <i>et al.</i> , 2004	Denmark, 1997-2001	Holstein	100	{1, 2, 3+}	[2, 224] d <i>pp</i>	BCS
Shamay <i>et al.</i> , 2005	Israël, 1999-2002	Israeli-Holstein	40	-	[150, 600] d of life	BCS
Berry <i>et al.</i> , 2006	Ireland, 1995-2002	Holstein-Friesian	422	{1, 2, 3}	[0, 305] d <i>pp</i>	BCS

1277 ^a*pp* = post partum.

1278

Table 4 References of published models of performance used for model evaluation.

Reference	Data			Animals		
	Source	Period	Variables	Breed ^{ab}	Parity	Model ^c
Turner;1928	US, Missouri	2 to 14 yr	BW	JER & GUE	-	$Y = a \cdot (1 - b \cdot \exp(-c \cdot t))$
Wood, 1969	UK, England (1964-65)	[1, 44] wk	MY	Friesian (859 lac)	{1, 2, 3, 4+}	
Wood, 1970	UK, England (1952-64)	? wk	MY	Friesian (1567 lac)	[1, 4]	
Decaen <i>et al.</i> , 1970	France (1952-64)	[4, 63] d	MY	FRI & Normande (665 lac)	[1, 4]	$Y = a \cdot t^{-2} + b \cdot t^{-1} + c + d \cdot t + e \cdot t^2$
Kellogg <i>et al.</i> , 1977	US, New Mexico	[1, 10] mo	MY	HOL (36)	[1, 4]	
Schaeffer <i>et al.</i> , 1977	Canada (1966-70)	[6, 305] d	MY	HOL (76753 lac) & JER (10383 lac)	{1, 2, 3+} x 2 age groups x 2 seasons	$Y = a \cdot \exp(-b \cdot (t - c)) \cdot (1 - \exp(-d \cdot (t - c))) / d$
Killen & Keane, 1978	Ireland (1966-75)	[1, 44] wk	MY, MC _{F,P}	Irish dairy cattle (1181 rec)	{1, 2, 3+}	
Madalena <i>et al.</i> , 1979	Brazil (1965-73)	[1, 300] d	MY	HFR & HFR x Gir (870 lac)	{1, 2, 3, 4, 5+}	

Wood <i>et al.</i> , 1980	UK, England (1972-73)	[1, 10] 2-wk	MY, MC _{F,P}	FRI (159), AYR (40), GUE (15) & JER (22)	{1, 2+}	
Wood, 1980	UK, England (1978-79)	[1, 44] wk	MY	FRI (579303), Shorthorn (6608), AYR (27374), JER (19529) & GUE (19760)	{1, 2, 3, 4+}	
Congleton & Everett, 1980	US, New York (1970-77)	[0, 300] d	MY	HOL (49633 lac x 11 production level)	{1, 2, 3+}	
Schneeberger, 1981	Switzerland (1976-77)	[1, 305] d	MY	BRS (159541)	[1, 4]	$Y = a.(t - b)^c.exp(-d.(t - b))$ (Wood, 1967, with time-lag)
Shanks <i>et al.</i> , 1981	US, California	[1,43] wk	MY	HOL (113705 lac)	{1, 2, 3, 4+}	
Rowlands <i>et al.</i> , 1982	UK, England (1976-79)	[1,43] wk	MY	British FRI (468 lac)	{1, 2, 3, 4, 5+}	
Batra, 1986	Canada (1972-77)	[1, 44] wk	MY	HOL, AYR, BRS & Norwegian Red (4228 pure- & crossline cows)	{1, 2, 3}	
Wilmink, 1987	The Netherlands (1981-82)	[1, 305] d	MY	Dutch FRI (14275)	{1, 2, 3+}	$Y = a_1 + a_2.t + a_3.exp(-0.05.t) + d.t^2$ where $a_i = p_i + q_i.T + r_i.ln(T)$ and T : age at calving in mo

Partie II Proposition de modèle
Modèle téléonomique (Martin and Sauvant, submitted)

Grossman & Koops, 1988	The Netherlands (1983-86)	[10, 290] d	MY	Dutch FRI & Meuse-Rhine- Yssel (33853 daily records)	{1, 2, 3} x 2 lactation lengths x 2 breeds	Diphasic function (Koops, 1986) $Y = \sum_{i:1 \rightarrow 2} a_i \cdot b_i \cdot (1 - \tanh^2(b_i \cdot (t - c_i)))$
Morant & Gnanasakthy, 1989	UK, England (1980-84)	[1, 300] d	MY	FRI (130 lac)	{1, 2, 3}	$\ln(Y) = a + b \cdot t' \cdot (1 + k \cdot t') + c \cdot t'^2 + d/t$ where $t' = (t - 150)/100$
Brunsschwig <i>et al.</i> , 1994	France	[1, 305] d	MC _{F,P}	HOL (107000 lac)	{1+}	$Y = a + f_i(t)$ where $f_i(t) = b_i \cdot t + c_i$ if $t \in [t_{i1}, t_{i2}]$ and $i=1, \dots, n$ (C _F : n=6, C _P : n=5)
Gallo <i>et al.</i> , 1996	Italy (1991-93)	[0, 300] d	BCS	HFR (1395)	{1, 2+} x 5 milk production levels	$Y = a + b \cdot t + c \cdot t^2 + d \cdot t^3$
Garcia-Muniz <i>et al.</i> , 1998	New Zealand	lifetime	BW	HFR (97)	2 genetic lines	$Y = a \cdot (1 - b \cdot \exp(-c \cdot t))^3$ (Von Bertalanffy)
Friggens <i>et al.</i> , 1999	UK, Scotland (1990-95)	[1, 240] d	MY	HFR (40)	{1, 2, 3}	$Y = a \cdot \exp(-\exp(a - b \cdot t)) \cdot \exp(-c \cdot t)$ (Emmans & Fisher, 1986)
Rotz <i>et al.</i> , 1999	US, literature survey (1936-87)	[1, 56] wk	MC _F , BW	HOL	{1, 2+} x 3 body sizes	$Y = a \cdot (t+b)^c \cdot \exp(-d \cdot (t+b))$ (Wood, 1967 with time-lag)

Partie II Proposition de modèle
Modèle téléonomique (Martin and Sauvant, submitted)

Lopez <i>et al.</i> , 2000	UK, England	lifetime	BW	HOL (16)	-	$Y = (a \cdot b^c + d \cdot t^c) / (b^c + t^c)$
Tekerli <i>et al.</i> , 2000	Turkey (1989-94)	[1, 305] d	MY	Turkish HOL (754 lac)	{1, 2, 3+}	
Vargas <i>et al.</i> , 2000	Costa Rica (1987-94)	[1, 305] d	MY	HOL (lactation length = 10mo, calving to conception interval = 4 mo, 71225 rec)	{1, 2+}	Diphasic function (Koops, 1986) $Y = \sum_{i:1 \rightarrow 2} a_i \cdot b_i \cdot (1 - \tanh^2(b_i \cdot (t - c_i)))$
Lopez-Villalobos <i>et al.</i> , 2001	New Zealand (1998-99)	[1, 200] d	MY, BCS	HOL heavy (40) & light (44) lines	{1, 2+} x 2 line sizes	
Martin & Sauvant, 2002	Worldwide, metaanalysis of 37 articles (1959-99)	[1, 45] wk	MY, BW	HFR, Swedish Red & White, AYR, JER & GUE (120 lac)	{1, 2+}	$Y = a + b \cdot (t - c_1) - d \cdot f_1(t) + e \cdot f_2(t)$ where $f_i(t) = \ln((\exp(g \cdot t) + \exp(g \cdot c_i)) / (1 + \exp(g \cdot c_i)))$ (Grossman <i>et al.</i> , 1999)
Val-Arreola <i>et al.</i> , 2004	Mexico (1989-2001)	[1, 400] d	MY	Dairy cattle (1283 rec)	{1, 2, 3+} x 2 management systems	$Y = a \cdot \exp(b \cdot (1 - \exp(-c \cdot t)) / c - d \cdot t)$ (Dijkstra <i>et al.</i> , 1997)
Choumei <i>et al.</i> , 2006	Japan (1979-98)	[1, 20] wk	MY	HOL (745)	{2, 3, 4, 5+}	
Hansen <i>et al.</i> , 2006	Denmark	[1, 180] d	MY	Danish Red, Danish HOL &	{1, 2, 3}	$Y = a \cdot \exp(-\exp(a - b \cdot t)) \cdot \exp(-c \cdot t)$

	(1996-2001)			JER (604 lac)		(Emmans & Fisher, 1986)
Pérez-Cabal <i>et al.</i> , 2006	Spain	lifetime	BW	HOL	-	$Y = a \cdot (1 - (1 - (b/a)^{1/3}) \cdot \exp(-c \cdot t))^3$
Quinn <i>et al.</i> , 2006	Ireland	[1, 44] wk	MC _{F,P}	Irish dairy cattle (14956 lac) {1+}		$Y = a + b \cdot \exp(-c \cdot t) + d \cdot t$ (Wilmink, 1987)
Roche <i>et al.</i> , 2006	New Zealand (2002-04)	[1, 270] d	MC _{F,P}	HFR (113 lac)	{1+}	$Y = a + b \cdot \exp(-c \cdot t) + d \cdot t$ (Wilmink, 1987)
Faverdin <i>et al.</i> , 2007	France	[1, 44] wk	MY	?	{1, 2+}	$Y = a \cdot (b - c \cdot \exp(-d \cdot t) - e \cdot t - f \cdot \exp(-g \cdot (45 - t')))$ where t': wk gestant
Friggens & Badsberg, 2007	Denmark (1996-2001)	[0, 375] d	BCS _[1-5]	Danish HOL (112), Danish Red (97) & JER (78)	{1, 2, 3}	$Y = a + b \cdot \exp(-c \cdot t) + d \cdot \exp(-e \cdot (283 - t'))$ where t' : days from conception,
Roche <i>et al.</i> , 2007	New Zealand (1986-2004)	[0, 350] d	BCS _[1-10]	HFR & JER (3209 lac)	{1, 2, 3, 4, 5, 6+}	$Y = \sum_{i=1 \rightarrow 4} (a_i + b_i \cdot t) / Z_i$ where i=1: $Z_i = 1 + \exp(-c_i \cdot (d_i - t))$ i=2,3: $Z_i = (1 + \exp(c_{i-1} \cdot (d_{i-1} - t))) \cdot (1 + \exp(c_i \cdot (d_i - t)))$ i=4: $Z_i = 1 + \exp(-c_{i-1} \cdot (d_{i-1} - t))$

1279 ^aAYR : Ayrshire, BRS : Brown Swiss, FRI : Friesian, GUE : Guernsey , HFR : Holstein-Friesian, HOL : Holstein, JER: Jersey.

1280 ^bin brackets : number of cows, lactations (lac) or daily records (rec).

1281 ^cif not mentionned, model of Wood (1967): $Y = a \cdot t^b \cdot \exp(-c \cdot t)$.

1282 **Table 5** References of published models of dry matter intake (*DMI*, kg/d) used for model evaluation.

Reference	Equation ^a
Journet <i>et al.</i> , 1965	$6.7 + 0.0074 \cdot BW + 0.27 \cdot MY$
Johnson <i>et al.</i> , 1966	$6.71 + 1.46 \cdot wim + 0.08 \cdot MY + 0.09 \cdot dBW/dt + 1.08 \cdot BCS$ if $wim \leq 15$ $14.57 + 0.05 \cdot MY + 0.09 \cdot dBW/dt - 5 \cdot BCS - 0.12 \cdot wip$ if $wim > 15$
McCullough, 1973	$5.38 + 0.008 \cdot BW + 0.359 \cdot MY_4 - 0.028 \cdot DM_{CO}$
MAFF, 1975	$0.025 \cdot BW + 0.1 \cdot MY$ for lactating cow $(31.4 - 0.03 \cdot BW) \cdot BW/1000$ for growing cattle
Brown <i>et al.</i> , 1977	$\exp(0.5198 + 0.000675 \cdot BW - 0.000827 \cdot dim + 0.14807 \cdot h(dim) + 0.33922 \cdot \ln(MY) + 0.09927 \cdot MY_F + 0.018 \cdot CF - 0.000557 \cdot CF^2)$
Bines, 1979	$(1 + 0.2 \cdot factor) \cdot (4.25 + 0.0113 \cdot BW + 0.16 \cdot MY + 2.45 \cdot dBW/dt)$ with factor = 0 if parity = 1 and factor = 1 if parity > 1
ARC, 1980	$(0.135 \cdot BW^{0.75} + 0.2 \cdot (MY - 21.4 \cdot wim^{0.2} \cdot \exp(-0.04 \cdot wim))) \cdot factor_{mo}$ with factor _{mo:1 to 10} = {0.81, 0.98, 1.07, 1.08, 1.09, 1.08, 1.01, 0.99, 0.97, 0.93} for lactating cow
McCullough, 1981	$-5.54 + 0.022 \cdot BW + 0.511 \cdot MY_4 - 0.0024 \cdot MY_4^2$
Yungblut <i>et al.</i> , 1981	$3.37 + 0.01 \cdot BW + 0.34 \cdot MY + 5.3 \cdot MC_F + 0.34 \cdot parity - 0.11 \cdot ADF$
Neal <i>et al.</i> , 1984	$0.022 \cdot BW + 0.2 \cdot MY$
NRC, 1987	$(1.896 \cdot BW^{0.593} \cdot MY_4^{0.33} \cdot \exp(0.16 \cdot dBW_dt) / (DE \cdot 4.18))$ for lactating cows $(1.896 \cdot BW^{0.593} \cdot \exp(0.16 \cdot dBW_dt) / (DE \cdot 4.18))$ for nonlactating pregnant cows
NRC, 1989	$-0.293 + 0.372 \cdot MY_4 + 0.0968 \cdot BW^{0.75}$

Kertz <i>et al.</i> , 1991	$0.010936 \cdot BW + 0.2627 \cdot MY_4 + 0.1938 \cdot \text{dim} - 0.001805 \cdot \text{dim}^2 + 0.00000570 \cdot \text{dim}^3$ if $\text{dim} \leq 140$ and parity = 1 $0.006136 \cdot BW + 0.3139 \cdot MY_4 + 0.3036 \cdot \text{dim} - 0.003165 \cdot \text{dim}^2 + 0.00001100 \cdot \text{dim}^3$ if $\text{dim} \leq 140$ and parity > 1
Fox <i>et al.</i> , 1992	$0.0185 \cdot BW + 0.305 \cdot MY_4$, for lactating cattle $0.02 \cdot BW$, for non-lactating cattle
Rayburn and Fox, 1993	$0.0117 \cdot BW + 0.0749 \cdot \text{dim} + 0.281 \cdot MY_4$ if $\text{dim} \leq 84$ $0.023 \cdot BW + 0.0201 \cdot \text{dim} + 0.286 \cdot MY_4 - 0.0979 \cdot \text{NDF}$ if $\text{dim} > 70$
Roseler <i>et al.</i> , 1997b	$(3.7 + 0.012 \cdot BW + 0.84 \cdot \text{dBW}/\text{dt} + 12.2 \cdot MY_p - 0.011 \cdot \text{dip}) \cdot (1 - \exp(-(0.564 - 0.124 \cdot T) \cdot (\text{wim} + K)))$ for parity = 1 with T: mo of peak MY and K = 2.36 for T = {1, 2}, K = 3.67 for T=3 $0.6 + 0.005 \cdot BW + 0.77 \cdot \text{dBW}/\text{dt} + 10.4 \cdot MY_p - 0.013 \cdot \text{dip} - 0.17 \cdot \text{wim} + 4.59 \cdot \ln(\text{wim})$
NRC, 2001	$(0.372 \cdot MY_4 + 0.0968 \cdot BW^{0.75}) \cdot (1 - \exp(-0.192 \cdot (\text{dim} + 3.67)))$
Martin and Sauvant, 2002	$15.69 + 0.94 \cdot (\text{wim} - 6.7) - 0.141 \cdot \ln((\exp(K) + \exp(44.66))/(1 + \exp(44.66))) - 0.012 \cdot \ln((\exp(K) + \exp(176))/(1 + \exp(176)))$ for parity = 1 $18.63 + 1.16 \cdot (\text{wim} - 5.8) - 0.174 \cdot \ln((\exp(K) + \exp(38.66))/(1 + \exp(38.66))) - 0.0255 \cdot \ln((\exp(K) + \exp(84))/(1 + \exp(84)))$ for parity > 1 with K = $\text{wim}/0.15$
Fox <i>et al.</i> , 2004	$(0.0185 \cdot BW + 0.305 \cdot MY_4) \cdot (1 - \exp(-(0.564 - 0.124 \cdot T) \cdot (\text{wim} + K)))$ with T: mo of peak MY and K = 2.36 for T = {1, 2}, K = 3.67 for T=3
Faverdin <i>et al.</i> , 2007	$(13.9 + 0.015 \cdot (BW - 600) + 0.15 \cdot MY_{\text{POT}} + 1.5 \cdot (3 - \text{BCS})) \cdot \text{IL} \cdot \text{IG} \cdot \text{IM}$ with $MY_{\text{POT}} = MY_{\text{MAX}} \cdot (1.084 - 0.7 \cdot \exp(-0.46 \cdot \text{wim}) - 0.009 \cdot \text{wim} - 0.69 \cdot \exp(-0.16 \cdot (45 - \text{wip})))$ for parity = 1

$$MY_{POT} = MY_{MAX} \cdot (1.047 - 0.69 \cdot \exp(-0.90 \cdot wim) - 0.0127 \cdot wim - 0.50 \cdot \exp(-0.12 \cdot (45 - wip))) \text{ for parity } > 1$$

$$IL = a + (1-a) \cdot (1 - \exp(-0.16 \cdot wim)) \text{ where } a = 0.6 \text{ if parity } 1 \text{ and } a = 0.7 \text{ if parity } > 1$$

$$IG = 0.8 + 0.2 \cdot (1 - \exp(-0.25 \cdot (40 - wip)))$$

$$IM = -0.1 + 1.1 \cdot (1 - \exp(-0.08 \cdot tP(c)/30))$$

Martin and Sauvant, 2007 $0.531 \cdot (8.48 + 3.36 \cdot MY_{max}/10) \cdot dim^{0.19} \cdot \exp(-0.0025 \cdot dim)$

1283 ^aPerformance variables involved as predictors: body weight (BW , kg), body weight change (dBW/dt , kg/d), body condition score (BCS , 0-5 scale), milk
1284 yield (MY , kg/d), 4% milk yield (MY_4 , kg/d), milk fat yield (MY_F , kg/d), milk protein yield milk (MY_P , kg/d), fat content (MC_F , kg/kg), day in milk (dim , d
1285 after parturition), week in milk (wim , wk after parturition), day in pregnancy (dip , d after conception), week in pregnancy (wip , wk after conception), age at
1286 parturition of reproductive cycle c ($t_p(c)$, d of life). Assumed diet composition on a dry matter (DM) basis: concentrate ($DM_{CO} = 0.40$ kg/kg DM), crude
1287 fiber ($CF = 0.26$ kg/kg DM), acid detergent fiber ($ADF = 0.31$ kg/kg DM), neutral detergent fiber ($NDF = 0.43$ kg/kg DM), digestible energy
1288 ($DE = 3.3$ Mcal/kg DM).
1289

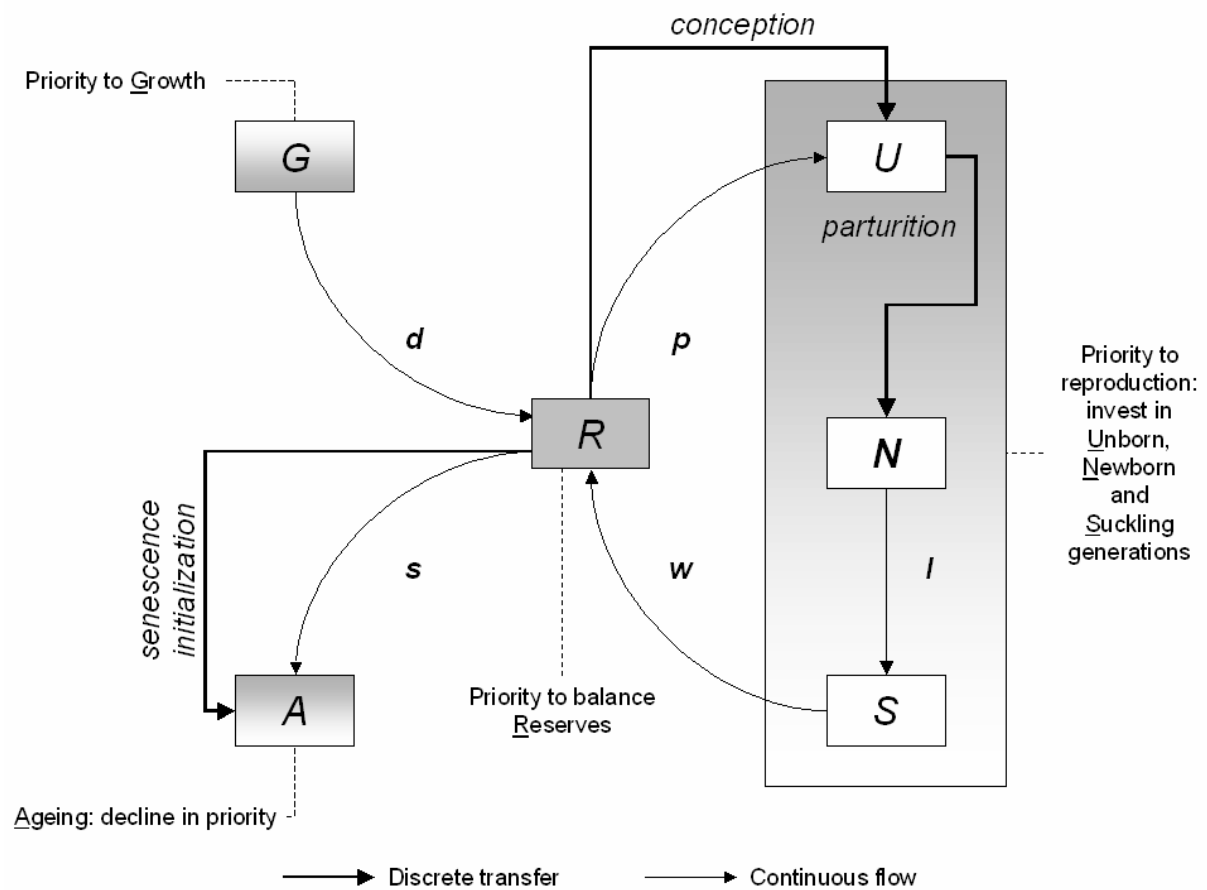


Figure 1.1 Regulating sub-model diagram. Compartments refers to animal priorities *G* : growth, *A* : ageing, *R* : balance of body reserves, *U* : survival of the unborn generation, *N* : survival of the newborn generation, and *S* : survival of the suckling generation.

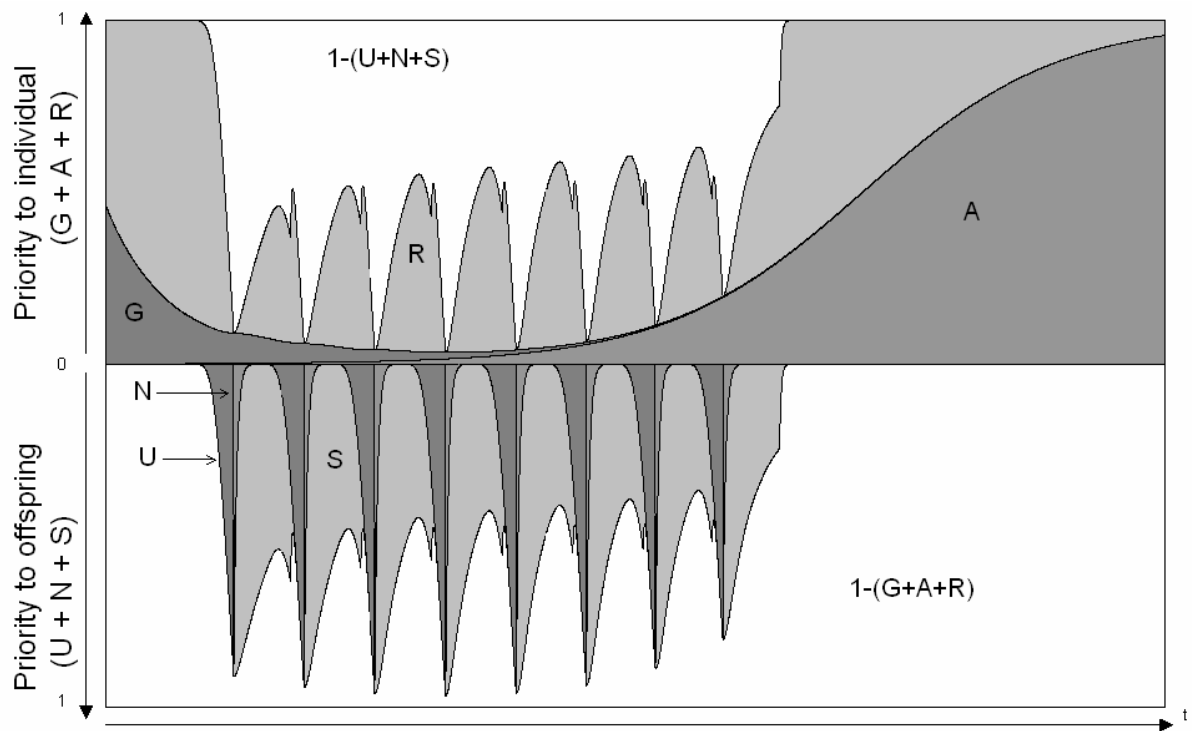


Figure 1.2 Trajectories of priorities G : growth, A : ageing, R : balance of body reserves, U : survival of the unborn generation, N : survival of the newborn generation, and S : survival of the suckling generation over 20 yr of life.

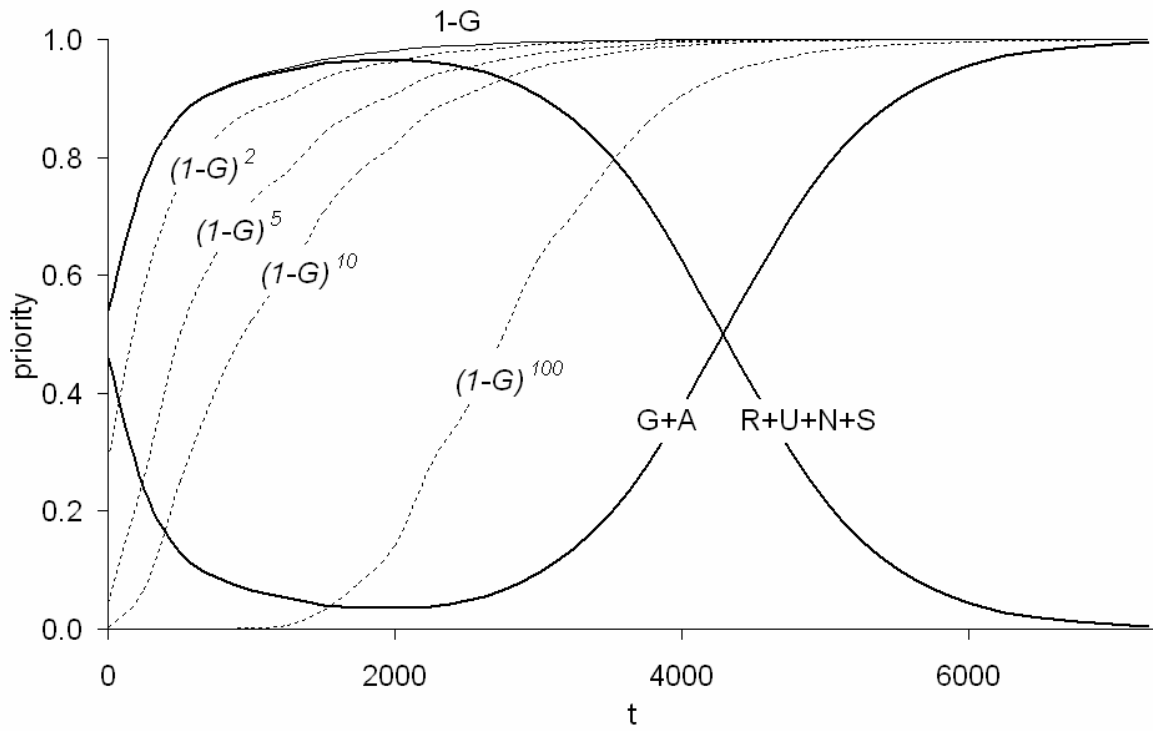
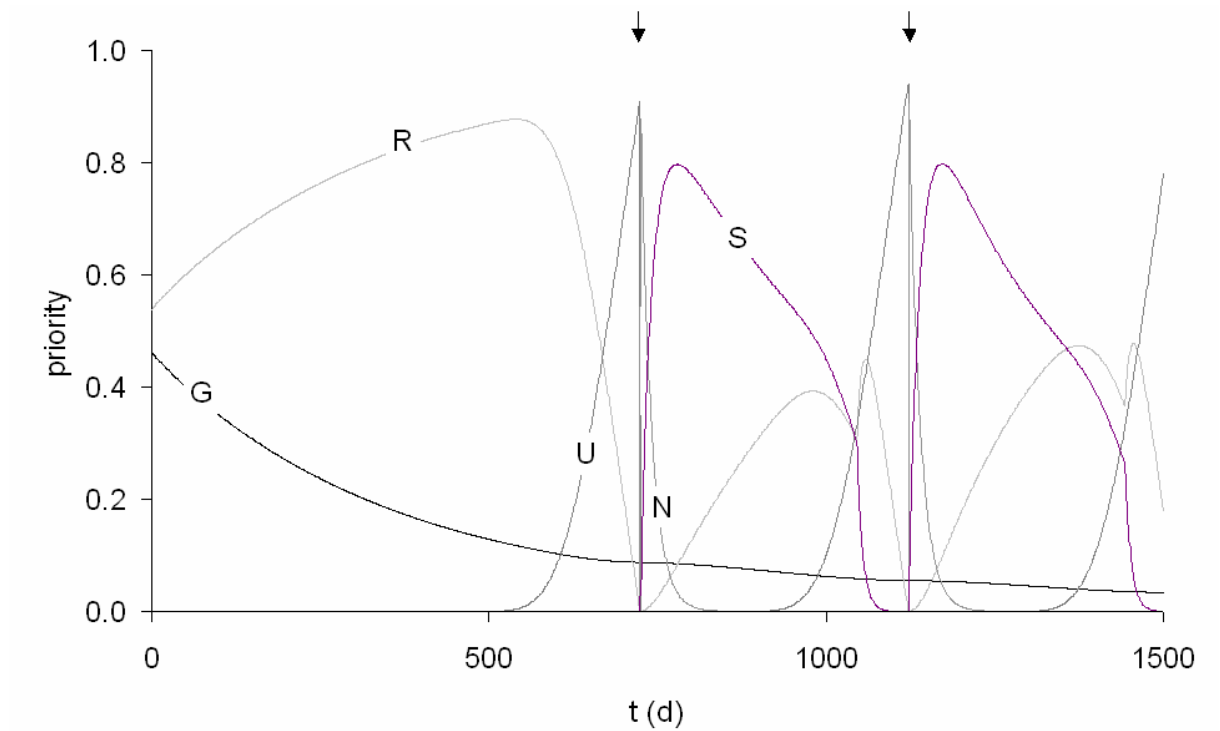


Figure 1.3 Trajectories of global priorities ($1 - G$, $G + A$ and $R + U + N + S$), and differential priority $(1 - G)^K$ for $K = \{2, 5, 10, 100\}$ over 20 years of life (with priorities G : growth, A : ageing, R : balance of body reserves, U : survival of the unborn generation, N : survival of the newborn generation, and S : survival of the suckling generation).



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Figure 1.4 Trajectories of priorities *G* : growth, *A* : ageing, *R* : balance of body reserves, *U* : survival of the unborn generation, *N* : survival of the newborn generation, and *S* : survival of the suckling generation over 1500 d of life. Arrows indicate parturition times of two successive reproductive cycles.

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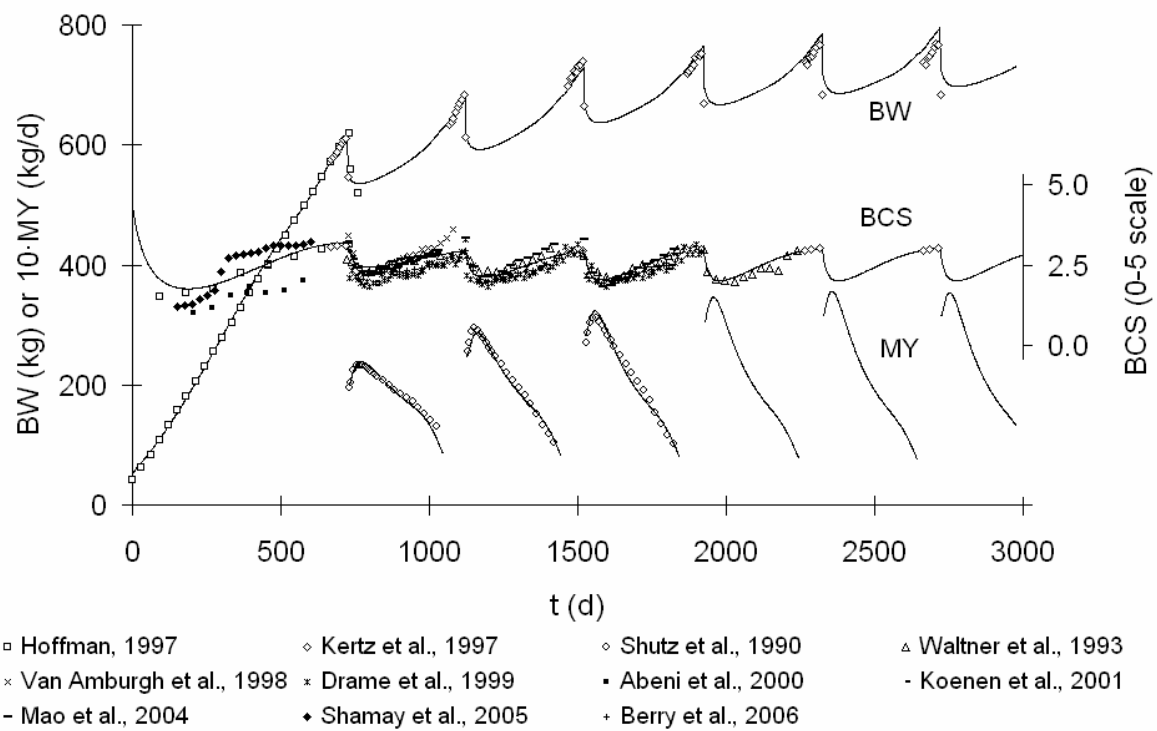
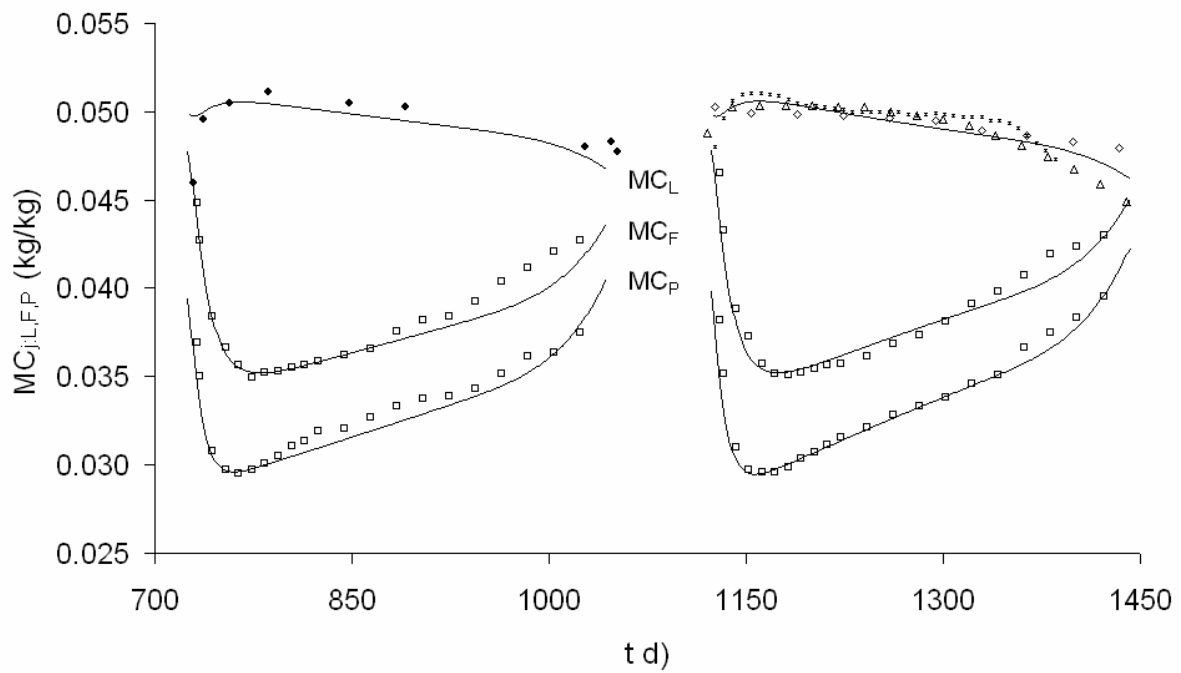


Figure 1.5 Model simulations of body weight (BW , kg), body condition score (BCS , 0-5 scale), and milk yield (MY , kg) from birth to 3000 d of life plotted with data used for model calibration.



□ Shutz et al., 1990 ◇ Jenness, 1985 △ O'Mahony, 1988 · Roche, 2003 • Ostensen et al., 1997

Figure 1.6 Model simulations of milk fat (MC_F , kg/kg), protein (MC_P , kg/kg) and lactose (MC_L , kg/kg) contents (kg/kg) during the 1st and 2nd parity plotted with data used for model calibration.

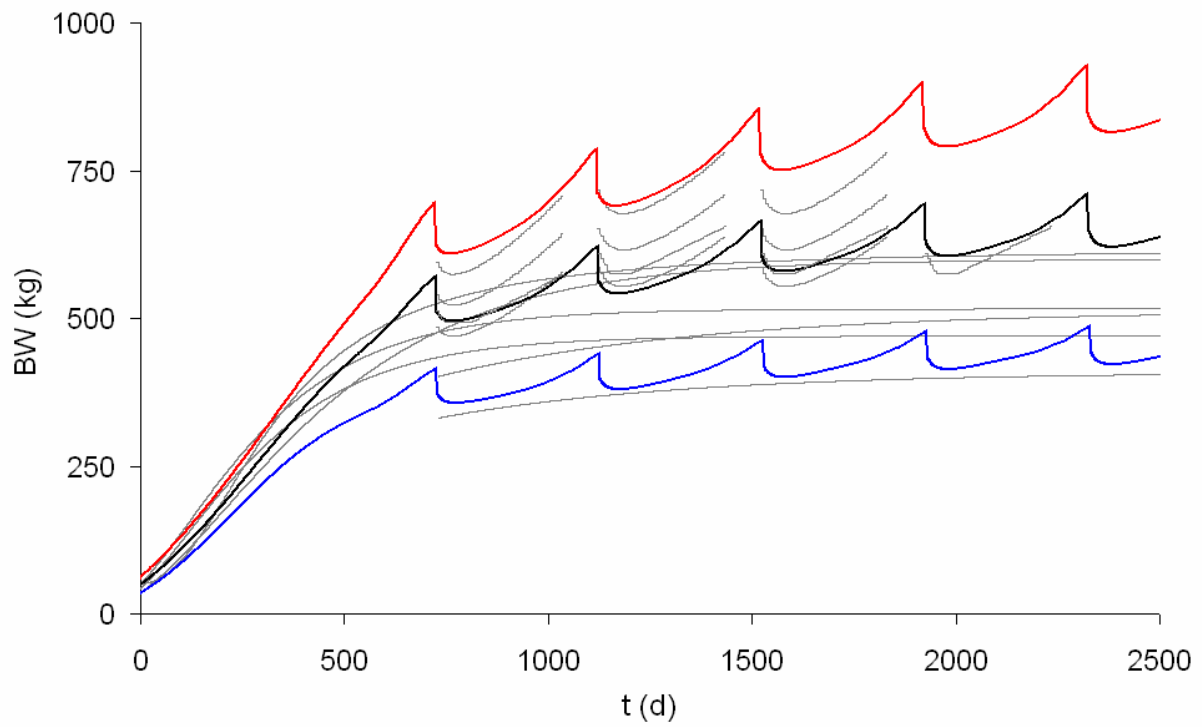
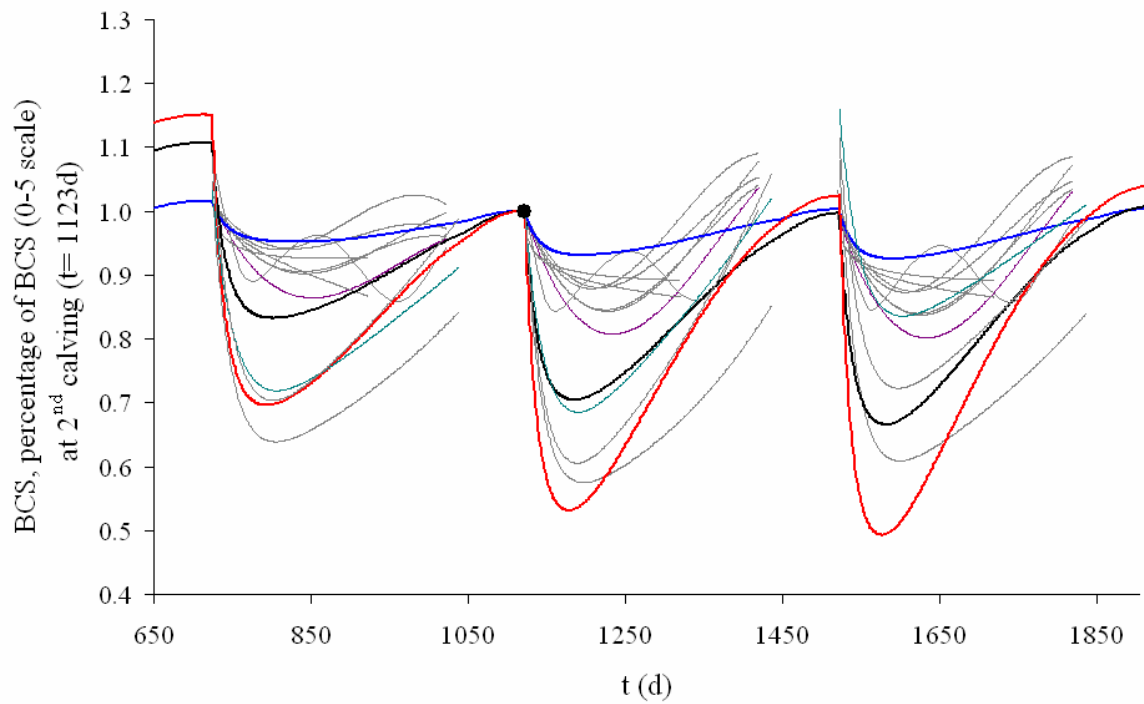
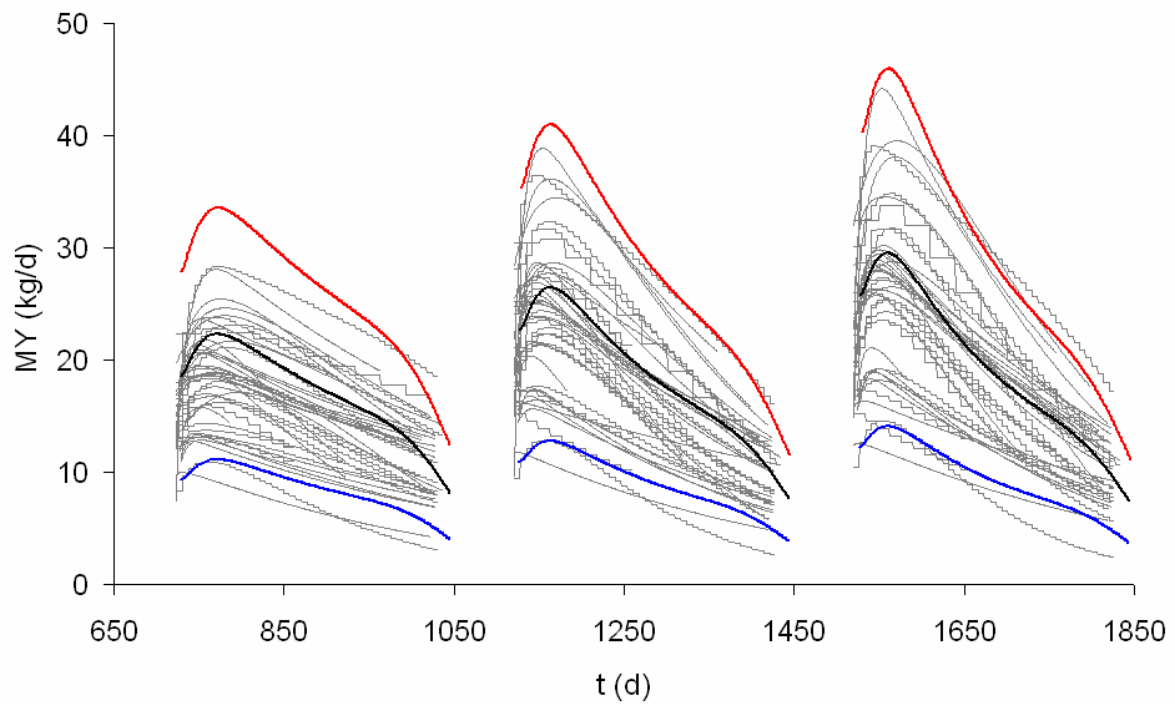


Figure 1.7 Model simulations of body weight (BW , kg) for increasing values of the input parameter scaling body size ($W_M = \{300, 450, 600\}$ kg) plotted with simulations of published models for different dairy cattle breeds and sizes within breeds (see **Table 4**).



1317

1318 **Figure 1.8** Model simulations of body condition score (*BCS* , 0-5 scale) expressed in % of *BCS* at
 1319 2nd calving (t = 1121 d of age) for increasing values of the input genetic parameter scaling individual
 1320 body reserves mobilization potential ($\nu_x = \{0.2, 1.0, 1.8\}$) plotted with simulations of published
 1321 models (see **Table 4**).



1322

1323 **Figure 1.9** Model simulations of milk yield (MY , kg/d) in 1st to 3rd parity for increasing values of the
1324 input genetic parameter scaling individual milk yield potential ($\nu_y = \{0.5, 1.0, 1.5\}$) plotted with
1325 simulations of published models (see **Table 4**).

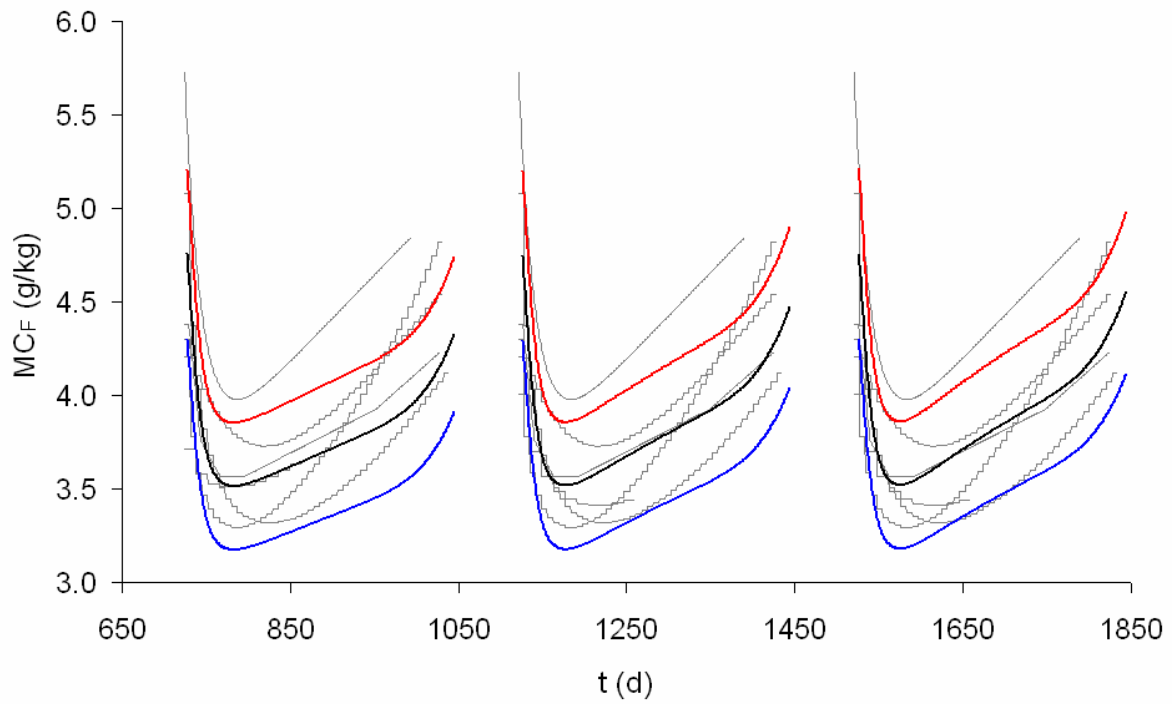
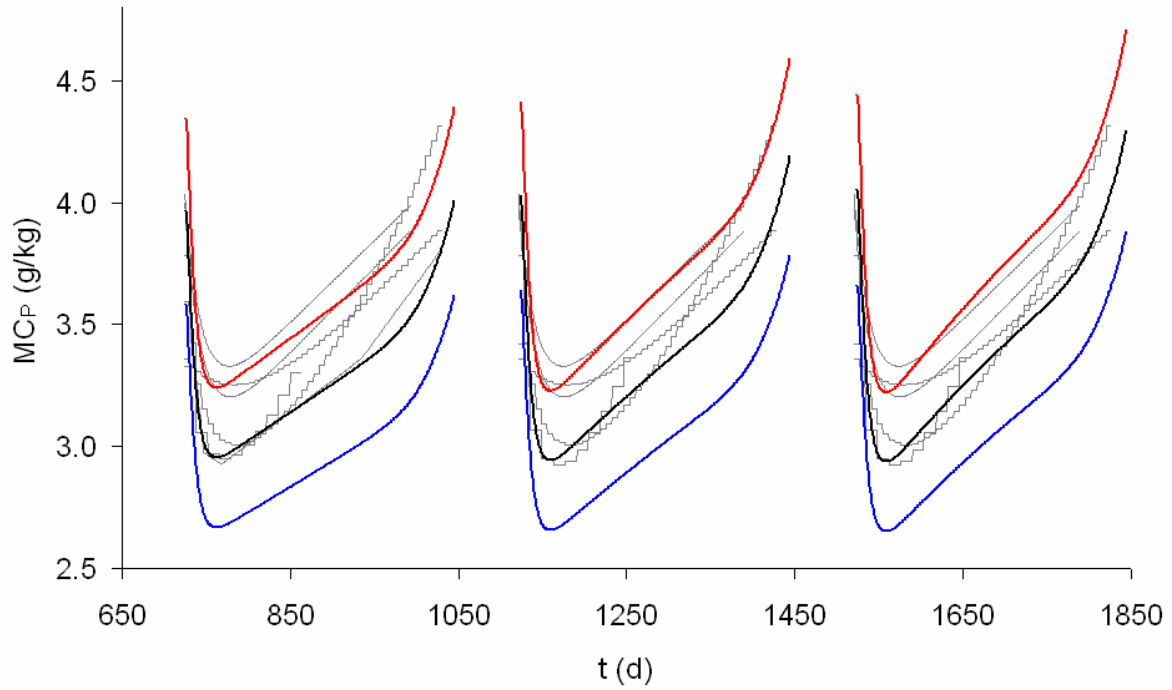
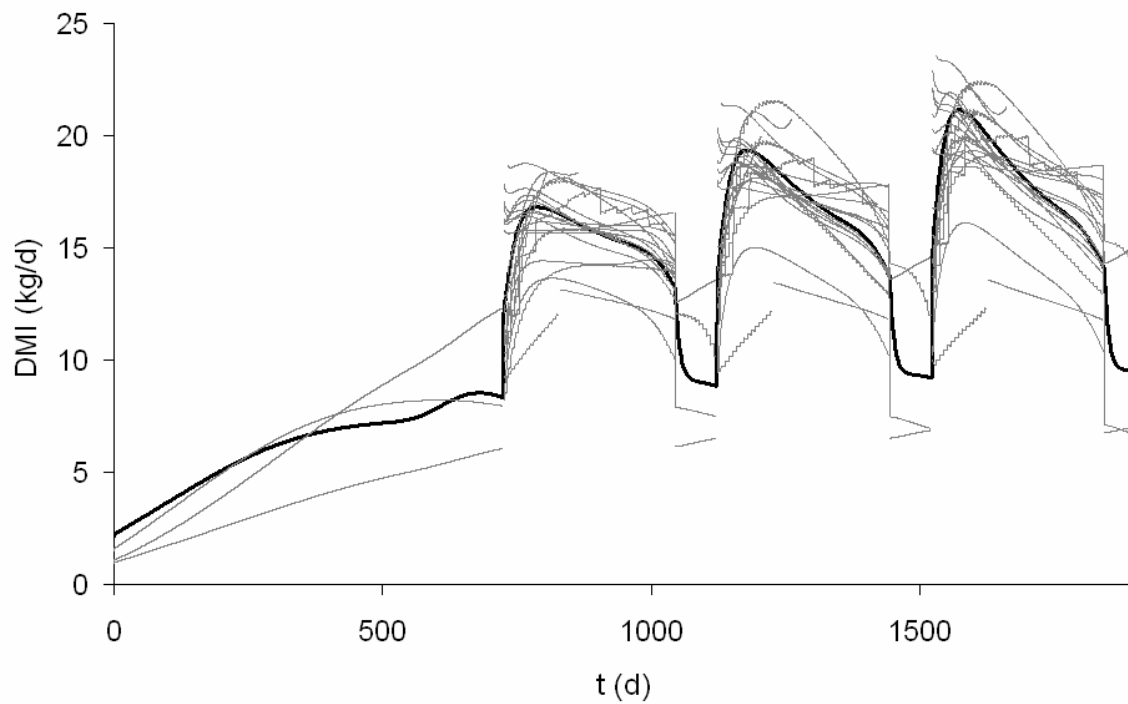


Figure 1.10 Model simulations of milk fat content ($100 \times MC_F$, g/kg) in 1st to 3rd parity for increasing values of the input genetic parameter scaling individual milk fat yield potential ($\nu_F = \{0.9, 1.0, 1.1\}$) plotted with simulations of published models (see **Table 4**).



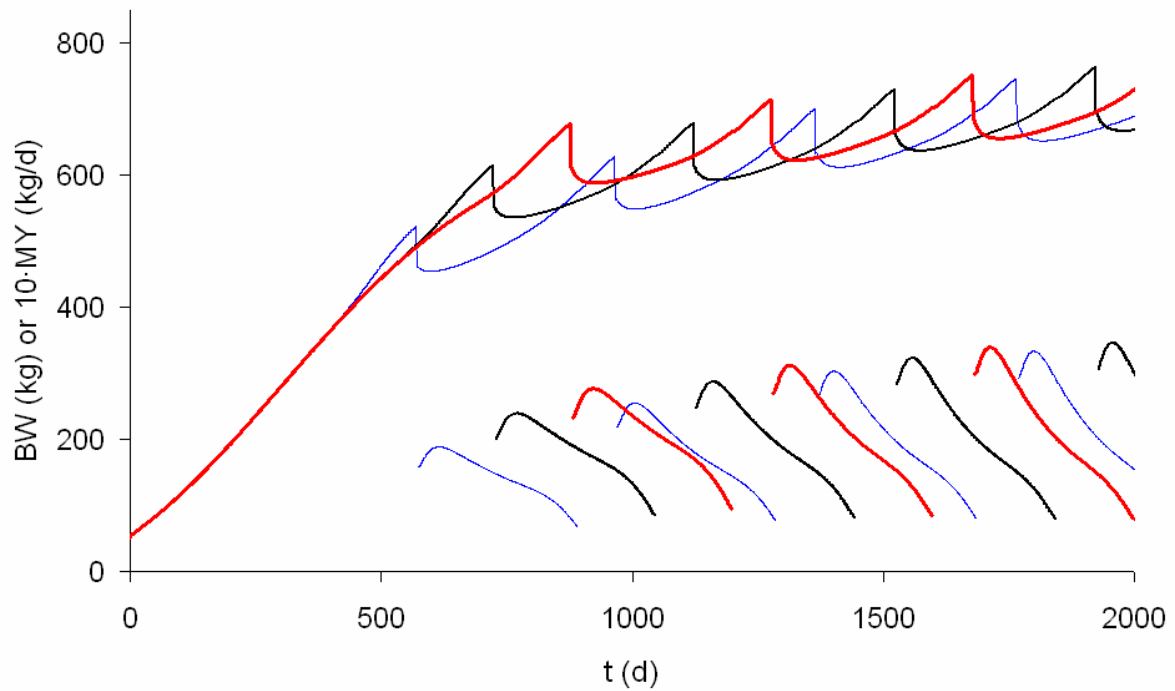
1330

1331 **Figure 1.11** Model simulations of milk protein content ($100 \times MC_p$, g/kg) in 1st to 3rd parity for
 1332 increasing values of the input genetic parameter scaling individual milk protein yield potential
 1333 ($v_p = \{0.9, 1.0, 1.1\}$) plotted with simulations of published models (see **Table 4**).



1334

1335 **Figure 1.12** Model simulations of dry matter intake (*DMI* , kg/d) from birth to 2500d of life plotted with
1336 simulations of published models (see **Table 5**).



1337

1338 **Figure 1.13** Model simulations of body weight (BW , kg) and milk yield (MY , kg/d) from birth to
 1339 2000d of life for increasing values of the input parameter setting age at first conception
 1340 ($PCI(0) = \{300, 450, 600\}$ d).

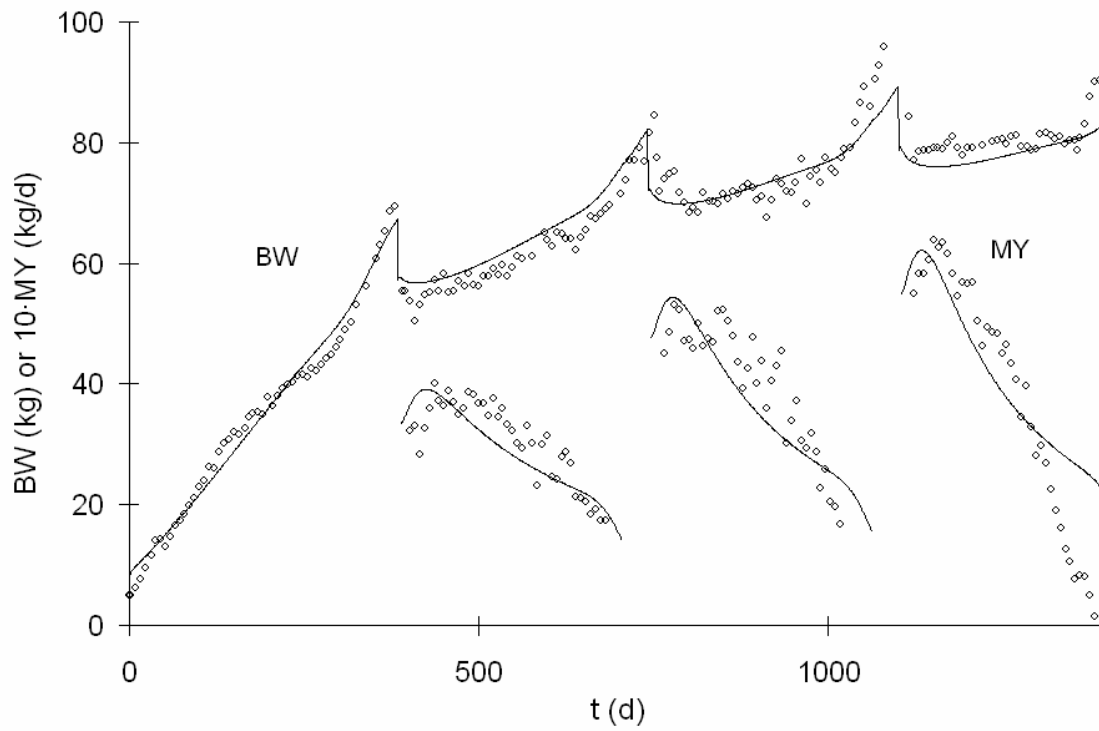


Figure 1.14 Model simulations applied to dairy goat of body weight (BW , kg) and milk yield (MY , kg/d) from birth to 1400 d of life plotted with individual experimental records.

2 Modèle énergétique

La description du modèle énergétique est présentée sous la forme d'un article soumis à la revue Animal :

Martin O and Sauvant D 2009. Modelling dairy livestock lifetime performance. 2.Homeorhetic drive and homeostatic control of energy partitioning. Animal (submitted ²⁶).

²⁶ Accepté après la soutenance de thèse sous la forme : **Martin, O. and Sauvant, D., 2010b. A teleonomic model describing performance (body, milk and intake) during growth and over repeated reproductive cycles throughout the lifespan of dairy cattle. 2. Voluntary intake and energy partitioning. Animal (in press).**

1 Modelling dairy livestock lifetime performance.

2 2. Homeorhetic drive and homeostatic control of energy 3 partitioning

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9

10 *This is the second paper of a short series of two accompanying papers describing a*
11 *teleonomic model of lifetime performance of female livestock. The model described in the*
12 *first paper is based on the coupling of a regulating sub-model of the dynamic partitioning of a*
13 *mammal's female priority over lifetime with an operating sub-model of whole-animal*
14 *performance. The model provides a reference pattern of performance under normal*
15 *husbandry and feed regimen, which is expressed in the present paper in a reference*
16 *dynamic pattern of energy partitioning and adapted to changes in nutrient supply. Firstly, a*
17 *model of intake regulation accounting for feeding allowance, physical limitation of the*
18 *digestive tract and energy demand, is used to determine the actual intake, which may*
19 *generate a deviation from the energy input under the reference pattern of partitioning.*
20 *Secondly, a theoretical model is proposed to apportion the energy deviation between flows*
21 *involved in performance and thus model lifetime performance when actual intake is above or*
22 *below requirements. The model explicitly involves a homeorhetic drive by the way of the*
23 *tendency to home on to the teleonomic trajectory and a homeostatic control by the way of the*
24 *tendency to maintain an energetic equilibrium in response to nutritional constraints. The*
25 *model was developed and evaluated through simulations reproducing typical feeding trials in*

dairy cows. Model simulations shown in graphs concern the effect of dietary energy content on intake, body weight and condition score, and milk yield. Results highlight the ability of the model to simulate the combination of physical and energetic regulation of intake, the accelerated, retarded and compensatory patterns of growth, and the short and long-term residual effects of prepartum and postpartum feeding on lactation.

Keywords: Homeostasis; Homeorhesis; Model; Dairy cow; Lactation; Body reserves

Implications

This model of lifetime performance of dairy livestock opens new perspectives in the field of modelling animal physiology and provides a prototype of an integrative whole animal model. This work involves (1) an innovative conceptual framework by focusing on priorities for physiological functions, (2) a holistic view of growth, reproduction and nutrition, (3) a combination of genotype and environmental effects in the prediction of performance, and (4) a generic formalism with scaling parameters allowing to simulate different animal genotypes.

Introduction

This is the second part in the short series of two papers on the modelling of female livestock lifetime performance aimed at proposing a conceptual framework and developing a simulation tool.

The general principle of the proposed modelling approach relies on the coupling of a regulating sub-model describing the dynamic partitioning of a mammal's female priority over lifetime with an operating sub-model describing dairy livestock intake

and production variables. The regulating sub-model provides teleonomic trajectories used as a driving force to rule the work of the operating sub-model. The coupling is designed to formalize homeorhetic drive and homeostatic control of energy partitioning (see companion paper).

The first paper in this short series described the regulating sub-model coupled with a condensed version of the operating sub-model. This coupling provides a reference pattern of lifetime performance in dairy cows under normal husbandry conditions and feed regimens. Scaling genetic parameters were used to simulate the variability of performance between individuals of the same breed or between breeds of dairy cattle. In this second paper, the same formalism is used to provide a reference pattern of performance expressed in terms of a reference partitioning of energy. This pattern corresponds to a situation of intake supplying the exact coverage of requirements. A model of intake regulation accounting for feeding allowance, physical limitation of the digestive tract and energy demand, is used to determine the actual intake, which may generate a deviation from the energy input under the reference pattern of partitioning. A homeostatic function is proposed to adjust the reference partition by apportioning the energy deviation between flows involved in performance. The effective energy partitioning is then converted into an effective pattern of performance, which explicitly involves a homeorhetic drive by the way of the tendency to home on to the teleonomic trajectory and a homeostatic control by the way of the tendency to maintain an energetic equilibrium in response to nutritional constraints.

The whole model allows to simulate milk yield and composition, foetal growth, calf birth weight, intake, and body mass and composition changes in dairy cows over lifespan and during repeated gestation/lactation cycles.

The operating sub-model presented afterwards is a compartmental, dynamic and deterministic model of metabolizable energy partitioning between growth, maintenance, pregnancy, milk production and body reserves mobilization and storage. It incorporates major concepts described by Van Es (1978) and shared by updated dairy energy feeding systems used around the world (e.g., NRC, 2001; Fox et al., 2004; INRA, 2007).

The following sections deal with the model description and development and its evaluation through simulations designed to reproduce classic trials performed on dairy cows.

Model description

Regulating sub-model

A comprehensive description of the regulating sub-model is given in the companion paper. Briefly, the model describes the partition of a mammal's female priority over lifetime t and during successive reproductive cycles between six elementary goals: G : achieve growth, A : achieve ageing, R : balance body reserves, U : complete intrauterine growth of offspring, N : supply nutrients to the neonate, and S : supply nutrients to the nursing young. Priority is formalized as a dimensionless quantity flowing from G to R during growth, from R to A with ageing, and cyclically through R , U , N and S during reproductive cycles such as $G + A + R + U + N + S = 1$. The so-called *GARUNS* dynamic pattern defines a teleonomic trajectory providing rules for the time-based orchestrated changes in energy metabolism. An exhaustive compendium of model equations is presented in Table 1.

Operating sub-model

Structure. The operating sub-model (**Figure 2.1**) describes the partitioning of metabolizable energy between major life functions of the cow over her lifetime: growth, maintenance, body reserves storage and mobilization, pregnancy and lactation. The main state variables of the operating sub-model concern the composition of full body weight (BW , kg) and the amount of available food in a fresh matter (FM) basis (AF , kg FM).

As in the companion paper, variable BW (kg) is given by

$$BW = W + X + DT + GU, \quad (35)$$

where W (kg) is the non-labile body mass weight which determines the animal frame size, X (kg) is the labile body mass weight (X standing for extra-weight) which represents the energy reservoir, DT (kg) is the digestive tract contents weight, and GU (kg) is the gravid uterus weight including the foetus weight (W_F) and foetal annexes (placentome, fetus, membranes and fluids). Other variables are source or sink compartments of energy (*maintenance*) or material (*milk*, *foodstuffs*, *faeces* and *calf & annexes*).

The central compartment of the model is the metabolizable energy zero pool (ME , Mcal) which links inflowing and outflowing energy flows, metabolizable energy being a common unit.

The differential equation for ME is

$$\frac{dME}{dt} = I - A_w - A_x + C_x - P - Y - M, \quad (36)$$

where I (Mcal/d) is the energy inflowing from diet, A_w (Mcal/d) is the energy involved in W growth, A_x (Mcal/d) is the energy involved in X storage, C_x (Mcal/d) is the energy issued from X mobilization, P (Mcal/d) is the energy involved in

pregnancy, Y (Mcal/d) is the energy involved in milk secretion and M (Mcal/d) is the energy involved in maintenance expenditure.

The daily raw milk yield (MY , kg/d) is given by

$$MY = \sum_{j:F,L,P,H} MY_j, \quad (37)$$

where MY_j is the daily yield of milk constituent j ($j : F$ for milk fat, $j : P$ for milk protein, $j : L$ for milk lactose, and $j : H$ for milk water). The yield of milk mineral constituents is not considered in this work.

Other continuous flows of material include the daily amount of fresh food offered (FMO , kg FM /d), refused (FMR , kg FM /d), ingested (FMI , kg FM /d), and excreted (FME , kg FM /d). The flow FMO is defined by the feeding system of the cow and is an input of the model potentially generating a limit to the voluntary intake, conventionally expressed in a DM basis (DMI , kg DM /d) as the flow providing the dietary metabolizable. The daily intake FMI is the current material flow entering the digestive tract.

Other model inputs concern characteristics of diet ingredients i ($i : fo$ for forage, $i : co$ for concentrate and/or $i : tm$ for a mixture of forage and concentrate in a complete diet) and the proportion of forage in tm on a FM basis (p_{tm} , kg FM /kg FM). Given their diet concentration (FM_i , kg FM /kg FM), their dry matter content (DM_i , kg DM /kg FM) and their digestible organic matter content (DOM_i , kg/kg DM), the diet metabolizable energy content (e_D , Mcal/kg DM) is given by

$$e_D = 4.29 \cdot \frac{\sum_i (FM_i \cdot DM_i \cdot DOM_i)}{\sum_i (FM_i \cdot DM_i)} - 0.31, \quad (38)$$

where 4.29 (± 0.06) and 0.31 (± 0.04) are estimates derived from a meta-analytic study involving 713 various ruminants diets ($R^2 = 0.89$, $RMSE = 0.13$ Mcal/kg DM , Sauvant and Giger-Reverdin, unpublished).

The diet DM content (DMC , kg DM / kg FM) is given by

$$DMC = \frac{\sum_i (FM_i \cdot DM_i)}{\sum_i FM_i}. \quad (39)$$

Model first steps of development were achieved with a standard mixed diet characterized by $FM_{tm} = 1$, $p = 0.6$, $DM_{tm} = 0.6$ and $DOM_{tm} = 0.70$ giving $e_D = 2.68$, and $DMC = 0.6$.

As in the companion paper, the differential equation for digestive tract contents weight is given by

$$\frac{dDT}{dt} = FMI - FME, \quad (40)$$

with $DT_{t=0} = \delta \cdot W_B$ and

$$FME = k_0 \cdot (DT - \delta \cdot W), \quad (41)$$

where k_0 (d^{-1}) is the fractional rate of daily DT removal and δ (kg/kg) is a parameter scaling the minimal and permanent digestive tract content fresh weight.

The differential equation for AF is simply given by

$$\frac{dAF}{dt} = FMO - FMI - FMR, \quad (42)$$

where

$$FMR = FMO - FMI, \quad (43)$$

with the assumption that food refusals are daily removed and that AF is a zero pool compartment.

The flow V (kg/d) is a discrete transfer of material occurring at parturition and represents calving, *i.e.*, the expulsion of the newborn calf and the foetal annexes from the cow's gravid uterus.

Intake. Given the daily *ME* requirement I^* derived from the reference pattern of performance defined in companion paper (see Table 1 and Table 2) and the dietary *ME* content e_D , the level of *DM* intake covering energy requirements (DMI^* , kg *DM* /d) is given by

$$DMI^* = I^*/e_D. \quad (44)$$

This reference level of intake defines the theoretical realization of the animal energetic demand under homeorhetic drive, given the diet characteristics.

The food intake capacity (DMI_C , kg *DM* /d) limiting intake to a digestive tract maximal fill is simply given by

$$DMI_C = \left(\frac{e_D}{e_D^*} \right) \cdot I^*/e_D^*, \quad (45)$$

where e_D^* is defined as the theoretical optimal dietary *ME* content maximizing intake.

By the way of I^* , this level of maximal intake relies on the assumption that the dynamic pattern of food intake capacity is under homeorhetic drive, meaning that the digestive tract size follows a specific dynamic pattern along the animal lifetime and during the reproductive cycle. This approach is consistent with the INRA Fill Unit System of voluntary dry matter intake prediction in dairy cows recently proposed by Faverdin et al. (2007), which involves corrective indexes of maturity, gestation and lactation. By the way of e_D^* , this level of maximal intake relies on the assumption that

an optimum diet is associated with the exact coverage of energy requirement, which is, here limited to energy, the basis of livestock nutrition.

Giving the amounts of offered ($DMO = FMO / DMC$, kg DM /d), maximum (DMI_C) and required (DMI^*) intake, the actual DMI is defined as the minimum value between DMO , DMI_C and an optimum food intake amount lying between DMI^* and DMI_C , and is given by

$$DMI = \min(DMO, DMI_C, q \cdot DMI_C + (1 - q) \cdot DMI^*), \quad (46)$$

where $q \cdot DMI_C + (1 - q) \cdot DMI^*$ is an optimum food intake, defined when $DMI^* \leq DMI_C$ according to the value of q given by

$$q = 1 / \left(1 + \left(\frac{X/W}{\chi_I} \right)^5 \right), \quad (47)$$

where χ_I (kg/kg) is a threshold parameter for the labile to non-labile body mass ratio.

The actual ME intake is then given by

$$I = e_D \cdot DMI. \quad (48)$$

This formalism assumes that when the digestive tract fill is not limiting (*i.e.*, when $DMI^* < DMI_C$), food intake tends to exceed the energy requirement based amount DMI^* and to reach the intake capacity DMI_C in lean animals ($X/W < \chi_I$). Inversely, in fatty animals ($X/W > \chi_I$), food intake tends to the strict coverage of energy requirements. This formalism is consistent with the lipostatic theory of Kennedy (1953) suggesting that the long term regulation of food intake is linked to the regulation of body reserves. The recent researches on leptin identified as an “adipostat” and thought to be a metabolic signal involved in energy balance

regulation are reminiscent of the lipostatic theory (Houseknecht et al., 1998). This simple representation of food intake allows to simulate the physical limitation of intake of low density energy diets ($e_D < e_D^*$) and situations of overfeeding of high density diets ($e_D > e_D^*$) leading to excessive fattening. Moreover, this model allows to simulate a compensatory higher intake following a restricted feeding period (Faverdin et al., 2007).

Rationale. An essential feature of the model is the conservation of energy which is given by

$$\frac{dME}{dt} = 0, \quad (49)$$

and implies that

$$I = A_w + A_x - C_x + P + Y + M, \quad (50)$$

Flows A_w , A_x , C_x , P , Y and M are described with the following generic formalism:

$$flow = flow^* + \partial flow, \quad (51)$$

where $flow$ is the simulated daily ME inflowing/outflowing from ME , $flow^*$ is the homeorhetic version of $flow$ driven by the *GARUNS* pattern, and $\partial flow$ is the homeostatic adjustment of $flow^*$. It is thus basically assumed that the actual dynamic of $flow$ is the realization of the dynamic of $flow^*$ corrected daily in an additive manner with $\partial flow$.

The trajectory of priority defined in the regulating sub-model proposed in the companion paper directs energy metabolism and determines a standard dynamic pattern of energy partition such as

$$I^* = A_w^* + A_x^* - C_x^* + P^* + Y^* + M^* , \quad (52)$$

210 This partition is aimed at supporting the priority in energetic supply and is thus an
211 homeorhetic drive.

212 The flow I^* represents the inflow of metabolizable energy allowing to strickly cover
213 the energy requirements defined through this drive. The actual inflow I is derived
214 from the actual DMI . Flows I (and DMI) and I^* (and DMI^*) are respectively the
215 supply and the demand in energy (and food). The flow I can thus be equal, superior
216 or inferior to I^* which is given by

$$I = I^* + \partial I . \quad (53)$$

217 If the actual intake I is different from the reference amount I^* in underfeeding
218 ($I < I^*$ and $\partial I < 0$) or overfeeding ($I > I^*$ and $\partial I > 0$) situations, the deviation ∂I
219 characterizes an energetic imbalance ($I = A_w^* + A_x^* - C_x^* + P^* + Y^* + M^* + \partial I$) and
220 the deviation ∂I is divided up between these flows through deviations $\partial flow$ such as

$$\partial I = \partial A_w + \partial A_x - \partial C_x + \partial P + \partial Y + \partial M . \quad (54)$$

221 The way ∂I is apportioned between flows A_w , A_x , C_x , P , Y and M is defined
222 through a model of partition of energy taking into account levels of priority to lactation
223 (S) and growth (G), of body reserve and of dietary energy input. This partition is
224 aimed at the preservation of an energetic equilibrium and is thus a homeostatic
225 control.

226 In the following sections are described (1) the partition between A_w^* , A_x^* , C_x^* , P^* , Y^*
227 and M^* generating the demand I^* (homeorhetic drive of $flow^*$), (2) the partition of
228 ∂I generated by actual supply, between ∂A_w , ∂A_x , ∂C_x , ∂P , ∂Y and ∂M
229 (homeostatic control of $\partial flow$), and (3) the calculation of body and milk composition

according to energetic flows obtained by the combinations $flow^* + \partial flow$. An important point to keep in mind is that the homeorhetic drive of $flow^*$ is built independently of the current level of feeding but with respect to the body reserve size, which reflects previous feeding.

Homeorhetic drive of $flow^$* . The formalism for variables dW/dt , dX/dt , dGU/dt , MY_j , and DMI defined in the companion paper (see Table 2) as a reference dynamic pattern of lifetime performance is denoted with a star exponent and converted afterwards in a reference dynamic pattern of energy partitioning. This trajectory represent the homeorhetic drive of $flow^*$.

The daily *ME* flow channelled to growth is given by

$$A_w^* = e_w \cdot \frac{dW^*}{dt}, \quad (55)$$

where e_w (Mcal/kg) is the growth *ME* requirement (for the accretion of 1kg *W*).

The labile body mass anabolic and catabolic *ME* flows A_x^* and C_x^* represent the net result associated with changes in body reserves *X* and are given by

$$A_x^* = \begin{cases} e_{xa} \cdot \frac{dX^*}{dt} & \text{if } \frac{dX^*}{dt} > 0 \\ 0 & \text{elsewhere} \end{cases}, \quad (56)$$

and

$$C_x^* = \begin{cases} e_{xc} \cdot \frac{dX^*}{dt} & \text{if } \frac{dX^*}{dt} < 0 \\ 0 & \text{elsewhere} \end{cases}, \quad (57)$$

245 where e_{Xa} (Mcal/kg) is the *ME* requirement for the storage of 1 kg X and e_{Xc}
246 (Mcal/kg) is the *ME* supplied by the mobilization of 1 kg X (see Appendix B in the
247 companion paper).

248 Daily investment of *ME* in pregnancy is defined as the energy required to supply the
249 reference gravid uterus growth dGU^*/dt tied to foetal growth (see Appendix A in the
250 companion paper) and is given by

$$P^* = e_U \cdot \frac{dGU^*}{dt}, \quad (58)$$

251 where e_U (Mcal/kg) is the pregnancy *ME* requirement (for the accretion of 1kg GU)
252 Energy flow Y^* channelled to milk secretion supply is considered as the sum of *ME*
253 flows involved in the secretion of milk constituents j :

$$Y^* = \sum_j e_j \cdot MY_j^*, \quad (59)$$

254 where e_j (Mcal/kg) is the *ME* requirement for the yield of milk constituent j .

255 Maintenance *ME* energy expenditure is given by

$$M^* = e_M \cdot BW^{0.75}, \quad (60)$$

256 where e_M (Mcal/kg) is the maintenance *ME* requirement.

257

258 *Homeostatic control of flow*. Giving the actual energy input I resulting of the *DMI*
259 model (see (46) and (48)) and the reference required energy input I^* , the relative
260 energetic feeding level f is given by

$$f = \frac{I}{I^*}. \quad (61)$$

Components $\partial flow$ correspond to an adjustment (homeostatic control) of the energy partitioning defined with variables $flow^*$ (homeorhetic drive). They are defined as a proportion of deviation ∂I with a general formalism given by

$$\partial flow = \partial I \cdot \Theta_{flow} . \quad (62)$$

where Θ_{flow} is a specific function of partitioning defined for variables $flow$ (A_w , A_x , C_x , P , Y and M) such as $\sum_{flow} \partial flow = 0$.

Thus, the difference ∂I (by construction $\Theta_I = 1$) between energetic supply and demand is integrally diverted between flows which may be increased or decreased in relation to their reference value $flow^*$ according to the sign of ∂I ($\partial I < 0$ and $f < 1$: energy deficit, $\partial I > 0$ and $f > 1$: energy surplus:). In particular a deficit of energy may induce a slowing down in growth, a decrease in body reserve storage, an increase in body reserve mobilization, a decrease in foetal growth and/or a decrease in milk production. Inversely, a surplus of energy may induce a speeding up of growth, an increase in body reserve storage, a decrease in body reserve mobilization and/or an increase in milk production.

This model of partition assumed that maintenance requirements (M) are unaffected by the level of energetic feeding, which is given by

$$\Theta_M = 0 , \quad (63)$$

which implies $\partial M = 0$ and $M = M^*$ whatever ∂I .

Quantification of other functions Θ_{flow} is assumed to depend on priorities G and S of the *GARUNS* pattern of relative priorities defined in the regulating sub-model in the companion paper, on the relative energetic feeding level f and on the level of body reserves (X_L) given by

$$X_L = \frac{X}{W}, \quad (64)$$

282 which corresponds to the ratio of labile to non-labile body mass.

283 The proposed theoretical formalism involves a simple logistic function Ψ of f , which
284 acts as a pivot and has the property to smoothly shift from 1 to 0 when f increase
285 from below to above 1, *i.e.*, from energy deficit to surplus. This function is given by

$$\Psi = \frac{1}{1 + f^{20}}, \quad (65)$$

286 where the exponent 20 was set to ensure a shift mostly completed for f ranging
287 from 0.85 to 1.15. The function Ψ is used to direct the model behaviour to either the
288 energy deficit response or the energy surplus response, which is thus assumed to be
289 fully reached at a $\pm 15\%$ deviation from requirements.

290 The general formalism for Θ_{flow} is given by

$$\Theta_{flow} = f_{fat}(\Psi) - \frac{f_{fat}(\Psi) - f_{lean}(\Psi)}{1 + \left(\frac{X_L}{\chi_{flow}} \right)^{\theta_{flow}}}, \quad (66)$$

291 where $f_{lean}(\Psi)$ is the theoretical function used to describe the change of Θ_{flow} with
292 the relative energetic feeding level f when $X_L = 0$ (extremely lean animal), and
293 $f_{fat}(\Psi)$ is the theoretical function used to describe the change of Θ_{flow} with the
294 relative energetic feeding level f when $X_L \geq 0.5$ (extremely fat animal). The function
295 of partition is thus built by the way of theoretical responses in unrealistic extreme
296 situations in order to obtain a comprehensive surface response within the range of
297 realistic values of f (approximately 0.75 to 1.25) and X_L (approximately 0.05 to 0.5
298 leading to a body condition score (BCS) ranging from 0.5 to 4.5 on a 0 to 5 scale).

299 The effect of changes in the level of energetic feeding on the diversion of energy into
300 milk is regulated by the function Θ_Y given by

$$\Theta_Y = S \cdot (1 - \Psi) - \frac{S \cdot (1 - \Psi) - \frac{Y^*}{I^*} \cdot \Psi}{1 + \left(\frac{X_L}{\chi_Y} \right)^{\theta_Y}}, \quad (67)$$

301 where χ_Y (kg/kg) and θ_Y (unitless) are parameters governing the shape of the
302 surface response shown in **Figure 2.2** and where the term S is the priority to
303 lactation defined in the companion paper. This function generates a smooth transition
304 of energy partitioning profile according to the animal state and can be easily read by
305 focusing on areas defined by values of the couple (f, X_L) of the response surface:

- 306 • $(f < 1, X_L < \chi_Y)$ is a situation of energy deficit detrimental to milk secretion as
307 the state of body reserves not allows mobilization (the maximal value of Θ_Y
308 equals Y^*/I^* which implies $\partial Y \rightarrow Y^*$ when $\partial I \rightarrow I^*$);
- 309 • $(f < 1, X_L > \chi_Y)$ is a situation of energy deficit not detrimental to milk
310 secretion as the state of body reserves allows mobilization;
- 311 • $(f > 1, X_L < \chi_Y)$ is a situation of energy surplus in which energy is channelled
312 to body reserves recovery rather that diverted into milk yield;
- 313 • $(f > 1, X_L > \chi_Y)$ is a situation of energy surplus diverted into milk yield
314 according to the level of priority S .

315 The modulation of Θ_Y by priority S traduces the fact that conceptually, homeostasis
316 and homeorhesis are goal-seeking and concerted mechanisms, the former
317 contributing to the “environmentally” compatible realization of the plan drawn by the
318 latter. This construction is consistent with the more pronounced effect of

underfeeding on milk production in early lactation (Broster, 1972) and the favoured diversion of energy surplus into milk when this option is available rather than into body reserves (Friggens *et al.*, 2004). Since the quantity of energy surplus ∂I is function of requirements I^* driven by homeorhesis and of actual input of energy limited by intake, the quantity of milk yield has an implicit physiological limit, which is not redundantly formalized at this level of energy deviation partitioning.

The effect of changes in the level of energetic feeding on the diversion of energy into pregnancy is regulated by the function Θ_p given by

$$\Theta_p = \frac{\frac{P^*}{I^*} \cdot \Psi}{1 + \left(\frac{X_L}{\chi_p} \right)^{\theta_p}}, \quad (68)$$

where χ_p (kg/kg) and θ_p (unitless) are parameters governing the shape of the surface response shown in **Figure 2.3**.

This function implies:

- ($f < 1$, $X_L < \chi_p$) is a situation of energy deficit detrimental to pregnancy as the state of body reserves not allows mobilization (the maximal value of Θ_p equals P^*/I^* which implies $\partial P \rightarrow P^*$ when $\partial I \rightarrow I^*$);
- ($f < 1$, $X_L > \chi_p$) is a situation of energy deficit not detrimental to pregnancy as the state of body reserves allows mobilization;
- ($f > 1$, $X_L < \chi_p$) and ($f > 1$, $X_L > \chi_p$) are situations of energy surplus in which energy is not channelled to pregnancy.

As in the model of energy requirements of the pregnant ewe developed by Geisler and Neal (1979), the supply of energy to ensure an optimal fetal growth is seen as a “protected” function. This formalism implicitly assumes that the flow P^* corresponds

to an optimal fetal growth. Overfeeding during pregnancy induces body reserve formation and underfeeding is associated with body reserves mobilization to supply fetal growth requirements (Lins *et al.*, 2003). As energy deficit increases, a greater part is detrimental to foetal growth (Wade and Schneider, 1992). The effect of changes in the level of energetic feeding on the diversion of energy into growth is regulated by the function Θ_{AW} given by

$$\Theta_{AW} = G \cdot (1 - \Psi) - \frac{G \cdot (1 - \Psi) - \frac{G}{G_{t=0}} \cdot (1 - \Psi) - \frac{A_w^*}{I^*} \cdot \Psi}{1 + \left(\frac{X_L}{\chi_{AW}} \right)^{\theta_{AW}}}, \quad (69)$$

where χ_{AW} (kg/kg) and θ_{AW} (unitless) are parameters governing the shape of the surface response shown in **Figure 2.4**.

This function implies:

- ($f < 1$, $X_L < \chi_{AW}$) is a situation of energy deficit detrimental to growth as the state of body reserves not allows mobilization (the maximal value of Θ_{AW} equals A_w^*/I^* which implies $\partial A_w \rightarrow A_w^*$ when $\partial I \rightarrow I^*$);
- ($f < 1$, $X_L > \chi_{AW}$) is a situation of energy deficit not detrimental to growth as the state of body reserves allows mobilization;
- ($f > 1$, $X_L < \chi_{AW}$) is a situation of energy surplus associated with a lean body in which energy is channelled to growth (this situation corresponds to a compensatory growth in young animals);
- ($f > 1$, $X_L > \chi_{AW}$) is a situation of energy surplus diverted to growth with respect to the partition $A_w^*/I^* = G \cdot (G + A + R)$ which corresponds to the

reference growth rate increased or decreased according to priority to growth and inhibited during reproductive stages of life when $U + N + S > 0$.

Parameters χ_Y , χ_P and χ_{AW} correspond to thresholds of the labile to non-labile body mass ratio at which the homeostatic function shifts the channelling of energy deficit or surplus. For instance, a high value of χ_Y implies that body reserves recovery prevails over milk yield, that an energy surplus is diverted into milk yield when body reserves are at a high level, and that an energy deficit is primarily detrimental to milk yield. A low value of χ_P defines the level of protection of the pregnancy function: an energy deficit is detrimental to foetal growth only when body reserves fall under a critical value. Analogously, the value of χ_{AW} determines the level of body reserves at which an energy deficit start to be detrimental to growth and an energy surplus enhances growth. To exemplify the modelling principle, these parameters were set to $\chi_Y = 0.22$, $\chi_P = 0.16$ and $\chi_{AW} = 0.10$ which correspond approximately to BCS of 2.0, 1.5 and 1.0 respectively (on 0-5 scale). Parameters θ_Y , θ_P and θ_{AW} govern the speed of the shift at these threshold points and were set to $\theta_Y = \theta_P = \theta_{AW} = 5$.

The partition of energy deviation defined by Θ_Y , Θ_P and Θ_{AW} implicates body reserve mobilization or storage with a net result (∂B_X , Mcal/d) given by

$$\partial B_X = \partial I \cdot \Theta_X, \quad (70)$$

where

$$\Theta_X = 1 - \Theta_Y - \Theta_P - \Theta_{AW} - \Theta_M, \quad (71)$$

and achieved through changes in body reserve mobilization or storage relative to the reference levels A_X^* and C_X^* such as

$$\partial B_X = \partial A_X - \partial C_X, \quad (72)$$

379 with

$$\partial A_X = \max(-A_X^*, \partial B_X - C_X^*), \quad (73)$$

380 and

$$\partial B_X = \max(-\partial B_X - A_X^*, -C_X^*). \quad (74)$$

381 These equations traduce the fact that an increase in body reserve storage is
382 achieved by reducing C_X^* if $C_X^* > 0$ or by increasing A_X^* if $A_X^* > 0$ and that an
383 increase in body reserve mobilization is achieved by reducing A_X^* if $A_X^* > 0$ or by
384 increasing C_X^* if $C_X^* > 0$.

385 This model explicitly consider body reserves as an energy buffer, *i.e.*, an energy
386 source to partially compensate the effect of underfeeding and an energy sink
387 formalizing the fattening effect of overfeeding.

388 Actualised values of *flow* are then given by

$$A_W = A_W^* + \partial A_W, \quad (75)$$

$$A_X = A_X^* + \partial A_X, \quad (76)$$

$$C_X = C_X^* + \partial C_X, \quad (77)$$

$$P = P^* + \partial P, \quad (78)$$

$$Y = Y^* + \partial Y, \quad (79)$$

389 and

$$M = M^* + \partial M. \quad (80)$$

390 The above model of energy partitioning implies that
391 $\partial A_W + \partial A_X - \partial C_X + \partial P + \partial Y + \partial M = \partial I$, traducing that the energetic deviation ∂I is
392 integrally apportioned to adjust flows A_W , A_X , C_X , P and Y . This partition is

assumed to affect simultaneously all flows, which reflects the coordinated aspect of homeostatic energy regulation and especially the harmonized use of energy reserves to counter temporary energy deficit or take advantage of favourable conditions to constitute energy reserves. Severe energetic deficit are detrimental to the completion of lactation and gestation which traduces situations where milk production and foetal growth are severely reduced as body reserve mobilization becomes inefficient to lessen the effect of underfeeding.

By the way of the homeorhetic driven variables $flow^*$ and the homeostatic corrections $\partial flow$, the model combines push and pull approaches (Drackley *et al.*, 2006) (input makes output vs output makes input): trajectories of physiological functions determine reference dynamic energy requirements (homeorhetic pull standpoint) and lifetime animal performance are corrected according to effective energy supply (homeostatic push standpoint).

The formalism applied in the companion paper to convert references values of $flow^*$ into animal performance is applied afterwards to adjusted values of $flow = flow^* + \partial flow$.

Performance. Giving the effective flows A_w , A_x and C_x labile and non labile body mass changes are given by

$$\frac{dW}{dt} = \frac{A_w}{e_w}, \quad (81)$$

and

$$\frac{dX}{dt} = \frac{A_x}{e_{xa}} - \frac{C_x}{e_{xc}}. \quad (82)$$

413 Giving the effective flow P , the gravid uterus weight changes are given by

$$\frac{dGU}{dt} = \frac{P}{e_u}, \quad (83)$$

414 with $GU = 0$ at discrete event parturition as in the companion paper.

415 The effective dynamic of BW is then derived from its components changes dW/dt ,

416 dX/dt , dGU/dt and dDT/dt and the effective dynamic of BCS is calculated with the

417 formalism used in the companion paper (see Table 2).

418 The variation in milk composition resulting of changes in energy input is considered

419 through the changes in the origin of the energy channelled to the udder. The variation

420 ∂Y resulting from the deviation ∂I involves a change in energy inflowing from diet

421 denoted $\partial Y_D = \partial I - \partial M - \partial P - \partial A_w - \partial A_x$ and a change in energy issued from body

422 reserves mobilization denoted $\partial Y_x = \partial C_x$ such as $\partial Y = \partial Y_D + \partial Y_x$.

423 The partition of ∂Y between flows $Y_{j:L,P,F}$ is modelled with respect to the partition of

424 ∂Y between ∂Y_D and ∂Y_x , and is given by

$$Y_j = Y_j^* + \partial Y_j^D + \partial Y_j^x, \quad (84)$$

425 where

$$\partial Y_j^D = u_j^D \cdot \partial Y_D, \quad (85)$$

426 and

$$\partial Y_j^x = u_j^x \cdot \partial Y_x, \quad (86)$$

427 with $\sum_j u_j^D = 1$ and $\sum_j u_j^x = 1$.

428 Coefficients u_j^D and u_j^x depict respectively how a change in dietary energy supply

429 and body reserve mobilization affect energy channelled to the udder for the secretion

430 of milk constituent j .

431 Daily yield of milk constituent j is then given by

$$MY_j = \begin{cases} \text{milking} \cdot \frac{Y_j}{e_j} & \text{for } j : \text{lactose, protein, water} \\ \text{milking} \cdot \left(\frac{Y_F^* + \partial Y_F^D}{e_F} + \frac{\partial Y_F^X}{e_F^X} \right) & \text{for fat} \end{cases}, \quad (87)$$

432 where e_j (Mcal/kg) is the ME requirement for the yield of milk constituent j ,
 433 assuming that $e_F^X = 0.8 \cdot e_F$ is the lower ME required for the secretion of milk fat
 434 fuelled by body reserves mobilization. The use of two different coefficients of energy
 435 requirement for milk fat secretion fuelled from dietary energy and milk fat secretion
 436 fuelled from body reserves energy relies on the difference between milk fat
 437 biochemical precursors. As suggested by Van Es and Van der Honing (1979), the
 438 theoretical maximum efficiency of fat synthesis is close to 90% when dietary fat or
 439 long-chain fatty acids (such as non-esterified fatty acids released by lipomobilization)
 440 are used directly as substrate, while the corresponding efficiency from volatile fatty
 441 acids (*i.e.*, from diet digestive processes) is only about 70%. In the present version of
 442 the model, coefficients u_j^D and u_j^X were defined in a simple way by assuming that
 443 changes in energy issued from body reserves only affect milk fat secretion ($u_F^X = 1$
 444 and $u_{j:L,P,H}^X = 0$) and that no changes occur in the partition of energy inflowing from
 445 diet channelled to milk constituents ($u_j^D = Y_j^*/Y^*$). This formalism is conceived as a
 446 null hypothesis to be evaluated in further specific work.
 447 Finally, milk content of constituent j is given by

$$MC_j = \begin{cases} \frac{MY_j}{MY} & \text{if } MY > 0 \\ 0 & \text{elsewhere} \end{cases}. \quad (88)$$

The discrete event *parturition* sets *milking* to one while the additional discrete event *drying off* is used to set *milking* to zero after 320 days in milk to simulate dairy production context.

Model evaluation

The model was implemented with Modelmaker version 3.0 software (Cherwell Scientific Ltd, 2000) using the Runge-Kutta 4 numerical integration procedure and a fixed integration step of 1 d from $t = 0$ to $t = 2500$ d. Settings of parameters of the regulating and operating sub-model are described in the companion paper.

Model evaluation is aimed at presenting through graphic results the ability of the model to produce realistic dynamic patterns of lifetime performance of dairy cows under nutritional challenging contexts. The dynamic response of the model is induced by changing the dietary metabolizable energy content e_D reflecting changes in diet composition and inducing changes in intake, while the theoretical optimal dietary metabolizable energy content maximizing intake is set to $e_D^* = 2.7$ Mcal/kg *DM*. These virtual experimentations were designed to reproduce classic features of dairy cow intake and performance during growth, peripartum period and lactation.

Overall diet effect on intake

The **Figure 2.5** shows the simulated changes in weekly average *DMI* and *I* during the 5th week of lactation of a second parity cow associated with changes in e_D ranging from 50% to 150% of e_D^* . The model produces the typical pattern of physical

fill effect limiting *DMI* of low density diet and the plateau response of *I* to the level of requirement resulting of a decrease of *DMI* (e.g., Faverdin, 1992).

Feeding effect on growth

The **Figure 2.6** shows the simulated effect on *BW* and *BCS* of two dietary *ME* energy content (H: $e_D = 3.0$ Mcal/kg *DM* and L: $e_D = 2.4$ Mcal/kg *DM*) during two periods of age (200 to 400d and 400 to 600d). The model produces typical patterns (e.g., Crichton et al., 1960) of retarded (LL and HL), accelerated (HH) and compensatory growth (LH).

Prepartum feeding effect on performance

The **Figure 2.7** shows the simulated effect of six levels of feeding ($e_D = 2.2 \rightarrow 3.2$ Mcal/kg *DM*) three months prepartum on *BW*, *BCS* and *MY* of a 2nd parity cow. The model produces main known features of such treatment (e.g., Garnsworthy and Topps, 1982), i.e., prepartum weight gain and increase in body condition, increase body weight loss with body condition at calving, return to an apparently defended level of body weight and score during lactation, the residual difference between treatment groups at the end of the subsequent lactation being reduce, and detrimental effect on milk yield.

Feeding effect during lactation

The **Figure 2.8** shows the simulated effect on body weight and milk yield of two dietary *ME* energy contents (H: $e_D = 3.0$ Mcal/kg *DM* and L: $e_D = 2.4$ Mcal/kg *DM*) during two stages of lactation (0 to 70 d and 70 to 140 d). The model produces the

classical pattern of such feeding trial (e.g., Broster et al., 1969) and simulate the residual effect of early lactation feeding level on milk yield and body weight change in the following course of lactation.

Discussion

The model as a predictive tool

The application of the conceptual framework yielded to a prototype of a dairy cow lifetime performance predictive tool. This approach is complementary to our previous work aimed at associating a given pattern of performance with metabolic pathways in dairy cows (Martin and Sauvant, 2007). As whole, the proposed model of energy metabolism resemble to the growth models of the Metabolic Theory of Ecology (MTE; Brown et al., 2004) and the earlier theory of Dynamic Energy Budgets (DEB; Kooijman, 1986). All these approaches are founded on simple mechanistic descriptions of how individual organisms take up and use energy and material. The MTE is based on the physics and geometry of supply networks and the DEB is based on relationships between surface area and volume (Van der Meer, 2008). The model is also related to the model developed by Vetharaniam et al. (2001) based on the concept of absorbed energy and designed to predict performance of different genotypes under different feeding regimes. The main differences of our approach are the more detailed representation of the sequence of reproductive cycles and the involvement of teleonomic trajectories for life functions. Our approach is resolutely dedicated to the development of an operational tool rather than the construction of a new theory. The *GARUNS* model is intended to artificially simulate rather than explain the biological basis of energy partitioning. In non-reproductive stages of life, the

priority to growth is consistent with the formalism proposed by West *et al.* (2001) in a general model of growth.

The lactation part of the model involves a two-stage empirical control by priorities to ensure the transition between gestation and lactation, and that of providing nutrients to the calf. This approach is not directly based on the known biology of the mammary gland during pregnancy and lactation, which is the rationale of models developed by Neal and Thornley (1983), Dijkstra *et al.* (1997), Pollott (2004) and Vetharaniam *et al.* (2003a, 2003b), but follows the same principle of modelling an underlying mechanism giving rise to lactation. The model describes the raw milk yield as the sum of milk constituents' yields. The use of different exponents for the differential priorities to secrete these constituents allows simulating properly their standard kinetic shapes. The use of simple partition coefficients to modulate milk composition according to nutritional deviation from demand allows to simulate an overall response consistent with results derived from meta-analysis studies on milk response to feeding (Sauvant, 2003). However, the ability of an energy based model to simulate accurately the udder synthesis system remains in question.

The intake part of the model involves a body reserves dependant trade-off between the saturation of the intake capacity to take benefit from a liberal feeding situation to improve body condition and the exact coverage of energy demand. This two-ways modelling principle, initially proposed by Conrad *et al.* (1964) is the basis of several published models of intake. The originality of our approach is to formalize possible intermediary levels of intake between energy and fill based prediction that account for a long-term energy demand relying on a target body reserves level to reach. Contrary to numerous intake models using production variables as inputs, intake is predicted as a full-fledged performance as milk production and body weight.

Animal is thus considered as a whole, on a lifetime scale, with its own “agenda” and the model simulates *ad libitum* feeding situations as well as situations of restricted feeding. As the dietary energy content is the only feed characteristic used as input, the model provides a synthetic but reductive view of nutrition. Simulated trajectories of $DMI \times MY$ daily values falls within the scatter plot shown by Hristov et al. (2004), gathering a large set of data reported in the literature.

The decomposition of body mass into structural/non-labile and reserve/labile compartments is a classic representation in animal science energy based models of growth (Hoch et al., 2004) and lactation (Bywater and Dent, 1976). It allows to incorporate the energy buffer role of reserves and the changes in body weight during reproductive cycles. In the future, the principle of differential priority could be used to model growth of anatomic body components and to improve the representation of energy transactions and material exchange between metabolic and body systems. The modelling of body weight changes occurring during the lactation course, though identified as a pertinent indicator for diagnostic and management purposes (Maltz, 1997) has been subject to little modelling studies (Quinn et al., 2006). A major problem relates to the prediction of digestive tract contents accounting for up to 20 to 25% of live weight, mainly determined by the fiber content of the diet (Martin and Sauvant, 2003) and subjected to within-day changes in relation to the alimentary behaviour along the nycthemeron. The incorporation of the gravid uterus weight as a body component allows to produce realistic simulations of the changes in body weight during gestation and at parturition. The prediction of the body condition score allows to express the amount of body reserves consistently with records made in the field. An improvement of the operating sub-model concerns the modelling of the initiation of body reserves mobilization occurring a few days before parturition and

detected through the increase in plasma non-esterified fatty acids concentrations (Vazquez-Añon et al., 1994). This issue could be fixed by incorporating a control by the priority U to the unborn generation in the mobilization function. The principle of differential priority with a high value exponent could be used to simulate the initiation of mobilization at high level of priority U . Another improvement of the model concerns the opportunity of incorporation of a genetic parameter in the function of balancing body reserves to represent differences between animals and breeds in the ability to replenish body reserves.

As such the predicted performance are based on the modulation of a reference, so called optimal performance, assumed to mirror the animal potential pertaining to its genotype. This underlying pattern can not be recorded as such and specific investigations should be done to allow a model parameterisation for individual animals. We intend to go further in this direction.

The model as a conceptual framework

The model described in the first paper of this short series allows to simulate lifetime performance of dairy cows under standard husbandry conditions and feed regimens without any environmental constraints.. This reference pattern of performance corresponds to a theoretical equilibrium profile pertaining to a genetically pre-determined ability and an optimal level of feeding. The present sophistication of the model is aimed at accounting for the effect of variations in feed intake around this level and thus yield a prediction of performance based on a combination of genotype and energy-based nutrition factors. The basic principle is to model the partitioning of energy deviation from the optimal reference between functions to generate an adjusted pattern of performance. The performance (P) is thus expressed as the

trajectory of a genotype (G) in a constraining nutritional environment (E). Contrary to the classical additive formalism $P = G + E + (G \times E)$ (Bryant *et al.*, 2005) the proposed model explicitly focus on the interaction $G \times E$ and formulates performance through a whole function $P = f(G, E)$. A time-based pattern of priorities determines an optimal requirement according to physiological status and body condition, and the effective energy supply determines the effective performance, which in turns modifies the animal status and consequently updates the optimal requirement. Lifetime performance are thus the result of the long-term tendency to home on to a goal-directed trajectory giving a genetically determined ability and the short-term tendency to ensure an energetic equilibrium giving an environmentally determined resource. This approach relies on a comprehensive coupling of homeorhetic drive and homeostatic control.

The concepts of homeostasis and homeorhesis have been widely used in animal nutritional science to explain regulations of nutrient partitioning (Bauman and Currie, 1980 ; Sauvant, 1994). Both are properties of living systems to return to a particular state, a particular setpoint in the physiological parameters space for homeostasis and a set of points composing a dynamic trajectory for homeorhesis. From a modeling standpoint, it was assumed that the formalization of this trajectory, coined a chreod by Waddington (1957), should be the starting point rather than an exhaustive representation of metabolic pathways, composing the piping of an animal model. This approach echoes on the suggestions of Friggens and Newbold (2007) to focus on “*why does partition changes with time?*” rather than “*how do animal partition nutrients?*”. The **Figure 2.9** shows a schematic representation of the properties of homeorhesis and homeostasis, seen respectively as the long- and short-term components of the general process that make living organisms follow a trajectory in

their physiological parameters space despite disturbing environmental conditions. This trajectory being compatible with life, genetically determined and targeted to ensured species continuation. This schematic representation illustrates the rationale of the modeling framework proposed in this short series of companion papers.

As a consequence of this construction, body reserves follow a genetically driven pattern acting as an equilibrium reference. This pattern results of the tendency to balance body reserves to a target level from which mobilization forces a deviation in early lactation of each reproductive cycle. The target level corresponds to a favorable body condition to be reach before parturition. The monitoring of body reserves is thus considered as a full-fledged function intimately implicated in reproduction. Body reserves represent an energy buffer being either an energy source in restricted feeding context or an energy sink in liberal feeding contexts. The homeostatic functions establishing the apportioning of energy surplus or deficit between functions of growth, lactation and gestation are modulated according to the level of body reserves. Structurally, the body reserves level is thus a central variable of control regulating the partitioning of energy in situations of energy deviation from the reference pattern of requirements. Moreover, body condition is assumed to regulate the trade-off at the regulating sub-model level between priorities to lactate or replenish body reserves by the way of a safeguarding level. This threshold is thus involved in the change of energy requirement and consequently intake, relying on the lipostatic theory of the long-term regulation of intake by adipose tissue. Results of Ellis *et al.* (2006) have shown that the incorporation of the lipostatic theory into a dynamic model of energy balance significantly improves prediction of intake and body weight changes. In the present model, body reserves follow a trajectory passing by strategic setpoints at parturition, temporary altered to counter nutritional supply

inadequacy to requirements and remaining within a range of tolerable values. At any time, through homeostatic functions, the level of body reserves determines to which extent an energy deficit is detrimental to growth, lactation and pregnancy and to which extent an energy surplus is diverted to growth, lactation or body reserves replenishment.

In parallel with the descending control from the regulating to the operating sub-model, the body size maturity and the body reserves level give information from the operating to the regulating sub-model. These state variables reflect the effective energy channeled to functions permitted by the feeding context. The so-called homeostatic model used to adjust the reference partitioning of energy to an effective supply is a theoretical formalization of the modulation of animal response to nutrient supply. This problem has been tackled with the aim to integrate the basic knowledge and further work will be necessary to accurately predict a wide range of feeding contexts at different physiological stages. Refinements of this specific component of the whole model can be done while keeping the principle of a model diverting an energy deficit or surplus between processes. An interesting question to tackle concerns the incorporation of genetic parameters into the homeostatic function to account for differences between animals and breeds in the ability to cope with challenging feeding contexts. Our purpose is to keep as much as possible the overall model structure with a generic regulating sub-system at the specie level and a specific operating sub-system at the individual level. From that standpoint, the regulating sub-model is intended to embody invariant determining factors in the process of performance elaboration and the operating sub-model is intended to express the way a given genotype performs in a given nutritional environment.

The present model evaluation remains on illustrative typical properties and has not been performed quantitatively. A first step should concern the repeated fit of the model to various data sets and the study of parameter estimates variability. This work should allow quantifying the dependencies between genetic parameters of the model, and especially between the abilities to secrete milk constituents and that of mobilize body reserves. A second step concerns the investigation of the model ability to represent dairy and beef breeds, as well as animals of other dairy livestock species such as goats, ewes, red deers, camels, ...

Conclusion

We proposed a model of lifetime performance of female livestock accounting for changes in energy supply. We conjecture that this work provides a novel conceptual framework. This approach explicitly incorporated a homeorhetic drive by the way of the tendency to home on to the teleonomic trajectory defined in the companion paper and a homeostatic control by the way of the tendency to maintain an energetic equilibrium in response to nutritional constraints. The model formalized lifetime performance as a defended trajectory. Applied to dairy cows, this framework allowed to build a whole animal predictive model defined as an autonomous entity with its “own agenda”, and ultimately as a “virtual cow”. The quantification of the predictive ability of the model and its application to other lactating species remain to be tested.

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- 790
- 791

Table 6 Compendium of regulating sub-model equations described in the companion paper giving the dynamics of priorities G , A , R , U , N and S for age t ranging from 0 to 2500 d, where W , W_B and X are body mass variables in the operating sub-model and with input scaling parameter $W_M = 480$, reproductive events timing parameters $PCI(0) = 450$ and $PCI(c > 0) = 120$, pregnancy scaling parameters $\pi = 285$, $\alpha = 0.0111$ and $\varpi = 3.5 \cdot 10^{-6}$, fractional rates $\mu = 0.06$, $\lambda_0 = 0.0017$, $\lambda_1 = 0.0055$, $\gamma = 0.03$, $\tau = 0.1$ and $\sigma = 0.0018$, and body reserves threshold parameters $\chi_M = 1/3$ and $\chi_S = 1/5$.

		Discrete event of reproductive cycle number c			
		Conception if $A < 0.2$ at $t = t_c(c)$		Parturition	Drying off
Variable	Equation	Initial value	if $c = 0$	if $c > 1$	at $U \geq 1 - (G + A) - \varepsilon$ at $\dim \geq 320$
Control					
c		0	$c = c + 1$	$c = c + 1$	
$milking$		0			$milking = 1$ $milking = 0$
$t_c(c)$	$t_c(c) = t_p(c) + PCI(c)$	$PCI(0)$			
$t_p(c)$		0			$t_p(c) = t$
$\dim$	$\dim_{t+1} = \dim_t + milking$	0			$\dim = 0$
State					
G	$dG/dt = -d$	$1 - (W_B/W_M)^{1/4}$			

A	$dA/dt = s$	0	$A_{t+1} = A_t + 10^{-3}$		
R	$dR/dt = d - s - p + w$	$(W_B/W_M)^{1/4}$	$R_{t+1} = R_t - \varepsilon - 10^{-3}$	$R_{t+1} = R_t - \varepsilon$	
U	$dU/dt = p$	0	$U_{t+1} = U_t + \varepsilon$	$U_{t+1} = U_t + \varepsilon$	$U_{t+1} = 0$
N	$dN/dt = -l$	0			$N_{t+1} = N_t + U_t$
S	$dS/dt = l - w$	0			

Auxiliary

d	$d = (4 \cdot W_M^{1/4} \cdot W^{3/4})^{-1} \cdot dW/dt$
s	$s = \sigma \cdot A \cdot (1 - A)$
p	$p = \alpha \cdot \ln\left(\frac{Z}{U}\right) \cdot U$ if $\varepsilon \leq U < 1 - (G + A) - \varepsilon$ 0
l	$l = \mu \cdot N$
w	$w = (\lambda_0 + \Lambda_x + \gamma \cdot U + \tau \cdot (1 - \text{milking})) \cdot S$
ε	$\varepsilon = \varpi/W_B$
Z	$Z = \varepsilon \cdot \exp(-\ln(\varepsilon)/(1 - \exp(-\alpha \cdot \pi)))$
Λ_x	$\Lambda_x = \lambda_l / (1 + ((X/W)/\chi_s)^{\frac{1}{\beta}})$

Table 7 Compendium of operating sub-model equations described in the companion paper giving the reference performance and the associated metabolizable energy (ME) partitioning for age t ranging from 0 to 2500 d where $p = dU/dt$ and G , R , U , N and S are relative priorities defined in the regulating sub-model, $milking$ is a control variable of mammary stimulation, δ , χ_M , β_W , β_X and ϕ are body mass composition parameters, W_M , ν_Y , ν_X and ν_j are scaling parameters (where j : milk fat, protein, lactose and water), b_0 , m_0 and k_0 are body change parameters, x , y , y_{jN} and y_{jS} are scaling exponents of differential priority control, k_{jN} and k_{jS} are parameters of milk constituents secretion, DMC is the diet DM content and e_D , e_U , e_M , e_W , e_{Xa} , e_{Xc} and e_j are ME conversion factors.

Variable	Equation	Initial value (at birth)	Description	Unit
State				
EBW	$EBW = W + X$	$EBW_B = 0.197 \cdot (W_M \cdot (1 + \chi_M))^{0.83}$	Empty body weight	kg
BW	$BW = EBW + GU + DT$	$BW_B = EBW_B + DT_B$	Full body weight	kg
Performance				
W	$dW/dt = G \cdot (G + A + R) \cdot I/e_w$	$W_B = 0.97 \cdot EBW_B$	Non-labile body mass	kg
X	$dX/dt = bal - mob$	$X_B = 0.03 \cdot EBW_B$	Labile body mass	kg
GU	$dGU/dt = p \cdot W_B/\phi$ and $GU = 0$ at discrete event <i>parturition</i>	$GU_B = 0$	Gravid uterus weight (set to 0 at <i>parturition</i>)	kg
DT	$dDT/dt = DMI/DMC - k_0 \cdot (DT - \delta \cdot W)$	$DT_B = \delta \cdot W_B$	Digestive tract contents weight	kg

MY	$MY = milking \cdot \sum_{j:F,P,L,H} MY_j$	Daily raw milk yield	kg/d
MY_j	$MY_j = (1 - G)^y \cdot \left(k_{jn} \cdot N^{y_{jn}} + k_{js} \cdot S^{y_{js}} \right) \cdot W_M \cdot v_Y \cdot v_j$	Daily milk constituent j yielda	kg/d
Energy			
I	$I = (M + Y + P + A_X - C_X) / (1 - G \cdot (G + A + R))$	ME intake	
DMI	$DMI = I / e_D$	Dry matter intake	kg/d
M	$M = e_M \cdot BW^{0.75}$	Maintenance ME requirement	Mcal/d
Y	$Y = \sum_{j:F,P,L,H} e_j \cdot MY_j$	Milk ME requirement	Mcal/d
P	$P = e_U \cdot dGU/dt$	Pregnancy ME requirement	Mcal/d
A_X	$A_X = e_{Xa} \cdot bal$	ME requirement for X anabolism	Mcal/d
C_X	$C_X = e_{Xc} \cdot mob$	ME requirement for X catabolism	Mcal/d
Auxiliary			
bal	$bal = (1 - G)^x \cdot b_0 \cdot \left(1 - (X/W_M) / \chi_M \right) \cdot R$	Labile body mass balance	kg/d
mob	$mob = (1 - G)^x \cdot m_0 \cdot N \cdot X \cdot v_X$	Labile body mass mobilization	kg/d
EBF	$EBF = \beta_W \cdot W/W_M + \beta_X \cdot X$	Empty body fat	kg/d
BCS	$BCS = (EBF / (1 - \exp(-0.0068 \cdot (EBW - EBF)^{3.7235})) - 17.9) / 39.8$	Body condition score	[0-5]

$$MC_j \quad MC_j = MY_j / MY$$

Milk constituent j content kg/kg

804

805

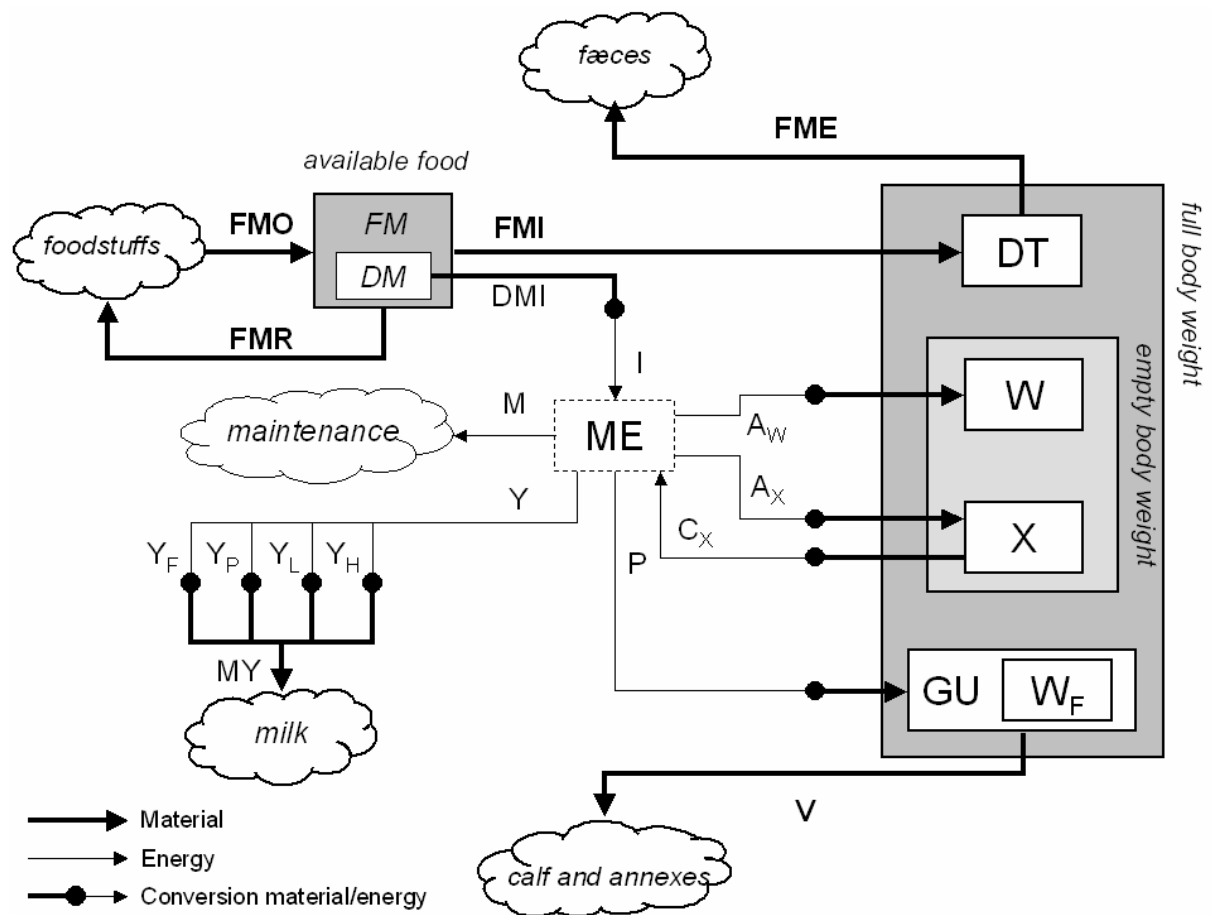


Figure 2.1 Operating sub-model diagram. *ME* : metabolizable energy “zero pool”; I , M , Y , Y_j (j : fat, protein, lactose, water), P , A_W , A_X , C_X : *ME* flows; *FMO*, *FMR*, *FMI*, *FME* : dietary fresh matter flows; *DMI* : dry matter intake; *MY* : raw milk yield; *V* : parturition; components of empty body weight : *W* : non labile mass, *X* : labile mass; components of full body weight: *DT* : digestive tract contents, *GU* : gravid uterus including fetus (W_F) and annexes.

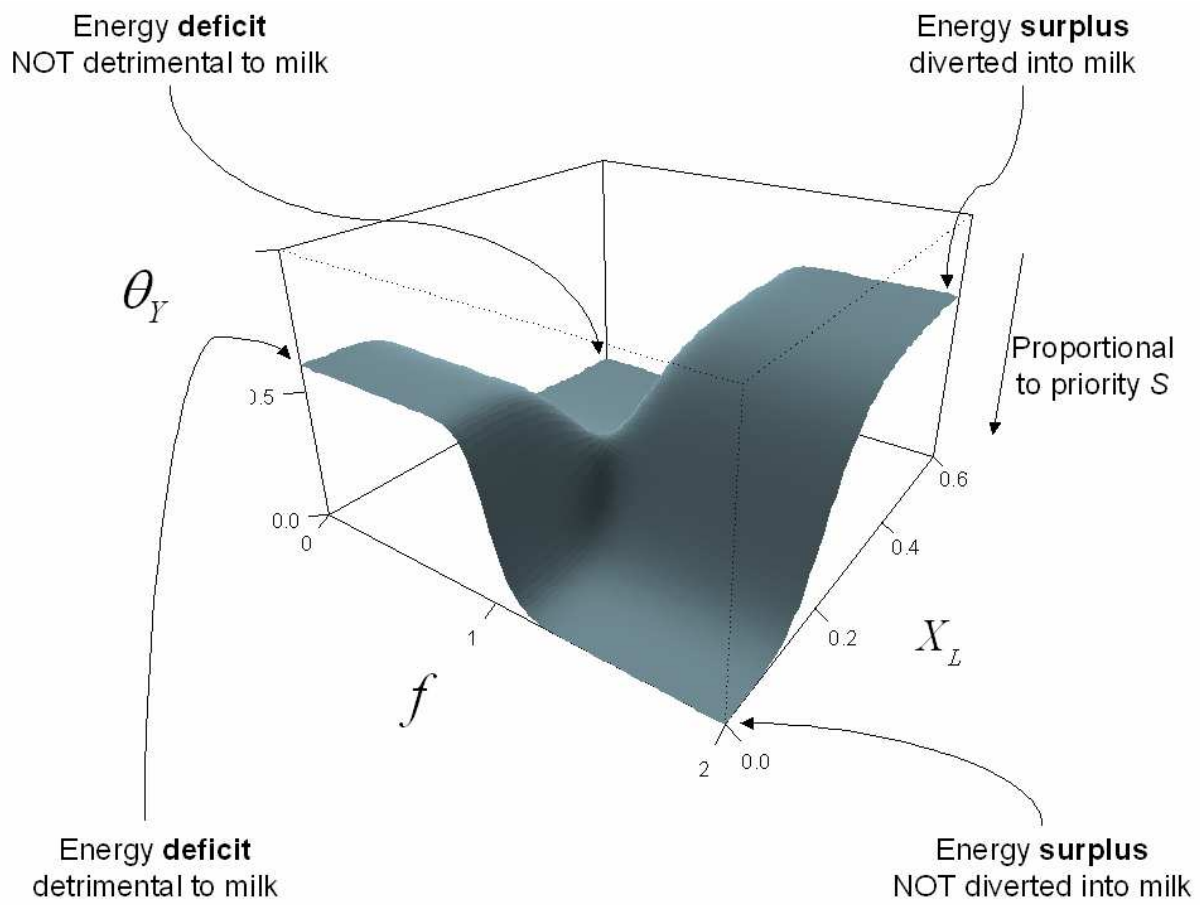


Figure 2.2 Surface response of the function partitioning energy deviation from requirement to milk yield (Θ_Y) according to feed level (f , Mcal/Mcal) and body reserves level (X_L , kg/kg).

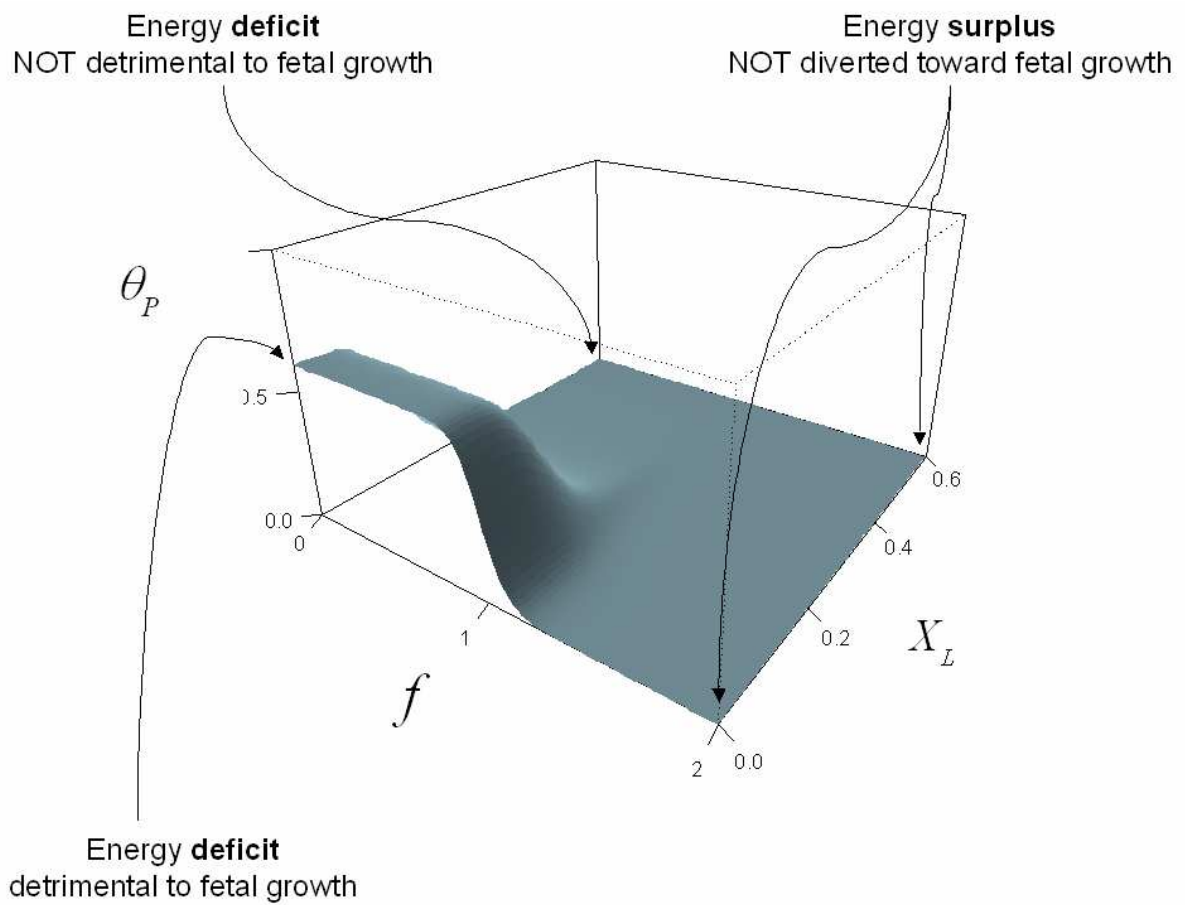


Figure 2.3 Surface response of the function partitioning energy deviation from requirement to fetal growth (Θ_P) according to feed level (f , Mcal/Mcal) and body reserves level (X_L , kg/kg).

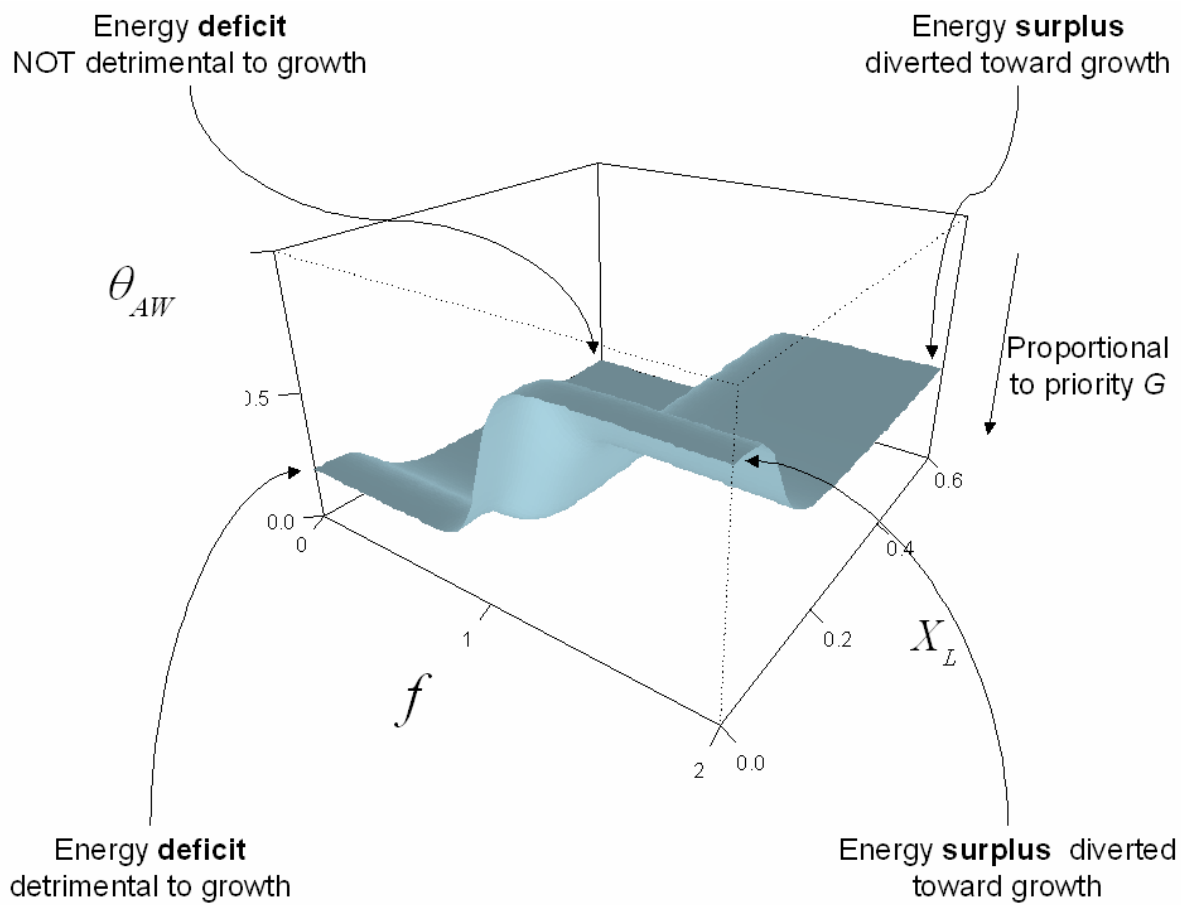


Figure 2.4 Surface response of the function partitioning energy deviation from requirement to growth (Θ_{AW}) according to feed level (f , Mcal/Mcal) and body reserves level (X_L , kg/kg).

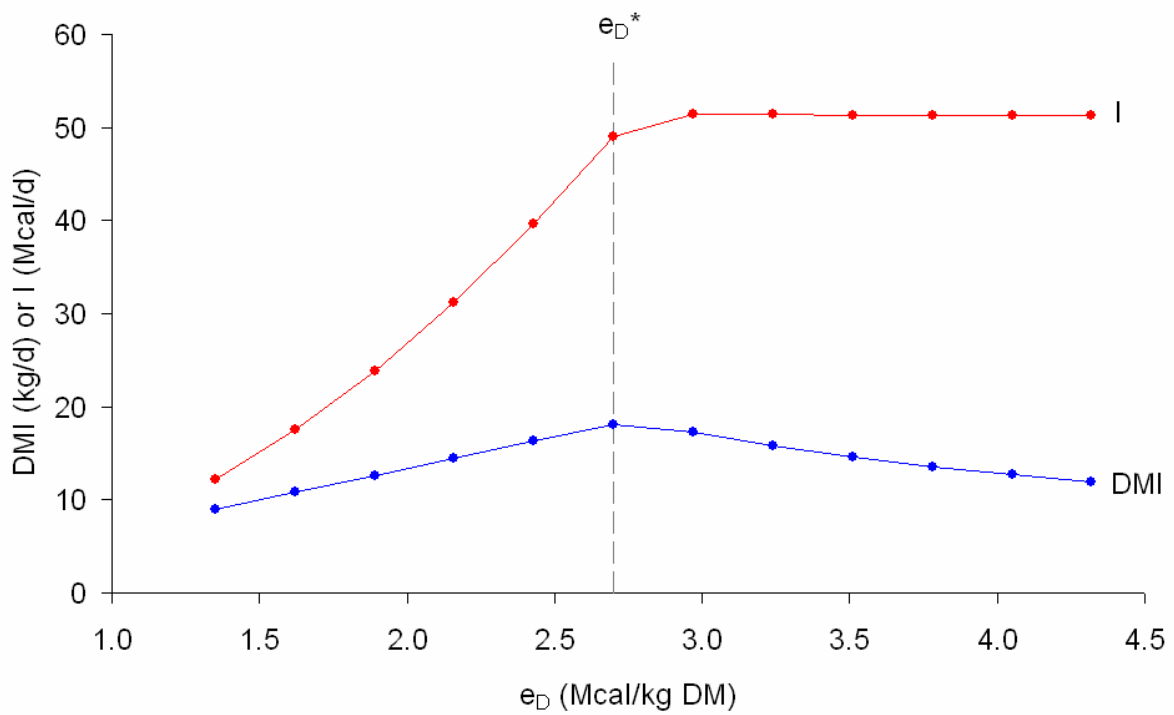


Figure 2.5 Model simulations of average intake of metabolizable energy (I , Mcal/kg) and dry matter (DMI , kg/d) in the 5th week of lactation according to the dietary metabolizable energy content e_D (Mcal/kg DM) where e_D^* is the dietary metabolizable energy content maximizing intake.

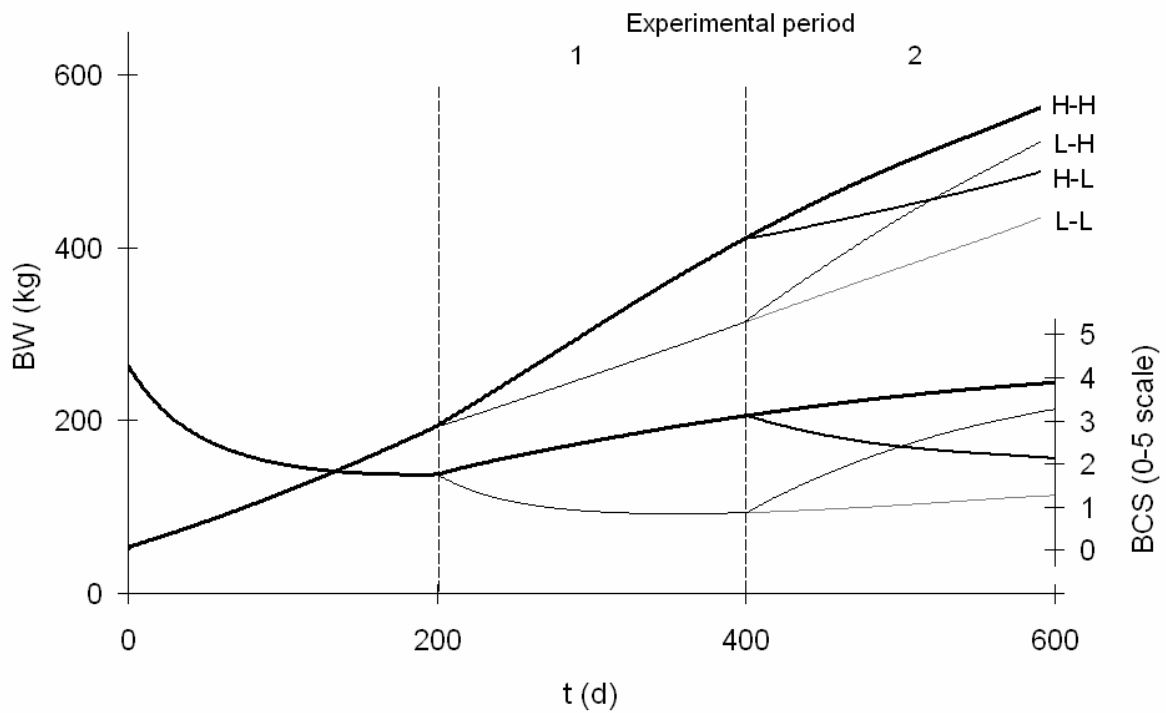


Figure 2.6 Model simulated effect of two dietary metabolizable energy contents (H: $e_D = 3.0$ Mcal/kg DM vs. L: $e_D = 2.4$ Mcal/kg DM) during two experimental periods (200-400d and 400-600d) on body weight (BW , kg) and body condition score (BCS , 0-5 scale) changes during growth.

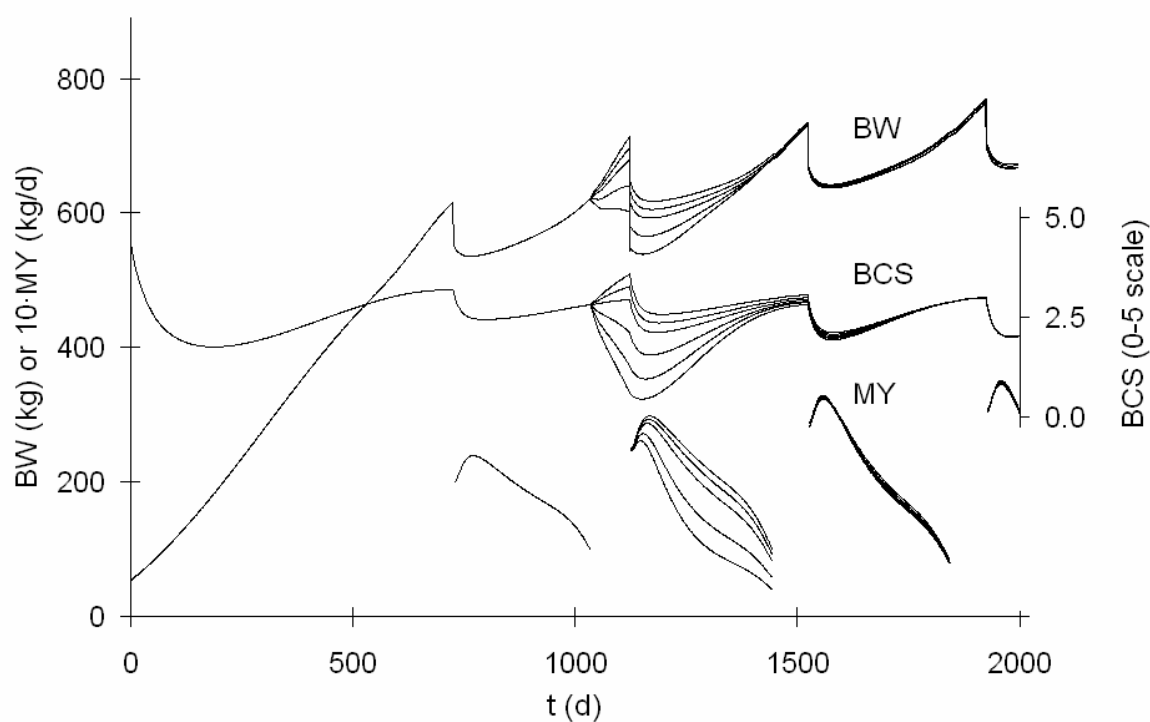


Figure 2.7 Model simulated effect of six dietary metabolizable energy contents ($e_d = 2.2 \rightarrow 3.2$ Mcal/kg DM) three months prepartum on body weight (BW , kg), body condition score (BCS , 0-5 scale) and milk yield (MY , kg/d) of a 2nd parity cow.

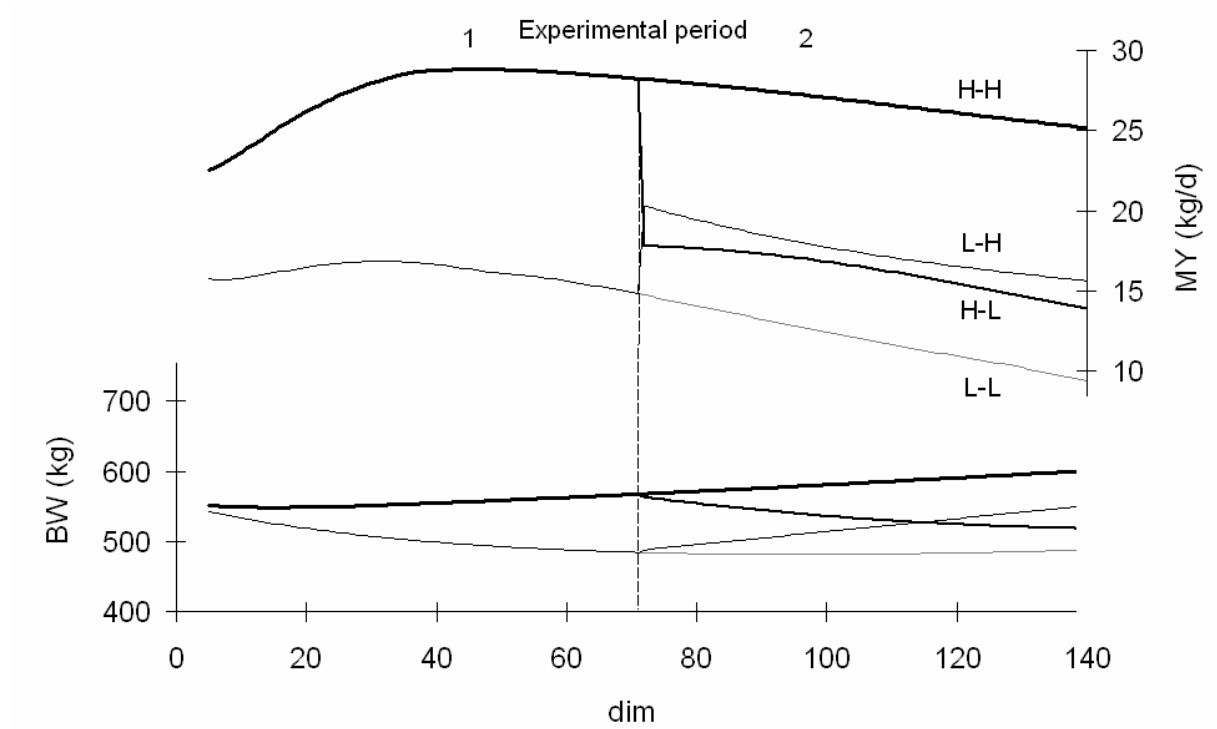


Figure 2.8 Model simulated effect of two dietary metabolizable energy contents (H: $e_D = 3.0$ Mcal/kg DM vs. L: $e_D = 2.4$ Mcal/kg DM) during two experimental periods (0-70d and 70-140d of lactation) on body weight (BW , kg) and (MY , kg/d) of 1st parity cow.

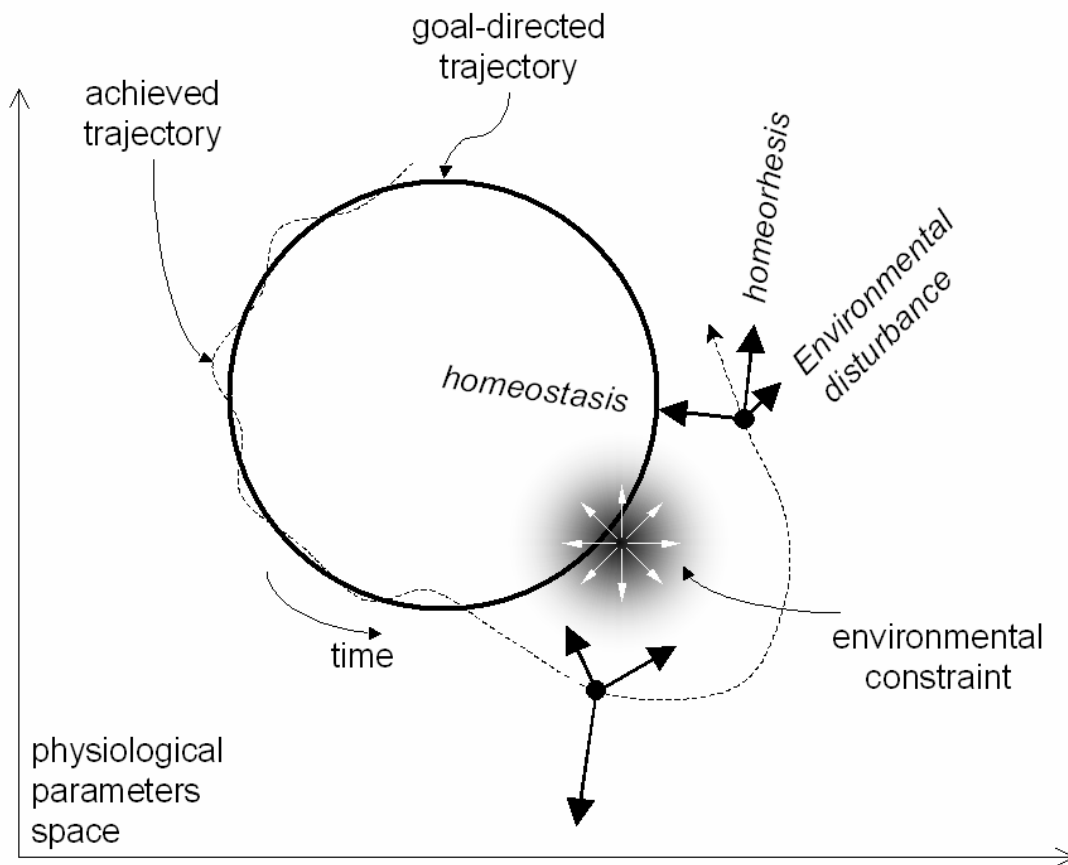


Figure 2.9 Conceptual representation of an organism life seen as a trajectory in a physiological parameters space. Environmental constraints impose a disturbance that deviates the trajectory from the equilibrium goal-directed trajectory. Homeostasis and homeorhesis are forces acting respectively to return to the nearest equilibrium state and to return to the trajectory at this point. The achieved trajectory in the disturbing environment is the result of disturbance, homeostasis and homeorhesis.

3 Modèle métabolique

La description du modèle métabolique est présentée sous la forme d'un article publié dans la revue Animal :

Martin O and Sauvant D 2007. Dynamic model of the lactating dairy cow metabolism. *Animal* 1, 1143-1166.

Animal (2007), 1:8, pp 1143–1166 © The Animal Consortium 2007
doi: 10.1017/S1751731107000377



Dynamic model of the lactating dairy cow metabolism

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(Received 28 August 2006; Accepted 2 May 2007)

The whole-animal model described in this paper is intended to be a research model with an intermediary structure between sophisticated and simple cow models. The mechanistic model structure integrates the main metabolic pathways of the lactating dairy cow. Milk yield and related feed intake for varying production potentials were considered to be the driving forces and were empirically defined. The model was designed to explain the main metabolic flows and variations in body reserves associated with the push of nutrients from dry matter intake and their pull by the mammary gland to synthesise milk components throughout lactation. The digestive part of the model uses either known feed unit systems (e.g. PDI system for protein) or published empirical equations for the prediction of digestive flows of organic matter, starch and fatty acids and ruminal volatile fatty acid production. The metabolic sub-system is made up of four tissue compartments (body protein, body lipid, protein in the uterus and triglycerides in the liver) and five circulating metabolites (glucose, amino acids, acetate + butyrate, propionate, and triglycerides and non-esterified fatty acids). A major original aspect of the model is its homeorhetic control system. It was assumed that flows relating to adipose and protein tissue anabolism and catabolism were driven by a couple of linked theoretical hormones controlling mobilisation and anabolism. The evolution in body composition and body weight were outcomes of this control. Another originality of the model is its suitability for milk yields varying from 10 to 50 kg at peak production. This was achieved by homeorhetic control of milk potential acting on several key metabolic flows. Homeostatic regulation was also introduced in order to confine the behaviour of the model within realistic physiological values. For some basic aspects (e.g. Uterine involution, standard kinetics of body protein and fat), it was necessary to build specific databases from the literature and interpret these by meta-analysis. Fairly realistic simulated kinetics were obtained for body composition, liver triglycerides, blood plasma metabolite concentrations, milk protein and fat contents, and also for major groups of milk fatty acids.

Keywords: dynamic model, lactation, dairy cow, metabolism

Introduction

The pioneering work of Baldwin has demonstrated the importance of mathematical modeling of nutritional processes. In dairy ruminant nutrition modeling, several complete models have been proposed by Baldwin *et al.* (1987a, b and c and 1995), Danfaer (1990, 2005a and b), Paul (1990) and Smith (1970). The development of these models was made possible by the accumulation of experimental data concerning size and turnover of tissue and metabolic compartments and also data related to metabolic flows. However, all these models have a major limitation which is the representation (or lack thereof) of the regulatory subsystem of metabolism (Sauvant, 1994 and 1996). Therefore, the objective of the present work was to develop a mathematical model of metabolism during lactation,

which includes a theoretical regulatory subsystem. The aim of this whole animal, dynamic and mechanistic model was to link the kinetics of dry matter intake, milk yield and live weight throughout the course of lactation with a minimal active structure, which allows digestive flows, metabolic pathways and milk composition to be simulated during lactation. An empirical model was used to describe feeding pattern and the lactation curve, and a theoretical drive for the balance between tissue anabolism and catabolism was used. Using these features at defined levels of milk production, the model provided a mechanistic representation of the animal's metabolism. Thus, in our model, an empirical regulatory sub-system was associated with a mechanistic operating sub-system based on the representation of the flows of six major pools of metabolites through eight major anatomical modules. A 4-min time step of integration was chosen, which is consistent with the high turnover rate of metabolites such

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as plasma NEFA. However, model outputs were pooled into daily means.

The principles described in this paper are valid for all lactating ruminants although the calibration of the parameters was only considered for the dairy cow. The basic principles behind this model have been published by Sauvant and Phocas (1992).

Material and methods

Model conception and description

General principles. The organism was considered as a compartmental system including two major sub-systems connected by flows of information (Sauvant, 1992 and 1994). The operating sub-system was made up of tissue compartments, pools, and flows of digesta and metabolites. The regulatory sub-system used internal auxiliary variables that control metabolic flows. Since the present work focused on the long-term aspects of lactation, mainly homeostatic controls (Bauman and Currie, 1980) were included in the model although several homeostatic systems of regulation were also introduced. Therefore, in the present version of the model and based on the above-mentioned principle, the model aims to simulate major metabolite flows and the resulting evolution in body weight associated with a given pattern of feed intake and milk production. An empirical model was used to create standard intake and lactation curves.

Model modules, compartments and flows. The model was subdivided into eight major modules corresponding to

anatomical components: rumen (RU), intestines (IN), blood plasma and lymph (BL), protein tissue (PT), adipose tissue (AT), liver (LI), udder (UD) and uterus (UT). The milk synthesized in the udder and stored in the mammary gland cisterns (MI) was defined as a specific module of the model as well. These sub-sections encompassed compartments or metabolite pools (Table 1). Pools of the same metabolite can be present in different model modules (e.g. glucose in BL, AT, PT and UD), and a metabolite can occur in different forms (e.g. amino acids in proteins, free or deaminated). The main metabolites represented in the model are glucose (GLU), amino acids (AA), acetate-butyrate (ACB), which combines acetate and the pool of 4-carbon molecules considered to be metabolically similar to acetate (butyrate, β -OH-butyrate, aceto-acetate), triglycerides (TG) and fatty acids (FA). Lactose (LA), lactate (LAC), propionate (PRO) and glycerol (GLY) were also included in the metabolic pathways described in the model. Flows of metabolites within and between modules were either transfer flows of a metabolite (e.g. TG release from liver to blood plasma denoted $TG_{LI \rightarrow BL}$) or conversion flows of a metabolite (e.g. milk lactose synthesis in the udder from glucose denoted $GLU_{UD \rightarrow LA_{MI}}$). A flow was systematically expressed in the units of the starting compartment, a conversion factor being applied to the receiving compartment if necessary.

The blood plasma and lymph, liver, adipose tissue, protein tissue, uterus and udder modules were considered as sub-parts of the model through which metabolic pathways involved in milk production and animal maintenance metabolism occurred. The rumen and intestines are the only modules where nutrients can enter the metabolic pathways,

Table 1 Components of the model: anatomic modules and metabolite pools

			Model module [†]						
Metabolite pool	Form	Coding	BL	LI	AT	PT	UT	UD	M
Glucose		GLU	■ [*]		□ [*]	□		□	
Lactose		LA							■
Amino acids	Deaminated	DAA	□						
	Free	AA	■					□	
	In protein	AAP				■	■		■
Acetate-butyrate		ACB	■		□	□		□	
Lactate		LAC				□			
Propionate		PRO	□						
Fatty acids	Free (non-esterified)	FA	■	□	□			□	
	In triglyceride	FATG	■	■	■				
	Short chain in triglyceride	SFATG							■
	Long chain in triglyceride	LFATG							■
Glycerol	Free	GLY	□		□			□	
	In triglyceride	GLYTG	■	■	■				■
Triglyceride	All sizes of FA	TG	■	■	■				■
	Long chain	LTG							■
	Short chain	STG							■

[†]BL = blood and lymph, LI = liver, AT = adipose tissue, PT = protein tissue, UT = uterus, UD = udder, MI = milk.

■: standard compartment, □: "zero pool" compartment, ■: sink compartment.

and the milk module is the sink for the lactation process. Inputs to the mechanistic part of the model were rumen volatile fatty acids (VFAs; ACB and PRO) and intestinally absorbed major nutrients (GLU, AA and FA). Since depicting the digestive process was not the main focus of the current model, it was considered in a very simple way using recent empirical equations. Except for the zero pools, the dynamic behavior of each compartment was modeled with differential equations depicting these flows.

Model calibration. Given the evolution in intake and milk yield throughout lactation, model calibration (i.e. assigning values to model parameters) was performed to achieve realistic blood concentrations of AA, GLU, ACB, TG and NEFA together with realistic milk fat and protein content. The aim was not to yield a reliably accurate simulation but to match the standard behavior of the system and to generate compatible results.

Oxidative flows were either *a priori* fixed or built by fitting procedures in order to equilibrate inflows and outflows of a 'zero pool' compartment. In addition, general knowledge of dairy cow physiology was used to define reality constraints, for example concerning the proportion of *de novo* fatty acid synthesized in adipose tissue or relative contributions of precursors to liver gluconeogenesis. Moreover, empirical functions were introduced in order to stabilise the model's behavior whatever the level of milk production (assuming a predefined potential ranging from 2000 to 11 000 kg 305-day milk yield). Due to space limitations and its heuristic, cyclic and 'by trial and error' nature, the work performed to complete the whole model calibration is not described in the present paper. Thus, several values for parameters are given in equations without giving details on how they were obtained.

Model simulation. The dynamic simulation was performed with Modelmaker 4.0 (Modelkinetix, Oxford). The model diagram, the listing of the model equations, the run options and the table of the parameter values in ModelMaker are available as an appendix at <http://www.animal-journal.eu/>. Numerical integration of differential equations was completed with Runge-Kutta's method with a fixed step of integration of $1/360 = 2.778 \times 10^{-3}$ day, which corresponds to a 4-min interval. In the model, the independent variable t indicates days in milk ranging from 1 to 300 days after calving. Initial values were given for $t = 0$, at calving. State variables characterising compartment size were expressed in mol and flows characterizing exchanges between compartments were expressed in mol/day. The model simulated the major metabolic traits of a 'standard multiparous cow' weighing 620 to 660 kg after calving (550 kg empty body and 70–110 kg gut fill according to level of feed intake) and producing between 10 and 50 kg/day of raw milk yield (RMV, kg/day) at the peak of production according to its potential. The cow received a mixed diet of forage and concentrate (Table 2). The proportion of concentrate (CO,

Dynamic model of the lactating dairy cow metabolism

Table 2 Characteristics of the diet

Item	Forage (kg/kg DM)	Concentrate (kg/kg)
OM	0.92	0.92
NDF	0.53	0.28
ST*	0.20	0.40
CP	0.13	0.18
EE*	0.04	0.05
OMD*	0.60	0.80
CPd*	0.70	0.55
Std*	0.60	0.60

*OM = organic matter, NDF = neutral-detergent fibre, ST = starch, CP = crude protein, EE = ether extract, OMD = OM digestibility, *Assumed digestibility of crude protein and starch.

kg/kg DM (1)) was of 50% of diet dry matter during the first month of lactation; thereafter, it decreased at a constant rate of approximately 0.15% per day finishing at 8% after 300 days of lactation (the proportion of forage was $FO = 1 - CO$). The following continuous model was used to simulate this classical scheme of concentrate distribution:

$$CO = 0.50 - 0.00147[1 - \exp(-0.01 t)]t. \quad (1)$$

Animal characteristics

Standard feed intake curve. The alternative form of the Wood (1967) model proposed by Dhanoa (1981) was used to simulate the curve of dry matter intake (DMI, kg/day (2)) according to the milk potential expressed as POT, which was an index equal to 10^{-1} times the maximum RMV ($1 < POT < 5$). The relationship between maximum DMI and POT, and mean values for the time of peak DMI (parameter b) and the decrease in DMI after the peak (parameter c) were derived from the database described by Martin and Sauvant (2002). Finally, the following equation system was used and assumed to provide realistic DMI curve associated with milk potential, which varied between 10 and 50 kg at peak (Figure 1):

$$DMI = at^{bc} \exp(-ct), \quad (2)$$

with

$$\begin{aligned} DMI_{\max} &= 8.48 + 3.36 \text{ POT}, \\ a &= DMI_{\max} / [b^{bc} \exp(-cb)], \\ b &= 76, \\ c &= 0.0025. \end{aligned}$$

Standard lactation curve. The Dhanoa (1981) model was also used to simulate the curve of RMV (3) according to POT. The relationship between POT and the time of lactation peak (parameter e), and mean value for the decrease in RMV after the peak (parameter f) were derived from the database described in Martin and Sauvant (2002). Finally, the following equation system was used and assumed to

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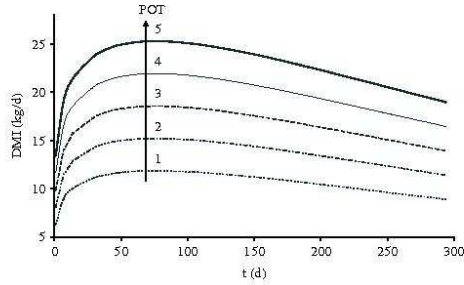


Figure 1 Standard dry matter intake (DMI) curves throughout lactation for increasing values of milk potential (POT = 1, 2, 3, 4, 5).

provide realistic RMY curves associated with milk potential, which varied between 10 and 50 kg at peak (Figure 2):

$$RMY = dt^{ef} \exp(-ft), \quad (3)$$

with

$$\begin{aligned} RMY_{\max} &= 10 \text{ POT}, \\ d &= RMY_{\max} / [e^{ef} \exp(-fe)], \\ e &= 17.74 + 6.23 \text{ POT}, \\ f &= 0.0054. \end{aligned}$$

Equations (2) and (3) allowed the simulation of typical, consistent patterns of DMI and RMY curves for different levels of milk production. These models were found to be in good agreement with classical published kinetics of intake and production, for example by Faverdin *et al.* (1987). Moreover, the overall scatter plot of simulated values of RMY v. DMI was close to that published by Hristov *et al.* (2004). The model (3) simulated an increase of 232 kg in 305-day RMY when peak RMY increased by 1 kg. This is consistent with the values cited by Young (2002).

Body system. Auxiliary variables were used to compute the weight of body modules corresponding to tissue components implicated in body weight changes during lactation: adipose tissue and protein tissue, and, to a lesser extent, the uterus. The weight of lipids in adipose tissue (LIP_{AT} , kg (31)) was derived from the quantity of stored TG in adipose tissue (TG_{AT} , mol (32)), assuming a molar weight of 810 g/mol for TG. The weight of protein in protein tissue (PRT_{PT} , kg (48)) and in the uterus (PRT_{UT} , kg (60)) was derived from the quantity of AA stored in protein tissue (AAP_{PT} , mol (49)) and the uterus (AAP_{UT} , mol (61)), assuming a molar weight of 110 g/mol for polymerised AA. It was assumed that the empty body at calving was chemically composed of 113 kg lipid ($LIP = LIP_{AT}$), 95 kg protein ($PRT_{PT} = 93$ kg, $PRT_{UT} = 2$ kg, $PRT = PRT_{PT} + PRT_{UT}$), 25 kg ash (ASH , kg (4)) and 319 kg water (H_2O , L (5)). This composition, which corresponds to a mean body condition score (BCS ~ 3.0 on a 0–5 scale), was determined using the model proposed by Martin and Sauvant (2005). The following formulas, derived

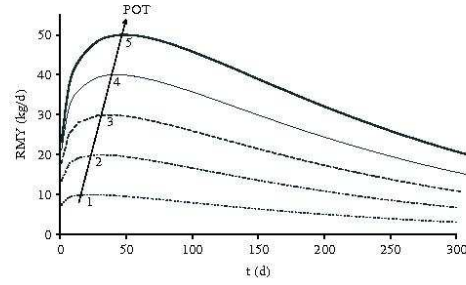


Figure 2 Standard milk yield (RMY) curves throughout lactation for increasing values of milk potential (POT = 1, 2, 3, 4, 5).

from Martin and Sauvant (2005), were used throughout the course of lactation to modify the empty body water and ash weights according to changes in empty body protein. The empty body weight (EBW, kg (6)) was calculated by summing the weights of body components:

$$ASH = 0.267 \text{ PRT}, \quad (4)$$

$$H_2O = 2.650(\text{PRT} + ASH), \quad (5)$$

$$EBW = H_2O + LIP + PRT + ASH. \quad (6)$$

The live weight (LW, kg (8)) was then calculated using both EBW and expected changes in gastrointestinal fill related to intake. The digestive tract contents (DTC, kg (7)) were predicted from NDF intake (NDFI, kg/day) using the equation published by Martin and Sauvant (2003) with a mean time post-feeding of 6 h:

$$DTC = (30.7 + 8.13 \text{ NDFI}) / 0.696, \quad (7)$$

$$LW = EBW + DTC. \quad (8)$$

From a literature review, blood plasma volume (PLV, L (9)) and lymph volume (LYV, L (10)) were assumed to average 10% H_2O and 25% H_2O , respectively; the remaining 65% H_2O was intracellular water:

$$PLV = 0.10 \text{ } H_2O, \quad (9)$$

$$LYV = 0.25 \text{ } H_2O. \quad (10)$$

The blood plasma concentrations of GLU ($[GLU_{BL}]$, mmol/l (11)), NEFA ($[NEFA_{BL}]$, mmol/l (12)), TG ($[TG_{BL}]$, mmol/l (13)) and AA ($[AA_{BL}]$, mmol/l (14)) were calculated:

$$[GLU_{BL}] = (GLU_{BL} 10^3) / PLV, \quad (11)$$

$$[NEFA_{BL}] = (NEFA_{BL} 10^3) / PLV, \quad (12)$$

$$[TG_{BL}] = (TG_{BL} 10^3) / PLV \text{ and } [FATG_{BL}] = 3 [TG_{BL}], \quad (13)$$

$$[AA_{BL}] = (AA_{BL} 10^3) / PLV. \quad (14)$$

The blood plasma and lymph ACB concentration ($[ACB_{BL}]$, mmol/l (15)) was calculated:

$$[ACB_{BL}] = (ACB_{BL} 10^3) / (PLV + LYV). \quad (15)$$

Mammary blood flow (MBF, l/day (16)) was predicted from RMY using the following equation obtained by a re-evaluation of the model proposed by Lescoat *et al.* (1996)

$$MBF = 3048 + 414 RMY. \quad (16)$$

This equation allows the simulation of daily udder nutrient extraction rate associated with specific realistic values of RMY and MBF.

Nutritional inputs

Ruminal production and absorption of volatile fatty acids. There is at the present time no generally accepted method to simply predict the flow of VFA absorption from dietary parameters. We compared five simple methods that could be used (Sauvant, 1996). There were fairly large differences between the simulated values calculated by the different methods. One of the methods was chosen for the present model because it used the partitioning of OM digestibility, which is well documented. In order to calculate VFA production, a table of estimations proposed by Vermorel (1978) and inspired from the data of Murphy *et al.* (1982) was transformed into equations. VFA production was predicted from dietary organic matter content (OM, kg/kg DM, see Table 2), from whole tract diet OM digestibility ($OMD = CO \cdot OMD_{CO} + FO \cdot OMD_{FO}$, kg/kg DM, see Table 2), and from DMI as estimated above. The equations to predict the flow of absorbed acetate (including butyrate or β -OH-butyrate) from rumen to blood ($ACB_{RU} \rightarrow ACB_{BL}$, mol/day (17)) and the flow of absorbed propionate (including LAC produced from PRO) from rumen to blood ($PRO_{RU} \rightarrow PRO_{BL}$, mol/day (18)) were:

$$ACB_{RU} \rightarrow ACB_{BL} = 0.7 [1.1 DMI OM OMD \times (-17.4 OMD + 20.6)], \quad (17)$$

$$PRO_{RU} \rightarrow PRO_{BL} = 0.8 [1.1 DMI OM OMD (2.2 OMD + 0.2)]. \quad (18)$$

Equations (17) and (18) produced realistic values of the ruminal molar ratio ACB/PRO (Sauvant, unpublished). The coefficients 0.7 and 0.8 used, respectively, in (17) and (18) took into account the VFA metabolised by the rumen wall. Values obtained for $ACB_{RU} \rightarrow ACB_{BL}$ and $PRO_{RU} \rightarrow PRO_{BL}$ were well within the range of VFA absorbed per kg of digestible dry matter as proposed by Sutton (1985) based on a literature review. Minor VFA were not considered in this model and VFA production from starch and fibre in the hindgut was considered to be negligible.

Intestinal absorption of glucose. The flow of absorbed glucose from the intestine to blood ($ST_{IN} \rightarrow GLU_{BL}$, mol glucose per day (22)) was estimated using four calculation

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steps based on the starch content of diet ($ST = CO \cdot ST_{CO} + FO \cdot ST_{FO}$, kg/kg DM, see Table 2). Firstly, ruminal starch digestibility (ST_{DR} , kg/kg (19)) was calculated from dietary starch *in sacco* effective degradability ($STD = (CO \cdot ST_{CO} \cdot STD_{CO} + FO \cdot ST_{FO} \cdot STD_{FO}) / ST$, kg/kg, see Table 2) with STD for both concentrate and forage obtained from *in sacco* kinetics (Offner and Sauvant, 2004b) and from DMI in terms of percentage LW. Secondly, non-ruminally digestible (by-pass) starch flow (ST_{BP} , g/day (20)) was then calculated from DMI and small intestinal starch digestibility (ST_{DI} , g/g (21)) using the equation published by Offner and Sauvant (2004b) from ST_{BP} and DMI. Finally, $ST_{IN} \rightarrow GLU_{BL}$ (mol/day (22)) was predicted assuming a molar weight of 180 g/mol for glucose:

$$ST_{DR} = 0.680 STD + 0.439 - 8.3 DMI / LW, \quad (19)$$

$$ST_{BP} = DMI ST (1 - ST_{DR}) 10^3, \quad (20)$$

$$ST_{DI} = 0.740 - 1.22 ST_{BP} / (DMI 10^3), \quad (21)$$

$$ST_{IN} \rightarrow GLU_{BL} = 0.75 ST_{BP} ST_{DI} / 180. \quad (22)$$

The proportion of GLU flow metabolised by the intestinal wall was assumed to be constant and equal to 25%. However, it probably varies according to the amount of GLU absorbed.

Intestinal absorption of amino acids. The calculation of absorbed AA flow from the intestine to blood ($AA_{IN} \rightarrow AA_{BL}$, mol/day (26)) was based on the equations of the French PDI system (Vérité *et al.*, 1987). Thus, the non-ruminally degradable (by-pass) AA flow (AA_{BP} , g/day (23)) was predicted from DMI, dietary crude protein content ($CP = CO \cdot CP_{CO} + FO \cdot CP_{FO}$, kg/kg DM, see Table 2), and dietary crude protein effective degradability ($CPd = (CO \cdot CP_{CO} \cdot CPd_{CO} + FO \cdot CP_{FO} \cdot CPd_{FO}) / CP$, kg/kg, see Table 2) with CPd for both concentrate and forage obtained from *in sacco* kinetics:

$$AA_{BP} = DMI CP 1.11 (1 - CPd) 10^3. \quad (23)$$

The duodenal microbial AA flow (AA_M , g/day (25)) was predicted from ruminal fermentable OM (RFOM, g/day (24)) calculated as follows:

$$RFOM = OMD DMI 10^3 - AA_{BP} - EE DMI 10^3 - ST_{BP}, \quad (24)$$

where EE was the dietary ether extract content ($EE = CO \cdot EE_{CO} + FO \cdot EE_{FO}$, kg/kg DM, see Table 2). The influence of silage organic acid content was considered to be negligible. However, as proposed by Tamminga *et al.* (1994), by-pass starch was taken into account. Thus, using an average of 145 g AA per kg RFOM:

$$AA_M = 0.145 RFOM. \quad (25)$$

Finally, $AA_{IN} \rightarrow AA_{BL}$ was predicted assuming a molar weight of 110 g/mol for AA, a proportion of 0.80 for AA in microbial crude protein, and intestinal digestibilities of 0.80

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and 0.85 for microbial and by-pass dietary proteins, respectively.

$$AA_{IN} \rightarrow AA_{BL} = 0.70(0.80 \times 0.80 AA_M + 0.85 AA_{BP})/110. \quad (26)$$

The absorbed AA flow was the sum of AA flows from microbial and dietary sources. This implies that N recycling through urea was sufficient to maintain a normal level of microbial activity. It was also assumed that only 70% of intestinal digestible protein was available in the blood circulation, the remaining 30% being lost across the portal-drained viscera (Hanigan *et al.*, 1998).

Intestinal absorption of triglycerides. In the model, TG were not considered as such, but estimated via the GLY moiety and FA. Thus, GLY and FA were either incorporated into TG (GLYT_G and FAT_G) or free (GLY and FA). The notation NEFA was used for the blood-plasma-free fatty acid pool (NEFA_{BL}) while the notation FA was used for the liver, adipose tissue and udder zero-pools (FA_L, FA_{AT} and FA_{UD}). The absorbed TG flow from the intestine to blood (FAT_{G_{IN}} → FAT_{G_{BL}}, mol/day (28) and associated GLYT_{G_{IN}} → GLYT_{G_{BL}}, mol/day (29)) was calculated by using the equation published by Sauvant and Bas (2001) from a literature review. The equation predicts duodenal by-pass fatty acid flow (FA_{BP}, g/day (27)) from dietary FA content (FA = 0.98 CO EE_{CO} + 0.43 FO EE_{FO}, kg/kg DM, see Table 2) and DMI. The value of FA was estimated from the dietary ether extract content using a ratio FA/EE of 0.43 and 0.98 for forage and concentrate feeds, respectively (Sauvant *et al.*, 2002). Finally, FAT_{G_{IN}} → FAT_{G_{BL}} was predicted assuming a molar weight of 270 g/mol for FA and a mean digestibility of FA of 75% in the small intestine:

$$FA_{BP} = DMI 10^3 (0.84 + 83 FA)/100, \quad (27)$$

$$FAT_{G_{IN}} \rightarrow FAT_{G_{BL}} = 0.75(FA_{BP}/270). \quad (28)$$

Body reserves

Regulatory sub-system. The concept of the regulatory sub-system was based on the hypothesis that there exist two directly connected theoretical hormones for mobilisation (HM (30)) and anabolism (HA). The values for the variables HM and HA were between 0.1 and 1. HM and HA were assumed to be proportional to the biological effects of homeorhetic hormones involved in mobilisation and anabolism, respectively. Moreover, HM and HA were linked by the following relationship:

$$HM HA = 0.1. \quad (29)$$

The hyperbolic nature of this relationship indicates that high levels of mobilisation and anabolism cannot occur simultaneously. This principle is consistent with data of Robelin and Chilliard (1984). Inspired by the approach of Neal and Thornley (1983), it was assumed that the hormone

HM presented an exponential decay as a function of time throughout lactation:

$$HM = 0.1 + 0.9 f_1 \exp(-f_2 t), \quad (30)$$

where

$$f_1 = (4 + POT)/9,$$

$$f_2 = (1.426 + \ln(f_1))/(8 POT).$$

The coefficients f_1 and f_2 , were built to be dependent on milk potential (POT), inducing a higher level of HM at $t = 0$ ($HM_{t=0}$) and a slower decrease in HM with increasing values of POT. The function, f_1 , which controls the value $HM_{t=0}$ linearly, depends on POT assuming that $HM_{t=0} = 1$ when $POT = 5$ (RMY = 50 kg/day at peak). Moreover, this implies that $HM_{t=0}$ decreased linearly by 0.1 units when POT decreased by 1 unit. The control of the rate of decay of HM by the function, f_2 , was conceived to be consistent with the fact that the length of the mobilisation phase is related to the potential milk yield (Faverdin *et al.*, 1987). Hence, the basic assumption was made that the time $T_{HM=HA}$ at which $HM = HA = \sqrt{0.1}$ (with respect to (29)) was proportional to POT ($T_{HM=HA} = 8 POT$) and f_2 was defined accordingly ($1.426 = -\ln((\sqrt{0.1} - 0.1)/0.9)$). The value of 8 was applied to produce realistic patterns of EBW kinetics (Figure 14) reaching a minimum between weeks 4 and 12 of lactation (Martin and Sauvant, 2002). Figure 3 indicates the pattern of HM and HA throughout lactation for increasing values of POT (1 to 5).

Adipose tissue metabolism. The sub-model diagram of adipose tissue metabolism is presented in Figure 4. Body lipids were assumed to be stored in adipose tissue as triglycerides (TG_{AT}, mol (32)), their molar weight was fixed at 810 g/mol. Thus, at $t = 0$, $LIP_{AT(t=0)} = 113$ kg corresponding to $TG_{AT(t=0)} = 139.5$ mol:

$$LIP_{AT} = TG_{AT} 810 \times 10^{-3}. \quad (31)$$

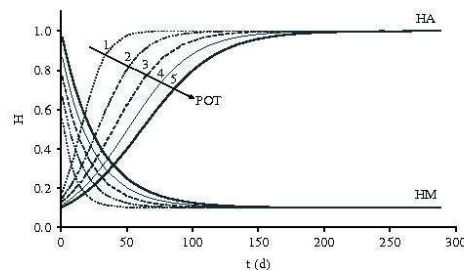


Figure 3 Pattern of theoretical anabolic (HA) and mobilisation (HM) hormones throughout lactation for increasing values of milk potential (POT = 1, 2, 3, 4, 5).

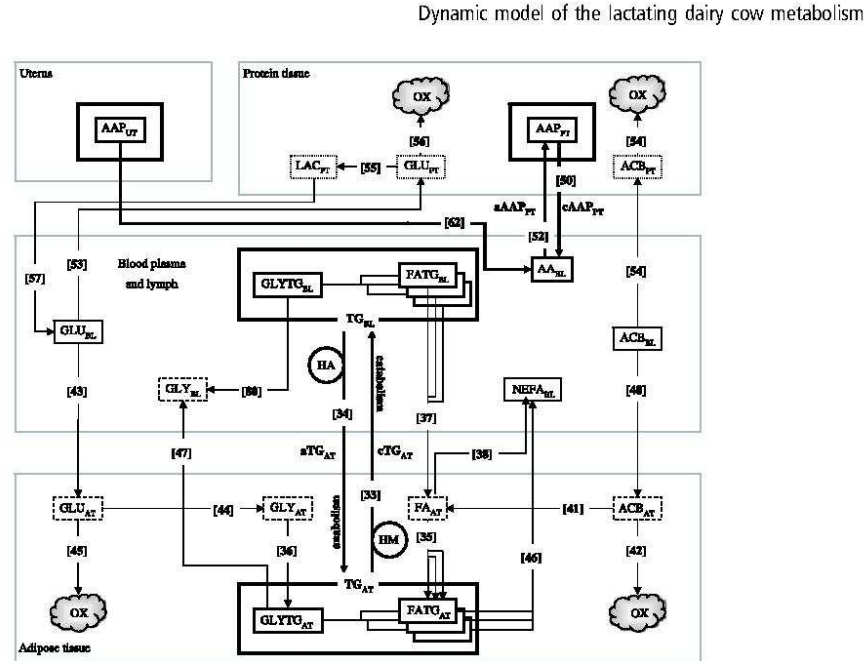


Figure 4 Model diagram of adipose and protein tissue metabolism.

The stored TG pool in adipose tissue varied according to the balance between body lipid catabolism (cTG_{AT} , mol/day (33)) and anabolism (aTG_{AT} , mol/day (34)):

$$dTG_{AT}/dt = aTG_{AT} - cTG_{AT}. \quad (32)$$

The catabolic flow of TG was proportional to TG_{AT} and assumed to be driven by HM:

$$cTG_{AT} = 0.0332 \text{ HM } TG_{AT}. \quad (33)$$

This equation allowed the calculation of a fractional turnover of TG (lipolysis) between 0.003 and 0.03 per day. This range of values is consistent with the values published by Riis (1983) and that of 0.02 per day in the model of Baldwin *et al.* (1987a).

The anabolic flow of TG was assumed to be proportional to HA and to the amount of stored TG at time zero ($TG_{AT(t=0)}$), which was considered to be a fixed value:

$$aTG_{AT} = 0.0043 \text{ HA } TG_{AT(t=0)}. \quad (34)$$

The two flows describing adipose tissue anabolism and catabolism were split up into the corresponding flows of their TG components, i.e. the glycerol skeleton (GLY_{AT} → $GLYT_{AT}$ (36) and $GLYT_{AT}$ → GLY_{BL} (47)) and the FA chains (FA_{AT} → $FATG_{AT}$ (35) and $FATG_{AT}$ → $NEFA_{BL}$ (46)), with the stoichiometry of 1 mol GLY and 3 mol FA per mol TG. Anabolic flows involved 'zero pools' of adipose tissue

FA (FA_{AT}) and GLY (GLY_{AT}):

$$FA_{AT} \rightarrow FATG_{AT} = 3 aTG_{AT}, \quad (35)$$

$$GLY_{AT} \rightarrow GLYT_{AT} = aTG_{AT}. \quad (36)$$

The anabolic process leading to TG storage in adipocytes was assumed to be the driving force of blood metabolite removal by AT. The metabolites removed from blood by adipose tissue were FA (37), ACB (40) and GLU (43).

The FA inflow ($FATG_{BL} \rightarrow FA_{AT}$ (37)) was due to the hydrolysis of blood TG by lipoprotein lipase:

$$FATG_{BL} \rightarrow FA_{AT} = ((1 - K_{SYN})/0.9)FA_{AT} \rightarrow FATG_{AT}. \quad (37)$$

It was assumed that a proportion $(1 - K_{SYN})$ of FA fixed in stored TG came from blood FA, the remaining proportion (K_{SYN}) was synthesised from ACB chains ($ACB_{AT} \rightarrow FA_{AT}$ (41)). In addition, it was assumed that 90% of the FA released by hydrolysis of blood TG were actually used by adipocytes for TG storage, while the remainder entered the blood NEFA pool ($FA_{AT} \rightarrow NEFA_{BL}$ (38)):

$$FA_{AT} \rightarrow NEFA_{BL} = 0.1 FATG_{BL} \rightarrow FA_{AT}. \quad (38)$$

The glycerol released by the hydrolysis of blood TG entered in its entirety the blood GLY pool ($GLYT_{BL} \rightarrow GLY_{BL}$ (80)) without passing through the adipose tissue GLY pool. The flow of FA derived from blood TG hydrolysis was

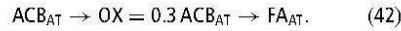
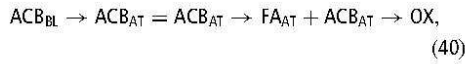
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thus built to include FA intended for TG storage and FA not used by adipocytes. The parameter K_{SYN} (39) was a sigmoidal decreasing function of the blood plasma TG concentration ($[\text{TG}_{\text{BL}}]$, mol/l (13)).

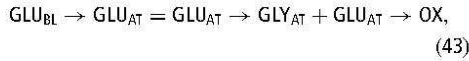
$$K_{\text{SYN}} = 1 / (1 + ([\text{TG}_{\text{BL}}]/0.2)^3). \quad (39)$$

The equation yielded values ranging from 0.05 to 0.75. This enabled our model to regulate blood plasma TG concentrations and to inhibit *de novo* FA lipogenesis in early lactation. This is consistent with *in vitro* observations in dairy (McNamara and Hillers, 1986; McNamara and Baldwin, 2000) and beef cows (Mills *et al.*, 1989).

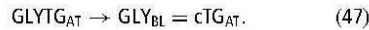
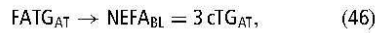
The ACB removed from blood ($\text{ACB}_{\text{BL}} \rightarrow \text{ACB}_{\text{AT}}$ (40)) provided carbon chains for *de novo* FA synthesis ($\text{ACB}_{\text{AT}} \rightarrow \text{FA}_{\text{AT}}$ (41)) with a conversion factor of 8.5 mol ACB per mol FA synthesised, and was locally oxidised ($\text{ACB}_{\text{AT}} \rightarrow \text{OX}$ (42)), thus contributing to adipocyte energy expenditure (assuming 0.5 mol ACB oxidised per mol ACB converted to FA):



The GLU removed from blood ($\text{GLU}_{\text{BL}} \rightarrow \text{GLU}_{\text{AT}}$ (43)) provided carbon atoms for glycerol skeletons ($\text{GLU}_{\text{AT}} \rightarrow \text{GLY}_{\text{AT}}$ (44)) and NADPH via glucose oxidation ($\text{GLU}_{\text{AT}} \rightarrow \text{OX}$ (45)), with 1 mol GLU oxidised per 2 mol GLU converted to GLY:



The glycerol and the FA released by adipose tissue TG catabolism entered NEFA ($\text{FATG}_{\text{AT}} \rightarrow \text{NEFA}_{\text{BL}}$ (46)) and GLY ($\text{GLYT}_{\text{AT}} \rightarrow \text{GLY}_{\text{BL}}$ (47)) blood plasma pools:



The compartments GLU_{AT} , GLY_{AT} , FA_{AT} and ACB_{AT} were 'zero pool' compartments, the sum of inputs being equal to the sum of outputs, and were built in order to partition flows correctly.

Protein tissue metabolism. The sub-model diagram of protein tissue metabolism is presented in Figure 4. The mean molar weight of AA stored in protein tissue (AAP_{PT} , mol AA (49)) was fixed at 110 g/mol. Thus, at

$t = 0$, $\text{PRT}_{\text{PT}(t=0)} = 93 \text{ kg}$ corresponding to $\text{AAP}_{\text{PT}(t=0)} = 846.4 \text{ mol}$:

$$\text{PRT}_{\text{PT}} = \text{AAP}_{\text{PT}} 110 \times 10^{-3}. \quad (48)$$

The stored AA pool in protein varied according to the balance between AA flows of protein catabolism (cAAP_{PT} , mol/day (50)) and anabolism (aAAP_{PT} , mol/day (51)):

$$d\text{AAP}_{\text{PT}}/dt = \text{aAAP}_{\text{PT}} - \text{cAAP}_{\text{PT}}. \quad (49)$$

The catabolic flow of AA was proportional to AAP_{PT} and assumed to be driven by HM:

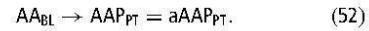
$$\text{cAAP}_{\text{PT}} = 0.0062 \text{HM} \text{AAP}_{\text{PT}}. \quad (50)$$

The anabolic flow of AA was not dependent on the plasma AA pool, but was proportional to HA and to the body protein pool at time zero ($\text{AAP}_{\text{PT}(t=0)}$) and considered to be a set value:

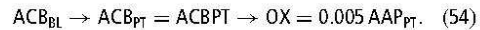
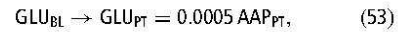
$$\text{aAAP}_{\text{PT}} = 0.001 \text{HA} \text{cAAP}_{\text{PT}(t=0)}. \quad (51)$$

As in the case of AT, the anabolic process leading to AA storage in protein tissue was assumed to be the driving force of blood metabolite removal by protein tissue. The metabolites removed from blood by protein tissue were AA, GLU and ACB.

The uptake of AA from blood was only for protein storage ($\text{AA}_{\text{BL}} \rightarrow \text{AAP}_{\text{PT}}$ (52)).



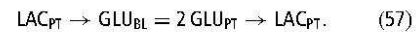
The inflows of GLU and ACB, denoted, respectively, as $\text{GLU}_{\text{BL}} \rightarrow \text{GLU}_{\text{PT}}$ (53) and $\text{ACB}_{\text{BL}} \rightarrow \text{ACB}_{\text{PT}}$ (54), were assumed to be proportional to the protein tissue AA pool and were to cover protein tissue turnover and energy maintenance requirements:



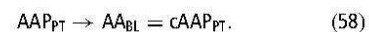
It was assumed that the production of LAC by protein tissue was equal, on a molar basis, to glucose removal. That meant that 50% of GLU was recycled through LAC production ($\text{GLU}_{\text{PT}} \rightarrow \text{LAC}_{\text{PT}}$ (55)), the remainder being oxidised ($\text{GLU}_{\text{PT}} \rightarrow \text{OX}$ (56)):



All the recycled LAC was then used in gluconeogenesis ($\text{LAC}_{\text{PT}} \rightarrow \text{GLU}_{\text{BL}}$ (57)):



The AA released by protein catabolism entered the blood AA pool ($\text{AAP}_{\text{PT}} \rightarrow \text{AA}_{\text{BL}}$ (58)):



The compartments ACB_{PT} , GLU_{PT} and LAC_{PT} were 'zero pool' compartments, the sum of inputs being equal to the sum of outputs, and were built in order to partition flows correctly.

Uterine involution. Initial simulations showed that AA mobilization was insufficient to cover udder demand, particularly in early stages of lactation. It was assumed that this could be due to the fact that uterine involution was ignored at the onset of lactation. Therefore, the uterus compartment was modeled (UT , kg (59)) and was considered to be a pool of protein (PRT_{UT} , kg (60)). It was assumed that the uterus weighed 2.2% EBW after parturition with a crude protein content of 16% (Ferrell *et al.*, 1976; Andrew *et al.*, 1994). As in (48), the mean molar weight of AA stored in uterine protein tissue (AAP_{UT} , mol (61)) was fixed to 110 g/mol. Thus, at $t = 0$, $PRT_{UT}(t=0) = 1.9$ kg, $UT(t=0) = 12.1$ kg and $AAP_{UT}(t=0) = 17.6$ mol:

$$UT = PRT_{UT}/0.16, \quad (59)$$

$$PRT_{UT} = AAP_{UT} 110 \times 10^{-3}, \quad (60)$$

$$dAAP_{UT}/dt = -AAP_{UT} \rightarrow AA_{BL}. \quad (61)$$

The uterine involution process was modeled using data from Gier and Marion (1968). Thus, the release of AA from uterus to blood ($AAP_{UT} \rightarrow AA_{BL}$ (60)) was proportional to the size of the AAP_{UT} compartment when AAP_{UT} was greater or equal to its normal non-gravid size.

$$AAP_{UT} \rightarrow AA_{BL} = \begin{cases} c0.2 AAP_{UT} & \text{if } AAP_{UT} \geq 1.5 \text{ mol AA} \\ 0.0 & \text{if } AAP_{UT} = 1.5 \text{ mol AA} \end{cases} \quad (62)$$

With this formula, uterine involution was complete after 5 weeks of lactation and the uterus had returned to its basic weight of 1 kg ($UT = 1$ kg, $PRT_{UT} = 0.16$ kg, $AAP_{UT} = 1.5$ mol AA).

Body lipid and protein kinetics. The values of coefficients in equations driving catabolism and anabolism of body lipids and proteins, respectively, (33), (34), (50) and (51) were fixed to obtained a realistic evolution in empty body weight and composition for the standard lactation ($POT = 3$). Thus, the shape of the evolution in EBW was controlled so that it was close to an average curve as derived from results of a meta-analysis of lactation kinetics (Martin and Sauvant, 2002). Moreover, based on data of Komaragiri *et al.* (1998), Komaragiri and Erdman (1997), Gibb *et al.* (1992), Chilliard *et al.* (1991), Butler-Hogg *et al.* (1985), Martin and Ehle (1984) and Belyea *et al.* (1978), it was assumed that the LIP and PRT compartments reached a minimum of, respectively, 65% and 90% of their initial pre-calving value during a standard lactation. Additionally, it was assumed that calving EBW was recovered by 300 days of a standard

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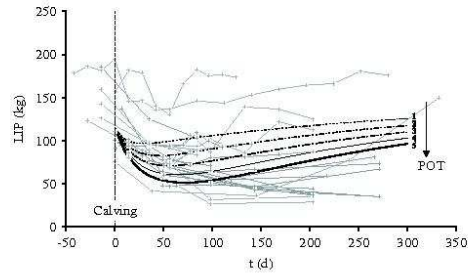


Figure 5 Evolution of the size of the body lipid compartment (LIP, kg) throughout lactation for increasing values of milk potential ($POT = 1, 2, 3, 4, 5$) together with data from literature (see text for references).

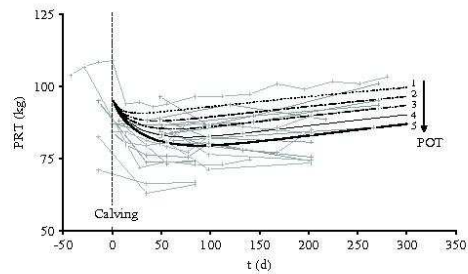


Figure 6 Evolution of the size of the body protein compartment (PRT, kg) throughout lactation for increasing values of milk potential ($POT = 1, 2, 3, 4, 5$) together with data from literature (see text for references).

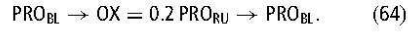
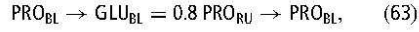
lactation. Given these assumptions for $POT = 3$, the patterns of the kinetics of LIP and PRT for values of POT smaller or greater than 3 were calculated by the theoretical model proposed for catabolism and anabolism influenced by HM and HA. These patterns were considered to be satisfactory as can be seen in Figures 5 and 6 showing the evolution of lipid and protein masses, respectively, simulated by the model for increasing values of POT together with data from the literature (previously mentioned references plus: Bath *et al.*, 1965; Chilliard, 1987; McGuffey *et al.*, 1991; Andrew *et al.*, 1994). Finally, the model yielded a decrease in EBW ranging from 37 to 134 kg for increasing values of POT . This corresponds to 47% lipids, 11% protein, 38% water and 3% ash.

Blood plasma metabolite compartments and flows

Blood plasma propionate. Metabolic pathways of blood plasma PRO are shown in Figure 8. The blood plasma propionate pool (PRO_{BL}) was considered as a 'zero pool' compartment, assuming that 80% of the propionate inflow from ruminal absorption ($PRO_{RU} \rightarrow PRO_{BL}$ (18)) was involved in gluconeogenesis with a conversion factor of 2 mol PRO per 1 mol GLU ($PRO_{BL} \rightarrow GLU_{BL}$ (63)), the

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remaining 20% being oxidised ($PRO_{BL} \rightarrow OX$ (64)):



Blood plasma glucose. Metabolic pathways of blood plasma GLU are shown in Figure 7.

The differential equation of the blood plasma GLU pool (GLU_{BL} (65)) was

$$\begin{aligned} dGLU_{BL}/dt = & ST_{IN} \rightarrow GLU_{BL} \\ & + 0.5 PRO_{BL} \rightarrow GLU_{BL} + 0.5 DAA_{BL} \rightarrow GLU_{BL} \\ & + 0.5 GLY_{BL} \rightarrow GLU_{BL} + 0.5 LAC_{PT} \rightarrow GLU_{BL} \\ & - GLU_{BL} \rightarrow GLU_{UD} - GLU_{BL} \rightarrow GLU_{PT} \\ & - GLU_{BL} \rightarrow GLU_{AT} - GLU_{BL} \rightarrow OX. \end{aligned} \quad (65)$$

The initial size of GLU_{BL} was fixed at 0.074 mol, which corresponds to $[GLU_{BL}] = 2.3$ mmol/l.

The blood plasma glucose pool was fed by five inflows, one from intestinal absorption of digested dietary starch ($ST_{IN} \rightarrow GLU_{BL}$ (22)) and four derived from metabolites involved in liver gluconeogenesis: PRO ($PRO_{BL} \rightarrow GLU_{BL}$ (63)), deaminated AA ($DAA_{BL} \rightarrow GLU_{BL}$ (88)), GLY ($GLY_{BL} \rightarrow GLU_{BL}$ (83)) and endogenous LAC produced by protein tissues ($LAC_{PT} \rightarrow GLU_{BL}$ (57)). Four outflows were considered, corresponding to the glucose removed from this pool by the udder ($GLU_{BL} \rightarrow GLU_{UD}$ (105)), by protein tissues ($GLU_{BL} \rightarrow GLU_{PT}$ (53)), by adipose tissue ($GLU_{BL} \rightarrow GLU_{AT}$ (43)) and by oxidation processes ($GLU_{BL} \rightarrow OX$ (66)). The rate of blood plasma GLU oxidation, summing the

overall oxidation processes, was modeled by mass action kinetics, in which the rate factor is described by an increasing sigmoid function of blood plasma concentration ($[GLU_{BL}]$, mmol/l (11)). This equation allowed glucose to be spared during hypoglycemia: the rate factor of oxidation at $[GLU_{BL}] = 2.0$ mmol/l represented about 30% of its value at $[GLU_{BL}] = 2.5$ mmol/l:

$$GLU_{BL} \rightarrow OX = 59.5 (1 - \exp(-0.001 ([GLU_{BL}]^{7.5}))) GLU_{BL}. \quad (66)$$

Blood plasma and lymph acetate + butyrate. Metabolic pathways of blood plasma and lymph ACB are shown in Figure 8.

The differential equation of blood plasma and lymph ACB pool (ACB_{BL} (67)) was

$$\begin{aligned} dACB_{BL}/dt = & ACB_{RU} \rightarrow ACB_{BL} + 8.5 FA_{LI} \rightarrow ACB_{BL} \\ & + 2 DAA_{BL} \rightarrow ACB_{BL} - ACB_{BL} \rightarrow ACB_{PT} \\ & - ACB_{BL} \rightarrow ACB_{AT} - ACB_{BL} \rightarrow ACB_{UD} \\ & - ACB_{BL} \rightarrow OX. \end{aligned} \quad (67)$$

The initial size of ACB_{BL} was fixed at 0.234 mol, which corresponds to $[ACB_{BL}] = 2.1$ mmol/l.

The blood and lymph ACB pool originated from three sources. The first one was ruminal ($ACB_{RU} \rightarrow ACB_{BL}$ (17)). The second inflow came from the partial liver oxidation of NEFA ($FA_{LI} \rightarrow ACB_{BL}$ (68)). It was the NEFA remaining after liver uptake ($NEFA_{BL} \rightarrow FA_{LI}$ (73)) for liver TG synthesis ($FA_{LI} \rightarrow FAT_{GLI}$ (92)) and which had not been completely oxidized ($FA_{LI} \rightarrow OX$ (94)). A proportion $K_{FA_{LIOX}}$ (95) of

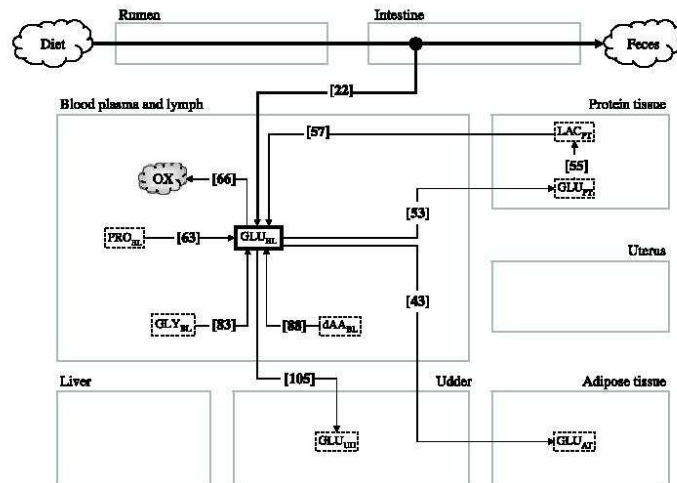


Figure 7 Model diagram of glucose (GLU) metabolism.

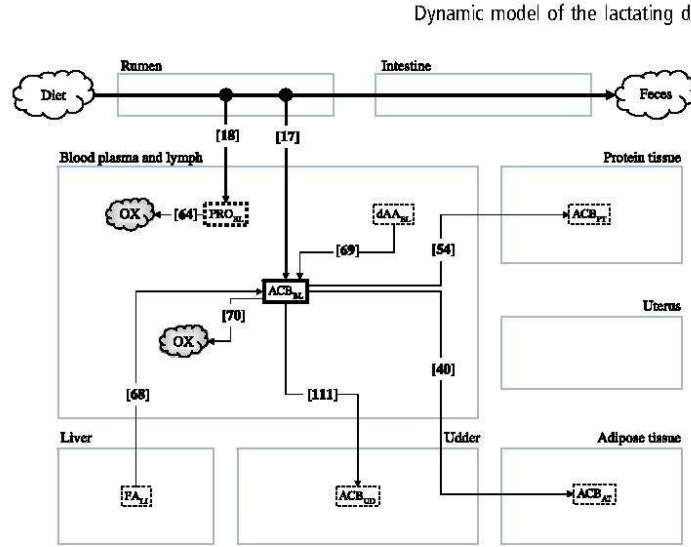


Figure 8 Model diagram of acetate + butyrate (ACB) and propionate (PRO) metabolism.

NEFA not involved in liver TG synthesis was completely oxidized, the remaining proportion $1 - K_{FAUOX}$ being converted to ACB using a factor of 8.5 mol ACB per 1 mol FA:

$$FA_U \rightarrow ACB_{BL} = (1 - K_{FAUOX}) \times (NEFA_{BL} \rightarrow FA_U - FA_U \rightarrow FATG_U). \quad (68)$$

The third inflow of ACB ($DAA_{BL} \rightarrow ACB_{BL}$ (69)) was derived from hydrolysed ketogenic AA representing the flow of deaminated AA ($AA_{BL} \rightarrow DAA_{BL}$ (85)) not involved in gluconeogenesis ($DAA_{BL} \rightarrow GLU_{BL}$ (88)), and assuming that each ketogenic AA provided four carbon units:

$$DAA_{BL} \rightarrow ACB_{BL} = AA_{BL} \rightarrow DAA_{BL} - DAA_{BL} \rightarrow GLU_{BL}. \quad (69)$$

Acetate was removed by the udder ($ACB_{BL} \rightarrow ACB_{UD}$ (111)) to contribute to milk FA synthesis and to local oxidation (see udder part). It was also removed by peripheral non-mammary tissues: body protein ($ACB_{BL} \rightarrow ACB_{PT}$ (54)) and adipose tissues ($ACB_{BL} \rightarrow ACB_{AT}$ (40)). Acetate was also oxidised ($ACB_{BL} \rightarrow OX$ (70)) in the major tissues according to a daily rate proportional to POT:

$$ACB_{BL} \rightarrow OX = (65.7 + 17.1 \text{ POT}) ACB_{BL}. \quad (70)$$

Blood plasma non-esterified fatty acids. Metabolic pathways related to NEFA are shown in Figure 9. The NEFA pool was ignored in the models published for the cow (Baldwin *et al.*, 1987a, b and c) and the sow (Pettigrew *et al.*, 1992). Taking into consideration the specific nature and the significant role of these metabolites during the phase of

mobilisation, it was included in the current model, as suggested by Danfaer (1990).

The differential equation of the blood plasma NEFA pool ($NEFA_{BL}$ (71)) was

$$\begin{aligned} dNEFA_{BL}/dt = & FATG_{AT} \rightarrow NEFA_{BL} + FA_{AT} \rightarrow NEFA_{BL} \\ & + FA_{UD} \rightarrow NEFA_{BL} - NEFA_{BL} \rightarrow FA_{UD} \\ & - NEFA_{BL} \rightarrow FALI - NEFA_{BL} \rightarrow OX. \end{aligned} \quad (71)$$

The initial size of $NEFA_{BL}$ was indexed to POT and was equal to $0.011 + 0.004 \text{ POT}$ mol, which corresponds to $[NEFA_{BL}]$ ranging from 0.5 to 1.0 mmol/l. This approach was adopted since the increase in blood plasma NEFA is known to start before parturition (see Vazquez-Añon *et al.*, 1994) and to reach higher levels when milk production and body weight loss increase (Harrison *et al.*, 1990).

A major NEFA pool inflow was adipose tissue mobilization ($FATG_{AT} \rightarrow NEFA_{BL}$ (46)) and was proportional to adipose tissue catabolism. Expressed per gram of adipose tissue, the simulated $FATG_{AT} \rightarrow NEFA_{BL}$ flow was within the range of data measured in cow subcutaneous adipose tissue (Yang and Baldwin, 1973; Metz and Van Den Bergh, 1977). Another inflow was the release of NEFA from blood TG hydrolysis under the influence of lipoprotein lipase ($FA_{AT} \rightarrow NEFA_{BL}$ (38)). The last inflow was mainly due to the release of NEFA from blood TG hydrolysis in udder vessels ($FA_{UD} \rightarrow NEFA_{BL}$ (72)) assuming that 10% of the FA, which could be potentially released from blood TG by mammary lipoprotein lipase ($FATG_{BL} \rightarrow FA_{UD}$ (116)), were recycled as NEFA:

$$FA_{UD} \rightarrow NEFA_{BL} = 0.1 \text{ FATG}_{BL} \rightarrow FA_{UD}. \quad (72)$$

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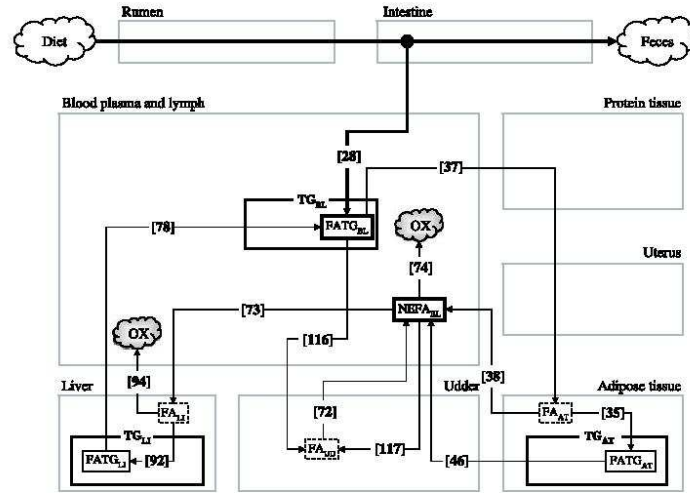


Figure 9 Model diagram of non-esterified fatty acid (NEFA) and triglyceride fatty acid (FATG) metabolism.

Three outflows from the NEFA blood pool were considered. The first flow of NEFA removal from blood plasma was due to the udder ($\text{NEFA}_{\text{BL}} \rightarrow \text{FA}_{\text{UD}}$ (117)). The second flow was due to liver extraction of NEFA ($\text{NEFA}_{\text{BL}} \rightarrow \text{FA}_{\text{LI}}$ (73)) built on the mass action law in which the rate factor was expressed as a sigmoid function of NEFA blood plasma concentration ($[\text{NEFA}_{\text{BL}}]$, mmol/l (12)). Moreover, the parameters driving the asymptote and the shape of the function were assumed to be linearly dependent on POT. Through this equation, higher rates of liver extraction were associated with lower values of POT and a higher sensitivity to $[\text{NEFA}_{\text{BL}}]$ was associated with higher values of POT:

$$\text{NEFA}_{\text{BL}} \rightarrow \text{FA}_{\text{LI}} = ((245 - 29 \text{ POT}) / (1 + 10 \exp \times (-54 - 9 \text{ POT})[\text{NEFA}_{\text{BL}}])) \text{NEFA}_{\text{BL}}. \quad (73)$$

The NEFA removed by the liver and which were not involved in TG synthesis ($\text{FA}_{\text{LI}} \rightarrow \text{FATG}_{\text{LI}}$ (92)) were completely oxidised ($\text{FA}_{\text{LI}} \rightarrow \text{OX}$ (94)) or partially oxidised into acetate or 4-carbon chains ($\text{FA}_{\text{LI}} \rightarrow \text{ACB}_{\text{BL}}$ (68)). Through these pathways, NEFA contributed to oxidative metabolism. The third outflow of NEFA was due to lean tissues (e.g. muscle, gut, heart) and was integrated as an oxidative flow ($\text{NEFA}_{\text{BL}} \rightarrow \text{OX}$ (74)):

$$\text{NEFA}_{\text{BL}} \rightarrow \text{OX} = 1.2 \text{ NEFA}_{\text{BL}} \rightarrow \text{FA}_{\text{LI}}. \quad (74)$$

As no specific value has been published for this flow, the definition adopted was fixed to achieve a slightly higher outflow for the muscle-gut-heart system than for the liver as suggested by Pethick and Dunshea (1994) in pregnant ewes. Moreover, simulated data were consistent with NEFA

values of utilisation by sheep muscle at maintenance (Pethick *et al.*, 1983).

Blood plasma triglycerides. Metabolic pathways related to FA and GLY components of TG are shown in Figures 9 and 10, respectively.

The differential equation of the blood plasma FATG pool (FATG_{BL} (75)) was

$$\begin{aligned} d\text{FATG}_{\text{BL}}/dt = & \text{FATG}_{\text{IN}} \rightarrow \text{FATG}_{\text{BL}} + \text{FATG}_{\text{LI}} \rightarrow \text{FATG}_{\text{BL}} \\ & - \text{FATG}_{\text{BL}} \rightarrow \text{FA}_{\text{UD}} - \text{FATG}_{\text{BL}} \rightarrow \text{FA}_{\text{AT}}. \end{aligned} \quad (75)$$

Analogously, the differential equation of the blood plasma GLYTG pool (GLYTG_{BL} (76)) was

$$\begin{aligned} d\text{GLYTG}_{\text{BL}}/dt = & \text{GLYTG}_{\text{IN}} \rightarrow \text{GLYTG}_{\text{BL}} \\ & + \text{GLYTG}_{\text{LI}} \rightarrow \text{GLYTG}_{\text{BL}} \\ & - \text{GLYTG}_{\text{BL}} \rightarrow \text{GLY}_{\text{UD}} \\ & - \text{GLYTG}_{\text{BL}} \rightarrow \text{GLY}_{\text{BL}}. \end{aligned} \quad (76)$$

The blood plasma TG pool (TG_{BL} (77)) was then deduced from the FATG or GLYTG blood plasma pool:

$$\text{TG}_{\text{BL}} = \text{GLYTG}_{\text{BL}} = \text{FATG}_{\text{BL}}/3. \quad (77)$$

The initial size of FATG_{BL} was fixed at 0.0096 mol and the initial size of GLYTG_{BL} was fixed at 0.0032 mol (1/3 of the initial size of FATG_{BL} for stoichiometric consistency), which corresponds to $[\text{TG}_{\text{BL}}] = 0.1 \text{ mmol/l}$.

The blood plasma TG pool, split up into its components GLYTG_{BL} (76) and FATG_{BL} (75), was fed by gut absorption of chylomicrons ($\text{FATG}_{\text{IN}} \rightarrow \text{FATG}_{\text{BL}}$ (28) and $\text{GLYTG}_{\text{IN}} \rightarrow$

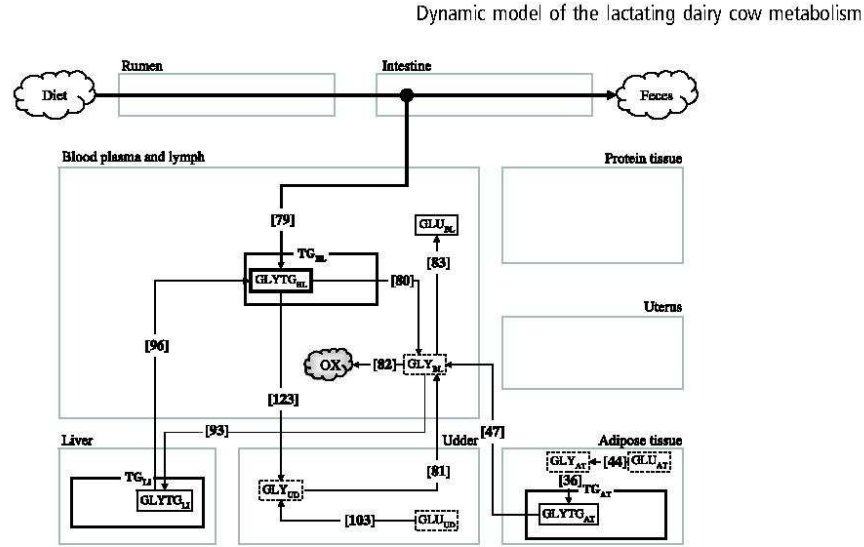


Figure 10 Model diagram of glycerol (GLY) metabolism.

GLYTG_{BL} (79)) and by liver release of lipoprotein (FATG_{LI} → FATG_{BL} (78) and GLYTG_{LI} → GLYTG_{BL} (96)). This latter flow was proportional to liver fat storage and was therefore increased by mobilisation. Moreover, this flow was assumed to be regulated by POT:

$$\text{FATG}_{LI} \rightarrow \text{FATG}_{BL} = (0.24 - 0.04 \text{ POT}) \text{FATG}_{LI}. \quad (78)$$

This equation was built to agree with experimental data on liver steatosis (Figure 15). Blood TG were removed by the udder to contribute to milk fat production requirements (FATG_{BL} → FA_{UD} (116) and GLYTG_{BL} → GLY_{UD} (123)). They were also hydrolysed in the blood by the lipoprotein lipase of peripheral tissues. The lipoprotein lipase activity was linked to adipose tissue anabolism and it only treated adipose tissue in the present model (FATG_{BL} → FA_{AT} (37) and GLYTG_{BL} → GLY_{BL} (80)).

Blood plasma glycerol. The glycerol blood pool was considered as a 'zero pool'. The first inflow of GLY came from adipose tissue mobilisation (GLYTG_{AT} → GLY_{BL} (47)). The second from glycerol derived from hydrolysis of blood TG (FATG_{BL} → FA_{AT} (37)) under tissue lipoprotein lipase action (GLYTG_{BL} → GLY_{BL} (80)) and not used by adipocytes and redirected in its totality toward the blood GLY pool.

$$\text{GLYTG}_{IN} \rightarrow \text{GLYTG}_{BL} = (1/3) \text{FATG}_{IN} \rightarrow \text{FATG}_{BL}, \quad (79)$$

$$\text{GLYTG}_{BL} \rightarrow \text{GLY}_{BL} = (1/3) \text{FATG}_{BL} \rightarrow \text{FA}_{AT}. \quad (80)$$

While the third glycerol inflow was derived from the hydrolysis of blood TG under mammary lipoprotein lipase action (GLYTG_{BL} → GLY_{UD} (123)) not used for milk fat and redirected toward the blood GLY_{BL} pool (GLY_{UD} → GLY_{BL} (81)).

Analogous to released FA (72), the value of 10% was used:

$$\text{GLY}_{UD} \rightarrow \text{GLY}_{BL} = 0.1 \text{GLYTG}_{BL} \rightarrow \text{GLY}_{UD}. \quad (81)$$

Blood plasma GLY was either removed by the liver to synthesise liver TG (GLY_{BL} → GLYTG_{LI} (93)) or oxidised (GLY_{BL} → OX (82)), the remaining being involved in gluconeogenesis (GLY_{BL} → GLU_{BL} (83)) where 2 mol GLY give 1 mol GLU. A daily oxidation rate of 20% of GLY inflow was assumed.

$$\begin{aligned} \text{GLY}_{BL} \rightarrow \text{OX} = & 0.2 (\text{GLYTG}_{AT} \rightarrow \text{GLY}_{BL} \\ & + \text{GLYTG}_{BL} \rightarrow \text{GLY}_{BL} \\ & + \text{GLY}_{UD} \rightarrow \text{GLY}_{BL}), \end{aligned} \quad (82)$$

$$\begin{aligned} \text{GLY}_{BL} \rightarrow \text{GLU}_{BL} = & \text{GLYTG}_{AT} \rightarrow \text{GLY}_{BL} + \text{GLYTG}_{BL} \\ & \rightarrow \text{GLY}_{BL} + \text{GLY}_{UD} \rightarrow \text{GLY}_{BL} \text{GLY}_{BL} \\ & \rightarrow \text{GLYTG}_{LI} - \text{GLY}_{BL} \rightarrow \text{OX}. \end{aligned} \quad (83)$$

Blood plasma amino acids. Metabolic pathways related to AA are shown in Figure 11.

The differential equation for the blood plasma AA pool (AA_{BL} (84)) was

$$\begin{aligned} d\text{AA}_{BL}/dt = & \text{AA}_{IN} \rightarrow \text{AA}_{BL} + \text{AAP}_{UT} \rightarrow \text{AA}_{BL} \\ & + \text{AAP}_{PT} \rightarrow \text{AA}_{BL} - \text{AA}_{BL} \rightarrow \text{DAA}_{BL} \\ & - \text{AA}_{BL} \rightarrow \text{AAP}_{PT} - \text{AA}_{BL} \rightarrow \text{AA}_{UD}. \end{aligned} \quad (84)$$

The initial size of AA_{BL} was fixed at 0.039 mol, which corresponds to [AA_{BL}] = 1.2 mmol/l (Figure 12).

The DAA blood pool was a 'zero pool'. Liver production of ammonia and urea was not considered in the model.

Liver sub-model

Liver metabolism. Liver metabolism was highly simplified. Indeed, most of its metabolic pathways (e.g. gluconeogenesis) have been described previously without a specific mention to this organ. It was considered that glycogen and labile protein pools were only important for within-day variations; thus only one liver pool was considered, liver TG (TG_{LI} (91)) through its components (FATG_{LI} (89) and GLYTG_{LI} (90)).

The differential equations for the liver FATG and GLYTG pools were thus (Figures 9 and 10):

$$dFATG_{LI}/dt = FA_{LI} \rightarrow FATG_{LI} - FATG_{LI} \rightarrow FATG_{BL}, \quad (89)$$

$$dGLYTG_{LI}/dt = GLY_{BL} \rightarrow GLYTG_{LI} - GLYTG_{LI} \rightarrow GLYTG_{BL}. \quad (90)$$

The liver TG pool (TG_{LI} (91)) was then calculated from the liver FATG or GLYTG pools:

$$TG_{LI} = GLYTG_{LI} = (1/3) FATG_{LI}. \quad (91)$$

The initial sizes of FATG_{LI} and GLYTG_{LI} were fixed at 0.321 and 0.107 mol (Figure 12).

The FA input into this pool (FA_{LI} → FATG_{LI} (92)) was assumed to depend linearly on the liver extraction flow of

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NEFA (NEFA_{BL} → FA_{LI} (73)):

$$FA_{LI} \rightarrow FATG_{LI} = 0.006 + 0.08 NEFA_{BL} \rightarrow FA_{LI}. \quad (92)$$

The associated flow of glycerol involved in liver TG storage (GLY_{BL} → GLYTG_{LI} (93)) was

$$GLY_{BL} \rightarrow GLYTG_{LI} = (1/3) FA_{LI} \rightarrow FATG_{LI}. \quad (93)$$

As described previously, the remaining NEFA removed by the liver (NEFA_{BL} → FA_{LI} (73)) and not involved in liver TG synthesis (FA_{LI} → FATG_{LI} (92)) were either completely (FA_{LI} → OX (94)) or partially (FA_{LI} → ACB_{BL} (68)) oxidised. The partitioning between these two oxidative flows, driven by the parameter K_{FALIOX} (95), was assumed to be a sigmoid function of the liver extracted NEFA flow (NEFA_{BL} → FA_{LI} (73)).

$$FA_{LI} \rightarrow OX = K_{FALIOX}(NEFA_{BL} \rightarrow FA_{LI} - FA_{LI} \rightarrow FATG_{LI}), \quad (94)$$

$$K_{FALIOX} = 1/(1 + 10 \exp(-2 NEFA_{BL} \rightarrow FA_{LI})). \quad (95)$$

This equation allowed the inflows of blood plasma ACB to be limited in early lactation and hence direct FA, resulting from adipose tissue mobilisation, toward oxidative processes to cover whole-body post-partum energy requirements. Thus, in early lactation 94% of liver FA was completely oxidised while during the remainder of lactation the proportions of FA directed toward TG, ACB and complete oxidation averaged, respectively, 4%, 76% and 20%.

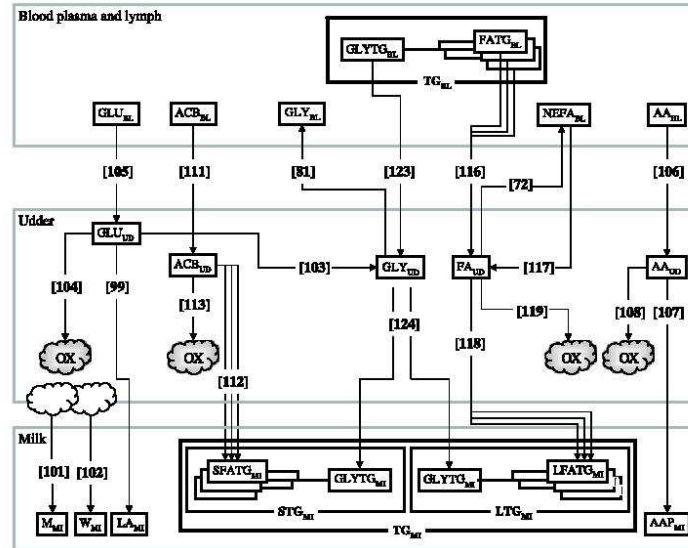


Figure 13 Model diagram of udder metabolism.

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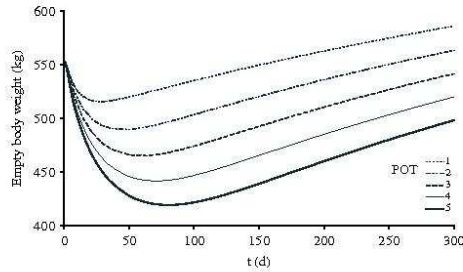


Figure 14 Evolution of empty body weight (EBW) throughout lactation for increasing values of milk potential (POT = 1, 2, 3, 4, 5).

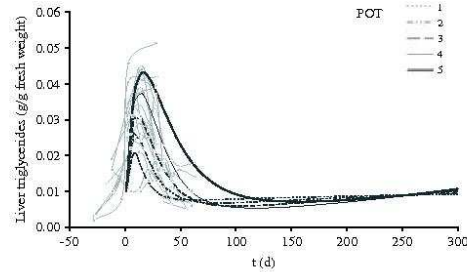


Figure 15 Evolution of liver triglyceride content throughout lactation for increasing values of milk potential (POT = 1, 2, 3, 4, 5) compared to literature data (references available upon request).

The outflow as lipoprotein entering the blood TG pool ($FATG_{LI} \rightarrow FATG_{BL}$ (78) and $GLYTG_{LI} \rightarrow GLYTG_{BL}$ (96)) was

$$GLYTG_{LI} \rightarrow GLYTG_{BL} = (1/3)FATG_{LI} \rightarrow FATG_{BL} \quad (96)$$

Liver weight and lipid content. At calving, a constant fresh liver weight of 8700 g was assumed (Smith and Baldwin, 1974) for non-lactating Holstein cows. It was then split into its lipid (LIP_{LI} , g (97)) and non-lipid ($NLIP_{LI}$) components. From an unpublished compilation of the literature, the TG content of fresh liver at calving was estimated to be 1% (i.e. 87 g, which is to 0.107 mol TG_{LI}) and a general relationship was established to predict the weight of liver lipids (LIP_{LI} , g) according to TG_{LI} (in mol, assuming a molar weight of 810 g/mol for liver TG):

$$LIP_{LI} = 243.2 + 1.45(810 TG_{LI}) \quad (97)$$

This equation, applied at calving, gave the following composition for liver: $LIP_{LI} = 369$ g and $NLIP_{LI} = 8331$ g. The non-lipid part of the liver was assumed to be constant during lactation while the lipid fraction was calculated according to variations in TG_{LI} with (97). Thus, the evolution in TG liver content characterised the degree of liver steatosis (STE , g/g (98)) and was estimated throughout lactation and compared to published results (Figure 15):

$$STE = 810 TG_{LI} / (LIP_{LI} + NLIP_{LI}) \quad (98)$$

Udder metabolism, milk secretion and composition

Milk constituents. Consistent with the global aim of the present model, this part was considered from a pull standpoint, the lactation curve (RMY (3)) being *a priori* defined using the parameter POT. The milk constituents considered in the model were lactose (LA_{MI} , kg), water (W_{MI} , kg), minerals (M_{MI} , kg), amino acids (AAP_{MI} , kg) and

triglycerides of short- and long-chain fatty acids (STG_{MI} and LTG_{MI} , kg). Thus, the outflows depicted in the model were milk lactose yield (MLY , kg/day (100)), milk mineral yield (MMY , kg/day (101)), milk water yield (MWY , kg/day (102)), milk protein yield (MPY , kg/day (109)) and milk fat yield (MFY , kg/day (121)). Milk lactose, mineral and water yields were calculated from RMY . The kinetics of udder lactose secretion and blood plasma glucose extraction were fixed in the model according to POT and the limits of glucose metabolism. Milk fat and protein yields were outcomes of the metabolic pathways regulated by POT.

Milk lactose, minerals and water. The milk lactose concentration was assumed to be constant ($MLC = 48$ g/kg). Thus, the milk lactose outflow ($GLU_{UD} \rightarrow LA_{MI}$ (99)) was the product of RMY and MLC assuming a molar weight of 342 g/mol for lactose and 2 mol GLU for 1 mol LA . This flow, expressed in kg of lactose per day, was the milk lactose yield:

$$GLU_{UD} \rightarrow LA_{MI} = 2 RMY MLC / 342, \quad (99)$$

$$MLY = RMY MLC 10^{-3}. \quad (100)$$

The associated milk water and mineral yields were estimated from RMY , MLY , MFY , MPY and MMY ($MMC = 7$ g/kg) with the underlying assumption that lactose secretion drove RMY through the action of osmotic pressure.

$$MMY = RMY MMC 10^{-3}, \quad (101)$$

$$MWY = RMY - (MLY + MFY + MPY + MMY). \quad (102)$$

There was no specific removal rate for glucose, which was extracted by the udder to cover its requirements. Therefore, GLU removed by the udder ($GLU_{BL} \rightarrow GLU_{UD}$ (105)) was used for lactose synthesis ($GLU_{UD} \rightarrow LA_{MI}$ (99)),

glycerol synthesis ($GLU_{UD} \rightarrow GLY_{UD}$ (103) and was oxidised ($GLU_{UD} \rightarrow OX$ (104)):

$$GLU_{UD} \rightarrow GLY_{UD} = 0.5 (GLY_{UD} \rightarrow GLYT_{GM} - (GLYT_{GBL} \rightarrow GLY_{UD} - GLY_{UD} \rightarrow GLY_{BL})), \quad (103)$$

$$GLU_{UD} \rightarrow OX = POT^{-0.8} GLU_{UD} \rightarrow LA_{MI}, \quad (104)$$

$$GLU_{BL} \rightarrow GLU_{UD} = GLU_{UD} \rightarrow LA_{MI} + GLU_{UD} \rightarrow GLY_{UD} + GLU_{UD} \rightarrow OX. \quad (105)$$

The proportion of glucose extracted by the udder for oxidation decreased from 48% to 20% when POT increased from 1 to 5.

The udder removal rate of FATG, NEFA and ACB from blood was calculated from mammary blood flow (MBF (16)) irrigating the udder and the specific removal rate of each metabolite. The metabolite flows entering the udder were the product of MBF and blood concentration of each of them.

Milk protein. For AA, a model with an extraction rate lead to unrealistic values of milk protein content. The flow of blood plasma AA to udder was therefore assumed to follow a mass action law with the rate decreasing as lactation progressed. Moreover, the model parameters for this rate factor were assumed to vary with POT: the initial rate of AA removal by the udder was proportional to POT and the decrease in this rate as lactation progressed diminished with increasing values of POT:

$$AA_{BL} \rightarrow AA_{UD} = 94.8 POT \exp(-(0.004 / (1 + (POT/6.4)^{2.3}))) t AA_{BL} / (t + 0.1 POT). \quad (106)$$

In this equation, the term $1/(1 + 0.1 POT)$ was introduced as a coefficient to smooth data. Since udder extraction of AA is not driven by mammary blood flow (contrary to NEFA, FATG and ACB), the coefficient used to smooth data was adopted to avoid abrupt AA removal from blood plasma. By this approach the udder AA extraction reached 90% of its value on day 1 for POT = 1 and on day 5 for POT = 5. Milk protein outflow was responsible for 95% of the AA removed ($AA_{UD} \rightarrow AAP_{MI}$ (107)), the remaining 5% were oxidised by the udder ($AA_{UD} \rightarrow OX$ (108)).

$$AA_{UD} \rightarrow AAP_{MI} = 0.95 AA_{BL} \rightarrow AA_{UD}, \quad (107)$$

$$AA_{UD} \rightarrow OX = 0.05 AA_{BL} \rightarrow AA_{UD}. \quad (108)$$

Assuming a molar weight for milk protein of 110 g/mol, the milk protein yield (109) and content (MPC, g/kg (110)) were determined.

$$MPY = 110 \times 10^{-3} AA_{UD} \rightarrow AAP_{MI}, \quad (109)$$

$$MPC = 10^3 MPY/RMY. \quad (110)$$

Dynamic model of the lactating dairy cow metabolism

Milk fat. Milk fat included TG with short- (4–16 carbon atoms) and long-chain (16–18 carbon atoms) fatty acids (STG_{MI} and LTG_{MI}, respectively). Milk TG of short-chain fatty acids (SFATG_{MI}) came from FA synthesised using the ACB removed from blood ($ACB_{BL} \rightarrow ACB_{UD}$ (111)) with an extraction rate increasing curvilinearly with POT. It was assumed that 60% of the precursors were actually incorporated into TG ($ACB_{UD} \rightarrow SFATG_{MI}$ (112)), the rest being oxidised ($ACB_{UD} \rightarrow OX$ (113)). This latter value ($K_{ACBUDOX}$ (114)) was moreover assumed to be higher in early lactation for a POT greater than 1 and to reach 80% at calving for POT = 5. This approach was adopted to avoid excessive milk fat yield in early lactation and was assumed to be consistent with the hypothesis of a specific energy requirement associated with the initiation of lactation.

$$ACB_{BL} \rightarrow ACB_{UD} = (0.00077 POT / (0.33 + POT)) [ACB_{BL}] MBF, \quad (111)$$

$$ACB_{UD} \rightarrow SFATG_{MI} = (1 - K_{ACBUDOX}) ACB_{BL} \rightarrow ACB_{UD}, \quad (112)$$

$$ACB_{UD} \rightarrow OX = K_{ACBUDOX} ACB_{BL} \rightarrow ACB_{UD}, \quad (113)$$

$$K_{ACBUDOX} = 0.4 + (0.1 POT - 0.1) \exp(-0.07 t). \quad (114)$$

Assuming a molar weight of 600 g/mol for STG_{MI} and a conversion factor of 6 mol ACB per 1 mol FA (mean carbon number 12), milk short-chain TG yield can be determined (MSTGY, kg/day (115)).

$$MSTGY = 600 \times 10^{-3} (ACB_{UD} \rightarrow SFATG_{MI} / 6) / 3. \quad (115)$$

Milk triglycerides of long-chain fatty acids (LFATG_{MI}) came from FA derived from the hydrolysis of blood TG ($FATG_{BL} \rightarrow FA_{UD}$ (116)) and from blood plasma NEFA. The extraction rate of FA from blood TG increased curvilinearly with POT and a total of 90% were used (see (72)). The extraction rate of NEFA was assumed to increase sigmoidally with blood NEFA concentration, the shape and asymptote of this function were linearly dependent on POT ($NEFA_{BL} \rightarrow FA_{UD}$ (117)). This structure allowed the model to express the increase in mammary NEFA uptake in early lactation and the increase in the proportion of long-chain FA (18-carbon chains) in milk at this time:

$$FATG_{BL} \rightarrow FA_{UD} = (0.00051 POT / (POT + 10.41)) [FATG_{BL}] MBF, \quad (116)$$

$$NEFA_{BL} \rightarrow FA_{UD} = ((5.8 + 0.1 POT) 10^{-4} / (1 + 10 \exp \times (-(5.6 + 19.8 POT)))) [NEFA_{BL}] MBF. \quad (117)$$

It was assumed that 80% of the FA removed were actually incorporated into milk fat ($FA_{UD} \rightarrow LFATG_{MI}$ (118)),

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the remaining 20% being oxidised ($FA_{UD} \rightarrow OX$ (119)):

$$\begin{aligned} FA_{UD} &\rightarrow LFATG_{MI} = 0.8(FATG_{BL} \rightarrow FA_{UD} + NEFA_{BL}) \\ &\rightarrow FA_{UD} - FA_{UD} \rightarrow NEFA_{BL}, \end{aligned} \quad (118)$$

$$\begin{aligned} FA_{UD} &\rightarrow OX = 0.2(FATG_{BL} \rightarrow FA_{UD} + NEFA_{BL}) \\ &\rightarrow FA_{UD} - FA_{UD} \rightarrow NEFA_{BL}. \end{aligned} \quad (119)$$

Assuming a molar weight of 800 g/mol for milk LTG_{MI} , the milk long-chain TG yield ($MLTGY$, kg/day (120)), the total daily milk fat yield (121) and the milk fat content (MFC , g/kg (122)) were determined:

$$MLTGY = 800 \times 10^{-3} FA_{UD} \rightarrow LFATG_{MI}/3, \quad (120)$$

$$MFY = MSTGY + MLTGY, \quad (121)$$

$$MFC = 10^3 MFY/RMY. \quad (122)$$

The parallel flows observed in glycerol required for udder FA secretion were:

$$GLYT_{GL} \rightarrow GLY_{UD} = (1/3)FATG_{BL} \rightarrow FA_{UD}, \quad (123)$$

$$\begin{aligned} GLY_{UD} &\rightarrow GLYT_{MI} = (1/3)(FA_{UD} \rightarrow LFATG_{MI} \\ &+ ACB_{UD} \rightarrow SFATG_{MI}/6). \end{aligned} \quad (124)$$

Glycerol was derived from blood TG hydrolysis with an utilisation of 10% of the released GLY (81) and from GLU conversion (96).

The compartments AA_{UD} , GLU_{UD} , GLY_{UD} , FA_{UD} and ACB_{UD} were 'zero pool' compartments, the sum of inputs being equal to the sum of outputs, and were only built in order to estimate correctly the partitioning of flows.

To obtain a prediction of milk FA composition and production according to the number of carbon atoms (C_{4-14} (125), C_{16} (127), and C_{18} (126)) throughout lactation, it was assumed that C_{16} represented a constant proportion of 25% in milk fat. The partitioning of its origin between mammary neosynthesis and long FA, from NEFA and TG, was proportional to $SFATG_{UD}/(SFATG_{UD} + LFATG_{UD})$ and $LFATG_{UD}/(SFATG_{UD} + LFATG_{UD})$:

$$C_{4-14} = 0.75 MSTGY, \quad (125)$$

$$C_{18} = 0.75 MLTGY, \quad (126)$$

$$C_{16} = 0.25 MFY. \quad (127)$$

Figures 16 and 17 show the evolution during lactation of MFC and MPC, and MFY and MPY, respectively. Figure 18 shows the evolution of short-chain (C_{4-14}) and long-chain (C_{18}) fatty acid secretion throughout lactation. This figure shows similar trends as experimental data (e.g. Decaen and Adda, 1967).

Figure 12 presents the dynamic pattern of blood plasma GLU , ACB , AA , TG and $NEFA$ concentrations throughout lactation. These patterns are of similar magnitude to those

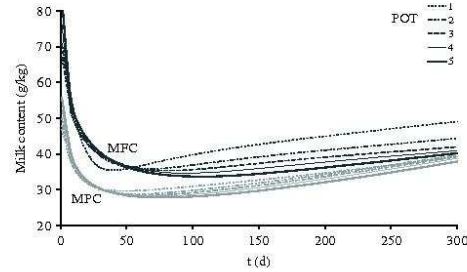


Figure 16 Evolution of milk fat content (MFC, black line) and milk protein content (MPC, gray line) throughout lactation for increasing values of milk potential (POT = 1, 2, 3, 4, 5).

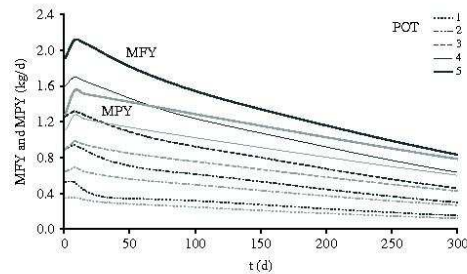


Figure 17 Evolution of milk fat yield (MFY, black line) and milk protein yield (MPY, gray line) throughout lactation for increasing values of milk potential (POT = 1, 2, 3, 4, 5).

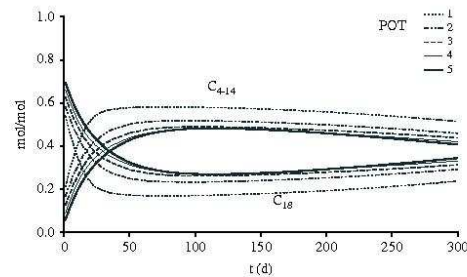


Figure 18 Milk fatty acid composition according to carbon chain size (C_{18} and C_{4-14}) throughout lactation for increasing values of milk potential (POT = 1, 2, 3, 4, 5).

generally observed and remained approximately stable regardless of milk production level.

Discussion

Model aim and structure

Anatomic modules within the operating sub-system.

Modules within the model were used to represent organs or

tissues having specific physiological functions: digestion for the rumen and intestines, storage of protein for protein tissue and uterus, storage of lipid for adipose tissue and liver, lactation for udder, and overall metabolism for blood plasma and lymph. This simplification was adopted as a minimal structure at the tissue/organ level to achieve realistic simulations at the animal level. Therefore, the current sub-models proposed for liver and udder were much simpler than those proposed by Freetly *et al.* (1993), Waghorn and Baldwin (1984), and Hanigan and Baldwin (1994) or included in the whole animal models of Danfaer (2005a and b), Paul (1990) and Baldwin *et al.* (1995). Body protein pools were considered in the model without a distinction being made between lean body and viscera proteins (Baldwin *et al.*, 1987).

Metabolite pools

Metabolites considered in the model were limited to major organic molecules involved in metabolism associated with digestion, catabolism and anabolism of body reserves, and lactation (i.e. VFAs, amino acids, triglycerides and glucose). Only two pools of VFAs were considered depending on their metabolism: propionate involved in gluconeogenesis and a pool of acetate + butyrate mainly involved in oxidative processes and *de novo* fatty acids synthesis in the mammary gland and in the adipose tissue. The amino acid pool was considered without making a distinction between non-essential and essential amino acids. The latter were assumed to be non-limiting. Furthermore, the associated nitrogen pathways through ammonia and urea were not depicted in the model. This metabolic pathway was integrated in the models of Danfaer (2005), Paul (1990) and Baldwin *et al.* (1995) without precise evaluation.

As in Danfaer (1990), it was considered that a minimum realistic feature of lipid metabolism could not be achieved by grouping all the circulating fatty acids into a single pool. Therefore, we propose to split lipids into two pools: triglycerides, reflecting lipoprotein transporters, and non-esterified fatty acids. Since this classification involved the relationship between fatty acids and glycerol, a minimal representation of glycerol metabolism was necessary. Glucose is largely synthesized *de novo* from sources such as propionate, certain amino acids, lactate and glycerol. In the present model, average contributions to gluconeogenesis over 300 days of lactation and over pooled values of POT ranging from 1 to 5, were 79% for propionate, 14% for amino acids, 4% for glycerol and 3% for lactate. These results stress the major role played by propionate. Maximal contributions from deaminated amino acids and glycerol occurred in early lactation, as the availability of these metabolites is enhanced by mobilization of adipose and protein tissue, and uterine involution. Compared to commonly accepted values (Drackley *et al.*, 2001), the model tended to overestimate the contribution of propionate and underestimated the contribution of lactate for gluconeogenesis. This was probably due to the fact that, in the

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model, lactate only originated from endogenous sources while propionate included exogenous lactate produced by fermentation. Glucose plays a central role in the model and despite a low level of entry from the digestive tract large quantities of glucose are involved in milk lactose synthesis during lactation. No glycogen compartment was considered, and thus no glucose storage mechanism was represented in the present model. This simple representation of glucose metabolism was chosen because it was considered on a daily output basis. However, despite this simplicity, realistic simulations of glucose metabolism were obtained. This was mainly achieved by the fact that alternative sources of endogenous glucose, from AA and from glycerol moieties, were consistently controlled by the HM-HA regulating system.

Based on the number of active compartments (NC) and differential equations at the tissue (NCt) and metabolic (NCm) levels, the current model (NCt = 4, NCm = 5) was much less sophisticated than the three major mechanistic models of the dairy cow (Danfaer, 2005a and b (NCt = 9 and NCm = 77), Paul, 1990 (NCt = 7 and NCm = 60) and Baldwin *et al.*, 1995 (NCt = 18 and NCm > 100)). In this aspect, our model was closer to the former metabolic model of Baldwin *et al.* (1987a), NCt = 3 and NCm = 4).

Differential equations were associated with pools of triglycerides (fatty acids and glycerol) in blood plasma, adipose tissue and liver, and with pools of amino acids in blood plasma, protein tissue and uterus. Differential equations were associated with pools of glucose, fatty acids and acetate + butyrate but only in the blood plasma and lymph. Other compartments in the different modules of the model were considered as 'zero pools' of metabolites and were only used to partition flows correctly. Moreover, the choice of depicting 'zero pools' was done to facilitate future additions to the model.

Flows

The overall framework of the model integrated numerous 'passive flows' of nutrients essentially considered to have a structural function rather than a key dynamic role as have 'active flows'. Flows of metabolites cover either digestive inputs of nutrients, anabolism and catabolism of lipid and protein, metabolic transactions, oxidative processes and milk component yields. Metabolic pathways depicted in the model, although simplified, were aimed at summarising elementary knowledge of dairy cow metabolism.

Contrasting with the cow models of Baldwin (1995) and Danfaer (2005a and b), the current choice was to create the simplest digestive sub-part. Published mechanistic models of rumen digestion were not used because it has been demonstrated that they suffer from serious limits in accuracy (Offner and Sauvant, 2004), which could lead to large biases in estimations of metabolism (McNamara, 2004). For this reason, empirical models of nutrient flows were used. Since they were fitted on extensive data sets, these equations are more robust than previous equations for predicting

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absorbed nutrients. Inflows of amino acids from the gut were calculated according to the PDI system (Vérité *et al.*, 1987). The recent equations proposed by Sauvant and Bas (2001) for the input of dietary fatty acids appear to be the most valid since they were based on a larger data set than previous proposals. Similarly, for starch digestion, the recent proposals of Offner and Sauvant (2004a and b) based on a large set of diets from feed tables (Sauvant *et al.*, 2002) were applied. This 'starch part' of the model allowed the correction of fermentable OM in the rumen from by-pass starch. This principle has been proposed in the Dutch version of the PDI system (Tamminga *et al.*, 1994). Finally, the mechanistic models of rumen digestive flows of VFA production and absorption were the least reliable aspect of the present model, even if the variations obtained for the ratio acetate + butyrate/propionate as a function of diet OM digestibility appeared to be fairly realistic.

In the present model, the balance between anabolism and catabolism of adipose tissue simulated mobilisation in early lactation and reconstitution of body fat reserves in late lactation. This is consistent with observations on body fat changes during lactation. Nevertheless, the present model expresses a net balance and does not describe the intracellular re-esterification of FA (Emery, 1979), and thus probably underestimates the total lipolytic activity of adipose tissue. Since glycerol released from adipose tissue covered not only apparent catabolism but also whole catabolism of triglycerides, the model may also underestimate glycerol release from adipose tissue.

In the model, oxidative flows were mainly conceived to equilibrate pathways according to the carbon conservation principle. The major contributor to oxidative processes in the model was acetate + butyrate: 77% of its carbon units were involved in oxidation over the 300 days lactation, compared to 9.2%, 5.3%, 4.7%, 3.6% and 0.1% for glucose, amino acids, propionate, fatty acids and glycerol, respectively. The value for fatty acids reached more than 20% in the first week of lactation. Over 300 days of lactation, 41.4% of carbon units involved in oxidative flows took place in the blood plasma and lymph module, compared to 30.8% through the rumen wall, 14.5% in udder, 6.9% through intestine wall, and 4.0% and 2.4%, respectively, in protein and adipose tissues. Metabolic models of lactation have rarely included ATP metabolism (Pettigrew *et al.*, 1992). Presently, this aspect was also not included for simplicity of the model and to avoid some methodological problems due to the high turnover rate of the ATP and ADP compartments. Thus, it was assumed that ATP availability was neither a limiting factor nor a regulatory element. Another reason for this choice was the current lack of experimental data on the origin of ATP sources from different substrates and the contribution of different organs in energy expenditure.

Although the milk lactose yield was conceived as a 'pull' mechanism, the milk protein and fat yields were outputs of the udder sub-model. The simulated milk fat and protein contents decreased, respectively, from 4.2% to 3.7% and

from 3.3% to 3.1% with increasing peak milk production level from 10 kg to 50 kg. Long-chain fatty acids represented about 60% and 30% of milk fatty acids in early and late lactation, respectively. These features were considered to provide a realistic simulation of milk composition.

Homeorhetic and homeostatic regulating sub-system

The first attempt to model homeorhesis in the lactating ruminant has been the modeling approach of the mammary gland of Neal and Thornley (1983). These authors assumed the existence of a theoretical hormone controlling the division rate of basic udder cells to provide active secretory cells. This hormone followed an exponential decay after an initial pulse at parturition. This first simple model was further developed by Dijkstra *et al.* (1997) and recently by Vetharaniam *et al.* (2003a and b) and Pollot (2004). These models constituted a trend in which a central role was played by the evolution of the mammary tissue. The present model did not follow this trend. In contrast, it described the organs and major metabolisms more accurately. Its main originality was the definition of the homeorhetic sub-system, which already existed in the first version (Sauvant and Phocas, 1992) and was based on three basic principles.

The first principle of expression of a homeorhetic drive for lactation is the consistent link between the kinetics of intake and milk production. This results in a pushing role of absorbed nutrients and a pulling one of the udder. This link was established through an empirical dynamic model derived from the database of lactation kinetics described by Martin and Sauvant (2002) and defining realistic and consistent patterns of DMI and RMY relevant with milk potential varying from 10 to 50 kg at peak production.

The second principle was the definition of a theoretical regulatory sub-system that adapted the nutrient flows to the level of intake and milk yield. It was mainly achieved by the key role of the parameter POT representing the milk production potential. Parameter values were estimated for milk potential varying from 10 to 50 kg at peak production and relationships between the most sensitive parameters and the parameter POT were modeled. Thus, the model produced realistic simulations of blood metabolite concentrations, regardless of the production level. In the present paper, the multiple influences of POT were not described in detail although introduced in several equations. Further studies will explore more systematically the sensitivity of the model to POT and some other major basic parameters.

The third principle was the hyperbolic relationship between HM and HA, which was also one of the major aspects of driving forces of the current model. This principle did not explicitly exist in other mechanistic model of lactating cows or sows. The shape of this relationship described the alternative influence between the activities of catabolism and anabolism and was consistent with the data of MacNamara (1989) and Chilliard and Robelin (1985). The

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theoretical and relevant approach of this aspect was chosen because of the lack of mechanistic information related to the complex hormonal systems driving lactation. Firstly, the hormones and neurotransmitters (including interrelationships), which are more or less directly involved in the lactation process, have not been sufficiently identified to be mechanistically described. Secondly, for each acting hormone, the mechanisms involved in synthesis and excretion, tissue sensitivity, receptor affinity, cellular metabolism after the internalisation of the hormone-receptor complex are poorly understood. Therefore, we tried to build the minimal mechanism to interpret the majority of the homeorhetic drives. The exponential decay of HM throughout lactation was adopted from observations on the evolution of plasma NEFA and milk long-chain fatty acids during lactation in the cow (Chilliard, 1987) and goat (Donshea and Bells, 1990). An advantage of the exponential expression was its flexibility and the possibility to express its two basic parameters as functions of POT. In the model of Baldwin *et al.* (1987), actual glycemia was considered as the major index of energy status and drove catabolic and anabolic flows. In the recent versions of this model, there was a lactation hormone (Lhor) that presented a first-order decrease in time as does the current HM. However, it did not seem to have any relationship with the potential of production. In the lactating sow model (Pettigrew *et al.*, 1992), a theoretical homeorhetic system has also been proposed. In this model, the hormone of lactation partly drove the potential value of the body protein and lipid catabolism, and also regulated milk secretion. In the model of Danfaer (1990), an empirical equation was fitted to data of Herbein *et al.* (1985) to provide kinetics of plasma growth hormone and insulin, which drove the major metabolic exchanges between the tissues and the udder. Theoretical principles of homeorhetic regulation and body mass turnover were also included in the model of pig growth proposed by Lovatto and Sauvant (2003). However, in their model, some basic principles of homeostasis were also explicitly taken into consideration to maintain the concentrations of the major blood metabolites within physiological ranges.

Some homeostatic controls concerned *de novo* fatty acid synthesis in adipose tissue controlled by blood plasma triglyceride ((37), (39)), gluconeogenesis from deaminated amino acids (88) and glucose oxidation (66) controlled by blood plasma glucose, liver extraction of fatty acids controlled by blood plasma non-esterified fatty acids (73) and the partition of liver extracted fatty acids between partial and complete oxidation ((68), (94), (95)). These homeostatic controls were necessary to ensure that model predictions were within physiological limits.

Present model and further developments

As underlined for previous models of the lactating cow (Baldwin *et al.*, 1987a, b and c; Danfaer, 1990) and lactating sow (Pettigrew *et al.*, 1992), only few experimental data were used to provide values for the basic parameters

of the models (e.g. rate, affinity and inhibition constants). Therefore, the model calibration was not completed globally but by successive partial optimisation processes focusing on a particular flow. This was generally performed by forcing selected flows through a model so that they simulated an expected trend in metabolism in order to estimate an unknown flow. For example, the flow of blood amino acids extracted by the udder was forced repeatedly through a model at different milk protein levels in order to build the blood amino acid deamination flow. Moreover, several experimental data sets have been developed to specifically determine values for model parameters. This was especially the case for uterine involution in early lactation and the evolution in body composition pattern.

Except for the simulation data, which was mainly focused on the influence of milk yield potential, no specific sensitivity study of the model was presented. This important phase will be described in future studies. Some external validations of the present model have been performed and they remained as simple as possible. The target was to check if the pattern of a given flow or compartment exhibited previously observed classical trends. This approach was applied to blood metabolites, body tissue components and udder flows of major fatty acids. In all these cases the results were globally satisfactory. Further external validations will have to be performed. In particular, since the data of measurements of flows of metabolites through organs have been published mainly in sheep or growing cattle, it will be necessary to build a database of blood flows measured in lactating cows and to validate the current model, taking into account major elements of animal husbandry (e.g. RMY, DMI). Another important aspect will be to compare, under similar dietary situations, the current model with the other whole-animal models already published. This will include not only the mechanistic dairy cow models Molly (Baldwin *et al.*, 1995) and Karoline (the latest version of Danfaer's model) but also the French dairy cow empirical model of INRA (2004) and the dairy cow module of the Cornell Net Carbohydrate and Protein System (CNCPS, 2000). Such a comparative evaluation of models is necessary to determine the modules where more work is needed in order to progress in the development of a minimal mechanistic structure able to aggregate the main features of dairy cow metabolism.

The initial purpose of applied animal nutrition has been to produce animal products as efficiently as possible. Therefore, the prediction of nutrient requirements at a given production potential has been a basic aspect of diet formulation. Today this sole objective is insufficient to answer current issues concerning product quality, environmental impact of animal production, animal welfare and food safety. For these reasons, the concept of multiple responses to diets and feeding practices was published over 10 years ago (Sauvant, 1992 and 1994) and is now largely accepted. This means that models should help our understanding and predict responses to diets rather than just estimate

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nutritional requirements. For example, the kinetics of lactation can be modified significantly by exogenous factors such as dietary strategy (Martin and Sauvant, 2002). The current model was not conceived to explore and predict the responses of dairy cows to variations in dietary strategies because it does not take into account the major dynamic principles of energy homeostasis around set values. This will be the next stage in development and a major challenge for the present model. Several other major aspects will have to be altered in view of this new perspective. The kinetics of milk protein, fat and major fatty acid levels were satisfactory. However, they will have to be challenged with diets varying in energy density and in fat content. Encouraging results were obtained with the major milk fatty acids and this model could be a good basis to integrate more information concerning fatty acid flows at the digestive, metabolic and udder levels.

Obviously, the next challenge will be to include the ability of the cow to respond to limited supplies of lysine and methionine (Rulquin *et al.* 1993). In order to do this, the rumen model of Lescoat and Sauvant (1995) will form a convenient first step as it includes lysine and methionine digestion. Several attempts to specifically model the metabolism of NH_3 and urea have already been performed (Sauvant, 1993; Faverdin and Verité, 2003) and the realistic simulated data, which were obtained with these models, suggest that they could be included fairly easily in the present model.

A further development of the sub-model of lipid digestion would be to separate the major groups of fatty acids (e.g. saturated, unsaturated), and hopefully some strategic minor fatty acids as *trans*-fatty acids and CLA (Chilliard *et al.*, 2001). One of the difficulties will probably be the estimation of ruminal hydrogenation and isomerisation processes.

In order to simulate hourly or minute-based processes concerning glucose metabolism it will be necessary to take into account the compartments of liver glycogen, and circulating insulin and glucagon (Lemosquet and Faverdin, 2001). All these homeostatic aspects will have to be taken into account when the target of the model is to simulate metabolic disorders such as ketosis.

Conclusion

The objective of this model was to integrate the mean kinetics of intake, milk production and its composition as well as body weight changes. The present model is an effective means to integrate experimental data of various origins. The results from simulations were satisfactory in the sense that the simulated values of all the parameters were globally realistic. One of the major advantages of such a model concerns its ability to behave reliably when milk yield potential varies. As such the current model could evolve in two major directions, firstly through its use in larger models of herd or even farm management, and secondly it could become more accurate and be completed by including the

major underlying mechanisms, which allow the prediction of responses to different dietary patterns during lactation.

Acknowledgments

The authors thank Pr. P. Schmidely for his suggestions and assistance.

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Conclusion et perspectives

« Les modèles que je propose ne sont que des points de départ pour la réflexion. En aucun cas des points d'arrivée. Ces modèles doivent être confrontés à la réalité et surtout à l'aléatoire. Ils doivent être agressés, détruits et reconstruits. Car ils ne peuvent évoluer que dans la confrontation et le discontinu. C'est à dire dans l'action »

Joël de Rosnay

Le comportement global du modèle est illustré à travers les **F18 à 27** présentées en Annexe 6. Ces figures correspondent aux compilations de données de la littérature présentées dans la Partie I.3 et mises ici en regard des simulations produites par le modèle global développé dans ce travail de thèse, situant ainsi de façon globale la plage de variation de son comportement.

Les principales propriétés des trois modèles présentés dans la Partie II sont rappelées dans le Tableau 2. Outre un couplage concrètement réalisé entre le modèle métabolique et le modèle énergétique, les perspectives d'évolution du montage formé par ces trois modèles reposent sur des modifications de chacun de ces modèles. En effet, chacun des modèles mérite un regard critique et doit être déconstruit pour être amélioré individuellement et pour faire progresser la démarche conceptuelle qui les relie.

Tableau 2 Propriétés des modèles téléonomique, énergétique et métabolique.

Modèle	Téléonomique	Énergétique	Métabolique
Objectif	Simuler la dynamique des priorités entre fonctions physiologiques.	Prédire les performances productives.	Interpréter les performances en termes de flux métaboliques.
Questionnement	Pourquoi ?	Combien ?	Comment ?
Concept	« <i>Chreod</i> »	Homéorhèse & Homéostasie	Conservation de matière
Niveau systémique	Espèce	Animal	Tissu/Organe
Représentation animale	Processus	Interface	Machine
Unité de base	Priorité	Énergie métabolisable	Mole
Variables clés	Croissance, reproduction, vieillissement, balance des réserves	Poids vif, lait, veau, aliment	Acides gras volatils, acides aminés, glucose, glycérol, acides gras, triglycérides
Input	Niveau de maturité	Génotype & alimentation	Performances
Output	Dynamique des priorités	Flux de matières	Flux de métabolites

Modèle métabolique

Le modèle métabolique est proposé comme une structure minimale au niveau tissu/organe représentant les **voies métaboliques majeures** des principales molécules organiques impliquées dans les fonctions d'intérêt zootechnique. Dans sa forme actuelle, le modèle métabolique n'utilise pas comme entrée les performances prédites au niveau du modèle énergétique mais, à l'échelle de la lactation, des équations empiriques de prédiction de la production laitière et de l'ingestion en fonction d'une variable de potentiel de production laitière (Figure 18). Par ailleurs, un sous-modèle d'homéorhèse gouverne la dynamique des processus d'anabolisme et de catabolisme des tissus de réserves adipeuse et protéique. Sa construction avec le statut d'interprétation du triplet de cinétiques {ingestion | poids | lait} en termes de flux de métabolites le rend compatible avec le montage des modèles téléonomique et énergétique.

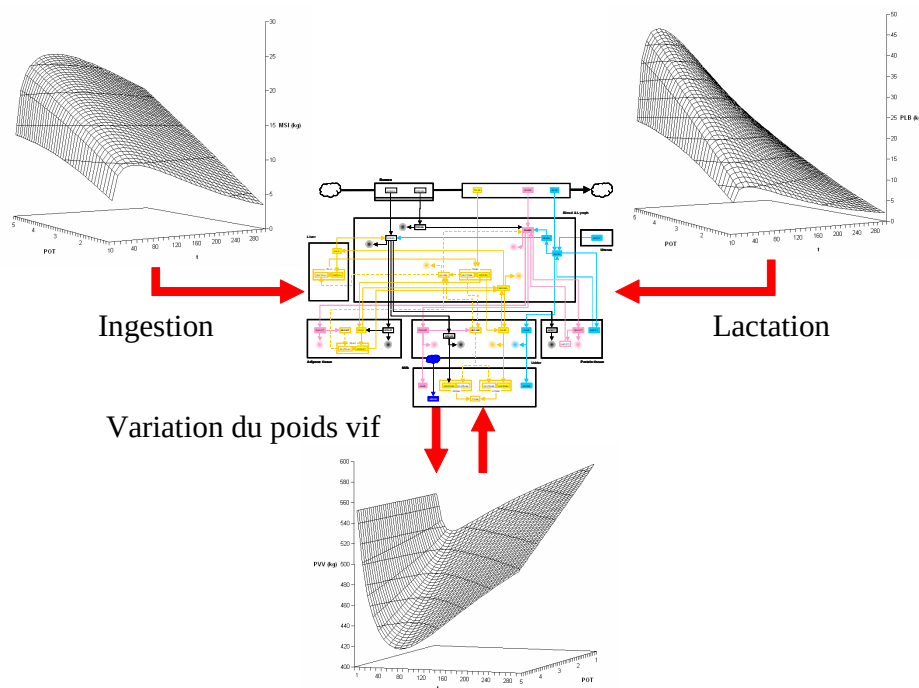


Figure 18 Fonction d'interprétation du modèle métabolique : métabolisme associé aux profils zootechniques selon le niveau de production laitière.

Cette connexion reste à formaliser concrètement, notamment à l'échelle non plus seulement de la lactation mais à celle de la vie de l'animal. En outre, d'autres perspectives peuvent être considérées à travers ce cadre général de décomposition des niveaux fonctionnels des modèles (gouvernance, prédiction, interprétation). En premier lieu, le fonctionnement du

modèle métabolique pourrait être exploité pour réguler le fonctionnement du modèle énergétique. Cette approche permettrait d'intégrer non plus seulement des modulations de la partition de l'énergie (AGV, glucose, acides gras) mais également celle d'autres nutriments tels que les acides aminés. Une limite actuelle du modèle est en effet son impasse sur l'effet de la nutrition protéique. Cette approche permettrait de moduler la réponse du point de vue énergétique par des indicateurs métaboliques, notamment au niveau du volet homéostatique du montage actuel. En second lieu, le pilotage dynamique par le modèle téléonomique pourrait être exploité directement au niveau du modèle métabolique. Cette approche permettrait de déployer la logique de construction actuelle sur l'énergie à l'ensemble des nutriments, en définissant un métabolisme de référence et ses modulations en fonction des apports. Ces pistes de travail permettraient de faire converger les enjeux explicatifs et prédictifs du modèle global. Actuellement, par exemple, le modèle métabolique utilise le niveau de production laitière pour déterminer le flux sanguin mammaire qui par la suite détermine les prélèvements de nutriments par la mamelle, formalisant ainsi une coordination homéorhéticque. Ce flux pourrait être directement déterminé à partir de la priorité à la fonction de lactation définie au niveau du modèle téléonomique. Un autre exemple concerne les flux d'anabolisme et de catabolisme qui pourraient être pilotés directement par des priorités différentielles pour les tissus protéiques, adipeux voire osseux dans une perspective de représentation du métabolisme phosphocalcique. Ces perspectives sont contingentes de celles concernant les modèles téléonomique et énergétique. Dans sa forme actuelle, le modèle métabolique constitue une représentation minimale du métabolisme, compromis entre une représentation mécaniste exhaustive et une représentation empirique agrégative. Ce format simple et qualifiable de réductionniste permet néanmoins d'appréhender de façon satisfaisante des processus tels que la stéatose hépatique (Partie II.3, Figure 15) ou la chute de glycémie *postpartum* (Partie II.3, Figure 12). L'idée de couplage d'un modèle prédictif à un modèle simple d'interprétation métabolique peut ainsi constituer une première étape intéressante pour enrichir la prédiction des performances d'indications sur le fonctionnement du métabolisme, notamment en lien avec des aspects sanitaires. Cet aspect est cohérent avec l'enjeu de modèle des lois de réponses multiples (Sauvant, 1992²⁷).

²⁷ Sauvant, D., 1992. Systemic modeling in nutrition. *Reproduction Nutrition Development* 32, 217-230.

Modèle énergétique

Le modèle énergétique est proposé comme une structure représentant la **partition de l'énergie** entre fonctions et dont la dynamique est gouvernée par le modèle téléonomique. Le comportement de ce montage à vocation prédictive entre les modèles téléonomique et énergétique est illustré en Annexe 5 à travers les Figure 27 à Figure 36. Ces figures superposent les principales sorties du modèle pour des niveaux variables de paramètres génétiques à des données de la littérature, montrant ainsi l'aptitude du modèle à épouser des plages de variations connues. Ce positionnement est globalement satisfaisant même si des défauts persistent dans le détail. Ainsi, le poids du veau à la naissance et les durées de gestation sont sous-estimés (Figure 31 et Figure 32) et les cinétiques de production laitière au cours des premières semaines de lactation sont sensiblement en décalage par rapport aux observations dans le sens d'une surestimation (Figure 33). Par ailleurs, le décalage entre les dates de pic de production laitière et de maximum d'ingestion n'est pas suffisamment marqué par rapport aux observations classiques. Ces défauts nécessitent, pour être corrigés, des modifications principalement des valeurs de paramètres du modèle. Ce travail implique une phase de calibration focalisée sur le début de lactation et reposant sur des jeux de données adaptés. D'autres modifications du modèle concernent sa structure. A titre d'exemple, ce modèle n'intègre pas actuellement le démarrage de la mobilisation des réserves corporelles au cours des 20 derniers jours avant la mise bas, classiquement observé par le biais de l'augmentation *prepartum* de la concentration plasmatique en acides gras non estérifiés (Figure 19).

Une modification simple du modèle pour pallier à ce défaut pourrait consister à intégrer un rôle de pilote de la priorité orientée vers la gestation (priorité U) pour déterminer la mobilisation *prepartum* des réserves. Par l'intermédiaire du principe de priorité différentielle il serait aisé de simuler un démarrage de la mobilisation des réserves corporelles en fin de gestation, pour des niveaux de priorité U élevés (valeur de k élevée dans le terme U^k).

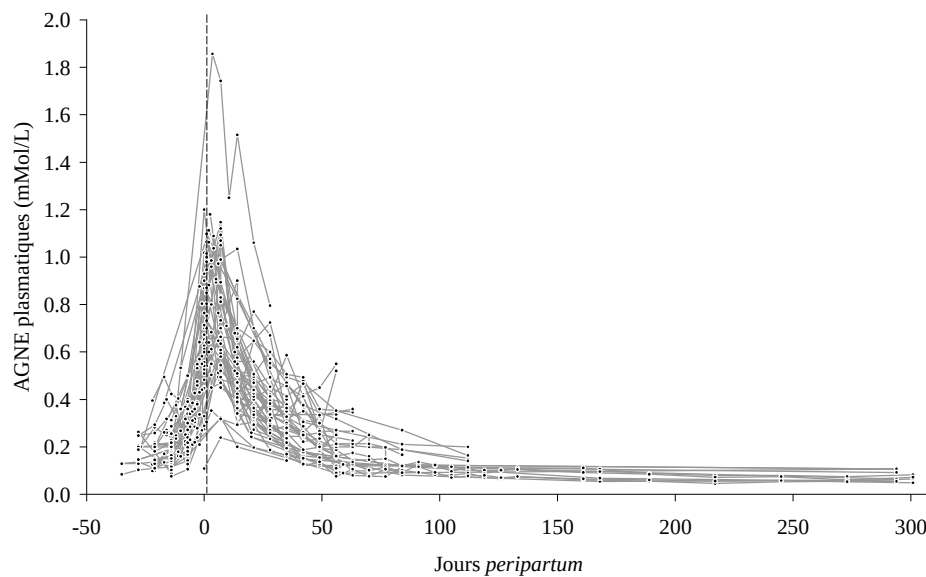


Figure 19 Évolution *peripartum* des acides gras non estérifiés plasmatiques chez des vaches laitières
Données de la littérature²⁸ (26 références, 61 groupes de traitement).

La relation entre niveaux de production laitière et d'ingestion produite par le modèle est globalement cohérente avec les données de la littérature compilées par Hristov *et al.* (2000²⁹ ; 2004³⁰). Les modulations imposées par des niveaux variables de potentiel génétique de production laitière et de densité énergétique de la ration produisent des trajectoires du couple (lait, ingestion) s'inscrivant de façon satisfaisante dans le champ des valeurs mesurées en station expérimentale (Figure 20).

²⁸ Reid *et al.*, 1979 ; Doreau *et al.*, 1981 ; Skaar *et al.*, 1989 ; Harrison *et al.*, 1990 ; Drackley *et al.*, 1991 ; Bertics *et al.*, 1992 ; Drackley *et al.*, 1992 ; Studer *et al.*, 1993 ; Vazquez-Añon *et al.*, 1994 ; Van den Top *et al.*, 1995 ; Grum *et al.*, 1996 ; Smith *et al.*, 1997 ; Vazquez-Añon *et al.*, 1997 ; Drackley *et al.*, 1998 ; Mäntysaari *et al.*, 1999 ; Putnam *et al.*, 1999 ; Rukkwamsuk *et al.*, 1999 ; Bremmer *et al.*, 2000 ; Greenfield *et al.*, 2000 ; Hartwell *et al.*, 2000 ; Doepel *et al.*, 2002 ; Grum *et al.*, 2002 ; Badinga *et al.*, 2004 ; Dann *et al.*, 2004 ; Grummer and Rastani, 2004 ; Rosendo *et al.*, 2004

²⁹ Hristov, A.N., Hristova, K.A. and Price, W.J., 2000. Relationship between dry matter intake, body weight, and milk yield in dairy cows: a summary of published data. *Journal of Dairy Science* 83 (Suppl.), 260.

³⁰ Hristov, A.N., Price, W.J. and Shafii, B., 2004. a meta-analysis examining the relationship among dietary factors, dry matter intake, and milk and milk protein yield in dairy cows. *Journal of Dairy Science* 87, 2184-2196.

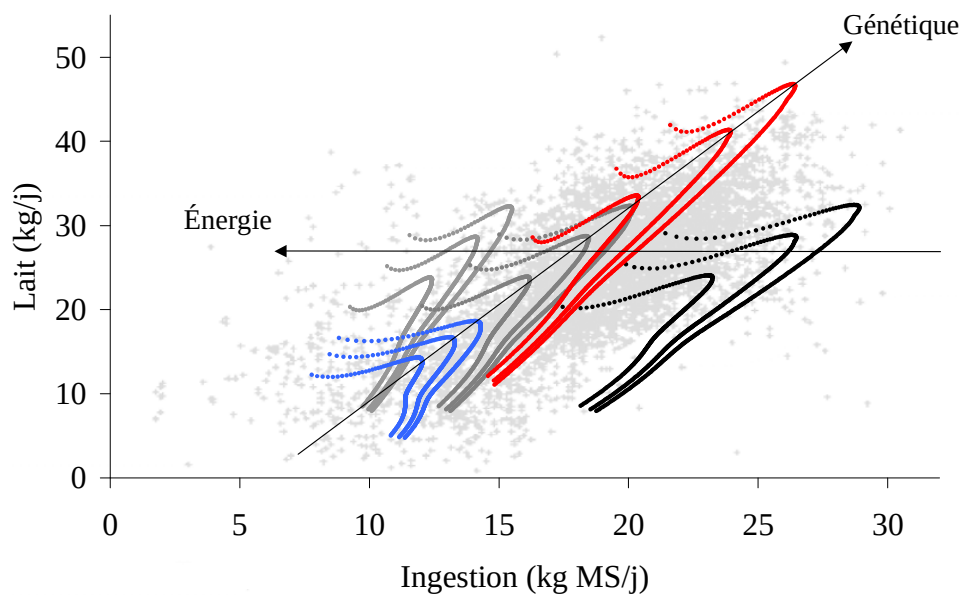


Figure 20 Relation entre niveau d'ingestion et production laitière journaliers sur trois lactations successives (rangs 1 à 3) pour des valeurs croissantes de paramètre génétique de niveau de production laitière (en bleu, gris et rouge) et des valeurs croissantes de densité énergétique de la ration (niveaux de gris). Superposition des simulations du modèle aux données de Hristov *et al.*, 2004 (Figure 1. Data from Hristov *et al.*, 2000, n = 5814).

A ce stade de développement, ce modèle peut ainsi être envisagé comme le prototype d'un outil de simulation global de la dynamique des performances d'une vache ou d'un troupeau (n vaches) avec une option de contrôle direct d'un niveau génétique. La construction d'un modèle à l'échelle d'un troupeau incorporant comme brique élémentaire un modèle animal au fonctionnement régulé individuellement et représentant un variant génotypique est actuellement en cours de développement au sein de l'UMR PNA pour l'espèce caprine (Puillet *et al.*, 2008a³¹). Le modèle animal développé ici, adapté à la chèvre laitière, pourrait être exploité en tant que maillon élémentaire venant se substituer à la version du modèle animal actuellement utilisée et conceptuellement apparentée (Puillet *et al.*, 2008b³²). L'interaction entre un modèle animal et une représentation d'un système de pratiques permet d'appréhender la diversité des carrières au sein d'un élevage comme un faisceau de

³¹ Puillet, L., Martin, O., Sauvant, D. and Tichit, M., 2008a. Lifetime performance diversity of dairy goats and feeding and reproduction practices: a modelling approach. *Recontres autour des Recherches sur les Ruminants* 15, 171-174.

³² Puillet, L., Martin, O., Tichit, M. and Sauvant, D., 2008b. Simple representation of physiological regulations in a model of lactating female: application to the dairy goat. *Animal* 2, 235-246.

trajectoires individuelles dans un environnement contrôlé, imposant des contraintes alimentaires et rythmant les cycles reproductifs.

Les propriétés du modèle en terme de modulation de la partition d'énergie selon le niveau d'apport alimentaire reposent sur une modélisation théorique globale n'ayant pas fait l'objet d'une validation fine. En effet, même si le modèle produit des réponses globalement cohérentes avec les connaissances actuelles, la précision de ses prédictions reste à évaluer. Cette étape indispensable devra reposer sur la confrontation du modèle à des jeux de données expérimentales exprimant des déformations des performances des animaux induites par des modulations dynamiques des apports alimentaires. De nombreux essais ont été publiés dans la littérature (compilation dans Martin and Sauvant, 2002³³) et peuvent être exploités pour notamment éclairer la représentation de la ventilation d'une variation de la quantité d'énergie exportée vers le lait entre ses composants. Cet aspect est actuellement intégré dans le modèle sous forme simple d'une hypothèse minimale de proportionnalité. Des essais spécifiques, destinés à l'évaluation du modèle, pourraient par ailleurs être menés afin d'explorer plus spécifiquement et d'améliorer le comportement du modèle à l'intersection des facteurs génétique et alimentaire. En particulier, un facteur génétique pourrait être incorporé dans le modèle pour représenter une variabilité de réponses à des modifications de niveau d'apport alimentaire.

La construction du modèle énergétique a été menée avec un objectif de compilation de l'état actuel des connaissances et de positionnement à un niveau moyen par rapport à celles-ci. Le paramétrage du besoin de gestation en énergie en est une illustration (Figure 21). Sur ce graphique, la forme sigmoïde de la courbe reflète l'indexation du besoin en fonction du taux de croissance fœtale contrairement aux autres modèles pour lesquels il est calé sur le poids fœtal. Ce positionnement moyen peut être envisagé comme une étape intermédiaire dans une perspective d'amélioration de la prédiction des besoins énergétiques. A titre d'exemple, le modèle pourrait être utilisé comme outil pour évaluer les formules de calcul du besoin

³³ Martin, O. and Sauvant, D., 2002. Metaanalysis of input/output kinetics in lactating dairy cows. *Journal of Dairy Science* 85, 3363-3381.

d'entretien classiquement utilisées et celles récemment proposées pour améliorer sa prédiction (Ellis *et al.*, 2006³⁴).

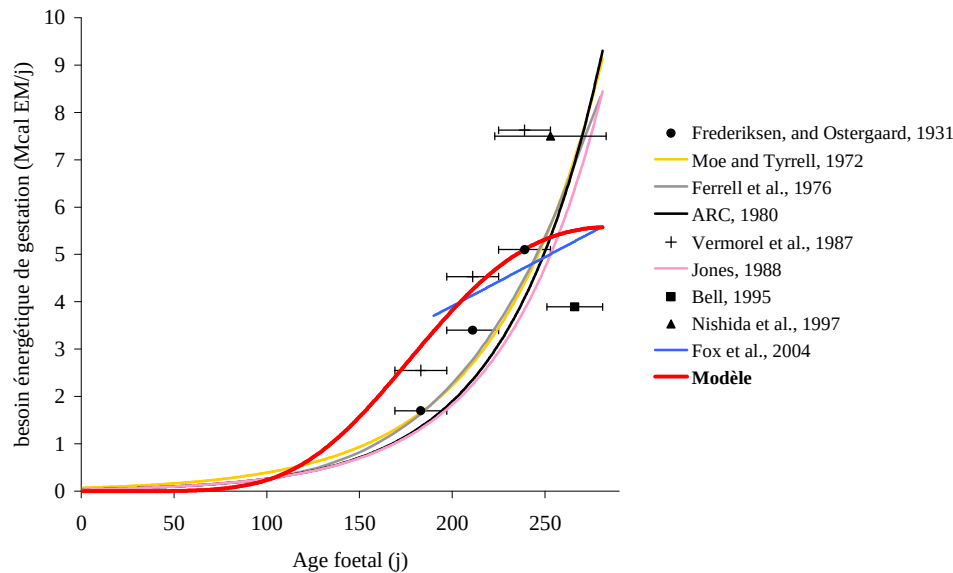


Figure 21 Comparaison de modèles^{35 36 37 38 39 40 41 42 43} de prédiction du besoin énergétique de gestation (Mcal énergie métabolisable (EM) / jour).

³⁴ Ellis, J.L., Qiao, F. and Cant, J.P., 2006. Evaluation of net energy expenditures of dairy cows according to body weight changes over a full Lactation. *Journal of Dairy Science* 89, 1546-1557.

³⁵ Frederiksen and Østergaard, 1931. Foderenheder og protein til mælkeproduktion. 136. Beretn. Landøkonomisk Forsøgslaboratorium, Frederiksberg, 256 p.

³⁶ Moe, P.W. and Tyrrell, H.F., 1972. Metabolizable energy requirement of pregnant dairy cows. *Journal of Dairy Science* 55, 480-483.

³⁷ Ferrell, C.L., Garrett, W.N., Hinman, N. and Grichting, G., 1976. Energy utilization by pregnant and non-pregnant heifers. *Journal of Animal Science* 42, 937-950.

³⁸ ARC, 1980. *Agricultural Research Council, The nutrient requirements of ruminant livestock*. Farnham Royal, UK: Commonwealth Agricultural Bureaux, 1980, 123 p.

³⁹ Vermorel, M., Coulon, J.B. and Journet, M., 1987. Révision du système des unités fourragères (UF). *Centre de Recherches Zootechniques et Veterinaires de Theix, Bulletin Technique* 70, 9-18.

⁴⁰ Jones, R.I., 1988. Final Report: Facet N6211/42/1/6. *Systems specifications and simulations for farm and extension use in stock and game farming: Development of microcomputer programs for dairy herd management*. Pietermaritzburg, South-Africa : Department of Agriculture, 1988.

⁴¹ Bell, A.W., 1995. Regulation of organic nutrient metabolism during transition from late pregnancy to early lactation. *Journal of Animal Science* 73, 2804-2819.

⁴² Nishida, T., Kurihara, M., Terada, F. and Shibata, M., 1997. Energy requirements of pregnant Holstein dairy cows carrying single or twin Japanese black fetuses in late pregnancy. *Animal Science and Technology* 68, 572-578.

⁴³ Fox, D.G., Tedeschi, L.O., Tylutki, T.P., Russell, J.B., Van Amburgh, M.E., Chase, L.E., Pell, A.N. and Overton, T.R., 2004. The Cornell Net Carbohydrate and Protein System model for evaluating herd nutrition and nutrient excretion. *Animal Feed Science and Technology* 112, 29-78.

La vocation du modèle énergétique est orientée vers une fonction d'outil pour tester des hypothèses et potentiellement comme un outil de recommandation. L'intégration de paramètres génétiques ouvre des perspectives pour des prédictions individualisées. Ces paramètres sont définis comme des paramètres d'échelles qui modulent les niveaux de réponse indépendamment de la structure générale du modèle. La recherche d'éventuelles liaisons entre les paramètres génétiques (potentiel laitier, labilité des réserves, composition du lait, poids vif mature) est par ailleurs une piste de travail. Par construction, dans une optique de segmentation des problématiques pour progresser, les déterminants génétiques ont été injectés au niveau du modèle énergétique pour déterminer les performances de référence. En revanche, ils n'interviennent pas explicitement au niveau du module d'homéostasie ni au niveau du modèle téléonomique. En effet, aucun paramètre génétique n'a été incorporé pour moduler la dynamique des priorités ni la ventilation d'une déviation d'énergie par rapport au besoin de référence. Ces hypothèses restent à tester : est-il nécessaire de tenir compte d'une variabilité génétique dans l'aptitude à moduler la partition de l'énergie dans des situations d'écart à la référence génétique ? Est-il nécessaire de tenir compte d'une variabilité génétique dans la dynamique des priorités entre fonctions au niveau téléonomique ?

Ces questions relèvent des concepts de flexibilité, d'élasticité et de plasticité (Alcaras and Lacroux, 1999⁴⁴) ou encore de robustesse et pourraient être interrogées par l'intermédiaire de ce modèle. Ces auteurs définissent les notions de flexibilité, d'élasticité et de plasticité d'un système par l'intermédiaire des aptitudes à modifier sa structure et/ou sa finalité. Ainsi, les systèmes élastiques résistent à des contraintes environnementales en supportant de façon temporaire des changements de leur structure tout en conservant leur finalité (constances structurelle et téléonomique). Les systèmes flexibles s'adaptent aux contraintes soit en modifiant leur structure tout en conservant leur finalité (déformation structurelle et constance téléonomique), soit en modifiant leur finalité tout en conservant leur structure (constance structurelle et déformation téléonomique). Enfin, les systèmes plastiques s'adaptent en modifiant leur structure et leur finalité (déformations structurelle et téléonomique). La construction du modèle global, reposant sur une séparation entre structure (modèle énergétique) et finalité (modèle téléonomique), est ainsi *a priori* « compatible » avec cette grille de lecture.

⁴⁴ Alcaras, J.R. and Lacroux, F., 1999. Planifier, c'est s'adapter. *Économie et Sociétés* 33, 7-37.

Modèle téléonomique

Le modèle téléonomique est dans sa version actuelle une représentation de la **dynamique des priorités** entre fonctions physiologiques. Cette construction est orientée vers une opérationnalité pour contrôler la dynamique de partition de l'énergie au niveau du modèle énergétique. Le modèle téléonomique doit constituer en soi un objet à même d'être considéré pour être amélioré. C'est notamment dans une perspective de comparaison des stratégies de reproduction de différentes espèces de mammifères que ce modèle pourrait être exploité. Ce travail s'inscrit dans le domaine de l'écologie au sens large et sort du champ strict de la zootechnie. Les pistes d'amélioration des propriétés du modèle concernent par exemple le flux de sénescence qui soustrait une « *quantité de priorité* » pour la fonction de reproduction à mesure que l'animal vieillit. Ce flux a été considéré de façon très simplifiée et sa formalisation devra probablement être reconsidérée à la lumière de connaissances sur le vieillissement. Une autre piste d'amélioration du modèle concerne une représentation démarrant dès la croissance intra-utérine de l'animal et non pas seulement dès sa naissance. Une telle formalisation, plus réaliste et plus élégante, permettrait de mettre en cohérence la croissance fœtale propre et celle portée par l'animal en terme de priorité. Le principe de priorité différentielle pourrait ainsi être exploité pour représenter la croissance des tissus corporels dès la conception. Dans l'état actuel seul le transfert de priorité entre « *lactation* » et « *équilibre des réserves* » est modulé par le statut de l'animal, en particulier le niveau de ces réserves et sa traite. Un niveau trop faible des réserves corporelles induit ainsi une accélération de ce transfert et une reconstitution privilégiée des réserves.

D'éventuelles modulations des autres transferts de priorité doivent être considérées, en particulier pour mieux maîtriser les variations de date du pic de production de lait ou de début de reprise de poids *postpartum*. L'hypothèse de base formulée actuellement repose sur l'inéluctabilité et l'invariance du transfert de priorité entre « *gestation* » et « *lactation* » par l'intermédiaire d'une priorité à la transition entre ces fonctions physiologiques. C'est la priorité à cette transition qui contrôle la mobilisation des réserves. Est-il nécessaire de représenter des variations de transfert de priorité induisant des modifications des performances en tout début de lactation ? Le niveau des réserves corporelles impacte-t-il uniquement la quantité de réserves mobilisée (hypothèse actuelle) ou module-t-il également sa dynamique ?

Couplage des modèles téléonomique et énergétique

Le couplage des modèles téléonomique et énergétique permet d'incorporer la régulation d'homéostasie à deux niveaux : (1) des fluctuations de l'environnement alimentaire induisent des déviations de la partition de l'énergie entre fonctions par rapport à une partition de référence pilotée par les priorités et (2) des modifications du niveau des réserves corporelles par rapport à des seuils de référence induisent directement des modifications de la partition dynamique des priorités entre fonctions. Ce dernier niveau formalise une interaction entre homéostasie et homéorhèse : la génétique fixe une norme de base (la chreod) qui prescrit (homéorhèse) une dynamique de fonctionnement physiologique, l'environnement module cette dynamique par rapport à la norme à court terme (homéostasie « *énergétique* ») et l'accumulation de déviations par rapport à cette norme impose un réajustement de la norme (homéostasie « *indirecte* »). Ce mécanisme formalise ainsi un « bassin d'attraction » autour d'une trajectoire de référence.

La cadre conceptuel formé par le triplet {chreod | homéorhèse | homéostasie} et sa formalisation par le couplage des modèles téléonomique et énergétique permet d'aboutir à un modèle de prédiction des performances possédant son propre « *agenda* ». Ce cadre est original et pertinent dans la mesure où il permet de proposer un modèle du « *système vache* » dans son ensemble (croissance, reproduction, nutrition), facilement transposable à la chèvre et la brebis, ou à tout autre organisme femelle de mammifère.

Perspective d'une plateforme de modélisation

Le montage des trois modèles est envisagé comme le **prototype d'un animal virtuel**. Virtuel est employé ici dans son sens dérivé du latin *virtus* (la vertu) : « *Est virtuel ce qui, sans être réel, a, avec force et de manière pleinement actuelle (c'est-à-dire non potentielle) les qualités du réel* » (Berthier, 2004⁴⁵). Le concept d'animal virtuel, en tant qu'objet technique médiatisé par une interface, correspond à un programme informatique compilant des équations mathématiques reproduisant le fonctionnement biologique d'un animal dans son ensemble et à l'échelle de sa vie. L'idée d'animal virtuel existe déjà sous la forme ludique

⁴⁵ Berthier, Denis, 2004. *Méditations sur le réel et le virtuel*. Paris : L'Harmattan, 2004, 280 p.

d'un compagnon artificiel sur console de jeu (tamagotchi) ou dans un élevage virtuel sur internet (par exemple www.vacheland.com). Ces applications, réalisées pour le jeu, n'ont pas de vocation scientifique d'intégration de connaissances ni de simulation fine des processus biologiques à l'origine des performances animales. Le terme « *animal virtuel* » est par ailleurs déjà utilisé dans des outils de simulation informatique d'élevage (Montel *et al.*, 2000⁴⁶) proposant une représentation de la conduite et des performances des animaux. Ce concept peut être vu comme une version moderne des UGB (Unités Gros Bovins) et des UZ (Unités Zootechniques) utilisées dans l'approche des systèmes de productions par les zootechniciens des années 1960-1970.

Le concept d'animal virtuel est utilisé ici pour insister sur l'autonomie du modèle et sur sa vocation, non plus seulement à simuler les entrées et sorties de l'animal vu comme une unité de production, mais à simuler le processus de vie de l'animal reconsidéré comme un organisme vivant dans sa globalité. Il s'agit d'un modèle, simulant de la naissance à la mort, le fonctionnement biologique d'un animal réel. Ce fonctionnement se limite à ce stade aux fonctions d'intérêt zootechnique et n'inclut pas son comportement, sa locomotion, ses interactions sociales, sa pathologie, etc. Sont ainsi représentées les principales fonctions des systèmes digestif, métabolique et reproducteur au cours de la croissance et des cycles reproductifs.

Le terme prototype est employé pour souligner l'intention d'initier un principe applicable de façon plus globale sous la forme d'une plateforme de modélisation dont ce modèle constituerait le squelette. L'idée étant de faire évoluer le modèle actuel en améliorant son fonctionnement et en incorporant d'autres fonctions biologiques pour affiner sa capacité à constituer une copie virtuelle d'un animal. La vocation de plateforme de recherche à court terme a pour ambition d'accueillir, de fédérer, de collecter et de compiler des travaux de recherches sur des aspects spécifiques du fonctionnement de l'animal. A long terme, le concept d'animal virtuel est envisagé comme un futur support d'agrégation et de diffusion des connaissances sur les femelles de ruminants. Ce support pouvant à terme être embarqué dans une carcasse logicielle pour l'aide à la décision et le pilotage sur le terrain.

⁴⁶ Montel, B., Van Milgen, J., Paboeuf, F. and Dourmad, J.Y., 2000. Construction d'un modèle de simulation des performances zootechniques et des rejets azotés d'une bande de porcs charcutiers. In : 32^{èmes} Journées de la Recherche Porcine en France, Paris, France, Février 1-3, 2000, 32, 51-58.

Les systèmes de recommandations alimentaires produits par les organismes de recherches en sciences animales à travers le monde correspondent déjà à des collections d'équations mathématiques plus ou moins sophistiquées et éventuellement incorporées dans un logiciel (Chalupa *et al.*, 2005⁴⁷). Le concept d'animal virtuel est principalement innovant dans sa vocation interdisciplinaire et fédératrice et dans son enjeu de représentation des mécanismes de régulations à travers laquelle l'animal est vu comme une entité autonome et non un « *bio-convertisseur* » de fourrages.

Il existe actuellement un fort engouement pour la modélisation, notamment à l'INRA (Goffinet *et al.*, 2006⁴⁸). Le potentiel analytique de cette approche est indéniable. Cependant, à mesure que les travaux de modélisation foisonnent et que les modèles naissent, le sens même de la modélisation doit probablement être questionné. Le point de vue adopté dans ce document retient deux idées clefs. En premier lieu, même si la systémique constitue une philosophie de représentation du réel et procède d'une véritable démarche scientifique, les modèles et la modélisation ne sont que des outils parmi d'autres dans la boîte à outil méthodologique du chercheur. Cette remarque désacralise la modélisation et renvoi le modèle à son rôle d'outil adapté à une tâche. En second lieu, il convient probablement d'envisager une issue commune à tous les modèles développés et un objectif commun aux travaux de modélisation en sciences animales. C'est le sens pris par le projet de la plateforme RECORD en agronomie (<http://record.toulouse.inra.fr/>). C'est le sens de la proposition de projet de plateforme de modélisation de la vache, et de façon générique des femelles de ruminants, auquel aboutit ce travail de thèse. Ce projet, envisagé comme la réalisation d'un animal virtuel, est voué à devenir un support d'intégration et d'interaction entre expérimentation (virtuelle et réelle) et modélisation, pour formaliser la connaissance et ses progrès et permettre sa diffusion. D'un point de vue prospectif, cette démarche s'inscrit dans le champ de la biologie intégrative, vers des modèles qui font émerger un fonctionnement global de l'agencement de processus élémentaires. Elle s'inscrit également dans la perspective de compréhension des invariants biologiques dans la diversité des génotypes. Elle doit permettre dans le futur de mieux formaliser les interactions entre génotype et environnement et de

⁴⁷ Chalupa, W., Boston, R. and Munson, R., 2004. Dairy nutrition models: their forms and applications. In : *Nutritional biotechnology in the feed and food industries. Proceedings of Alltech's 20th Annual Symposium: re-imagining the feed industry*, Lexington, Kentucky, USA, 23-26 May 2004, Pages: 187-193

⁴⁸ Goffinet, B. et le groupe de réflexion Modélisation, 2006. *La modélisation à l'INRA*. [en ligne], Paris, France : INRA, 2006, [référence du 25 avril 2007]. http://www.inra.fr/mia/doc/rapport_modelisation_VO.pdf

féderer les problématiques scientifiques émanant de différentes disciplines telles que l'éthologie, l'économie et l'écologie autour d'outils communs. A plus court terme, le développement d'une plateforme de modélisation de l'animal doit aider à faire progresser, au sein de l'UMR PNA, les travaux de modélisation centrés sur des organes tels que le rumen, sur des problématiques inter-organes telles que la partition de l'énergie et sur des activités telles que le comportement alimentaire. En exploitant un « squelette » minimal et fonctionnel d'un modèle animal, ces travaux pourraient être menés de façon conjointe et se nourrir mutuellement. Le travail de conception et de développement d'une telle plateforme se situe à l'intersection des mathématiques appliquées, de la biologie et de l'informatique appliquée et devra, pour aboutir sur le long terme, rassembler des compétences dans ces domaines. A très court terme, ce travail de thèse fournit une base pour démarrer ce projet ambitieux.

Annexes

Annexe 1 Revue historique sur la composition corporelle

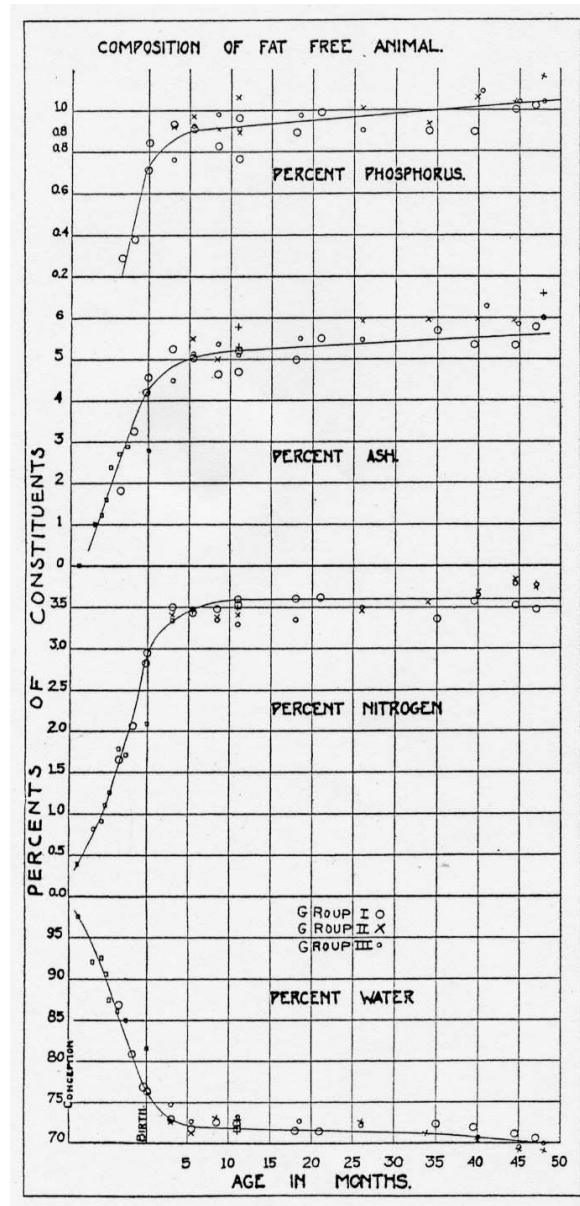


Figure 22 Moulton et al. (1922), Fig. 11, « Composition of the fat-free beef animal ».

Les travaux sur la composition corporelle des bovins ont été traditionnellement menés par des équipes travaillant sur la croissance et particulièrement dans le secteur de la production de viande. La composition du gain de poids des animaux détermine en effet le besoin énergétique associé à ce croît (Garrett *et al.*, 1959). Dans ce secteur, les investigations portent

généralement sur la composition de la carcasse, qui constitue la fraction commercialisable de l'animal, plutôt que sur celle de l'animal entier.

Von Bezold (1857 ; 1858) fut l'un des premiers auteurs à s'intéresser à la composition chimique du corps des animaux. Les conclusions de ses travaux sur des mammifères, des oiseaux, des amphibiens, des poissons et des crustacés à différents stades physiologiques, révèlent que l'âge est la principale source de variabilité de la composition corporelle d'un individu d'une espèce donnée. Dès 1880, plusieurs auteurs ont observé une réduction de la teneur en eau dans le corps vide avec l'accroissement de la teneur en lipides dans le corps vide (Henneberg, 1880 ; Von Hosslin, 1881 ; Pfeiffer, 1886), laissant supposer la notion de substitution de l'eau par les lipides lors du processus d'engraissement. Par ailleurs, la fraction lipidique du corps des animaux était déjà connue comme étant la fraction la plus variable.

En 1911, au terme d'une étude portant sur les différences de composition chimique d'animaux à sang chaud et à sang froid, Inaba conclut que des animaux morphologiquement similaires présentaient des compositions chimiques similaires.

En 1919 et 1922, Murray analysa les données de composition corporelle de bouvillons, de moutons et de cochons publiées par Lawes et Gilbert (1859), de bovins publiées par Haecker (1920) et de cochons publiées par Swanson (1921). Ses conclusions portent sur la relative constance des fractions aqueuse, protéique et minérale de la masse délipidée.

En 1922, Moulton *et al.* étudièrent la composition corporelle de bovins d'âges variant des stades précoces de la vie embryonnaire jusqu'à la maturité ainsi que d'embryons humains étudiés par Fehling (1877). Ils constatèrent une rapide réduction de la teneur en eau de la masse délipidée au cours de la vie embryonnaire puis une réduction plus faible de cette fraction au début de la vie autonome pour atteindre une valeur relativement constante (Figure 22). Cette évolution avec l'âge de la composition du corps vide avait déjà été soulignée par Inaba (1911) et Murray (1919 ; 1922).

En 1923, en conclusion d'une étude portant sur la composition corporelle du corps vide de différents mammifères, Moulton formula le concept de « *maturité chimique* » d'un animal défini comme l'âge auquel les fractions aqueuse, protéique et minérale de la masse corporelle délipidée atteignent une valeur approximativement constante. Dans un ouvrage de 1925, Armsby et Moulton situent la maturité chimique des bovins à un âge compris entre 150 et 300

jours. Bien que les mammifères étudiés atteignent la maturité chimique à des âges différents, ces auteurs notent que cet âge représente de 3.9 à 4.6% de la durée de vie totale de l'animal. Les conclusions de Moulton (1923) sont conformes à celles de Murray (1922) : la masse lipidique d'un animal d'une espèce donnée n'a pas d'influence sur la composition de la masse non-lipidique. Les travaux de Rubner (1924) et de Hastings (1940) confirment la validité de ce concept de composition approximativement constante de la masse délipidée d'un animal. De ce fait, reprenant la formulation de Reid *et al.* (1955), le principal effet de l'accroissement de la masse lipidique dans le corps vide sur les teneurs aqueuse, protéique et minérale du corps vide est un effet de dilution.

En 1945, Pace et Rathbun compilèrent des données de composition corporelle obtenues chez le rat, le cobaye, le lapin, le chat, le chien et le singe. Ils dégagèrent de cette étude une teneur moyenne en eau de la masse délipidée égale à 73.2% chez les Mammifères (de 69.9% à 76.3%). La revue de Shebaita (1977) reporte des valeurs allant de 72.2% à 75.2%.

Bien que la composition chimique d'un animal continue d'évoluer de façon marginale au stade adulte jusqu'à la mort, ce principe de constance approximative de la composition corporelle de la masse délipidée d'un animal a été retenu et dès lors largement utilisé pour l'estimation *in vivo* de la masse lipidique, notamment chez l'homme.

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Annexe 2 Méthodes de mesure de la composition corporelle

La mesure exacte de la composition chimique d'un animal entier implique son abattage et le dosage chimique des composants du corps vide après dissection, broyage et échantillonnage. L'analyse chimique fournit alors la décomposition de la masse corporelle en eau, en lipides (extrait étheré), en protéines ($N \times 6.25$) et en minéraux (cendres). En alternative à ce procédé long et coûteux, des procédures d'estimation indirecte de la composition chimique corporelle de l'animal entier ou de la carcasse ont été proposées.

Dissection anatomique

La masse corporelle des bovins comprend la carcasse (muscles, squelette et dépôts adipeux internes, sous-cutanés et intermusculaires) et le 5^{ème} quartier » (tête, cuir, viscères, tube digestif et dépôts adipeux viscéraux) (Robelin *et al.*, 1977). A maturité, selon le sexe et la race, les dépôts adipeux de la carcasse bovine représentent de 60 à 80% des dépôts adipeux totaux (Gibb *et al.*, 1992 ; Butler-Hogg *et al.*, 1985 ; Robelin and Geay, 1978 ; Cianza *et al.*, 1982 ; Robelin *et al.*, 1977 ; Holloway *et al.*, 1990). La masse totale des dépôts adipeux séparés par dissection n'est pas égale à la quantité de lipides déterminée par analyse chimique. En effet, d'une part le tissu adipeux n'est pas uniquement composé de lipides (de 75 à 85% à maturité) (Robelin, 1981 ; 1986) mais d'une matrice de tissu connectif et d'adipocytes contenant les lipides (Allen *et al.*, 1976) et d'autre part, tous les lipides ne sont pas contenus dans les dépôts adipeux (lipides intermusculaires, lipides du squelette, etc.) (Field *et al.*, 1974 ; Wright and Russel, 1984a). Robelin et Geay (1978) ont proposé une équation de prédiction de la quantité de lipides corporels à partir de la masse des dépôts adipeux de la carcasse et du 5^{ème} quartier sur des bovins de différentes races. De cette équation, il découle que les dépôts adipeux totaux de la carcasse et du 5^{ème} quartier représentent en moyenne 91.5% des lipides corporels totaux.

Finalement, d'après Robelin (1982), le « *gras total* » pesé après dissection anatomique est très proche du « *gras chimique* » dosé analytiquement. Par ailleurs, selon Lohman (1971) les erreurs de mesures associées à ces méthodes sont faibles par rapport à la variabilité biologique de la teneur en lipides corporels.

Analyse chimique partielle

L'analyse chimique est limitée à un élément dont la composition chimique est représentative de celle la carcasse (par exemple les 9-10-11^{èmes} côtes : Hopper, 1944 ; Hankins and Howe, 1946 ; Robelin *et al.*, 1975 ; Otto *et al.*, 1991).

Densitométrie

La densité de la carcasse est utilisée comme index de la teneur en dépôts adipeux et en eau corporelle (Kraybill *et al.*, 1952). Garrett et Hinman (1969) proposèrent des équations de prédiction des compositions chimiques de la carcasse et du corps vide à partir de la densité de la carcasse, permettant une estimation a posteriori de la composition corporelle. Des jeux d'équations analogues furent ensuite proposés par d'autres auteurs (Gil *et al.*, 1970 ; Ferrell *et al.*, 1976 ; Fortin *et al.*, 1981 ; Lanna *et al.*, 1990).

Dilution d'un marqueur de l'eau corporelle

Cette méthode se fondant sur le degré de dilution d'un marqueur après injection intraveineuse s'appuient sur l'hypothèse d'une teneur constante en eau dans la masse corporelle délipidée (Reid *et al.*, 1955 ; Shebaita, 1977). Ainsi la détermination de la masse lipidique, effectuée sur l'animal vivant, se ramène à celle de la quantité d'eau corporelle estimée par le biais de l'espace de diffusion du marqueur. Des molécules diffusant rapidement dans les fluides corporels, non toxiques, non métabolisées, stockées ou excrétées furent retenues comme marqueurs candidats (Soberman *et al.*, 1949). Différents marqueurs furent ainsi testés chez le bovin parmi lesquels l'antipyrine (Kraybill *et al.*, 1951) ou le 4-acetamidoantipyrine (4-AAP), l'un de ses dérivés (Whiting *et al.*, 1960), l'eau marquée (lourde (Byers, 1979) ou tritiée (Little and Morris, 1972), revue de Robelin, 1973) et l'urée (Preston and Koch, 1973).

Ces méthodes furent largement évaluées, discutées et comparées et de nombreux auteurs proposèrent par la suite des modèles de prédiction de la composition du corps vide ou de la carcasse (principalement l'eau et les lipides) à partir de l'espace de diffusion du marqueur considéré.

La précision de ces méthodes dépend de la vitesse de diffusion du marqueur dans le tube digestif (passage à travers la paroi du rumen ou par le biais de la salive dans le tube digestif, passage dans la vessie). Selon l'étendue de cette diffusion, l'espace de diffusion du marqueur fournit une estimation de l'eau du corps vide ou de l'eau corporelle totale. Dans certaines études, les animaux étaient privés d'eau avant l'expérience afin de réduire la quantité d'eau contenue dans le tractus digestif.

Bartle et Preston (1986) ont mis en évidence l'absence de passage rapide de l'urée dans le rumen, induisant une meilleure coïncidence de l'espace de diffusion de l'urée avec l'eau du corps vide qu'avec l'eau corporelle totale. Ce résultat est confirmé par Doreau *et al.* (1988) qui rapportent de plus une bonne correspondance entre l'espace de diffusion de l'eau lourde et l'eau corporelle totale. Selon Whitting *et al.* (1960) le 4-AAA présente l'avantage de ne diffuser dans le rumen que par le biais de la salive.

Marquage isotopique de la masse maigre

Les propriétés du potassium, principalement intracellulaire et quasiment absent dans les adipocytes furent exploitées pour estimer la masse protéique ou masse maigre des bovins. Ainsi, la détection par scintillation du ^{40}K en phase liquide fut proposée pour la détermination *in vivo* de la composition corporelle des bovins (Johnson and Ward, 1966). D'autres isotopes, tels que le césium (^{137}Cs) furent également testés (Ward and Johnson, 1965). Cette méthode, nécessitant un appareillage lourd et coûteux fut cependant peu exploitée.

Diamètre des adipocytes

Robelin (1982) proposa d'utiliser la taille des adipocytes sous-cutanés comme indicateur de la quantité de lipides corporels. Cette méthode est applicable aussi bien sur animaux vivants (par biopsie) que sur animaux abattus. Le système de prédiction (Robelin *et al.*, 1989 ;

Waltner *et al.*, 1994) utilise le diamètre des adipocytes et le poids vif comme prédicteurs de la quantité de lipides corporels.

Ultrasons

Principalement utilisée pour l'estimation de la composition de la carcasse, cette méthode repose sur la vélocité différentielle des ultrasons à travers des tissus de natures chimiques différentes (Temple *et al.*, 1956 ; revue de Simm, 1983). Wright et Russel (1984b), Garnsworthy *et al.* (1986) et Ivings *et al.* (1993) ont proposé des équations de prédiction de la composition du corps vide de vaches laitières à partir de mesures de vélocité d'ultrasons au niveau de l'arrière-train et de l'épaule.

Note d'état corporel

La note d'état corporel est un indicateur de terrain indépendant du poids vif et de la taille adulte de l'animal, développé pour apprécier simplement la quantité de réserves corporelles. Cette note est donnée après évaluation visuelle et palpation de zones particulières du corps et permet de classer les animaux par rapport à un type standard sur une échelle d'appréciation allant de « émacié » à « obèse ». Plusieurs échelles de notation ont été proposées pour les races laitières : de 1 à 5 (Wildman *et al.*, 1982 ; Edmonson *et al.*, 1985) ou de 0 à 5 (Lowman *et al.*, 1976 ; Mulvany, 1977 ; Bazin, 1984). Ces systèmes de notations sont largement utilisés pour évaluer le niveau de réserves corporelles et permettent de piloter les animaux en production.

D'autres techniques, parfois très sophistiquées comme les mesures d'impédance bioélectrique, la tomographie assistée par ordinateur, l'imagerie par résonance magnétique nucléaire, la photogrammétrie sont aujourd'hui proposées pour l'estimation *in vivo* de la composition corporelle des bovins ou de leur carcasse (revue de De Campeneere *et al.*, 2000). C'est aujourd'hui la technique de mesure de l'espace de diffusion de l'eau lourde qui est principalement utilisée chez les vaches en lactation afin de mesurer les variations quantitatives de lipides (et de protéines) au cours de la lactation.

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Annexe 3 Modèle empirique de la composition corporelle des vaches laitières

Cette annexe est présentée sous la forme d'un article publié dans les actes d'un congrès (6th International Workshop on Modelling Nutrient Utilization in Farm Animals, Wageningen, The Netherlands, 6-8 septembre 2004) :

Martin, O. and Sauvant, D., 2005. Empirical model of dairy cow body composition, 127-134. In : Kebreab, E., Dijkstra, J., Bannink, A., Gerrits, W.J.J. and France, J. (éd.), Nutrient Digestion And Utilization In Farm Animals: Modelling Approaches. Wallingford, UK : CAB International, 2006, 480 p.

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Empirical Model of Dairy Cow Body Composition

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Abstract

The knowledge of body condition and dynamic body reserve changes in dairy cows is of major importance in the understanding of lactation processes. An empirical model of dairy cow chemical body composition was developed and fitted to literature data. This model was aimed at predicting the concentrations of fat, protein, water, and minerals in empty body weight (EBW; kg) in relation to body condition score (BCS) on a 0–5 scale. Data were available for 239 groups of 1–36 animals. Body composition data were determined by direct analysis, anatomical dissection and organ weighing, or by indirect analysis. The relationship between body fat (F ; kg) and fat-free EBW (FFEBW; kg) was estimated with the sigmoidal model of Richards (1959), where the asymptote was assumed to be linearly dependent on BCS. This model, selected for its flexibility, was fitted to the data in two steps. First, the model was fitted to mean values of F by classes of FFEBW [<50 , 50 – 100), ..., $(400$ – $450)$, ≥ 450] assuming that these intraclass values were representative of a mean BCS (~ 2.5). Second, the asymptotic parameter of the Richards model was re-evaluated on each data for which BCS was available. The model finally obtained was $F = \{[117.4 + 39.8(\text{BCS} - 2.5)] \times [1 - \exp(-0.0068 \times \text{FFEBW})]^{3.7235}\}$ with an estimated root mean squared prediction error (RMSPE) of 20 kg. This model was not usable as such (since $\text{FFEBW} = \text{EBW} - F$) but, given EBW and BCS, the EB fat was the numerical solution of this equation. The ratios of body water (W ; kg) to FFEBW, body protein (P ; kg) and body minerals (M ; kg) to dry FFEBW ($\text{DFFEBW} = \text{FFEBW} - W$; kg) as well as their standard errors were estimated by bootstrap analysis on data limited to direct analysis: $100 \times W/\text{FFEBW} = 72.6 \pm 0.1\%$ ($n = 169$), $100 P/\text{DFFEBW} = 78.9 \pm 0.1\%$ ($n = 164$) and $100 M/\text{DFFEBW} = 21.0 \pm 0.1\%$ ($n = 164$). The complete chemical body composition of a cow ($\text{EBW} = F + P + W + M$) could therefore be simulated. The proposed model predicted body composition data in dairy cows from a broad experimental context and provided a practical prediction tool to study body reserves, particularly from a dynamic viewpoint.

Introduction

The condition and dynamic changes of body reserves in dairy cows during lactation are of major importance in the processes of lactation. It is therefore essential to estimate the animal state of reserves, especially of fat and protein.

The chemical body composition of an animal corresponds to the distribution of its body mass into fat, protein, water and minerals. This distribution is established on an empty body weight (EBW) basis, i.e. without digestive tract contents (reticulo-rumen and intestine digesta) and urogenital tract contents (urine, fetus, fluids and fetal membranes). Studies on cattle body composition have traditionally been done by researchers working on growth and were aimed at determining energy requirements, especially in beef cattle. Therefore, investigations rather dealt with carcass composition than empty body (EB) composition. As far back as 1923, Moulton (1923) had formulated the concept of 'chemical maturity' defined as the age at which the fat-free body composition remains approximately constant. Thus, as mentioned by Reid *et al.* (1955), the effect of an increasing EB fat on EB protein, water and mineral content is rather a dilution effect. Various indirect determination methods of EB chemical composition have been proposed (De Campeneere *et al.*, 2000) to avoid the slaughter of animals for direct chemical analysis. In the field, to simply assess the level of body reserves the body condition score (BCS) is used as an indicator independent of the body weight (BW; Lowman *et al.*, 1976).

The objective of this study is to develop an empirical model aimed at predicting EB composition of fat, protein, water and minerals related to EBW (kg) and BCS (0–5 scale) in dairy cows. An empirical model to predict EBW from neutral detergent factor (NDF) intake by estimating digestive tract fresh contents has been proposed elsewhere (Martin and Sauvant, 2003).

Compilation of the literature

Records of EB composition of growing, pregnant, lactating or dry dairy-type cows (mainly Holstein × Friesian) published between 1920 and 1998 in Europe (8 articles) and North America (17 articles) were gathered in a database. Collected data concerned 239 groups of 1–36 animals (154 individual data and 85 means of 13 ± 8 animals) and were obtained either by direct analysis (chemical analysis (170 groups), anatomical dissection and tissue weighing (10 groups) or by indirect analysis (deuterium dilution (38 groups), densitometry (17 groups), estimate from adipocyte cell size (4 groups). Direct and indirect analyses were assumed to furnish equivalent information. Moreover, no publication effect was taken into consideration, the database being considered only as a collection of body composition records rather than an experimental meta design. Notations used for empty body fat, protein, water, minerals, FFEBW, and DFFEBW were F (kg), P (kg), W (kg), M (kg), FFEBW ($EBW - F$; kg) and DFFEBW ($FFEBW - W$; kg), respectively.

Modelling empty body fat

The relationship between F and FFEBW was modelled with the sigmoidal model of Richards (1959), where the asymptote was assumed to be linearly dependent on BCS:

$$F = [f_0 + \beta(\text{BCS} - 2.5)] \times [1 - \exp(-f_1 \times \text{FFEBW})]^{f_2} \quad (13.1)$$

Since FFEBW and BCS were reported in 25 ($n = 239$) and 7 articles ($n = 38$) respectively (Fig. 13.1), this model, selected for its flexibility, was fitted to data in two steps corresponding to the estimate of parameters f_0 , f_1 , f_2 and β . First, the model was fitted to mean values of F by classes of FFEBW [<50 , (50–100), ..., (400–450), ≥ 450] assuming that these intraclass values were representative of a mean BCS (~ 2.5). Second, the asymptotic parameter f_0 was re-evaluated for each group of data for which BCS was available (Fig. 13.2):

$$f_0^* = F / [1 - \exp(-f_1 \times \text{FFEBW})]^{f_2} \quad (13.2)$$

The parameter β was then estimated as the linear intratrial slope of f_0^* on BCS (Fig. 13.3) with a mixed model integrating the random effect of trial on intercept ($\beta = df_0^*/d\text{BCS}$)

Quantitative descriptors of fit accuracy associated with the first step (fit of the model $F = f_0 \times [1 - \exp(-f_1 \times \text{FFEBW})]^{f_2}$ on mean values of F by classes of FFEBW) and the second step (fit of the model $f_0^* = (\mu + \sigma_{\text{trial}}) + \beta \times \text{BCS}$) are respectively $n = 13$, RMSPE = 8.2 kg, $f_0 = 117.4 \pm 22.1$, $f_1 = 0.0068 \pm 0.0030$, $f_2 = 3.7235 \pm 2.1130$, and $n = 38$, RMSPE = 20.8 kg, $\beta = 39.8 \pm 3.7$, $\sigma_{\text{trial}} = 25.8$ kg.

The model finally obtained was:

$$F = [117.4 + 39.8(\text{BCS} - 2.5)] \times [1 - \exp(-0.0068 \times \text{FFEBW})]^{3.7235} \quad (13.3)$$

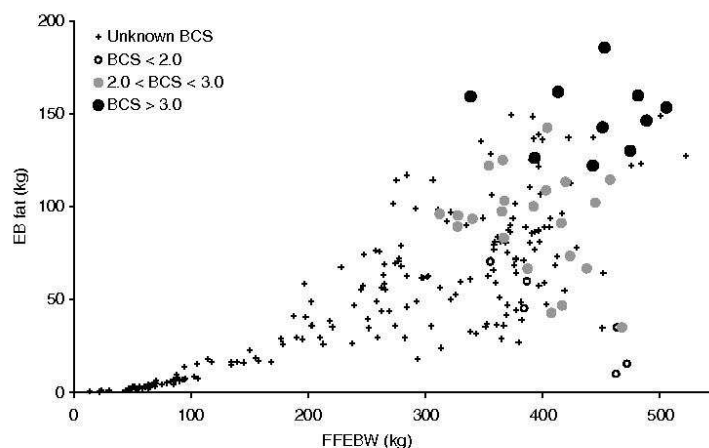


Fig. 13.1. Empty body (EB) fat data plotted against fat-free empty body weight (FFEBW; symbols encode for BCS).

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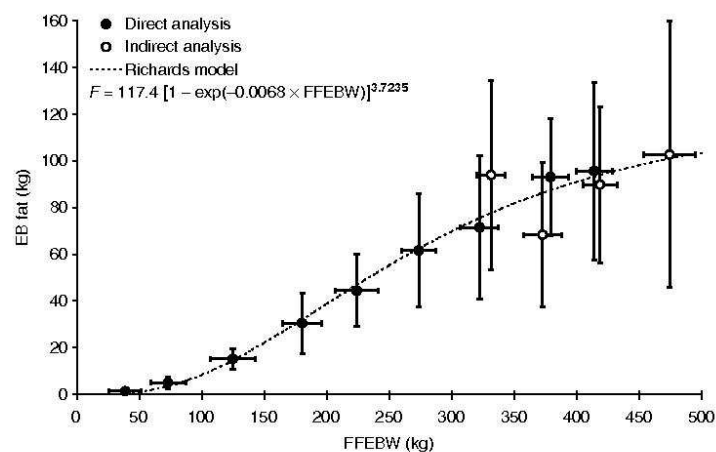


Fig. 13.2. Average empty body (EB) fat plotted against average fat-free empty body weight (FFEBW) by 50 kg classes (symbols encode for determination method).

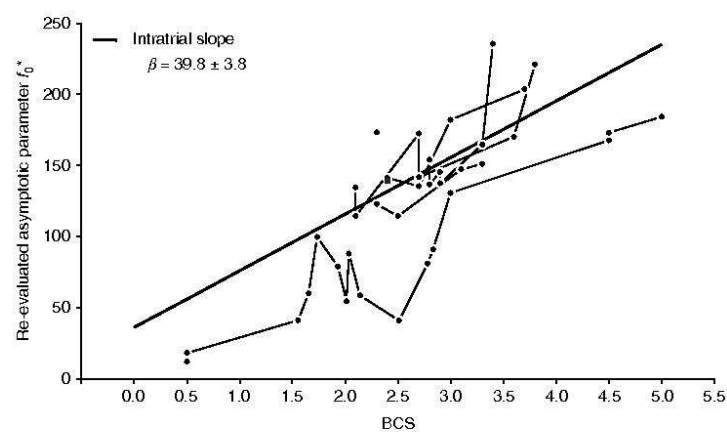


Fig. 13.3. Re-evaluated asymptotic parameter f_0^* plotted against body condition score (BCS; symbols linked by trial).

Since FFEBW is unknown in the field, this formula is not usable as such to estimate F . Given EBW and BCS, F is the numerical solution of the following equation (typically computed with the Newton-Raphson method):

$$F = [117.4 + 39.8(\text{BCS} - 2.5)] \times \{1 - \exp[-0.0068(\text{EBW} - F)]\}^{37235} \quad (13.4)$$

Fig. 13.4 shows simulated values of F plotted against EBW and BCS. The evaluated prediction error on F (unknown BCS assumed to be 2.5) is about ± 20 kg.

The following section was aimed at estimating body water content in FFEBW and body protein and minerals contents in DFFEBW. A first approach was performed using mixed model regression analysis taking into account the random effect of trial on intercept and slope of the regression $Y = f(X)$ where Y is the weight of the considered component into the total weight Y . Results showed that intercept was not significantly different from zero (and lower than residual error) and that random effects of trial on intercept and slope were not significant. It was therefore decided to quantify EB composition by the way of the ratio $Y:X$. The bootstrap analysis was then selected as the appropriate method to provide an unbiased estimate of the ratio and the estimate standard error of the estimated ratio.

Modelling fat-free empty body water content

The ratio W/FFEBW and its standard error were estimated by bootstrap analysis on data limited to direct analysis (Fig. 13.5):

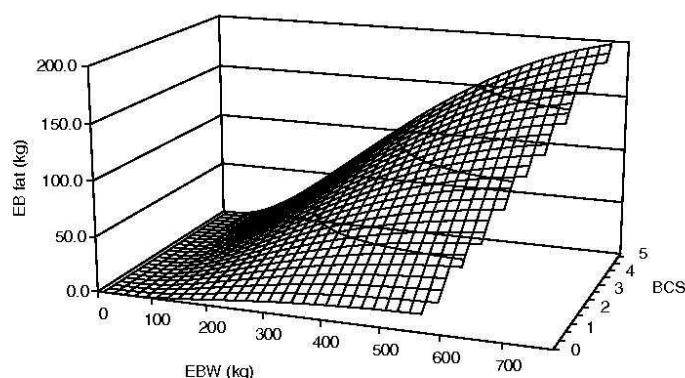


Fig. 13.4. Empty body (EB) fat (numerical solution of the model) plotted against empty body weight (EBW) and body condition score (BCS).

$$100W/FFEBW = 72.6 \pm 0.1\% \quad (n = 169) \quad (13.5)$$

Modelling dry fat-free empty body protein and minerals

The ratios $P:DFEBW$ and $M:DFEBW$ and their standard errors were estimated by bootstrap analysis on data limited to direct analysis (Fig. 13.6):

$$100 P/DFEBW = 78.9 \pm 0.1\% \quad (n = 164) \quad (13.6)$$

$$100 M/DFEBW = 21.0 \pm 0.1\% \quad (n = 164) \quad (13.7)$$

Discussion

The complete chemical body composition of a cow ($EBW = F + P + W + M$) at different BCS can be simulated stepwise with the proposed model. This modelling study synthesized body composition data in dairy cows from a broad experimental context and provided a practical prediction tool to study body reserves. Indeed, the model can be used to establish initial values of a mechanistic lactation model and to estimate the state of body reserves according to observed BCS changes during lactation. The proposed model gave predictions in average about 5% lower (10% for BCS 0 and 5) and 8% higher (regardless of BCS) values for EB fat and protein, respectively, of a 400

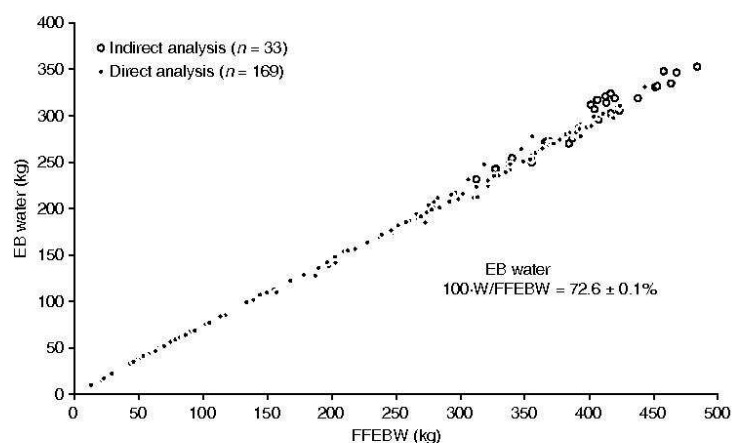


Fig. 13.5. Empty body (EB) water plotted against fat-free empty body weight (FFEBW; symbols encode for determination method).

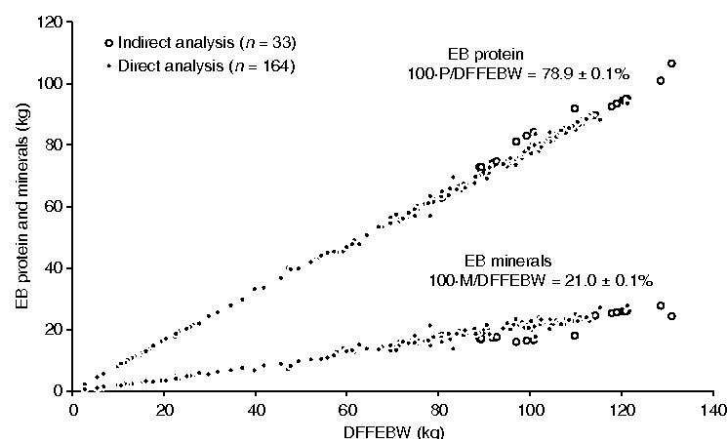


Fig. 13.6. Empty body (EB) protein and minerals plotted against dry fat-free empty body weight (DFFEBW; symbols encode for determination method).

kg EBW cow when compared to the model proposed by Fox *et al.* (1999). The estimated value of 39.8 kg fat per BCS unit used in the proposed model was in the range of the regression slopes of fat on BCS published in the literature (Wright and Russel, 1984; Rémond *et al.*, 1988; Chilliard *et al.*, 1991; Waltner *et al.*, 1994; Komaragiri and Erdman, 1997; Komaragiri *et al.*, 1998). Nevertheless, the present model has the advantage to integrate both the effects of BW and BCS. The model should be evaluated on a different data-set in order to verify its validity and to assess its associated prediction error.

Conclusion

The complete chemical body composition of a cow at different BCS was simulated with the proposed empirical model. The model can be used to establish initial values of a mechanistic lactation model and to estimate the state of body reserves according to observed BCS changes during lactation. The present model has the advantage to integrate both the effects of BW and BCS but requires further independent evaluation.

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Annexe 4 Meta-analyse des cinétiques de lactation chez la vache laitière

Cette annexe est présentée sous la forme d'un article publié dans la revue Journal of Dairy Science :

Martin O and Sauvant D 2002. Metaanalysis of input/output kinetics in lactating dairy cows. Journal of Dairy Science 85, 3363-3381.

J. Dairy Sci. 85:3363–3381

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Metaanalysis of Input/Output Kinetics in Lactating Dairy Cows

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ABSTRACT

The kinetics of dry matter intake, raw milk yield, milk fat yield, and body weight of 140 treatment groups of cows reported in 37 articles published between 1959 and 1999 were collected in a database. The majority of these experiments were performed with Holstein-Friesian cows (primiparous: $n = 51$, multiparous: $n = 89$). Animals were fed with forages and concentrates, offered separately ($n = 98$) or as a total mixed ration ($n = 42$). Empty body weight was calculated assuming that an increase of 1 kg in dry matter intake corresponded to an increase of 4 kg in gastrointestinal tract content. Each kinetic, denoted Y , was fitted with the model proposed by Grossman (1999) for raw milk yield. This model allowed the partitioning of the kinetic into three stages (early, middle, and late stages of lactation), each characterized by its own linear tendency. Kinetics were therefore summarized with parameter estimates of the model: the plateau value of Y in middle stage, the slopes of Y in early and late stages, and the weeks of start and end of the middle stage. The following additional variables were also calculated: the total increase of Y in early stage, the extrapolated value of Y at calving, and the persistency of Y defined as the duration of the middle stage. Variability of these parameters for each kinetic across treatment groups was examined through mixed models including the year of publication as covariate, parity as a fixed between-group factor, and trial as a random factor. Correlations between parameters within a Y -kinetic and between different Y -kinetics were calculated by parity group and feed allocation system. Finally we propose predictive models which emphasized (1) the effect of empty body weight at calving on the depletion of empty body weight in early lactation, (2) the incidence of the kinetic of dry matter intake on the kinetic of raw milk yield in middle and late stages of lactation, and (3) the relationships between the kinetics of raw milk yield and milk fat yield in middle and late stages of lactation.

(Key words: metaanalysis, milk yield, dry matter intake, body weight)

Abbreviation key: CO = concentrate, EBW = empty body weight, FO = forage, MEI = metabolizable energy intake, MFC = milk fat content, MFY = milk fat yield, MLC = milk lactose content, MLY = milk lactose yield, MPC = milk protein content, MPY = milk protein yield, Multi = multiparous cow, Primi = primiparous cow, RMSE = root mean square error, RMY = raw milk yield, YOP = year of publication.

INTRODUCTION

The majority of articles published on dairy nutrition and feeding have dealt with short periods of experimentation or with designs where animals receive successive experimental diets (e.g., Latin square designs). These trials provide static data, which allows empirical models of the effect of a particular type of diet or allocation system on animal production responses to be calculated for a given period of lactation. However, lactation is not a set of successive independent periods; it needs to be considered as a dynamic process (Broster and Broster, 1984). This is of practical importance. Knowledge regarding the impact of feeding on the kinetics of lactation is necessary for the optimization of a feeding strategy subject to constraints of feed inventory and fluctuating input and output prices. It therefore appeared important to examine the kinetic patterns that characterize the course of the lactation (DMI, yield, BW) and to model their interactions. In particular, the purposes of this study were: 1) to evaluate the variability of the kinetic patterns, their evolution through years of experimentation, and their differences according to parity; and 2) to highlight the dependencies within a given kinetic or between different kinetics, which determine a particular profile.

To achieve this goal, we decided to build a database by pooling the results from published trials dealing with the dynamic features of feeding, lactation, and BW. This paper presents the major characteristics of this collection of curves and the main effects revealed by a first metaanalysis approach.

Received October 3, 2001.
Accepted June 17, 2002.

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Table 1. Origin, data availability of main production variables, and experimental designs of the 37 articles collected in the database. Variables: DMI, metabolizable energy intake (MEI), raw milk yield (RMY), FCM, milk fat, protein, and lactose yield and content (MFY, MPY, MLY, MFC, MPC, and MLC), and BW.

Article	Origin	n ¹	[t ₀ -t ₃] ²	DMI	MEI	RMY	FCM	MF				ML				BW	Experimental design
								YC	YC	YC	YC	YC	YC	YC	YC		
Broster, 1969	UK, England	4	[1-18]	•	•	•	•	*								•	2 levels of feeding (H ³ or L ³) × 2 stages of lactation (wk [1-9] and [10-18]).
Broster, 1975	UK, England	6	[1-24]	•	•	•	•	**								•	6 patterns of CO ⁴ allocation: 3 levels of feeding (L, H or VH ⁵) applied for 5 stages of lactation (wk [1-4], [5-8], [9-12], [13-16] and [17-24]).
Cowan, 1970	Zimbabwe	4	[1-40]	•	•	•	•									•	4 TMR of different roughage content (5%, 20%, 35% or 50% in fresh matter basis).
Decaen, 1970	France	2	[1-40]	•	•	•	•	••								•	Secretion of fatty acids in 2 experimental farms.
DePeters, 1985	US, California	5	[1-44]	•	•	•	•	••								•	Parity (P or M) ⁶ × Number of daily milkings (2 or 3 times) + 2 dietary protocols for M cows milked 3 times daily.
DePeters, 1989	US, California	6	[1-16]	•	•	•	•									•	Parity (P or M) × Type of FO ⁴ (Chopped alfalfa hay: Cereal-vetch silage ratio: 100:0, 66:34 or 34:66 in DM basis).
Donker, 1983	US, Minnesota	12	[1-40]	•	•	•	•	••	••							•	Parity (P or M) × 2 sizes of cows (Small or Large) × 3 rates of feeding CO according to milk produced above 9.1 kg/d (L, S ³ or H).
Everson, 1976	US, Wisconsin	2	[1-44]	•	•	•	•	••								•	FO:CO ratio (Constant at 60:40 for wk [1-44] or variable at 50:50 for wk [1-21] and 66:36 for wk [22-44], in DM basis).
Garnsworthy, 1982	UK, Scotland	6	[1-16]	•	•	•	•									•	2 identical trials: 3 BCS at calving (L: [1.5-2.0], S: [2.5-3.0], H: [3.5-4.0]).
Holter, 1982	US, New Hampshire	10	[1-44]	•	•	•	•									•	Parity (P or M) × 5 programs of CO allocation according to milk produced.
Holter, 1984	US, New Hampshire	3	[1-40]	•	•	•	•									•	Wk [1-8]: 3 rates of feeding CO according to milk produced. Wk [9-40]: common decreasing program of CO allocation as percent of total CO consumed during wk [1-8].
Holter, 1992	US, New Hampshire	4	[1-43]	•	•	•	•	••								•	Parity (P or M) × Rate of feeding CO according to group or individual requirements.
Holter, 1993	US, New Hampshire	4	[1-40]	•	•	•	•	••								•	Parity (P or M) × Protein-Fat Bypass supplement (0% or 6% of FCM produced).
Johnson, 1977	UK, England	4	[1-20]	•	•	•	•	••								•	4 programs of CO allocation (2 graded levels (same total amount during wk [1-20]), 2 fixed levels (L or H)).
Johnson, 1979	UK, England	4	[1-20]	•	•	•	•	••								•	2 yield potential (L or H) in wk [7] × 2 levels of feeding CO in wk [9-20] (L or H).
Johnson, 1983	UK, England	2	[1-44]	•	•	•	•	••								•	2 programs of allocation of the same amount of CO in wk [6-20] (Graded or flat level).
Kertz, 1991	US, Missouri	2	[1-8]	•	•	•	•	••								•	Compilation of 18 trials over 6 yr: P or M.
Kronfeld, 1980	US, Pennsylvania	2	[2-26]	•	•	•	•	••								•	Control vs diet including protected tallow.
Krohn, 1983	Denmark	3	[1-36]	•	•	•	•	••								•	3 energy concentrations in TMR (VH, H or L) in wk [1-24].
Lahr, 1983	US, Minnesota	2	[2-44]	•	•	•	•									•	2 diets of different moisture content (Alfalfa silage or hay).
Lodge, 1975	Canada	2	[1-16]	•	•	•	•									•	2 levels of feeding prepartum (H or L).
Mohrenweiser, 1967	US, Minnesota	4	[1-40]	•	•	•	•									•	2 types of FO (Early-cut or Late-cut alfalfa hay) × Prepartum or postpartum.

continued

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Table 1. (continued) Origin, data availability of main production variables, and experimental designs of the 37 articles collected in the database. Variables: DMI, metabolizable energy intake (MEI), raw milk yield (RMY), FCM, milk fat, protein, and lactose yield and content (MFY, MPY, MLY, MFC, MPC, and MLC), and BW.

Article	Origin	n ¹	[t ₀ -t ₃] ²	DMI	MEI	RMY	FCM	MF			MP			ML			Experimental design
								YC	YC	YC	YC	YC	YC	YC	YC	YC	
Ostensen, 1997	Denmark	1	[1-24]	•	•	•	•	•	•	•	•	•	•	•	•	•	Kinetics of milk constituents.
Pinchasov, 1982	Israel	2	[1-23]	•	•	•	•	•	•	•	•	•	•	•	•	•	Control vs diet including liquid whey.
Rook, 1966	UK, England	2	[1-46]	•	•	•	•	•	•	•	•	•	•	•	•	•	2 programs of CO allocation (Constant daily or milk dependent amounts).
Soder, 1999	US, Pennsylvania	4	[1-13]	•	•	•	•	•	•	•	•	•	•	•	•	•	Control vs 3 diets including yeast, enzymes or yeast + enzymes.
Staples, 1990	US, Illinois	3	[1-9]	•	•	•	•	•	•	•	•	•	•	•	•	•	3 groups according to ovarian activity (Early, late or non-responders).
Swanson, 1967	US, Tennessee	2	[1-42]	•	•	•	•	•	•	•	•	•	•	•	•	•	Restricted vs Ad libitum FO allocation.
Taylor, 1984	UK, Scotland	6	[2-22]	•	•	•	•	•	•	•	•	•	•	•	•	•	Parity (P or M) × 3 systems of CO allocation (Constant or decreasing daily amounts or fixed daily amount according to milk produced in wk (2)).
Taylor, 1984	UK, Scotland	4	[3-27]	•	•	•	•	•	•	•	•	•	•	•	•	•	2 qualities of grass-silage (H or L digestibility) × 2 systems of CO allocation (Constant or variable daily amounts).
Tolkamp, 1998	UK, Scotland	3	[2-22]	•	•	•	•	•	•	•	•	•	•	•	•	•	2 control groups (Access to L or H protein feeds) an 1 choice group (access to both the L and H protein feeds).
Vérité, 1977	France	2	[1-13]	•	•	•	•	•	•	•	•	•	•	•	•	•	Control vs formaldehyde treated oil-meals.
Wallace, 1969	New Zealand	1	[9-32]	•	•	•	•	•	•	•	•	•	•	•	•	•	Study with identical twins (Lactating vs dry cow).
Wiktorsson, 1971	Sweden	6	[1-40]	•	•	•	•	•	•	•	•	•	•	•	•	•	3 levels of feeding (L, S or H) over 3 consecutive experimental lactations.
Wiktorsson, 1973	Sweden	2	[1-8]	•	•	•	•	•	•	•	•	•	•	•	•	•	Ad libitum vs restricted feeding of hay and CO.
Wohlt, 1978	US, Illinois	5	[1-43]	•	•	•	•	•	•	•	•	•	•	•	•	•	5 CO mixtures (No supplemental N, urea, L or H soybean meal, or urea + L soybean meal).
Wohlt, 1991	US, New Jersey	4	[1-18]	•	•	•	•	•	•	•	•	•	•	•	•	•	Control diet (12% CP) vs 3 protein sources (16% CP with soybean meal, fish meal or corn gluten meal).

• Data recorded weekly over the experimental period.

* Data recorded monthly over the experimental period.

¹ Number of treatment groups included in the database.² Recorded experimental period in weeks after calving; t₀ = first record, t₃ = last record.³ VH = Very high, H = High, S = Standard, L = Low.⁴ CO = concentrate, FO = forage.⁵ P = primiparous, M = multiparous.

MATERIALS AND METHODS

Compilation of the Literature

Articles and experimental designs. Experimental factors and results published in 37 articles covering input/output kinetics of lactating dairy cows were collected in the database. The articles, published between 1959 and 1999, reported trials performed in North America ($n = 17$), Europe ($n = 17$), Asia ($n = 1$), Africa ($n = 1$), and Oceania ($n = 1$; Table 1). The criteria used for inclusion were the existence of data concerning the kinetics of DMI (kg/d) and/or metabolizable energy intake (MEI, Mcal/d), raw milk yield (RMY, kg/d) and/or 4% FCM yield (kg/d), and BW (kg), all of which had to have been recorded for at least the first 8 wk of lactation. When available, the kinetics of milk fat yield (MFY, g/d) or content (MFC, g/kg) [MFC = MFY/RMY], milk protein yield (MPY, g/d) or content (MPC, g/kg) [MPC = MPY/RMY], and milk lactose yield (MLY, g/d) or content (MLC, g/kg) [MLC = MLY/RMY] were recorded (Table 1). The data sets used were weekly (32 articles) or monthly means (five articles) of daily records. Most of the data were published as graphs; consequently, they were stored in the database after digitalization. Each graph was scanned (IrfanView 3.36, Irfan Skiljan, <http://www.irfanview.com/>), and the picture file was incorporated as the background of an indexed graphical interface. Relative positions and scales of the picture axis were used to calibrate (X,Y) coordinates, and data points were translated into numerical values. These calculations were performed with Excel 2000 (Microsoft Corporation). This digitalization procedure was tested on simulated graphs. This method was found to be unbiased and accurate with less than 1% error.

The 37 articles included 140 treatments that were applied to groups of 3 to 277 cows (16.0 ± 27.6 animals/treatment group, mean $\pm$ SD). Most of these studies were aimed at investigating the effect of defined feeding strategies or types of diet on dynamic animal responses (Table 1). Cows were generally blocked into groups according to parity, BW, breed, calving date, and milk yield of previous lactation or early performance from the current lactation. They were then randomly assigned to each treatment group, generally at calving, and maintained in carefully controlled conditions of feeding and management over the experimental periods.

Animals and housing. The experiments were mainly conducted with Holstein-Friesian cows. However, the two trials reported by Wiktorsson (1971, 1973) were performed with cows of the Swedish Red and White breed. Ayrshire cows (pure- or cross-bred) comprised half of the livestock used in the experiment of

Garnsworthy (1982). Moreover, Ayrshire and Guernsey breeds were involved in the trial of Everson (1976), and Jersey cows in the trial of Swanson (1962). Within a treatment group, animals were predominantly of the same parity: 51 treatments used primiparous cows (Primi) and 89 multiparous cows (Multi; including 10 heterogeneous treatment groups with between 25 to 34% Primi which were treated as Multi). Animals were mostly housed individually in tie stalls or stanchion barns.

Diets and feeding. Cows from each treatment group were individually fed during one or several experimental subperiods according to a given nutritional plan. The dietary treatments were designed using combinations of the type of diet and its allocation system. The feeding regimens used three basic types of feeds: forage (FO), concentrate (CO), and TMR. The feed allocation systems were applied to either FO, CO or TMR, and there were four major types: 1) Restricted: allowance according to a predetermined flat rate or gradual increase up to a ceiling during the experimental period; 2) Ad libitum: feed allowance to appetite (seven papers reported a standard daily ort of 5 to 12% on a DM basis allowed); 3) Fitted: feed allowance adjusted at given intervals to current yield of milk (for production requirements) and/or BW (for maintenance requirements)—the rate of feeding per unit output (kg FCM, kg RMY, kg BW, or $\text{kg BW}^{0.75}$) was constant throughout the whole experimental period or gradually changed; and 4) Mixed: allowance of part of the ration in a restricted manner, the remainder being fed in a fitted manner. As a codifying rule, if a treatment group was fed more than 50% of the diet (in kg DM) ad libitum, fitted, or restricted, it was labeled as such. Since the fitted system was applied on the basis of expected nutrient requirements, the rate of feeding per unit output determined the allocation scheme. Thus, depending on the rate, the fitted system could be close to the ad libitum system (liberal allocation) or close to the restricted system (limited allocation). A total of 111 different feed-stuffs were used in these experiments: 29 TMR, 38 FO, and 44 CO. The FO were either hays (mainly meadow grass or alfalfa), grass or corn silages. The CO were mixtures of cereals (mainly barley, corn or oats), cereal byproducts (mainly wheat bran, brewers grains or corn gluten meal), oil meals (mainly soybean meal, peanut meal, rapeseed meal, coconut meal or cotton meal), and agro-industrial byproducts (mainly sugar beet pulp or molasses). The TMR were mixtures of roughages (mainly corn silage, meadow or alfalfa hay, or grass silage) and energy feeds (commercial dairy compound or mixtures of barley, corn, sugar beet pulp, brewers grains, and oil meals). All the available data concerning

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the chemical composition of feeds were systematically recorded in the database.

Analysis and records. In the majority of cases, feed allowance and intake were weighed daily. In most of the trials, samples of feed were collected weekly for pooled monthly chemical analyses, which were carried out according to conventional AOAC methods. Cows were generally machine-milked twice daily, except in Pinchasov (1982) and three treatment groups in DePeters (1985) for which cows were milked three times a day. Analysis of milk composition was generally performed monthly on weekly-pooled frozen samples. MFC was determined using the Babcock method (in the United States), the Gerber method (in Europe), or by infrared analysis (in the 1990's). MPC was assayed using Kjeldahl determination ($N \times 6.38$), orange G dye binding method (Udy, 1956), amido-black colorimetry (Posthumus, 1960) or infrared analysis. The MLC content was determined according to Somogyi (1952), Rook and Line (1961), or infrared analysis. The energy values of feeds were calculated or estimated by the authors according to the method generally used in the corresponding country. Animals were usually weighed twice per month on 2 consecutive d at the same hour.

Data Analysis

Additional variables. The percentages of FO and CO in diets allowed the calculation of the DMI of FO (kg/d), and CO (kg/d). DMI of the TMR was also noted (kg/d). The BW was used as such and also corrected for expected changes in gastrointestinal fill related to DMI, where a mean digestive tract content correction factor of 4 kg/kg DMI was used, assuming an increase in the weight of the reticulo-rumen content of 3 kg/kg DMI (Rémond, 1988) and an additional increase in intestinal content of 1 kg/kg DMI (Chilliard et al., 1987) [Empty BW (EBW, kg) = BW (kg) - 4 × DMI (kg)]. This correction was made to reduce the variability in the evolution of BW, especially in early lactation when DMI increased, and to estimate the real loss and gain of body reserves.

Treatment group general outcomes. Letting Y be the response variable (DMI, FO DMI, CO DMI, TMR DMI, MEL, RMY, FCM, MFY, MFC, MPY, MPC, MLY, MLC, BW, or EBW), the mean values of Y between wk 1 and 8 of lactation (Y[1-8]) were calculated for each treatment group. This measure was regarded as an overall level indicator of the Y-kinetic, from a static standpoint.

Two sequential mixed models were fitted with Proc MIXED of SAS (1992) to determine the effects of parity and year of publication (YOP) on Y[1-8]. The first model

focuses on the effect of parity on the slope of the regression:

$$Y[1-8]_{ijk} = P_j + t_k + B_j \cdot YOP + e_{ijk}, \quad [1]$$

where,

P_j = fixed effect of parity group j (j = 1, 2+),
 t_k = random effect of trial k (various number of trial according to Y[1-8]),
 B_j = regression coefficient of Y[1-8] on YOP for parity group j,
 e_{ijk} = error term ~ $N(0, \sigma_e^2)$.

A significant effect of P_j indicated that the intercepts of the slope of the linear regression of Y[1-8] on YOP were different from zero for at least one parity group. Therefore, a second model was fitted as follows:

$$Y[1-8]_{ijk} = \mu + P_j + t_k + (\beta_0 + \beta_j) \cdot YOP + e_{ijk}, \quad [2]$$

where symbols are as previously defined with the following changes:

μ = overall mean,
 β_0 = overall regression coefficient of Y[1-8] on YOP,
 β_j = deviation of regression coefficient of Y[1-8] on YOP from the overall regression coefficient for parity group j.

A significant β_j effect indicated that the slope of Y[1-8] on YOP was different for parity groups. Because of the unequal number of lactation (cow-year) between treatment groups and since the standard errors of Y by week were generally not known, least-squares were weighted with $\sqrt{N_i}$, where N_i was the number of lactations of treatment group i.

This first statistical model was aimed at giving an overview of the database without respect of dynamic aspects of lactation.

Modeling kinetics. Among the group of curves associated with lactation in the dairy cow, the kinetics of RMY have been most often described and modeled with time dependent functions (see reviews of Rowlands et al., 1982; Masselin et al., 1987; Papajcsik and Boderio, 1988; Rook et al., 1993). Among them, the gamma function $y(t) = a \cdot t^b \cdot e^{-ct}$ proposed by Wood (1967, 1968, 1969, 1977) has been extensively used to summarize the pattern of lactational performance. In this function, y(t) is the average daily milk yield in wk t of lactation, and a, b, and c are positive parameters that determine the scale and shape of the curve. While improving the pion-

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earing work of Wood, several authors have developed alternative forms of this model (Kuck et al., 1976; Cobby and Le Du, 1978; Dhanoa, 1981; Schneeberger, 1981). More recently, Goodall and Sprevak extended the fitting properties of Wood's model with stochastic (1984) and recursive (1985) procedures. Since the 1980's, numerous authors have suggested other mathematical approaches for fitting the milk yield $\times$ time data, either empirical (Emmans et al., 1983; Grossman and Koops, 1988; Morant and Gnanasakthy, 1989; Rook et al., 1993; Grossman et al., 1999), mechanistic (Neal and Thornley, 1983; Dijkstra et al., 1997), nonparametric (Elston et al., 1989) or autoregressive (Dhanoa and Le Du, 1982; Deluyker et al., 1990). Much less research has been undertaken on specific mathematical models to fit other curves characterizing the lactation profile. Nevertheless, several authors have proposed an application of their milk model to milk constituent yields (Schneeberger, 1979; Morant and Gnanasakthy, 1989) or contents (Wood, 1976), or to BW changes (Wood, 1979; Emmans et al., 1983). Stanton et al. (1992) proposed a statistical mixed model for milk, fat, and protein lactation curves. When fitting intake kinetics, Ostergaard (1979) proposed, in the context of ad libitum intake, to use the function $y(t) = a - b \cdot e^{-ct} - d \cdot t$, where $y(t)$ is the average daily DMI in wk t , and a , b , and c are positive parameters which determine the scale and shape of the curve. In the present paper, we wanted to use 1) the same model to fit the kinetics of all variables Y , and 2) a model which parameters quantified a specific and concrete aspect of the global pattern of the curve. This model was aimed at summarizing all curves with the same analytical rule in equivalent vectors of parameters. Observed kinetics of Y over the recorded experimental period $[t_0; t_3]$ ($t_0 \geq 1$ and $t_3 \leq 45$) of each treatment group were then summarized with the following triphasic model (only works concerning DMI, RMY, EBW, and MFY are considered in the present paper).

$$Y^*(t) = \begin{cases} Y_C + k_E \cdot t & \text{If } t \in [t_0; t_1] \\ Y_M & \text{If } t \in [t_1; t_2] \\ Y_M + k_L \cdot (t_2 - t) & \text{If } t \in [t_2; t_3] \end{cases} \quad [3]$$

where,

Y^* = predicted value of DMI, RMY, MFY, and EBW,

t = time, in weeks of lactation from calving,

$[t_0; t_1]$ = early stage of lactation,

$[t_1; t_2]$ = middle stage of lactation,

$[t_2; t_3]$ = late stage of lactation,

k_E = slope of Y as a function of time in early stage of lactation ($k_E \geq 0$ for Y = DMI, RMY, and MFY; $k_E \leq 0$ for Y = EBW),

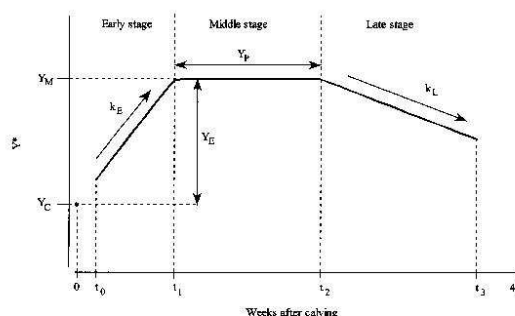


Figure 1. Model proposed by Grossman *et al.* (1999) (smoothing logistic transition between intersecting straight lines):

$$Y^*(t) = Y_M + k_E(t - t_1) - r_1 k_E \text{Ln} \left[\frac{e^{Y_F/r_1} + e^{t_1/r_1}}{1 + e^{t_1/r_1}} \right] + r_2 k_L \text{Ln} \left[\frac{e^{Y_F/r_2} + e^{t_2/r_2}}{1 + e^{t_2/r_2}} \right],$$

where Y_M = plateau value of Y in middle stage, k_E = slope of Y in early stage, t_1 = upper bound of early stage, r_1 and r_2 = durations of smoothing transition between linear phases set to 0.15 wk, k_L = slope of Y in late stage, and t_2 = upper bound of middle stage. Additional parameters: Y_C = extrapolated value of Y at calving time ($t = 0$), Y_E = total variation in Y during early stage, Y_F = duration of middle stage.

k_L = slope of Y as a function of time in late stage of lactation ($k_L \leq 0$ for Y = DMI, RMY, and MFY; $k_L \geq 0$ for Y = EBW),

Y_C = extrapolated value of Y for $t = 0$, calving time,

Y_M = plateau value of Y in middle stage lactation.

Using the above model, each stage was summarized by its linear trend: increasing or decreasing for early and late stages, constant for the middle stage. In order to build a smooth function from the linear equations system [3], we used the smoothing logistic transition between intersecting straight lines proposed by Koops and Grossman (1993) and employed by Grossman (1999) in the case of Y = RMY. Thus, the model finally used for each Y variable was (Figure 1):

$$Y^*(t) = Y_M + k_E(t - t_1) - r_1 k_E \text{Ln} \left[\frac{e^{Y_F/r_1} + e^{t_1/r_1}}{1 + e^{t_1/r_1}} \right] + r_2 k_L \text{Ln} \left[\frac{e^{Y_F/r_2} + e^{t_2/r_2}}{1 + e^{t_2/r_2}} \right]. \quad [4]$$

In equation [4], r_1 and r_2 were the measures of duration of smoothing transition between linear tendencies,

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from early to middle, and middle to late stages respectively. These two parameters governed the curvature of the model, with large values leading to smoother transitions. The values of the parameters r_1 and r_2 were fixed at 0.15 wk, which is equivalent to the value of 1 d used by Grossman (1999) for daily datasets. This low value only conferred smoothing properties to these parameters. As seen in Figures 2a and 2b, increasing

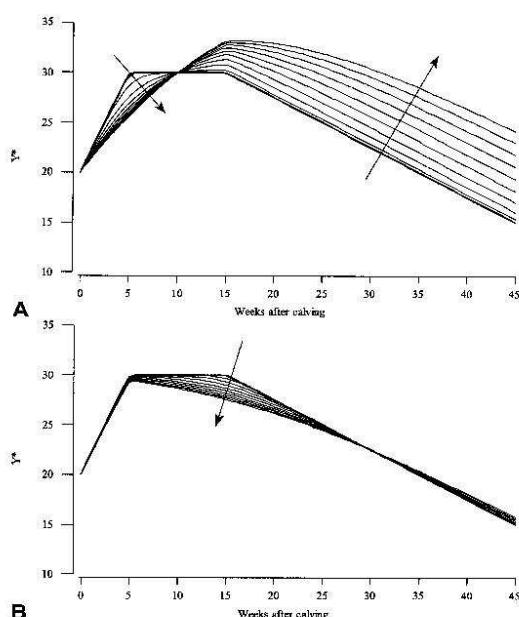


Figure 2a. Effect of increasing values of parameter r_1 on the shape of the model proposed by Grossman et al. (1999):

$$Y^*(t) = Y_M + k_E(t - t_1) - r_1 k_E \ln \left[\frac{e^{k_E t_1} + e^{t_1/r_1}}{1 + e^{t_1/r_1}} \right] + r_2 k_L \ln \left[\frac{e^{k_L t_2} + e^{t_2/r_2}}{1 + e^{t_2/r_2}} \right]$$

(Model parameters: $Y_M = 30.0$, $k_E = 2.0$, $k_L = -0.5$, $t_1 = 5$, $t_2 = 15$, $r_1 = \{0.15, 1, 2, 3, \dots, 9\}$, $r_2 = 0.15$).

Figure 2b. Effect of increasing values of parameter r_2 on the shape of the model proposed by Grossman et al. (1999):

$$Y^*(t) = Y_M + k_E(t - t_1) - r_1 k_E \ln \left[\frac{e^{k_E t_1} + e^{t_1/r_1}}{1 + e^{t_1/r_1}} \right] + r_2 k_L \ln \left[\frac{e^{k_L t_2} + e^{t_2/r_2}}{1 + e^{t_2/r_2}} \right]$$

(Model parameters: $Y_M = 30.0$, $k_E = 2.0$, $k_L = -0.5$, $t_1 = 5$, $t_2 = 15$, $r_1 = 0.15$, $r_2 = \{0.15, 1, 2, 3, \dots, 9\}$).

values of r_1 and r_2 spread the duration of the smooth transition and then distorted the curve from the pattern of Figure 1 (all the other parameters' values were constant). The model set to an arbitrary slightly smooth curve (1 d) is locked on the fitting pattern of Figure 1, with a valid assumption of the middle stage being a plateau at the level of Y_M , beginning in wk t_1 and ending in wk t_2 . Hence, the model was completely defined with the vector $[Y_M, t_1, t_2, k_E, k_L]$ and the constraint $t_2 \geq t_1$. Estimates for these five parameters were determined using nonlinear least squares methods using Proc NLIN of SAS (1992). Observed dependent variables were weekly means from the digitized dataset. No particular precaution was taken in the fitting procedure to deal with the natural serial correlation between observations. The coefficient of determination (R^2) and the root mean square error (RMSE) were computed and used as goodness-of-fit indicators. The asymptotic standard errors of the parameter estimates Y_M , t_1 , t_2 , k_E , k_L were denoted s_M , s_1 , s_2 , s_{kE} , and s_{kL} respectively. The total variation in Y (Y_E , in the unit of Y) during the early stage and its standard error s_E were estimated with the following formulas:

$$Y_E = k_E \cdot t_1 + \text{cov}(k_E, t_1), \quad [5a]$$

$$s_E^2 \approx k_E^2 s_1^2 + t_1^2 s_{kE}^2 + 2 k_E t_1 \text{cov}(k_E, t_1), \quad [5b]$$

where $\text{cov}(k_E, t_1)$ is the asymptotic covariance of parameter estimates k_E and t_1 . The extrapolated value of Y at calving (Y_C , in unit of Y) and its standard error s_C were estimated with the following formulas:

$$Y_C = Y_M - Y_E, \quad [6a]$$

$$s_C^2 \approx s_M^2 + k_E^2 s_1^2 + t_1^2 s_{kE}^2 - 2 k_E \text{cov}(Y_M, t_1) - 2 t_1 \text{cov}(Y_M, k_E) - 2 k_E t_1 \text{cov}(t_1, k_E), \quad [6b]$$

where $\text{cov}(Y_M, t_1)$ and $\text{cov}(Y_M, k_E)$ are the asymptotic covariances of parameter estimates Y_M and t_1 , and Y_M and k_E respectively. Grossman (1999) proposed to define the persistency of RMY as the duration of the middle stage. We employed this terminology for all kinetics. The persistency of Y (Y_P , in wk) and its standard error s_P were estimated with the following formulas:

$$Y_P = t_2 - t_1, \quad [7a]$$

$$s_P^2 \approx s_1^2 + s_2^2 - 2 \cdot \text{cov}(t_1, t_2), \quad [7b]$$

where $\text{cov}(t_1, t_2)$ is the asymptotic covariance of parameter estimates t_1 and t_2 . Estimates of parameters were used for further analysis if the following conditions were respected:

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- t_1 : $t_1 \neq t_0$ (early stage detected)
 t_2 : $t_2 \neq t_0$ and $t_2 \neq t_3$ (middle stage detected)
 k_E : $t_1 \neq t_0$ (early stage detected)
 k_L : $t_3 - t_2 > 3$ (slope estimated over at least 3 wk)
 Y_M : $t_3 > t_1$ (end of early stage detected)
 Y_E and Y_C : $Y_M > Y_C$ (valid estimate of a positive value of Y_E)
 Y_P : $t_2 \neq t_3$ (non null persistency)

Finally a database was created with, for each Y-kinetic of each treatment group, the vector of valid estimates of eight parameters Y_C , Y_E , Y_M , k_E , k_L , t_1 , t_2 , Y_P and their standard errors s_C , s_E , s_M , s_{k_E} , s_{k_L} , s_1 , s_2 , and s_P .

This modeling approach allows one to decompose and to quantify the pattern of each Y-kinetic by the use of two slopes (k_E and k_L), two times (t_1 and t_2), one duration (Y_P), two levels (Y_M and Y_C), and one change (Y_E).

Two sequential mixed models were fitted with Proc MIXED of SAS (1992) to determine the effects of parity and YOP on parameter estimates. The first model focuses on the effect of parity on the slope of regression:

$$(\theta_p)_{ijk} = P_j + t_k + B_j \cdot YOP + e_{ijk}, \quad [8]$$

where,

- $(\theta_p)_{ijk}$ = estimate of the parameter $\theta_p = \{Y_C, Y_E, Y_M, k_E, k_L, t_1, t_2, Y_P\}$ for the Y-kinetic of treatment group i in trial k (various number of treatment groups and trials according to Y-kinetic and parameter θ_p) for parity group j ($j = 1, 2, +$),
 P_j = fixed effect of parity group j ,
 t_k = random effect of trial k ,
 B_j = regression coefficient of θ_p on YOP for parity group j ,
 e_{ijk} = error term $\sim N(0, \sigma_e^2)$.

As in model [1], a significant effect of B_j indicated that the slope of the linear regression of θ_p on YOP was different from zero for at least one parity group. Therefore, a second model was fitted as follows:

$$(\theta_p)_{ijk} = \mu + P_j + t_k + (\beta_0 + \beta_j) \cdot YOP + e_{ijk}, \quad [9]$$

where symbols are as previously defined with the following changes:

- μ = overall mean,
 β_0 = overall regression coefficient of θ_p on YOP,
 β_j = deviation of regression coefficient of θ_p on YOP from the overall regression coefficient for parity group j .

As in model [2], a significant β_j effect indicated that the slope of θ_p on YOP was different for parity groups.

To account for unequal accuracy of estimates, least-squares means were weighted as follow: for parameter θ_p with standard error s_{θ_p} , w_1 is defined as the inverse of the squared of s_{θ_p} , and $\bar{w}$ as its mean value over available data. Thus, $w_2 = w_1/\bar{w}$ was used as weight (St-Pierre, 2001). This statistical model was aimed at quantifying the variability of the pattern of Y-kinetics across YOP and parity.

Three levels of correlations between parameter estimates were examined for kinetics of DMI, EBW, RMY and MFY:

- (1) Between parameter estimates of the same Y-kinetic within treatment group (e.g. DMI_{kE} and DMI_{kL} for the first treatment group of Johnson (1983)). These correlations straight out of NLIN were implied by the mathematical properties of model [4].
- (2) Between parameter estimates of the same Y-kinetic across treatment groups (e.g., EBW_C and EBW_E). These correlations provided information about the structural dependencies within the pattern of each Y-kinetic.
- (3) Between parameter estimates between Y-kinetics across treatment groups (parameters can be equivalent, e.g. DMI_M and RMY_M , or different, e.g. DMI_{kE} and RMY_{kL}). These correlations provided information about the relationships between the patterns of different Y-kinetics.

Asymptotic correlations of level (1) are model-dependent and therefore not different between Y-kinetics. The sign of parameters k_E (negative for EBW, positive for DMI, RMY, and MFY) and k_L (positive for EBW, negative for DMI, RMY, and MFY) determine the sign of all correlations except that between t_1 and t_2 . This latter correlation is always negative and induced by the structural constraint $t_2 \geq t_1$. Non null correlations exist within stages (within linear segments): between k_E and t_1 in early stage, between t_1 and Y_M and between Y_M and t_2 in middle stage, and between t_2 and k_L in late stage. Correlations between parameters of different stage were approximately null (in particular between k_E and Y_M , Y_M , and k_L , and k_E and k_L).

These results justify the corrections made with covariance components for unbiased estimates of parameter Y_E [5a] and standard error of parameters Y_E [5b], Y_C [6b], and Y_P [7b].

Correlations of levels (2) and (3) were all calculated within parity groups and within allocation systems A, F, and R. Only correlations with the same sign and an absolute value greater than 0.5 in each parity group and allocation system were retained. Correlations within Y-kinetic between parameters Y_P and Y_{t2} and between

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parameters Y_{kE} and Y_E were removed since they were implied by construction ([6a] and [7a]). Finally the conditions were matched for two couples of parameters within the EBW-kinetic and four couples of parameters between kinetics of DMI, RMY and MFY. These six correlations by parity group and allocation system are presented in Table 6.

The following five couples of parameters (θ_Y , θ_X) were retained for further analysis: (a) (EBW_E , EBW_C), (b) (RMY_M , DMI_M), (c) (RMY_{KL} , DMI_{KL}), (d) (MFY_M , RMY_M), and (e) (MFY_{KL} , RMY_{KL}). Four sequential mixed models were fitted with Proc MIXED of SAS (1992) to determine the effect of parameter θ_X on θ_Y within parity. The first model focuses on the effect of parity on the slope of the regression.

$$(\theta_Y)_{ijk} = P_j + t_k + B_j \cdot (\theta_X)_{ijk} + e_{ijk}, \quad [10]$$

where,

- $(\theta_Y)_{ijk}$ = estimate of the parameter $\theta_Y = \{Y_C, Y_E, Y_M, k_E, k_L, t_1, t_2, Y_P\}$ for the Y-kinetic of treatment group i in trial k (various number of treatment groups and trial according to couple of parameters (θ_Y , θ_X) and Y-kinetic) for parity group j ($j = 1, 2+$),
 P_j = fixed effect of parity group j,
 t_k = random effect of trial k;
 B_j = regression coefficient of θ_Y on θ_X for parity group j;
 $(\theta_X)_{ijk}$ = estimate of the parameter $\theta_X = \{Y_C, Y_E, Y_M, k_E, k_L, t_1, t_2, Y_P\}$ for the Y-kinetic of treatment group i for parity group j,
 e_{ijk} = error term $\sim N(0, \sigma^2_e)$.

As in model [1] and [5], a significant effect of B_j indicated that the slope of the linear regression of θ_Y on θ_X was different from zero for at least one parity group. Therefore, a second model was fitted as follows:

$$(\theta_Y)_{ijk} = \mu + P_j + t_k + (\beta_0 + \beta_j) \cdot (\theta_X)_{ijk} + e_{ijk}, \quad [11]$$

where symbols are as previously defined with the following changes:

- μ = overall mean,
 β_0 = overall regression coefficient of θ_Y on θ_X ;
 β_j = deviation of regression coefficient of θ_Y on θ_X from the overall regression coefficient for parity group j.

As in model [2] and [6], a significant β_j effect indicated that the slope of θ_Y on θ_X was different for parity groups. If not significant, a third model was fitted as follows:

$$(\theta_Y)_{ijk} = \mu + P_j + t_k + \beta_0 \cdot (\theta_X)_{ijk} + e_{ijk}, \quad [12]$$

where symbols are as previously defined.

A significant P_j effect indicated that the intercept of the regression of θ_Y on θ_X was different for parity groups. If not significant, a fourth model was fitted as follows:

$$(\theta_Y)_{ijk} = \mu + t_k + \beta_0 \cdot (\theta_X)_{ijk} + e_{ijk}, \quad [13]$$

where symbols are as previously defined.

To account for unequal accuracies of estimates, least-squares were weighted as follow: for parameters θ_X and θ_Y with respective standard errors s_X and s_Y , w_1 is defined as the inverse of the product $s_X \cdot s_Y$, and $\bar{w}$ as its mean value over available data. Thus, $w_2 = w_1/\bar{w}$ was used as weight (St-Pierre, 2001). By this way, both error on θ_X and θ_Y were used to estimate the regression coefficients.

These four models were aimed at quantifying the relationships between:

- the loss of EBW in early lactation and the EBW at calving,
- the plateau values of RMY and DMI in middle stage of lactation,
- the slopes of decrease of RMY and DMI in late stage of lactation,
- the plateau values of MFY and RMY in middle stage of lactation,
- the slopes of decrease of MFY and RMY in late stage of lactation.

The choice of independent (Y) vs dependent variable (X) was set in the sense of prediction of performances. Dependent variables were thus, either state at calving (EBW_C) for prediction of EBW loss, characteristics of intake pattern (DMI_M and DMI_{KL}) for prediction of equivalent characteristics of RMY, or characteristics of milk yield pattern (RMY_M and RMY_{KL}) for prediction of equivalent characteristics of MFY pattern.

In statistical models [1], [2], [8], [9], [10], [11], [12], and [13], trials were considered as blocks and their effect was incorporated as random intercept. When significant, random slopes (interaction of trial by dependent variable) were incorporated in the reduced models [10], [11], [12], and [13]. This methodology takes into account the fact that observations within a given trial have more in common than observations across trials (St-Pierre, 2001).

RESULTS

Database

Diets. Table 2 describes the average chemical composition of diets fed to the 140 treatment groups. The

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Table 2. Chemical composition of diets (DM basis).

Item	n _A ¹	n _T ²	Mean	CV (%)	Minimum	Maximum
DM, %	25	92	57.5	37.1	27.2	93.4
Ash, %	17	66	7.4	23.1	5.0	11.2
Phosphorus, %	8	33	0.5	21.7	0.3	0.7
Calcium, %	8	33	0.8	13.3	0.8	0.9
OM, %	17	66	92.6	1.8	88.8	96.0
Digestible OM, %	3	11	64.2	8.6	58.6	75.5
CP, %	26	102	16.0	12.0	10.1	20.5
Digestible CP, %	6	17	12.1	15.0	10.4	16.2
Ether extract, %	18	71	4.0	31.0	2.0	7.3
Crude fiber, %	17	63	18.3	26.5	3.4	32.2
ADF, %	10	45	22.9	12.0	18.1	27.5
Acid detergent lignin, %	2	11	5.1	10.4	4.5	5.7
NDF, %	6	24	35.3	6.6	31.2	39.6
Gross energy, Mcal/kg	5	15	4.5	2.7	4.2	4.6
Digestible energy, Mcal/kg	3	6	3.2	6.3	2.9	3.4
Metabolizable energy, Mcal/kg	24	84	2.7	10.1	1.5	3.0
NE _L , Mcal/kg	9	28	1.6	17.2	0.9	2.0

¹Number of articles providing item chemical content data.²Number of treatment groups including item chemical content data.

availability of data was variable amongst articles. The major sources of variability appeared to be associated with DM, ash, phosphorus, ether extract, and crude fiber content (Coefficient of variation greater than 20%). Metabolizable energy and CP contents, ranging from 1.5 to 3.0 Mcal/kg DM and from 10.1 to 20.5% reflect experimental designs investigated.

A subset of 94 treatment groups were fed CO and FO separately, which ranged respectively from 17.9% to 75.9% and from 24.1% to 82.1% (DM basis) over wk 1 to 8 of lactation. A subset of 42 treatment groups were fed a TMR, including 4 treatment groups in DePeters et al. (1989) for which animals were fed both a TMR and FO at 13.7% or 25.9% of the total DMI. A subset of 4 treatment groups were only fed FO ad libitum (Mohrenweiser and Donker, 1968).

Feeding systems. A summary of feeding systems used across the 140 treatment groups is given in Table 3. From 1970 to 1999, TMR were only fed ad libitum.

Restricted allowances of FO or CO were used before 1984. Fitted or ad libitum programs of feeding FO or CO were investigated from 1965 to 1999. Figure 3 shows the average fractions of diet fed A, F, and R according to the decade the article was published. The major part of DMI was mainly fed in a restricted way before 1970 (> 50% DMI) and was primarily fed ad libitum after 1980 (from 53% to 100% DMI amongst treatment groups). Before 1980, the underlying research was aimed at measuring the quantitative effects of intake on lactational performance (Table 1). Since 1980, ad libitum systems have been used predominantly, reflecting practical on-farm conditions: qualitative effects, mainly that of feed type, were therefore studied. Thus, data gathered across treatment groups were highly unbalanced with respect to feeding system.

Treatment group outcomes. Table 4 provides weighted least squares means of Y[1-8] by parity group (models [1] and [2]). Except for MFC and MPC, the

Table 3. Feeding systems applied for the 140 treatments.

Diet			n ¹			YOP ³
FO ²	CO ²	TMR	Multiparous	Primiparous	Total	
Ad libitum			0	4	4	1968
Ad libitum	Ad libitum		5	1	6	1973-1997
Ad libitum	Fitted		31	13	44	1967-1993
Ad libitum	Restricted		4	5	9	1984
Fitted	Fitted		2	2	4	1992
Restricted	Mixed		8	0	8	1971-1983
Restricted	Fitted		10	1	11	1965-1979
Restricted	Restricted		0	12	12	1969-1975
		Ad libitum	29	13	42	1970-1999
Total			89	51	140	1969-1999

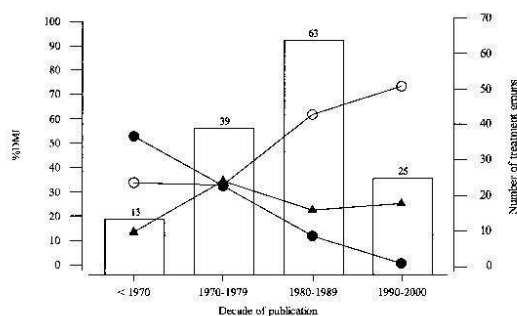
¹Number of treatment groups.²FO = forage, CO = concentrate.³YOP = year of publication.

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Table 4. Weighted least squares means and significance of effects of parity and year of publication on average dependant variables over the first 8 weeks of lactation.

Dependent variable ²	Multiparous			Primiparous			Effect of YOP ¹		
							Within parity ⁶		P value ⁷
	n ³	LSM ⁴	SEM ⁵	n	LSM	SEM	Multiparous	Primiparous	
DMI, kg/d	83	16.79 ^a	0.28	44	13.51 ^b	0.34	0.19 ^c	0.08 ^d	***
FO DMI, kg/d	56	7.40 ^a	0.58	33	6.13 ^b	0.67			NS
CO DMI, kg/d	54	9.10 ^a	0.48	27	7.09 ^b	0.66			NS
TMR DMI, kg/d ⁸	29	17.34 ^a	0.45	13	14.67 ^b	0.59	0.29	0.11	***
MEI, Mcal/d	64	42.61 ^a	1.10	32	34.66 ^b	1.39	0.59	0.41	***
RMV, kg/d	81	30.15 ^a	0.55	39	22.41 ^b	0.67	0.52 ^c	0.30 ^d	***
FCM, kg/d	53	28.06 ^a	0.58	25	20.89 ^b	0.71	0.37	0.38	***
MFY, g/d	45	1111 ^a	29	20	878 ^b	34	10	9	**
MFC, g/kg ⁹	73	37.80	0.77	30	39.15	0.89			NS
MPY, g/d	32	853 ^a	34	9	609 ^b	41	10	10	**
MPC, g/kg	54	31.64	0.59	13	31.31	0.66			NS
MLY, g/d	3	(1149) ¹⁰	(2)	3	(919)	(160)			ND ¹¹
MLC, g/kg ⁸	13	48.93	0.39	5	49.30	0.43	-0.13	0.08	*
BW, kg	89	578.7 ^a	4.9	50	503.0 ^b	5.8	2.3	1.2	***
EBW, kg	83	513.6 ^a	4.9	44	445.8 ^b	5.9	1.4	1.0	*

^{a,b}Least squares means within row with different superscripts differ ($P < 0.05$).^{c,d}Estimates of regression slope within row with different superscripts differ ($P < 0.05$).¹YOP = year of publication.²FO DMI = forage DMI, CO DMI = concentrate DMI, MEI = metabolizable energy intake, RMV = raw milk yield, MFY = milk fat yield, MFC = milk fat content, MPY = milk protein yield, MPC = milk protein content, MLY = milk lactose yield, MLC = milk lactose content, EBW = empty BW.³Number of treatment groups by parity group.⁴Weighted least squares mean of mixed model of dependent variable on YOP including fixed effect of parity and random effect of trial (see model [1]).⁵Standard error of the least squares mean.⁶Estimate of regression slope of dependent variable on YOP.⁷Regression slope of dependent variable on YOP different from zero for at least one parity group.⁸Random effect of trial not significant ($P > 0.1$).⁹Least squares means not significantly different at the level of 6%.¹⁰Group mean and standard error.¹¹Not determined.NS $P > 0.1$.* $P \leq 0.05$.** $P \leq 0.01$.*** $P \leq 0.001$.**Figure 3.** Number of treatment groups (histogram) and average fraction of diet (%DMI) fed, ad libitum (○), fitted to current performances (▲) or restricted (●) according to decade of article publication.

fixed effect of parity was significant ($P < 0.01$). Multi had higher DMI (+ 3.3 kg/d), higher FO DMI (+ 1.3 kg/d), higher CO DMI (+ 2.0 kg/d), higher TMDMI (+ 2.7 kg/d), and higher MEI (+ 8.0 Mcal/d) than Primi. Multi had higher RMV (+ 7.7 kg/d), higher FCM (+ 7.1 kg/d) than Primi. The higher level of RMV for Multi was associated with significantly higher levels of MFY (+ 233 g/d) and MPY (+ 244 g/d). Multi were heavier than Primi (BW: + 75.7 kg, EBW: + 67.8 kg). The effect of the YOP was found to be significant ($P < 0.01$) for at least one parity group for all variables except MFC, MPC, FO DMI, and CO DMI. Significant effects of the YOP were different between parity groups for variables DMI and RMV.

Kinetic Patterns

Table 5 provides weighted least squares means and standard errors of least squares means of parameter

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Table 5. Weighted least squares means and significance of effects of parity and year of publication on parameter estimates for kinetics of DMI, Raw milk yield (RMY), Milk fat yield (MFY), and Empty BW (EBW).

Kinetic	Parameter ²	Effect of YOP ¹								
		Multiparous			Primiparous			Within parity ⁶		
		n ³	LSM ⁴	SEM ⁵	n	LSM	SEM	Multiparous	Primiparous	P-value ⁷
DMI	DMI _C	75	12.46 ^a	0.49	37	10.01 ^b	0.56	0.16 ^c	0.02 ^d	*
	k _B	81	1.16 ^a	0.15	41	0.94 ^b	0.16			NS
	t ₁	81	5.8	0.4	41	6.7	0.5	0.0	0.2	*
	DMI _B	75	6.41	0.46	37	5.72	0.52	0.05	0.12	*
	DMI _M	83	18.63 ^a	0.41	41	16.69 ^b	0.33	0.22	0.13	***
	t ₂	62	12.6 ^b	1.4	36	26.4 ^a	1.7			NS
	k _L	53	-0.17 ^b	0.01	31	-0.08 ^a	0.02			NS
	DMI _P	58	6.9 ^b	1.2	36	19.8 ^a	1.5			NS
EBW	EBW _C	70	557.1 ^a	7.0	36	476.9 ^b	8.6	2.4	1.6	**
	k _B	81	-10.2	1.2	42	-8.0	1.5	-0.2	-0.3	*
	t ₁	81	4.4 ^a	0.2	42	3.3 ^b	0.3			NS
	EBW _B	70	-56.2 ^b	4.5	36	-42.0 ^a	5.4	-0.9	-0.7	†
	EBW _M	83	501.4 ^a	5.2	44	431.6 ^b	4.3	1.6	1.3	**
	t ₂	72	12.0	1.2	38	13.3	1.4	-0.2	-0.2	†
	k _L	68	2.4	0.2	38	2.5	0.2			NS
	EBW _P	60	8.7	0.9	34	8.8	1.1			NS
RMY	RMY _C	64	22.10 ^a	0.94	30	15.07 ^b	1.07	0.33	0.17	*
	k _B	75	2.62	0.39	36	2.31	0.41			NS
	t ₁	75	3.9	0.2	36	4.4	0.3			NS
	RMY _B	64	10.20 ^a	1.00	30	8.29 ^b	1.18			NS
	RMY _M	81	31.67 ^a	0.66	38	23.74 ^b	0.77	0.42	0.36	***
	t ₂	75	7.5 ^b	0.5	36	9.0 ^a	0.7	0.0	0.3	*
	k _L	78	-0.56 ^b	0.02	37	-0.29 ^a	0.03			NS
	RMY _P	66	4.1 ^b	0.4	26	8.1 ^a	0.7	0.1 ^d	0.3 ^e	*
MFY ⁸	MFY _C	2	ND ⁹	ND	2	ND	ND			ND
	k _B	13	11	3	10	10	4			NS
	t ₁	13	4.4	1.6	10	3.4	1.7			NS
	MFY _B	2	ND	ND	2	ND	ND			ND
	MFY _M	45	1201 ^a	38	20	900 ^b	42	0	15	†
	t ₂	25	6.6 ^b	1.0	15	9.8 ^a	1.2			NS
	k _L	45	-18 ^b	1	20	-11 ^a	1			NS
	MFY _P	8	3.9 ^b	0.9	8	4.2 ^a	1.2			NS

^{a,b}Least squares means within row with different superscripts differ ($P < 0.05$).¹YOP = year of publication.²Y_C = Y at calving, k_B and k_L = slope of Y in early and late lactation, t₁ and t₂ = lower and upper bounds of middle stage, Y_B = variation in Y in early stage, Y_M = plateau value of Y in middle stage, Y_P = duration of middle stage.³Number of treatment groups by parity.⁴Weighted least squares mean of mixed model of parameter on YOP including fixed effect of parity and random effect of trial (see model [8]).⁵Standard error of the least squares mean.⁶Estimate of regression slope of parameter on YOP.⁷Regression slope of parameter on YOP different from zero for at least one parity group.⁸Random intercept nonsignificant for all parameters ($P > 0.1$).⁹Not determined.NS $P > 0.1$.† $P \leq 0.1$.* $P \leq 0.05$.** $P \leq 0.01$.*** $P \leq 0.001$.

estimates by parity group for variables DMI, RMY, EBW, and MFY (models [8] and [9]). Values cited in the following text are weighted least squares means $\pm$ standard error within parity group.

Dry matter intake. Goodness-of-fit was not different between parity groups, and the overall average RMSE was 0.48 ± 0.24 kg/d. The distribution of the 124 R² calculated is given in Figure 4 ($R^2 = 91.3 \pm 7.9\%$).

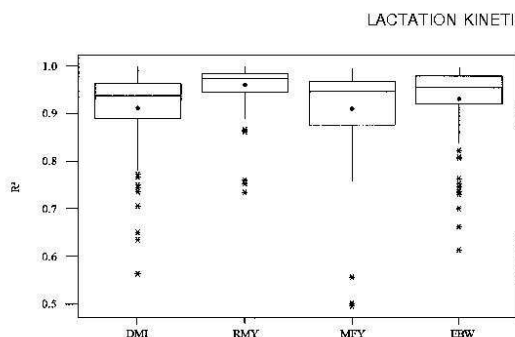


Figure 4. Box plot of R^2 of model of Grossman et al. (1999) fitted to treatment group kinetics of DMI, raw milk yield (RMY), milk fat yield (MFY), and empty BW (EBW). Bottom and top edges of the box are located at the sample 25th and 75th percentiles; center horizontal line is at the sample median; central filled circle is at the sample mean; asterisks are values more extreme than three interquartile ranges (distance between the 25th and 75th sample percentiles).

From 1959 to 1999, the annual increase in DMI_M was significant ($P < 0.001$; Multi: $+0.22$ kg/yr, Primi: $+0.13$ kg/yr). This increase was obtained with a higher level of intake at calving mainly for Multi (Multi: DMI_C : $+0.16$ kg/yr, Primi: DMI_C : $+0.02$ kg/yr) and a higher increase in intake in early lactation mainly for Primi (Multi: DMI_E : $+0.05$ kg/yr, Primi: DMI_E : $+0.12$ kg/yr). No significant effect of the YOP on the k_E was found. Nevertheless, the annual increase in t_1 was significant ($P < 0.05$) and nonnull for Primi ($+0.2$ wk/yr). Effect of YOP was not significant for parameters t_2 , k_L , and DMI_P .

Weighted least squares means of parameters were different between parity group except for t_1 (6.3 ± 0.5 wk for pooled parity groups) and DMI_E (6.18 ± 0.48 kg for pooled parity groups). Primi had a lower level of DMI at calving than Multi (DMI_C : -2.44 kg) and a lower slope of increase in early stage (Primi: $k_E = 0.94 \pm 0.16$ kg/wk, Multi: $k_E = 1.16 \pm 0.15$ kg/wk) which induced a lower level in middle stage (Primi: $DMI_M = 15.69 \pm 0.33$ kg, Multi: $DMI_M = 18.63 \pm 0.41$ kg). It should be mentioned that the range of k_E estimates was higher for restricted schemes of feeding than for others. The end of the plateau stage was reached significantly later by Primi ($t_2 = 26.4 \pm 1.7$ wk, $DMI_P = 19.8 \pm 1.5$ wk) than Multi ($t_2 = 12.6 \pm 1.4$ wk, $DMI_P = 6.9 \pm 1.2$ wk).

No correlation was retained within the kinetic of DMI. Only kinetics of the ad libitum allocation system could express animal requirements. Patterns of the fitted and restricted allocation systems are mainly determined by experimental designs.

Empty body weight. Goodness-of-fit was not different between parity groups, and the overall average

RMSE was 4.2 ± 1.8 kg. The distribution of the 128 R^2 calculated is given in Figure 4 ($R^2 = 93.1 \pm 7.4\%$).

From 1959 to 1999, the annual increases in EBW_M and EBW_C were significant ($P < 0.01$) and not different between parity groups (EBW_M : $+1.5$ kg/yr and EBW_C : $+2.1$ kg/yr for pooled parity groups). The effect of YOP was higher for EBW_C than for EBW_M because of the associated reduction in k_E while t_1 was not affected. Thus, Primi and Multi were heavier at calving and their total loss of EBW in early stage was greater (EBW_E : -0.8 kg/yr for pooled parity groups). Time t_2 was also influenced by the YOP for both parity groups (t_2 : -0.2 wk/yr for pooled parity groups). No significant effect of the YOP on parameters k_L and EBW_P was detected.

Weighted least squares means of parameters were different between parity group except for the slopes k_E and k_L (-9.4 ± 1.3 kg/wk and 2.4 ± 0.2 kg/wk respectively for pooled parity groups) and for the time t_2 (12.4 ± 1.3 wk for pooled parity groups). Multi had a higher level of EBW_C ($+80.2$ kg) and a higher level of EBW_M ($+69.8$ kg) induced by a greater EBW_E in early stage (-14.2 kg) achieved 1.1 wk later than Primi (Primi: $t_1 = 3.3 \pm 0.3$, Multi: $t_1 = 4.4 \pm 0.2$). Duration of the middle stage (plateau at minimum EBW before regrowth) was not different between parity groups ($EBW_P = 8.7 \pm 1.0$ wk).

The only correlations between parameters within Y-kinetics deemed coherent within parity and allocation system (Table 6) were found between EBW_E and EBW_C , and between EBW_M and EBW_C (respectively $\rho = -0.73$ and $\rho = +0.89$ for pooled data). These relationships stressed the primary influence of animal size at calving on the early decrease of BW.

The relationship between EBW_E and EBW_C is presented in Figure 5. Weighting factors applied were globally homogeneous across treatment groups. Slopes of EBW_E on EBW_C were different from zero within parity ($P < 0.001$, model [10]). The difference in the slopes between parity groups was not significant ($P = 0.688$, model [11]) and the difference in the intercepts between parity group was significant ($P < 0.001$, model [12]).

The regression equation proposed was obtained from [12]:

$$EBW_E \text{ (kg)} = (145.9 + \Delta) - 0.39 EBW_C \text{ (kg)}. \quad [14]$$

where $\Delta = 0.0$ for Primi and $\Delta = 19.6$ for Multi. This model was fitted for 104 treatment groups spread across 34 trials, and had a residual error of 9.0 kg (residual standard error of random intercept: 13.0 kg). Regression coefficient of model [14] gives an estimate of the within-trial effect of animal weight at calving on early depletion.

Raw milk yield. Goodness-of-fit was not different between parity groups and the overall average RMSE

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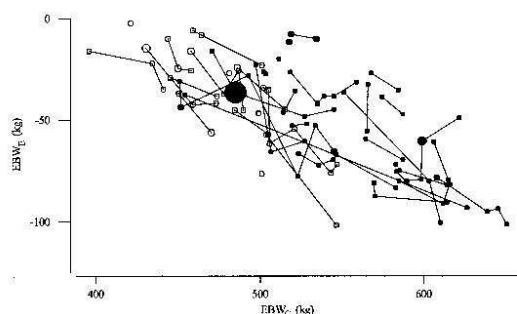


Figure 5. Plot of EBW_E (total loss of empty BW in early lactation) on EBW_C (empty BW at calving) for multiparous (●) and primiparous (○). Data are linked by trial and sized with respect to weight used in weighted least-squares analysis.

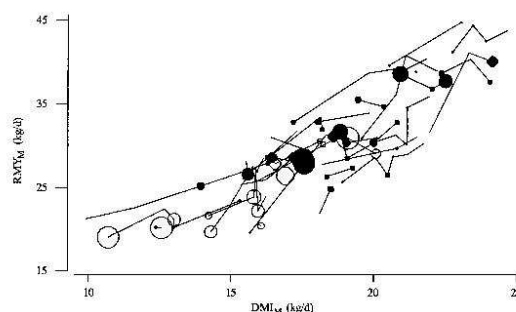


Figure 6. Plot of RMY_M (plateau value of raw milk yield in middle stage of lactation) on DMI_M (plateau value of DMI in middle stage of lactation) for multiparous (●) and primiparous (○). Data are linked by trial and sized with respect to weight used in weighted least-squares analysis.

was 0.66 ± 0.34 kg/d. The distribution of the 119 R^2 calculated is given in Figure 4 ($R^2 = 96.1 \pm 4.5\%$). These results were better than those obtained with the alternative form of the lactation model of Wood (Wood, 1967) proposed by Dhanoa (Dhanoa, 1981) using the same dataset ($RMSE = 0.79 \pm 0.36$ kg/d, $R^2 = 93.8 \pm 6.9\%$).

From 1959 to 1999, the annual increases in RMY_M and RMY_C were significant ($P < 0.05$) and not different between parity groups (RMY_M : $+0.40$ kg/yr and RMY_C : $+0.28$ kg/yr for pooled parity groups). The effect of YOP was significant on t_2 and RMY_P (t_2 : $+0.1$ wk/yr and DMI_P : $+0.2$ wk/yr for pooled parity groups). No significant effect of the YOP was detected on other parameters.

Weighted least squares means of parameters were different between parity group except for k_E and t_1 ($k_E = 2.52 \pm 0.40$ kg/wk and $t_1 = 4.1 \pm 0.2$ wk for pooled

parity groups). Multi had a higher level of RMY_C ($+7.03$ kg) and a higher level of RMY_M ($+7.93$ kg). Multi had a shorter persistency (Primi: $RMY_P = 8.1 \pm 0.7$ wk, Multi: $RMY_P = 4.1 \pm 0.4$ wk) obtained with an earlier time t_2 (Primi: $t_2 = 7.5 \pm 0.5$ wk, Multi: $t_2 = 9.0 \pm 0.7$ wk). The weekly rate of decrease in RMY in late stage was significantly higher for Primi ($k_L = -0.29 \pm 0.03$ kg/wk) than Multi ($k_L = -0.56 \pm 0.02$ kg/wk).

No correlation was retained within the kinetic of RMY. Nevertheless, the plateau value and the slope of decrease in RMY during late stage were found to be correlated with equivalent parameters for DMI. The relationship between RMY_M and DMI_M is presented in Figure 6. Since the accuracy of parameter estimates was not equivalent across treatment groups, the weighting factors applied were heterogeneous. The dif-

Table 6. Correlations between parameter estimates within and between kinetics (only correlations of same sign and with absolute value greater than 0.6 for both parity groups and allocation systems are presented).

Couple of parameters ²			Parity				Allocation system ¹					
			Multiparous		Primiparous		Ad libitum		Fitted		Restricted	
			n ³	r	n	r	n	r	n	r	n	r
Within EBW^4	EBW_E	EBW_C	70	-0.69	36	-0.77	58	-0.76	30	-0.60	18	-0.51
	EBW_M	EBW_C	70	0.81	36	0.79	58	0.91	30	0.83	18	0.79
Between kinetics ⁵	DMI_{kL}	RMY_{kL}	47	0.85	21	0.82	25	0.60	34	0.74	9	0.83
	DMI_M	RMY_M	75	0.80	29	0.84	57	0.82	35	0.85	12	0.58
	RMY_{kL}	MFY_{kL}	43	0.54	19	0.74	20	0.51	33	0.85	9	0.51
	RMY_M	MFY_M	45	0.77	20	0.82	23	0.78	33	0.84	9	0.61

¹Allocation system of the major part of the diet.

² Y_E = variation in Y in early stage, Y_C = Y at calving, Y_M = plateau value of Y in middle stage, k_L = slope of Y in late stage.

³Number of treatment groups involved by parity group or allocation system.

⁴ EBW = empty BW.

⁵ RMY = raw milk yield, MFY = milk fat yield.

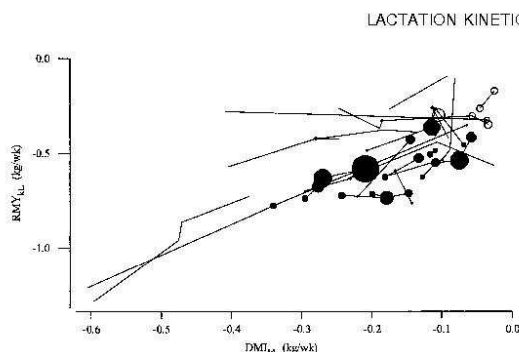


Figure 7. Plot of RMY_{kL} (slope of weekly decrease in raw milk yield in late stage of lactation) on DMI_{kL} (slope of weekly decrease in DMI in late stage of lactation) for multiparous (●) and primiparous (○). Data are linked by trial and sized with respect to weight used in weighted least-squares analysis.

ference in the slopes of RMY_M on DMI_M between parity group was significant ($P < 0.001$, model [11]). The difference in intercepts between parity groups was significant ($P < 0.01$, model [11]). Random effects on slope, on intercept, and random interaction between random slope and intercept were found to be significant (respectively $P = 0.068$, $P = 0.066$, and $P = 0.071$) and were therefore incorporated in retained model [10].

The regression equation for Multi is:

$$RMY_M \text{ (kg/d)} = (3.43) + 1.498 DMI_M \text{ (kg/d)}, \quad [15]$$

and the equation for Primi is:

$$RMY_M \text{ (kg/d)} = (19.16) + 0.374 DMI_M \text{ (kg/d)}. \quad [16]$$

This model was fitted for 119 treatment groups spread across 31 trials and had a residual error of 0.32 kg (residual standard error of random intercept: 13.7 kg). Regression coefficients of models [15] and [16] give an estimate of the within-trial increase in plateau value of milk yield associated with an increase in plateau value of DMI (about 1.5 and 0.4 kg RMY/kg DMI for Multi and Primi respectively).

The relationship between RMY_{kL} and DMI_{kL} is presented in Figure 7. Since the accuracy of parameter estimates was not equivalent across treatment groups, the weighting factors applied were heterogeneous. The difference in the slopes of RMY_{kL} on DMI_{kL} between parity group was significant ($P < 0.001$, model [11]) but only the slope within the Multi group was different from zero ($P < 0.001$, model [10]). The difference in the intercepts of RMY_{kL} on DMI_{kL} between parity group was also significant ($P < 0.05$, model [11]).

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The regression equation for Multi is (model [10]):

$$RMY_{kL} \text{ (kg/wk)} = (-0.366) + 1.239 DMI_{kL} \text{ (kg/wk)}, \quad [17]$$

and the equation for Primi is (model [10]):

$$RMY_{kL} \text{ (kg/wk)} = (-0.273) + 0.191 DMI_{kL} \text{ (kg/wk)}. \quad [18]$$

This model was fitted for 68 treatment groups spread across 21 trials and had a residual error of 0.06 kg/wk (residual standard error of random intercept: 0.06 kg/wk). The models [17] and [18] allow direct quantification of the incidence of the kinetic of intake on the kinetic of milk yield in late stage of lactation. This result emphasizes the potential effect that feeding management has on milk yield in late lactation.

Milk fat yield. Goodness-of-fit was significantly better for Primi (20 treatment groups, $RMSE = 27 \pm 10$ g/d) than Multi (45 treatment groups, $RMSE = 40 \pm 18$ g/d). The distribution of the 65 R^2 calculated is given in Figure 4 ($R^2 = 91.4 \pm 9.0\%$).

The effect of YOP was significant only for parameter MFY_M ($P < 0.1$) and only for Primi ($MFY_M: +15$ g/yr). A valid detection of an early stage with increasing MFY ($t_1 \neq t_0$) was only detected for 23 treatment groups, and a valid estimate of MFY_E in early stage was only calculated for 4 treatment groups. Due to the number of parameter estimates, models [8] and [9] were not applied to parameters MFY_C and MFY_E .

Weighted least squares means of parameters were different between parity groups for all parameters except k_E and t_1 ($k_E = 11 \pm 3$ g/wk and $t_1 = 4.0 \pm 1.6$ wk for pooled parity groups). Multi had a higher level of MFY_M ($+301$ g/d), an earlier time t_2 (-3.2 wk), and a higher slope of decrease in late stage (Primi: $k_L = -11 \pm 1$ g/wk, Multi: $k_L = -18 \pm 1$ g/wk). No correlation was retained within the kinetic of MFY . Nevertheless, the plateau value and the slope of decrease in MFY during late stage were found to be correlated with equivalent parameters for RMY .

The relationship between MFY_M and RMY_M is presented in Figure 8. Since the accuracy of parameter estimates was not equivalent across treatment groups, the weighting factors applied were heterogeneous. The difference in slopes between parity groups was significant ($P < 0.001$, model [11]), and the difference in intercepts between parity groups was also significant ($P < 0.05$, model [11]). Random effects on slope, on intercept, and random interaction between random slope and intercept were found to be significant ($P = 0.058$, $P = 0.049$, and $P = 0.057$, respectively) and were therefore incorporated in model [10].

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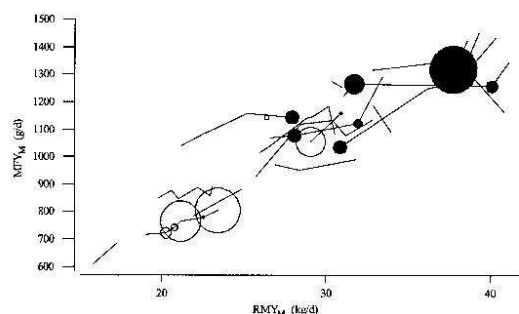


Figure 8. Plot of MFY_M (plateau value of milk fat yield in middle stage of lactation) on RMY_M (plateau value of raw milk yield in middle stage of lactation) for multiparous (●) and primiparous (○). Data are linked by trial and sized with respect to weight used in weighted least-squares analysis.

The regression equation for Multi is:

$$MFY_M \text{ (g/d)} = (803) + 11.2 RMY_M \text{ (kg/d)}, \quad [19]$$

and the equation for Primi is:

$$MFY_M \text{ (g/d)} = (-86) + 39.8 RMY_M \text{ (kg/d)}. \quad [20]$$

This model was fitted for 65 treatment groups spread across 18 trials and has a residual error of 6 g/d (residual standard error of random intercept: 16 g/d). Predictions of models [19] and [20] are consistent with observations of peak yield of milk and fat of Schutz et al. (1990) and Stanton et al. (1992).

The relationship between MFY_{KL} and RMY_{KL} is presented in Figure 9. Since the accuracy of parameter

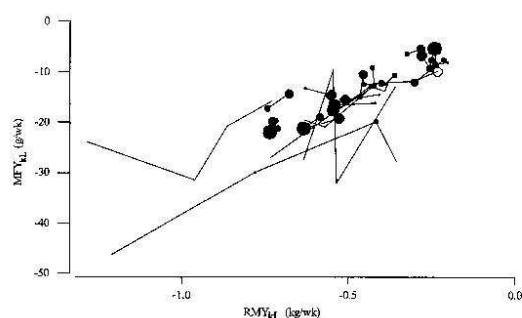


Figure 9. Plot of MFY_{KL} (slope of weekly decrease in milk fat yield in late stage of lactation) on RMY_{KL} (slope of weekly decrease in raw milk yield in late stage of lactation) for multiparous (●) and primiparous (○). Data are linked by trial and sized with respect to weight used in weighted least-squares analysis.

estimates was not equivalent across treatment groups, the weighting factors applied were heterogeneous. The difference in slopes between parity groups was not significant ($P = 0.283$, model [10]), and the difference in intercepts between parity groups was also not significant ($P = 0.088$, model [12]). The regression equation proposed for both parity groups is (model [13]):

$$MFY_{KL} \text{ (g/wk)} = (-1.82) + 27.65 RMY_{KL} \text{ (kg/wk)}. \quad [21]$$

This model was fitted for 62 treatment groups spread across 18 trials and has a residual error of 1.8 g/wk (residual standard error of random intercept: 3.0 g/wk). This model gives a direct quantification of dynamic yield of milk and fat during the late stage of lactation.

DISCUSSION

The challenge of metaanalysis is to identify the general features of a system through the study of pooled data from different origins. This approach was selected to examine lactation kinetics.

Each kinetic collected in the database was recorded in a particular experimental context which can be defined by animal factors (breed, genotype, potential, parity, age, health, etc.), feed factors (composition, digestibility, particle size, energy value, etc.), environmental conditions (temperature, calving season, etc.), farm management (housing, feeding, milking, weighing, etc.), experimental design (allocation system, etc.), and analysis techniques (chemical composition of diet, milk constituents content, etc.). Not all these factors were defined in the different experiments used. Moreover, the criteria used to select these data, which were based on the availability of the three pieces of information (DMI, RMY, BW), induced a bias in the sample. The database was used as a collection of various kinetics rather than an experimental metadesign. Hence, our purpose was to quantify the variability of these kinetics between treatment groups. This overall variability includes the between-trial variability (random effect), associated with experimental conditions, and the within-trial variability, associated with experimental factors. Only parity as fixed effect was incorporated in statistical models to deal with this latter source of variability.

The majority of the trials were carried out on Holstein-Friesian cows, but animals differed in size, intake, and milk yield potential. Values of DMI, RMY, and EBW ranged in middle stage of lactation between 10.1 to 24.7 kg, 15.5 to 44.4 kg, and 320 to 573 kg, respectively. The variability was mainly explained by parity and YOP effects. From 1969 to 1999, the DMI_M increased by 6.6 kg, while the RMY_M increased by 15.3

kg and the EBW_M increased by 51 kg. The increase with time reflects genetic selection and improved management. The corresponding annual increase in 44-wk milk yield was of 165 kg.

The correction of BW for gastrointestinal contents was aimed at calculating the unbiased changes in body reserves. Nevertheless, the correction factor of 4 was applied without taking into account the type of diet, especially the ratio of FO to CO. Several equations, already proposed to explain and predict the rumen volume, have been reviewed by Sauvant (1996) and provided very different estimations of rumen content for the same diet. If rumen load and therefore gut fill is more closely related to fiber or FO intake, as several data have suggested (Paquay et al., 1971), the EBW_E would have been overestimated in the present model for higher yielding animals. Moreover, corrections were not made for uterine involution in early lactation, gravid uterus growth in late lactation, and udder growth in early lactation. Gier and Marion (1968) reported a decrease of 8.5 kg in BW due to uterine involution during the first 3 wk of lactation. This could lead to an overestimation in the loss of body reserves in early lactation. In order to more precisely estimate the early depletion in BW due to mobilization, BW must be split into uterus weight, udder weight, total digestive tract weight, and EBW.

The model proposed by Grossman et al. (1999) summarizes the kinetics into main intersecting straight lines and, hence, into a vector of concrete parameters. We proposed to use this analytical approach on all kinetics of performance data during lactation. This allowed the quantification and the linking of patterns of intake, yield, and BW. In the case of milk yield, the overall goodness-of-fit was greater with this model than with the model of Wood-Dhanoo. Considering its goodness-of-fit, its use for each kind of kinetic, and the concrete signification of its five parameters, the model of Grossman could be a satisfying alternative tool for modeling the course of lactation.

The evolution in EBW was not found to be influenced by DMI, RMY or MFY in early lactation. The major effect that explained EBW loss was the level of EBW at calving (model [14]). This result agrees with the review of Broster and Broster (1984), who observed no clear buffering effect regarded as the "cow's ability to counter nutritional insults by withdrawal of body reserves to support milk production". This result needs to be validated in a context of severe under-nutrition in early lactation. Finally, the knowledge of the BCS at calving could probably improve the prediction of body reserve depletion. The evolution in RMY and in MFY exhibited very different shapes according to parity, especially according to the level of yield in midlactation

and the slope of decrease in late lactation. These results are consistent with results of Schutz et al. (1990) and Stanton et al. (1992). In particular, the current data confirmed the well-known influence of parity on lactation kinetics. Models [15], [16], [19], and [20] allowed the prediction of plateau values of RMY and MFY according to DMI and RMY respectively, by parity. Models [17] and [21] focused on dynamic aspect of the lactation through the relationships between slopes of decrease in intake and milk yield, and milk and fat yield. The choice of DMI as a predictor for RMY is coherent with a "push" viewpoint of lactation (Mertens, 1996) for which milk secretion is considered as a consequence of energy intake. From the opposite "pull" viewpoint, intake is a response to requirements. Only mechanistic models could integrate regulation systems gathering together "push" and "pull" concepts.

CONCLUSIONS

This metaanalysis has highlighted the importance of three main types of effect in the dynamics of lactation: general scale relationship within the couple (intake, yield), incidence of animal size on mobilization of body reserves in early lactation, and effect of lower plane of nutrition on decreasing milk yield and associated decrease in fat yield in late lactation. This work has also opened up the possibility of building an empirical model of lactation kinetics by use of parameter vectors of the model proposed by Grossman (1999). Further trials should be included in the database to validate the regression models obtained.

ACKNOWLEDGMENTS

The authors thank Dr. P. Schmidely, Dr. V. Berthelot, and Dr. S. Robin for suggestions and assistance.

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Annexe 5 Typologie des travaux de modélisation

Cette annexe consiste en un tour d’horizon des travaux de modélisation réalisés à différents niveaux systémiques impliquant une modélisation de la vache. Cette typologie est structurée à travers une grille de lecture systémique proposée comme alternative aux typologies classiques.

Un modèle mathématique peut se définir par l’expression $Y = M(X)$. Dans cette formule M est une méthode permettant de relier deux ensembles d’information X et Y ayant respectivement le statut d’entrée et de sortie. La méthode fait référence à des calculs numériques incorporant des règles, des formules et des paramètres ; X et Y correspondent à des vecteurs de variables pouvant être qualitatives ou quantitatives. Un modèle peut ainsi se définir formellement à travers les caractéristiques du triplet $\{M, X, Y\}$ en spécifiant par ailleurs ses objectifs en cohérence avec une problématique et son domaine d’application.

Typologies classiques

Classiquement, les typologies utilisées pour comparer des modèles mathématiques retiennent trois axes pertinents opposant les modèles stochastique et déterministe, les modèles dynamique et statique, et les modèles empirique et mécaniste (Thornley and France, 2007).

Les modèles stochastiques incorporent un ou plusieurs termes de nature aléatoire, dont la réalisation relève du hasard. La méthode M contient alors une ou plusieurs procédures de tirage aléatoire au sein d’une loi de probabilité, et une ou plusieurs sorties Y sont des variables aléatoires ou des variables synthétiques résumant leur distribution. Le comportement du modèle s’analyse alors à travers une répétition de simulations par opposition aux modèles déterministes dont le comportement peut être répétable et donc prévisible. Certains modèles déterministes basés sur des relations non-linéaires présentent un comportement imprévisible qualifié de chaotique ou d’erratique, d’apparence aléatoire.

Les modèles dynamiques se caractérisent par la présence du temps dans les variables d'entrées, par opposition aux modèles statiques qui sont indépendant de la chronologie du système objet d'étude. La méthode peut alors reposer directement sur une expression algébrique ou sur une expression différentielle, nécessitant une intégration numérique pour en approcher la solution. Dans le premier cas, le modèle repose sur une formalisation directe de l'évolution des variables Y en fonction du temps. Dans le second, le modèle repose sur une formalisation de leurs variations par unité de temps dY/dt .

Les modèles dits empiriques sont construits à partir de connaissances expérimentales, par opposition aux modèles dits mécanistes qui s'attachent à représenter des liens causaux entre composants du système objet d'étude. Typiquement, les modèles empiriques se fondent sur une représentation en « *boîte noire* » et les modèles mécanistes sur une représentation en « *boîte blanche* ». Ces définitions fournissent des archétypes et dans la pratique les modèles sont des hybrides. A ce titre, un modèle peut se fonder sur une représentation mécaniste du fonctionnement d'un système, c'est à dire en considérant les relations de causalité entre ses éléments constitutifs, mais en traduire le fonctionnement par l'intermédiaire d'un formalisme empirique. D'une manière générale, les modèles empiriques répondent à des impératifs opérationnels de prédiction et les modèles mécanistes sont développés pour expliquer, en impliquant des variables caractéristiques de niveaux d'organisation sous-jacents. Le ratio entre le nombre de variables prédictives et le nombre de variables prédites est généralement supérieur ou égal à un dans les modèles empiriques et inférieur à un dans les modèles mécanistes. En effet, ces modèles incorporent en cascade des variables auxiliaires.

Une autre catégorie concerne les modèles dits « *téléonomiques* » dont le fonctionnement est guidé par une finalité réelle ou imaginée (Thornley and France, 2007). Ces modèles incorporent une représentation explicite d'un pilotage assurant un fonctionnement autonome.

D'autres clefs de typologie des modèles peuvent être utilisées, opposant par exemple les modèles continus aux modèles discrets décrivant des événements ou opposant les modèles reposant sur des équations différentielles ordinaires aux modèles reposant sur des équations aux dérivées partielles utilisées notamment pour décrire la dynamique des structures.

Les modèles peuvent aussi être classés selon la discipline qui héberge leur développement et qui déterminent au moins partiellement leur spécificité (économie, épidémiologie, pharmacocinétique, etc.), ou encore selon leur champ d'application (générique vs spécifique).

Typologie alternative

Les typologies classiques sont efficaces d'un point de vue pédagogique pour caractériser la forme d'un modèle mais ne permettent pas de fournir une vision d'ensemble des travaux de modélisation concernant un domaine. Par ailleurs, les modèles sont souvent dans leur forme des hybrides. En outre, ces clefs ne renseignent pas sur l'objectif de la modélisation et sur le niveau de représentation systémique adopté pour le modèle.

La typologie d'analyse retenue ici pour procéder à un tour d'horizon des modèles publiés dans la littérature est fondée sur la localisation des variables en sortie du modèle. Les modèles sont ainsi classés en fonction du niveau systémique dont relèvent ses prédictions.

L'organisation des niveaux retenus est dérivée d'une analogie avec le modèle écosystémique de Bronfenbrenner (1979). Cette approche, développée dans le champ de la psychologie chez l'enfant, préconise d'étudier l'individu dans son environnement par des systèmes en interaction avec d'autres systèmes. Ce modèle de représentation propose une terminologie pour distinguer cinq niveaux systémiques: ontosystème, microsystème, mesosystème, exosystème et macrosystème. L'**ontosystème** correspond à l'organisme lui-même avec ses caractéristiques propres ; le **microsystème** est un environnement immédiat, lieu ou contexte d'interactions directes avec l'ontosystème ; le **mesosystème** correspond à un ensemble de liens et processus qui interviennent entre microsystèmes ; l'**exosystème** est le réseau externe d'influence des microsystèmes ; le **macrosystème** est la toile de fond qui englobe et influence tous les autres niveaux systémiques. Ces niveaux se réfèrent à des lieux physiques mais aussi aux personnes et objets qu'ils contiennent, aux activités et rôle qui s'y déroulent. En 1986, Bronfenbrenner ajoute le niveau chronosystème pour étudier les influences découlant du passage du temps et mettre l'individu dans une perspective axée sur son cycle de vie. Dans son développement original par Bronfenbrenner, l'ontosystème est l'enfant.

La transposition de cette structure de représentation globale à l'animal est proposée comme une grille de lecture :

- Le **macrosystème** correspond au territoire dans lequel est situé l'élevage. Il définit l'environnement dans ses dimensions technico-économique, socio-politique, bio-climatique et géo-physique (Figure 23).
- L'**exosystème** correspond au système biotechnique dans son ensemble : un lieu, des acteurs, des objets, des pratiques, etc. Les exosystèmes **agronomique et zootechnique** correspondent ainsi aux volets « *végétal* » et « *animal* » d'une exploitation agricole.
- Les **microsystèmes** (Figure 24) représentent des dimensions de l'animal dans son milieu: *individu* du microsystème **zoologique** (des animaux), *entité de gestion* du microsystème **humain** (des décisions et des pratiques), *utilisateur* du microsystème **physique** (des bâtiments et des équipements), *ligne budgétaire* du microsystème **économique** (des dépenses et des recettes), *transformateur* du microsystème **organique** (des flux de matière et/ou d'énergie). Les microsystèmes correspondent chacun à un point de vue sur l'ensemble des animaux dans l'exosystème zootechnique.
- Les **mesosytèmes** permettent d'identifier des aspects du fonctionnement de l'animal dont la signification au niveau de l'exosystème zootechnique s'articule entre les microsystèmes. Les quatre mesosytèmes pertinents envisagés sont les mesosytèmes productif, reproductif, coproductif et non-productif (Figure 25). Ils correspondent à une dimension de l'animal en tant qu'interface dans l'exosystème zootechnique.
 - Le **mesosystème productif** regroupe les processus d'**ingestion**, de **lactation** et de **croissance** et implique les éléments **aliment** (eau et ingrédients), **lait** et **tissus**.
 - Le **mesosystème coproductif** regroupe les processus d'**excrétion**, d'**échanges gazeux** impliqués dans la respiration et la digestion (absorption de dioxygène et rejet de dioxyde de carbone et de méthane) et d'**échanges thermiques**⁴⁹ entre l'animal et son milieu et implique les éléments **gaz**, **excréments** (matières fécales, urine et sueur) et **chaleur**.

⁴⁹ Les échanges thermiques consistent en un transfert d'énergie cinétique d'agitation microscopique et ne repose pas sur un échange de matière *sensu stricto*.

- Le **mesosystème non-productif** regroupe les processus de **contamination**, d'**infection** et de **traitement thérapeutique** et implique les éléments **pathogènes** et **agent thérapeutique**.
- Le **mesosystème reproductif** regroupe les processus d'**insémination** et de **gestation** et implique les éléments **semence** et **veau**.
- **L'ontosystème animal** correspond à l'animal dans son ensemble ;
- Les **endosystèmes**⁵⁰ **digestif**, **reproductif** et **métabolique** correspondent à une dimension de l'animal en tant que machine biologique.

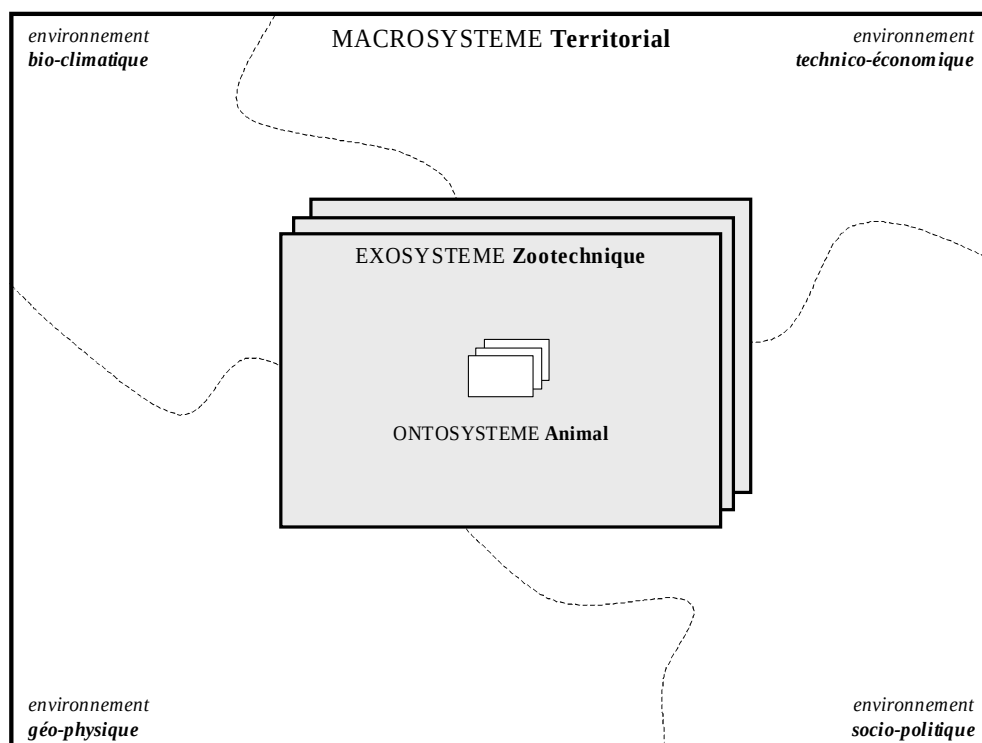


Figure 23 Emboîtement des niveaux « ontosystème animal » et « exosystème zootechnique » dans le macrosystème territorial.

⁵⁰ Le terme endosystème est ajouté ici à la terminologie proposée par Bronfenbrenner et correspond à un système biologique.

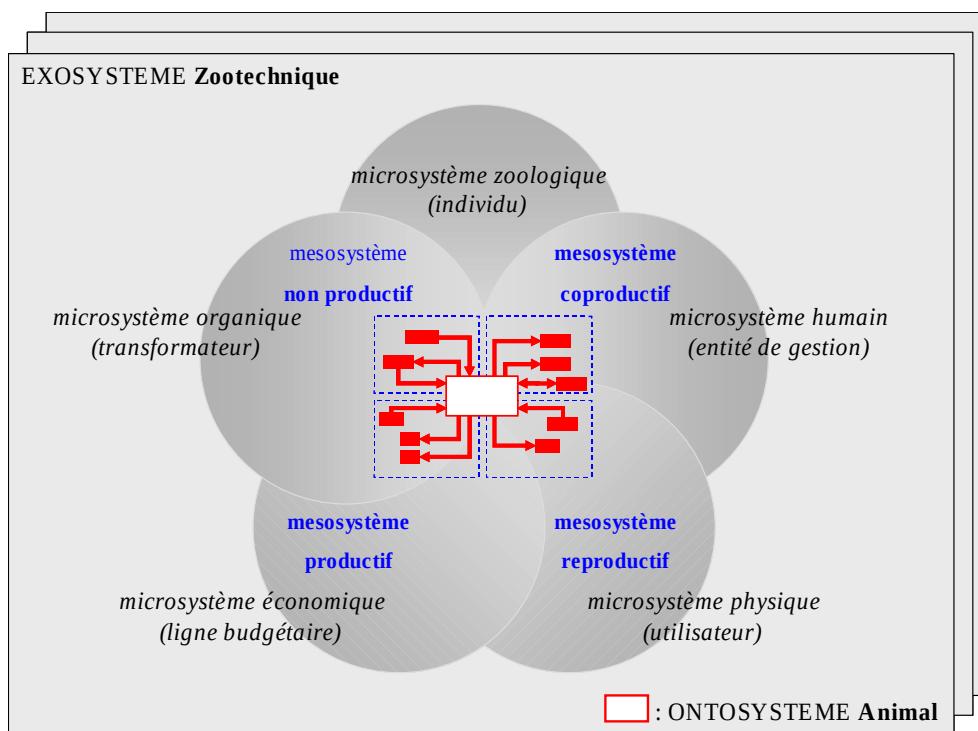


Figure 24 Articulation des microsystèmes et des mesosystèmes à l'interface entre ontosystème animal et exosystème zootechnique.

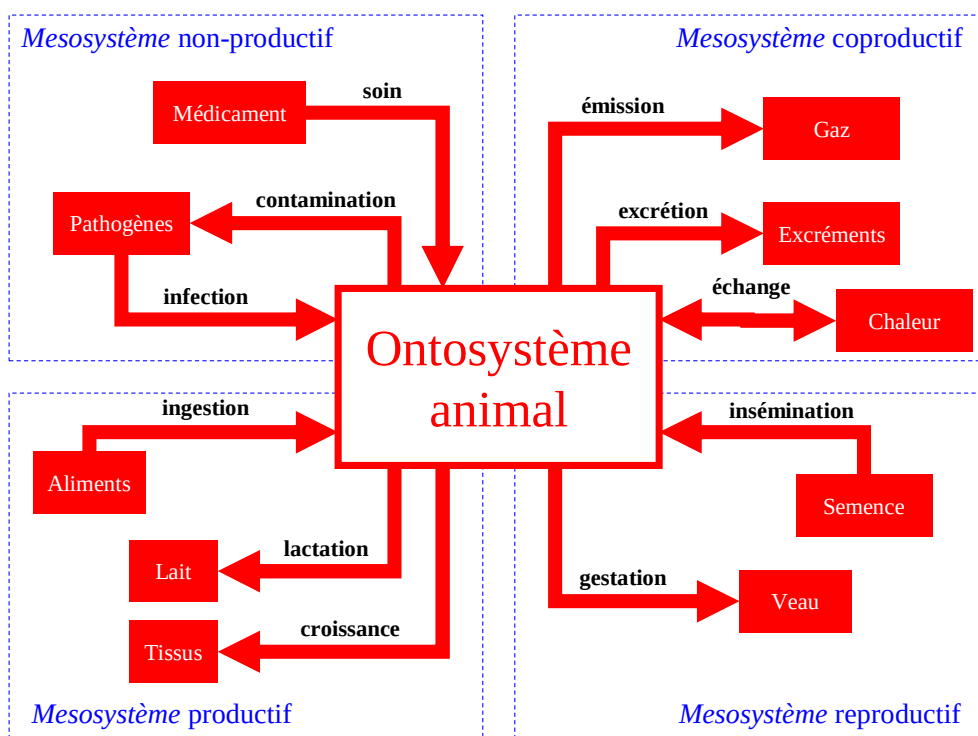


Figure 25 Processus et éléments impliqués dans les mesosystèmes productif, reproductif, coproductif et non-productif.

Les modèles développés dans le cadre de ce travail de thèse se situent au niveau du mesosystème productif pour le modèle énergétique et au niveau de l'endosystème métabolique pour le modèle métabolique.

Cette typologie par niveau systémique est utilisée dans la suite de cette partie pour localiser et classer les différents travaux de modélisation publiés dans la littérature impliquant une représentation de la vache. Elle est évoquée ici au titre d'une proposition de point de vue alternatif et fournit un référentiel permettant de segmenter les champs d'étude de l'animal.

Classification des modèles

Une collection d'articles de la littérature a été constituée pour ce travail en janvier 2008 (All databases sur le serveur ISI Web of Knowledge) en retenant les articles dont le titre contenait : (MODEL* ou PREDICT* ou SIMUL* ou MATH*) et (LIVESTOCK ou RUMINANT* OU CATTLE ou COW ou COWS ou LACTAT* ou HOLSTEIN ou DAIRY) et dont le nombre de citations était supérieur à 5 ou l'année de publication supérieure à 2006. Après dépouillement et exclusion des articles ne concernant pas le domaine des sciences animales au sens large⁵¹ ou concernant la génétique⁵², un nombre total d'environ 700 articles a été exploité. Sur la base des informations contenues dans le titre et le résumé de l'article explicitant les variables en sortie du modèle, chacune de ces références a été classée dans un niveau systémique ou positionnée au niveau d'un processus ou d'un élément d'un mesosystème. Les références citées ci-dessous le sont au titre de leur positionnement dans une classe de modèle sans avoir fait l'objet d'une lecture approfondie. La plupart de ces références sont à un niveau d'investigation non pertinent pour ce travail de thèse. L'enjeu est ici non seulement de procéder à un tour d'horizon des travaux de modélisation impliquant la vache mais aussi d'illustrer l'intérêt de cette grille d'analyse pour une vision hiérarchisée des modèles.

⁵¹Un exemple typique : Baesens and MacKay, 1997. Finite coherence length on equilibrium states of generalized adiabatic Holstein models. *Journal of Mathematical Physics* 38, 2104-2114.

⁵² Les travaux de génétique reposent généralement sur des approches mathématiques formalisant une prédiction de la valeur d'un individu dans une perspective de reproduction.

I. Macrosystème territorial

Dans les modèles au niveau du macrosystème territorial, les informations concernant la vache laitière sont intégrées indirectement à travers un ensemble d'exploitations composées d'ensembles d'animaux. Ces modèles représentent une très faible part de la littérature et sont en général des travaux singuliers. Les travaux suivants sont cités à titre d'exemple :

- modèle de croissance de la population de bovins au Brésil (Freitas et al., 2005) ;
- modèle de propagation de l'encéphalite spongiforme bovine en Grande Bretagne (Ferguson et al., 1997) ;
- modèle de propagation de la tuberculose dans les troupeaux de bovins en Nouvelle-Zélande (Barlow et al., 1997 ; 1998) .
- modèle de calcul de la distance minimisant les nuisances olfactives entre fermes d'élevage et zones résidentielles (Piringer and Schauburger, 1999) ;
- modèle d'émission des gaz à effet de serre par les fermes laitières européennes (Olesen et al., 2006).
- modèle d'application commerciale des techniques de transfert d'embryon chez les bovins laitiers en Europe (Van Arendonk and Bijma, 2003) :
- modèle d'implantation de fermes laitières de grande taille dans le Midwest (Bailey et al., 1997) ;
- modèle spatio-temporel des données de contrôle laitier en Nouvelle-Zélande (Clements et al., 2005).
- modèle des routes de distribution des produits laitiers (Muller, 2006).

II. Exosystèmes

i. Exosystème agronomique

Les modèles relevant de l'exosystème agronomique sortent du cadre de ce travail. Seuls les travaux impliquant indirectement les animaux, comme les modèles de l'effet du pâturage sur la végétation (Drewry, 2001 ; Clary, 2002 ; Finlayson, 2002), les modèles de croissance d'une

patûre (McCall, 2003) destinés à être couplés avec des modèles de ferme laitière, ou les modèles caractérisant le volet « *ressources* » d'une exploitation agricole (Senft, 1989) d'un modèle à l'échelle de l'exploitation dans sa globalité sont cités ici à titre d'exemple.

ii. Exosystème zootechnique

Dans les modèles relevant de l'exosystème zootechnique, les activités de la vache laitière sont agrégées au niveau d'une exploitation. Ces modèles simulent le fonctionnement d'une ferme laitière dans son ensemble, *i.e.* en impliquant plusieurs microsystèmes. Ces modèles ont en général pour vocation l'évaluation ou l'optimisation du fonctionnement d'un élevage ou d'un système de production (*e.g.*, Kristensen, 1998 ; Sorensen, 1992 ; Rotz, 1999 ; Mayer, 1996 ; Reyes, 1981 ; Shalloo et al., 2004 ; Hart, 1998 ; Cros, 2003 ; Herrero et al., 1999).

III. Microsystèmes

Dans les modèles positionnés au niveau d'un microsystème, les activités d'un ensemble de vaches sont interprétées spécifiquement à travers une dimension. Ces modèles produisent des sorties qui trouvent leur signification à l'échelle du troupeau, en impliquant plusieurs mesosystèmes. Ces approches reposent sur une représentation de l'animal en tant qu'individu (microsystème zoologique), en tant que transformateur (microsystème organique), en tant que ligne budgétaire (microsystème économique), en tant qu'utilisateur (microsystème physique/matériel), ou en tant qu'entité de gestion (microsystème humain).

i. Microsystème zoologique

Les modèles développés à ce niveau d'approche considèrent les performances des animaux à travers des indicateurs synthétiques à l'échelle du troupeau. Il s'agit principalement d'une part de modèles qui décrivent la structure et la taille du troupeau en lien avec les performances de reproduction et en réponse aux pratiques de renouvellement et de réforme, et d'autre part des modèles qui décrivent la prévalence et la propagation de maladies. Dans la première catégorie de modèles, se trouvent par exemple des modèles décrivant la reproduction du troupeau (Oltenacu et al., 1980), sa structure démographique (McCullough and Delorenzo, 1996), sa durée de vie productive (Ducrocq et al., 1988 ; Honnette et al., 1980 ; Caraviello et al., 2004), la durée des cycles de reproduction (Jalvingh, 1992 ; 1993) ou encore des

modèles/outils dédiés à la caractérisation/détection de l'état physiologique des animaux (Erb et al., 1985 ; Heuer et al., 1999 ; Friggens and Chagunda, 2005 ; De Mol et al., 1999). Dans ces modèles, les animaux sont décrits par des variables caractérisant leur état physiologique, leur fertilité, la durée de phases de leur cycle de reproduction, leur âge, leur survie, leur type, etc. Dans la seconde catégorie, c'est l'état sanitaire des animaux qui est considéré relativement à différents types de maladies ou de troubles sanitaires comme le déplacement de caillette (Leblanc et al., 2005), la paratuberculose (Collins and Morgan, 1991 ; Kudahl et al., 2007), la fièvre vitulaire (Østergaard et al., 2003), la diarrhée bovine virale (Innocent et al., 1997a ; 1997b), les mammites (Green et al., 2004 ; Østergaard et al., 2005), la cétose (Nielsen et al., 2005) ou d'une manière générale les troubles reproductifs (Klerx and Snolders, 1997) ou sanitaires (Sorensen and Enevoldsen, 1992).

C'est bien souvent dans ces catégories de modèles que les auteurs ont recours à des termes stochastiques pour réaliser des simulations. Cette catégorie de modèles contient également les modèles spatiaux, *i.e.* des modèles représentant les déplacements des animaux et les patterns de pression de pâturage (Senft et al., 1983 ; Pickup and Chewings, 1988).

ii. Microsystème organique

Les modèles appartenant à cette catégorie considèrent les animaux d'un élevage de vache laitière comme une unité élémentaire de transformation dans le cycle d'une molécule. C'est principalement la question de la volatilisation de l'ammoniaque qui a motivé ces travaux de modélisation (Monteny, 1998 ; Hutchings, 1996 ; Elzing, 1997). Inscrite également dans des problématiques environnementales, d'autres auteurs ont considéré l'excrétion de phosphore par les vaches (Davison, 1997 ; Gruber, 1996 ; Williams, 1990 ; Modin-Edman, 2007). Enfin, à travers le concept de la chaîne « *pâturage-vache-lait* », les transferts d'iode (Shaeffer, 1981 ; Crout, 1996) et de césium (Matthies et al., 1981 ; Mitchell, 1989) radioactifs ou encore de dioxine (Slob, 1993) ont donné lieu à des travaux de modélisation.

iii. Microsystème humain

Les modèles appartenant à cette catégorie sont principalement développés pour évaluer des stratégies de conduite des animaux (Congleton, 1984) ou de contrôle de maladies (Bennett, 1992 ; Collins, 1992). Ces modèles sont en général construits dans une perspective d'outils

d'aide à la décision et se focalisent sur les flux d'information émanant du système opérationnel (l'élevage) renseignant le système décisionnel (l'éleveur).

Bon nombre de modèles formalisent une prédiction au niveau du microsystème zoologique à partir de variables définies au niveau du microsystème humain (*i.e.*, effet de telle ou telle stratégie de conduite sur les performances). Le positionnement des modèles entre ces deux microsystèmes s'avère parfois délicate. Formellement, un modèle peut être positionné au niveau du microsystème humain lorsqu'il incorpore une représentation du processus de décision (Coleno and Duru, 1999 ; Muller, 1984 ; Dijkhuizen et al., 1986 ; Benari et al., 1983). C'est l'objet des travaux sur l'ontologie des systèmes pilotés (Martin-Clouaire and Rellier, 2003) qui reconsidèrent le volet « *humain* » dans la simulation des systèmes d'élevage (Garcia et al., 2005). Le modèle de Madelrieux et al. (2006) représentant l'organisation du travail dans une ferme rentre également dans cette catégorie.

iv. Microsystème physique

Les modèles appartenant à cette catégorie sont rares et concernent en général les bâtiments d'élevage du bétail au sens large. Ces modèles s'attachent à décrire les flux d'air (Timmons, 1984 ; Wu, 2001) et principalement au sens de leur implication dans les échanges thermiques (Gebremedhin, 2003) et la diffusion d'odeurs (Schauberger, 2002 ; 2006).

v. Microsystème économique

Les modèles appartenant à cette catégorie relèvent en général soit d'une interprétation économique de réponses relevant d'un ou de plusieurs autres microsystèmes soit du développement spécifique d'un modèle répondant à un objectif de maximisation du profit à court ou long terme. Les modèles de la première catégorie concernent par exemple l'interprétation économique en terme de coût ou de bénéfice de la construction des bâtiments (Pereira, 2003), d'un traitement contre les mammites (Swinkels, 2005), de l'utilisation d'hormone pour accroître la fertilité (Weaver, 1988), de changement de la durée de période de tarissement (Sorensen, 1993), du choix des pratiques de reproduction (Dijkhuizen, 1988), du potentiel génétique des animaux (Simm, 1994), de la mortalité des veaux (Martin and Wiggins, 1973), d'une épidémie de diarrhée (Sorensen, 1995), etc. De nombreux modèles mettent en relation les performances économiques de l'exploitation avec les performances de

reproduction des animaux (Plaizier, 1997 ; 1998 ; Groen, 1988). Les modèles de la seconde catégorie sont par exemple des outils d'optimisation des pratiques de mise à la reproduction et de politique de réforme (Groenendaal, 2004), de formulation des rations à moindre coût (Oconnor, 1989), ou d'analyse de l'impact de changements techniques (Berentsen and Giesen, 1995).

IV. Mesosytèmes

Les modèles développés à ce niveau systémique se focalisent en particulier sur un processus (*e.g.*, la lactation, la gestation), sur un élément donné (*e.g.*, le lait, les gaz) ou impliquent plusieurs processus et/ou plusieurs éléments, et sont de fait considérés comme des modèles du mesosystème dans son ensemble. Au niveau des mesosystèmes sont ainsi distingués les modèles focalisés sur son fonctionnement dans son ensemble, les modèles focalisés sur un processus en particulier (sa dynamique, son occurrence ou son efficacité) et les modèles focalisés sur un élément en particulier (sa quantité, sa composition ou sa valeur) (Figure 26).

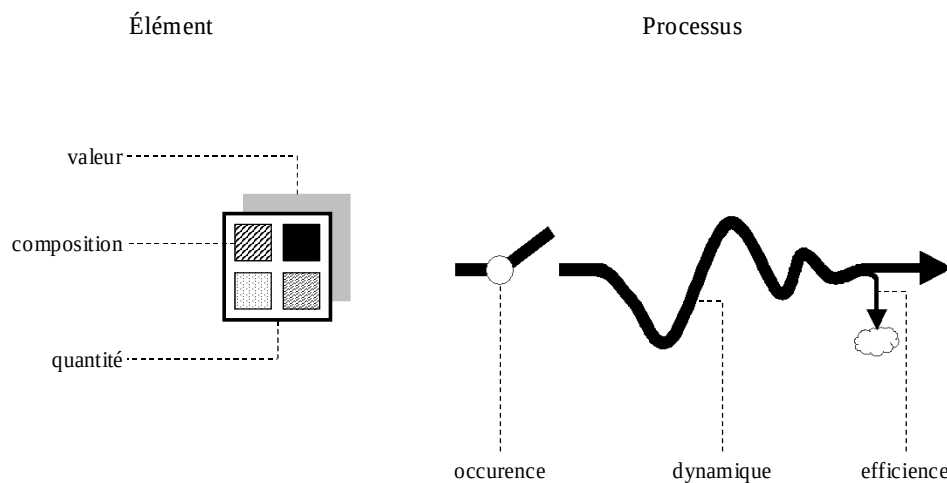


Figure 26 Illustration schématique des différents aspects considérés pour les deux composantes d'un mesosystème : valeur, composition ou quantité d'un élément ; occurrence, dynamique ou efficacité d'un processus.

i. Mesosystème non-productif

Il existe peu de travaux de modélisation relevant du niveau du mesosystème non-productif dans sa globalité et développés spécifiquement chez la vache laitière. *A priori*, de tels modèles décrivent à l'échelle de l'individu, les mécanismes d'infection et de contamination impliquant

des éléments pathogènes et les processus de traitement vétérinaire impliquant des agents thérapeutiques. Un exemple typique de modèle publié dans la littérature rentrant dans cette catégorie concerne l'effet de la désinfection de la mamelle sur le risque de mammite (Lam et al., 1996). Certains modèles se focalisent spécifiquement sur le risque individuel d'infection (*i.e.*, l'occurrence du processus d'infection) et concernent principalement les mammites (Lescourret et al., 1995 ; De Mol and Ouweltjes, 2001 ; Barnouln and Chassagne, 2001 ; Allore and Erb, 1999 ; Chassagne et al., 1998 ; Green et al., 2004 ; Odegard et al., 2003). Certains modèles se focalisent sur la réponse thérapeutique (*i.e.*, l'efficacité du processus de traitement) et concernent par exemple la prédiction, à partir de mesures physiologiques, du succès d'un traitement d'un déplacement de caillette (Staufenbiel et al., 2007). Rares sont les modèles focalisés sur la transmission de pathogènes à l'échelle de l'individu. Le modèle d'excrétion de *mycobacterium bovis* chez les bovins atteints de tuberculose développé par Neill et al., (1991) en est un exemple.

ii. Mesosystème reproductif

Aucun modèle représentant le mesosystème reproductif dans son ensemble n'a été identifié. Les modèles concernant l'axe reproductif à l'échelle de l'animal sont développés principalement pour prédire le risque de fécondation (*i.e.*, l'efficacité du processus d'insémination) généralement apprécié à travers des critères de fertilité tels que l'intervalle de temps entre la mise bas et l'insémination fécondante, à partir de critères prédictifs tels que la note d'état corporel (Suriyasathaporn et al., 1998 ; Prandi et al., 1999) ou la balance énergétique (De Vries et al., 1999). Les modèles développés pour représenter la dynamique du processus de gestation correspondent à des modèles de croissance fœtale (Sager, 1985), développés le plus souvent pour les mammifères en général (Laird, 1966). D'autres modèles concernent la prédiction du risque de mortalité embryonnaire (*i.e.*, l'efficacité du processus de gestation) (Curtis et al., 1988 ; 1993) mais relèvent plus du microsysteme zoologique dans la mesure où ces modèles décrivent son occurrence à l'échelle du troupeau et non ses déterminants à l'échelle de l'animal.

Deux modèles concernant les éléments « veau » et « semence » ont été identifiés : ils concernent la prédiction du sexe à partir du niveau de testostérone dans le fluide allantoïdien (Bongso et al., 1976) et la modélisation de la mobilité des spermatozoïdes (Serrano et al., 2006).

iii. Mesosystème productif

Les modèles développés à l'échelle du mesosystème productif dans son ensemble concernent des prédictions relatives à au moins deux des processus du triplet ingestion|croissance|lactation. Les sorties de ces modèles sont ainsi la dynamique du poids vif et/ou de la quantité d'aliments ingérés et/ou de la quantité de lait produit à l'échelle de la lactation. Il existe trois catégories de modèles à ce niveau de représentation : les modèles reposant sur le calcul de la balance énergétique de l'animal (*e.g.*, Bruce et al., 1984 ; Williams et al., 1989 ; Walter and Mac, 1989 ; Heuer et al., 2000 ; Schwager-Suter et al., 2001 ; Banos et al., 2005), les modèles proposant des jeux d'équations reliant ces processus (Brown et al., 1977 ; Shem et al., 1995 ; Holter et al., 1996 ; 1997 ; Miller et al., 1973 ; Gibson, 1987) et les modèles proposant une formalisation empirique de ces cinétiques conjointement (Wood, 1979 ; Menchaca and Ruiz, 1987 ; Martin and Sauvant, 2005).

D'autres modèles se focalisent exclusivement sur un seul des processus impliqués au niveau du mesosystème productif. Ces travaux constituent le front de recherche le plus dense de la littérature à l'intersection de la modélisation et des vaches laitières.

Croissance

Les modèles s'attachant à décrire la dynamique de la masse corporelle sont développés à l'échelle de la vie de l'animal et généralement pour les bovins en général (*e.g.*, Nesetrilova, 2005) ou de sa lactation (*e.g.*, Quinn et al., 2006). Ces modèles utilisent des fonctions mathématiques du temps avec l'objectif de décrire la cinétique des variations de poids vif ou de sa composition (Friggens et al., 2004 ; Williams and Jenkins, 1997) ou reposent sur une représentation mécaniste des mécanismes sous-jacents, avec l'objectif de décrire les variations de composition du croît (Tedeschi et al., 2004 ; Williams, 2005 ; Oltjen et al., 2005).

D'autres modèles sont développés pour prédire de façon statique le poids vif ou le poids vif vide à partir d'informations relatives à l'animal et sa ration (Holter et al., 1986 ; Williams et al., 1992) ou à partir de mesures morphologiques telles que la circonférence corporelle (Heinrichs et al., 1992 ; 2007 ; Khare et al., 2007).

Certains modèles, encore statiques sont développés pour prédire la composition du poids vif (Agnew et al., 2005) ou de la carcasse (Gresham et al., 1986), en incorporant parfois

comme prédicteurs des mesures de diffusion de marqueurs (Bird et al., 1982 ; Meissner et al., 1980) ou des mesures de composition de constituants anatomiques (Klawuhn and Staufenbiel, 1997 ; Alhassan et al., 1975). Enfin, d'autres auteurs ont cherché à relier composition corporelle et note d'état (Martin and Sauvant, 2005 ; Yan et al., 2005).

Ingestion

Il existe dans la littérature de nombreux modèles représentant la dynamique d'ingestion à l'échelle de la lactation et ce sujet continue à mobiliser les efforts (*e.g.*, Shah and Murphy, 2006, Williams et al., 2006 ; Halachmi et al., 2004 ; Hayirli et al., 2003). Plusieurs revues comparatives ont par ailleurs été publiées sur ce sujet (Faverdin, 1992 ; Roseler et al., 1997 ; Neal et al., 1984 ; Ingvarsten, 1994 ; Lopes et al., 2005 ; Keady et al., 2004). Certains de ces travaux sont focalisés sur la régulation de l'ingestion à l'échelle de la lactation (Ellis et al., 2006b ; Petruzzi and Danfaer, 2004) ou à court terme (Dove, 1996 ; Fisher, 1996 ; Forbes, 1980 ; Pittroff and Soca, 2006).

Tout un pan de cette littérature est orienté vers la prédiction de la quantité ingérée, généralement de façon statique, en fonction des aliments mis à disposition des animaux (Orskov et al., 1988 ; Dulphy and Demarquilly, 1994 ; Huhtanen et al., 2002 ; Jarrige et al., 1986 ; Steen et al., 1998). Formellement, ces modèles sont développés du point de vue de l'aliment en considérant son ingestibilité par l'animal. Une autre famille de modèles s'attache à représenter et/ou prédire d'autres critères de valeur des aliments liés à leur composition (Lindgren, 1981 ; Oconnor et al., 1993 ; Lyons and Stuth, 1992 ; Rotz et al., 1989 ; Hulme et al., 1986 ; Offner and Sauvant, 2004 ; Dhanoa et al., 2000 ; Baumont et al., 1999 ; Dewhurst et al., 1986 ; Golding et al., 1976).

Lactation

Depuis les travaux de Brody et al. (1923) en passant par les travaux incontournables de Wood (1967) jusqu'à nos jours (*e.g.*, Prasad, 2007 ; Dematawewa et al., 2007 ; Grzesiak et al., 2006), la modélisation de la courbe de lactation a fait l'objet d'une multitude de travaux et de nombreuses revues existent à ce sujet (*e.g.*, Masselin et al., 1987). Ces modèles proposent des formalismes incorporant principalement l'effet du temps écoulé depuis le vêlage avec des modulations liées aux caractéristiques de la ration et à la race de l'animal. D'autres travaux de modélisation, cette fois statiques, fournissent des outils de prédiction de la production de lait

et/ ou de ses principaux constituants sur l'ensemble de la lactation (Sharma et al., 2006 ; 2007 ; Grzesiak et al., 2003 ; Baranan et al., 1988 ; Wilmink, 1987 ; Schaeffer et al., 1977), ou encore de la durée de la lactation (Piper and Parks, 1996) ou de la traite (Thomas et al., 1993). D'autres modèles sont focalisés sur la prédiction de la composition du lait (Hermansen, 1995 ; Casper and Schingoethe, 1989) ou de sa valeur énergétique (Crovetto and Vanderhonong, 1984 ; Tyrrell and Reid, 1965). Certains auteurs se focalisent enfin sur l'effet de troubles sanitaires sur la production laitière, tels que les mammites (Lescourret and Coulon, 1994) ou la cétose (Grohn et al., 1999).

iv. Mesosystème coproductif

Aucun modèle représentant le mesosystème coproductif dans son ensemble n'a été identifié. Les modèles publiés dans la littérature se focalisent principalement sur l'excrétion d'azote urinaire et fécal (Kohn et al., 2005 ; Gruber and Poetsch, 2006 ; Nennich et al., 2006 ; Yan et al., 2006) et sur l'émission de méthane (Holter and Young, 1992 ; Wilkerson et al., 1995 ; Benchaar et al., 1998 ; Yan et al., 2000 ; Mills et al., 2003 ; Pelchen et al., 1998). Le modèle développé par Benchaar et al. (2001) a en particulier pour objectif l'évaluation de stratégies alimentaires pour réduire les émissions de méthane. Les travaux de Turnpenny et al. (2000a ; 2000b) concernent les échanges thermiques de l'animal avec son environnement, ce modèle étant développés pour le bétail en général et le modèle de Stevens (1981) concerne les pertes hydriques liées à la respiration. Le modèle de Dhanoa et al., (1985) a quant à lui été développé spécifiquement pour décrire l'excrétion de marqueurs dans une optique de mise au point méthodologique.

V. Ontosystème animal

Dans les modèles au niveau de l'ontosystème animal, les activités d'une vache résultent du fonctionnement de plusieurs endosystèmes. Ces modèles sont à l'échelle de l'animal dans son ensemble considéré comme une « *boîte blanche* ». Ces modèles intègrent simultanément les fonctions biologiques de croissance, d'entretien et de reproduction, en général à l'échelle de la vie de l'animal (Vetharaniam, 2005). Leur principal objet est la performance de l'animal, exprimée en termes de besoins (Reynoso-Campos, 2004). La question scientifique fondamentale que ces travaux cherchent à résoudre est celle de l'évolution de la partition des

nutriments entre les fonctions biologiques de l'animal (Baldwin, 1987 ; Friggens and Newbold, 2007 ; Kebreab, 2004 ; Bywater and Dent, 1976 ; Bywater, 1976). Ces modèles sont souvent le socle des systèmes de recommandations alimentaires construits à travers le monde (Fox, 2004 ; Danfaer, 2005a ; 2005b). Certains travaux cherchent par ailleurs explicitement à exprimer les performances comme le résultat d'une équation dont les termes sont le génotype de l'animal, son environnement et l'interaction génotype x environnement (Bryant, 2005).

VI. Endosystème

Les modèles au niveau d'un endosystème sont focalisés sur tout ou partie des phénomènes biologiques réalisant différentes fonctions et impliquant différents organes. Ces modèles sont à l'échelle des systèmes biologiques. Les travaux de modélisation publiés dans la littérature produisant des sorties à cette échelle concernent les endosystèmes digestif, reproductif et métabolique.

i. Endosystème digestif

Ces modèles concernent la digestion dans son ensemble depuis l'ingestion d'aliments jusqu'à l'absorption de nutriments (Bywater, 1984 ; Murphy et al., 1986 ; Baldwin, 1987 ; Illius and Gordon, 1991 ; Mills et al., 2001 ; Dijkstra et al., 2006). D'autres travaux ne considèrent qu'un segment du tractus digestif, en particulier en se focalisant sur le rumen (Petruzzi et al., 2002) ou un aspect particulier de la digestion ruminale comme les fermentations (Sveinbjornsson et al., 2005 ; Craninx et al., 2006), la méthanogénèse (Vlaeminck and Fievez, 2005) ou la cinétique de dégradation des aliments (France et al., 2000 ; Paengkoum, 2005). La dynamique du transit des aliments dans le tractus digestif est un aspect ayant donné lieu à de nombreux travaux de modélisation (Arnold and Trenkle, 1986 ; Pond et al., 1988 ; Quiroz et al., 1988, Beauchemin and Buchanansmith, 1989 ; Collao-Saenz et al., 2005a ; 2005b ; Seo et al., 2006a ; 2006b ; 2006c ; Seo et al., 2007). Enfin, certains auteurs se sont attachés à représenter la digestion d'un constituant particulier de la ration alimentaire, comme l'amidon (Mills et al., 1999a ; 1999b), les fibres (Mertens and Ely, 1979) ou les protéines (Journet and Vérité, 1979 ; Madsen and Hvelplund, 1984 ; Rohr et al., 1986 ;

Hvelplund and Madsen, 1989 ; Dijkstra et al., 1998 ; Rulquin et al., 1998 ; Bateman et al., 2001a ; 2001b ; Bateman et al., 2005).

ii. Endosystème métabolique

Certains modèles développés à ce niveau considèrent le métabolisme dans son ensemble (Baldwin et al., 1987 ; McNamara, 2004 ; 2005 ; Hanigan et al., 2006 ; Markantonatos et al., 2006). D'autres modèles se focalisent sur les organes clefs impliqués dans le métabolisme, principalement le foie (Freetly et al., 1993), le tissu adipeux (Baldwin et al., 1976 ; McNamara, 1994 ; McNamara and Baldwin, 2000) et les tissus splanchniques (Hanigan, 2005). D'autres auteurs ont considéré le métabolisme non pas à travers des flux de métabolites mais en terme d'énergie (Williams and Jenkins, 2003a ; 2003b ; 2003c). Enfin, une dernière catégorie de modèle concernant le métabolisme d'une molécule en particulier, comme le glucose (Horsfiel et al., 1974) ou les protéines et les acides aminés (Hanigan et al., 1997 ; Baldwin et al., 2003 ; Hanigan et al., 2004), ou d'un élément chimique en particulier, comme l'azote (Roffler and Satter, 1975a ; 1975b ; Jonker et al., 1998 ; Kebreab et al., 2002), le phosphore (Kebreab et al., 2006) ou le cuivre (Buckley, 1991). En marge, d'une modélisation dans le champ de la nutrition, il existe des travaux de modélisation pharmacocinétique décrivant le devenir de certaines toxines chez la vache (Derks et al., 1994 ; Sweetman et al., 1999 ; Mclachlan, 1994).

iii. Endosystème reproductif

Il convient de distinguer les travaux de modélisation concernant le volet gestation de la reproduction et impliquant une représentation de l'appareil reproducteur, des travaux de modélisation concernant le volet lactation et impliquant une représentation de la glande mammaire. Les modèles reposant sur une description plus ou moins fine de la glande mammaire sont quantitativement plus nombreux et considèrent des flux de métabolites qui la parcourent (Waghorn and Baldwin, 1984 ; Hanigan and Baldwin, 1994 ; Cant and McBride, 1995 ; France et al., 1997 ; Maas et al., 1997 ; Hanigan et al., 2001) ou décrivent la dynamique de ses modifications structurelles au cours de la croissance et de la lactation (Dijkstra et al., 1997 ; Hanigan et al., 2007 ; Vetharanim et al., 2003a ; 2003b).

Les travaux de modélisation à l'échelle de l'appareil reproducteur sont relativement rares en vache laitière (Blanc et al., 2001) alors que des avancées significatives ont été réalisées dans ce domaine en brebis laitière (Martin et al., 1987 ; Scaramuzzi et al., 1993). Chez les bovins, ils concernent principalement les profils dynamiques des signaux endocrines régulant l'axe reproducteur (Peters and Lamming, 1986 ; Yenikoye et al., 1981), principalement la dynamique du cycle ovarien. Formellement, ces modèles concernent en réalité l'intersection de l'endosystème endocrine avec l'endosystème reproducteur.

Synthèse

L'ensemble des références citées précédemment pour illustrer la diversité des modèles publiés dans la littérature ne constitue pas une liste exhaustive. De part la sélection des mots clefs utilisés et la restriction selon le nombre de citations, de nombreux travaux significatifs ne sont pas mentionnés. Ainsi, le travail de modélisation de la fonction ovarienne réalisé par Clément et al. (2002) ne concerne pas spécifiquement l'espèce bovine en particulier mais se positionne au niveau générique des mammifères. Un autre exemple concerne le modèle de digestion ruminale publié par Lescoat et Sauviant (1995) dont ni le titre ni les mots clefs ne font référence à une espèce en particulier et qui se positionne au niveau générique des ruminants. L'objectif de cette revue bibliographique est de produire une vision d'ensemble hiérarchisée des travaux de modélisation impliquant une représentation de la vache laitière.

Ce tour d'horizon montre que des modèles ont été produits à tous les niveaux d'organisation depuis l'organe jusqu'au territoire. En revanche, ces approches restent cloisonnées, focalisées sur les variables d'un niveau systémique et souvent inféodées à une discipline. Ce cloisonnement procède d'un effet de zoom détaillant certains aspects au détriment d'autres, abordés de façon simplifiés. Ainsi, par exemple, la construction d'un modèle des fermentations ruminales peut être développée à partir d'une représentation minimale de l'ingestion. Il existe une légitimité opérationnelle dans cette procédure et elle permet d'allonger la liste des processus ayant été mis en équations. En revanche, l'implication dans un processus agrégatif vers un modèle global n'est pas inscrite au cahier des charges des projets de modélisation. Certains modèles sont construits par compilation d'autres modèles déjà développés par ailleurs (Freer et al., 1997). Ce type d'approche peut par ailleurs poser des problèmes d'homogénéité technique et conceptuelle.

Il n'existe pas encore aujourd'hui une réelle démarche d'agrégation des modèles permettant par exemple d'impliquer une représentation fine du métabolisme de l'azote dans un modèle consacré à la volatilisation de l'ammoniaque à l'échelle d'un élevage. Le niveau animal constitue la brique centrale de ce cadre d'agrégation, en tant que niveau d'expression global des processus biologiques et niveau d'expression élémentaire des processus biotechniques. A ce titre, le développement d'un modèle à l'échelle de l'animal est un enjeu clef. A l'échelle de l'animal entier, persiste aujourd'hui une opposition entre des modèles « *encyclopédiques* » tendant vers une représentation exhaustive des processus biologiques et des modèles « *opérationnels* » permettant de simuler et de prédire. De façon schématique, les modèles mécanistes font progresser l'explicatif au détriment du prédictif. L'enjeu d'une modélisation à l'échelle de l'animal est de réconcilier ces deux fronts pour que l'agrégation des connaissances à l'échelle « *infra* » nourrisse de façon pertinente les besoins de simulation à l'échelle « *supra* ».

Dans son ensemble, le travail de modélisation présenté dans la suite de ce manuscrit se positionne au niveau de l'animal. Il constitue un prototype de modèle impliquant une représentation du métabolisme à l'échelle inter-organes et produisant une entité élémentaire de simulation, unité de production et variant génétique, à même d'être utilisée comme brique dans la construction d'un modèle à l'échelle de l'élevage.

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Annexe 6 Comportement global du modèle

Les Figures présentées dans cette annexe correspondent aux compilations de données de la littérature présentées dans la Partie I.3 et mises ici en regard des simulations produites par le modèle développé dans ce travail de thèse.

Cette annexe illustre le comportement global du modèle et situe la plage de variation de son comportement.

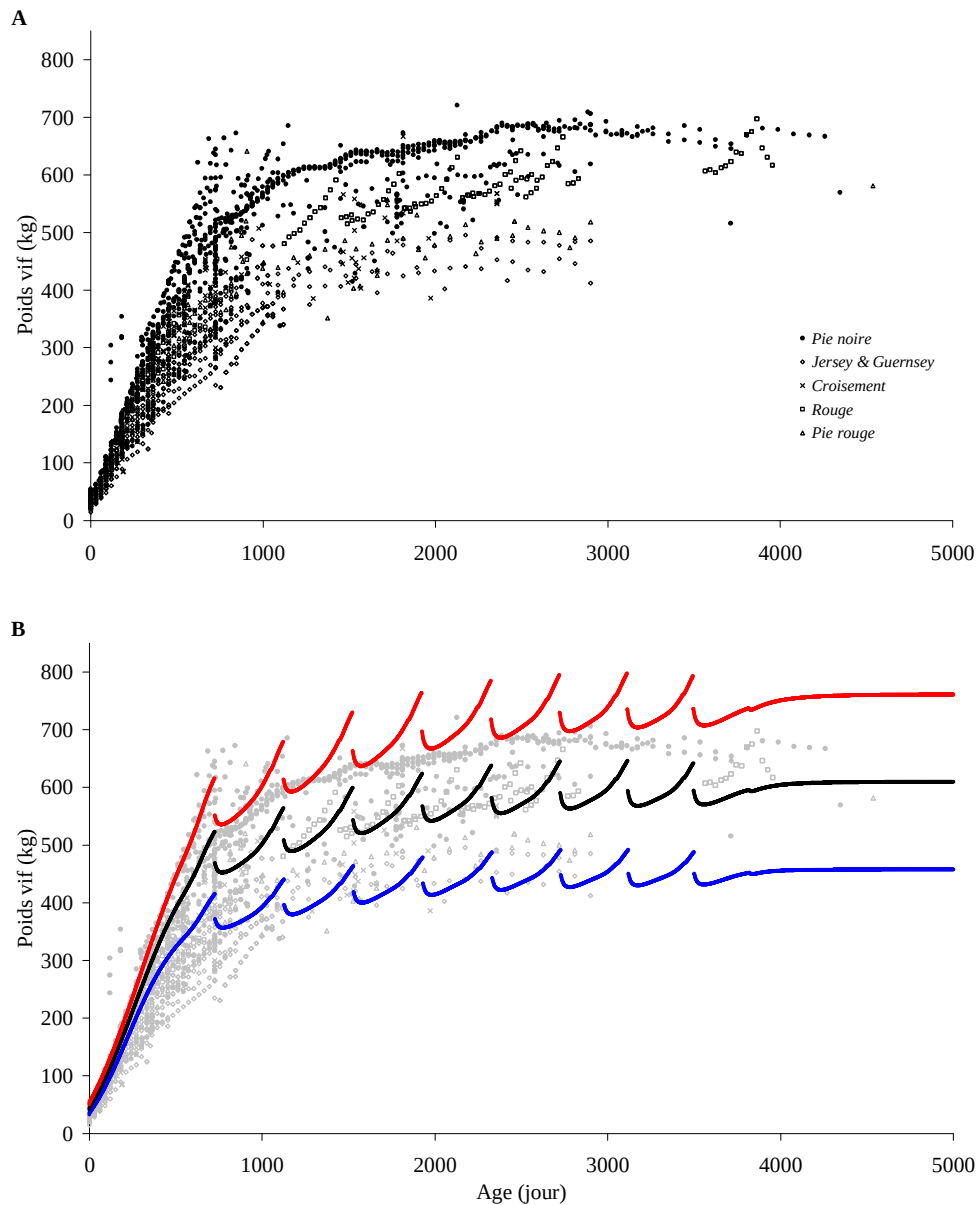


Figure 27 Evolution du poids vif avec l'âge de vaches laitières. A : Données de la littérature⁵³ pour différentes races (Pie Noire, Jersey & Guernsey, Croisement, Rouge, Pie Rouge) à différents stades physiologiques (croissance, entretien, lactation, gestation, stades *pre-* ou *postpartum*). B : Superposition des simulations du modèle pour différents formats à maturité (*en bleu, noir et rouge*).

⁵³ Eckles, 1920 ; McCandlish, 1922 ; Bartlett, 1926a ; Bartlett, 1926b ; Espe *et al.*, 1932 ; Ragsdale, 1934 ; Hilder and Fohrman, 1949 ; Ellenberger *et al.*, 1950 ; Reid *et al.*, 1951 ; Campbell and Flux, 1952 ; Matthews and Fohrman, 1954 ; Davis and Hathaway, 1956 ; Morrison, 1956 ; Burt, 1957 ; Davis, 1957 ; Crichton *et al.*, 1959 ; Crichton *et al.*, 1960 ; Swanson, 1960 ; Martin *et al.*, 1962 ; Wickersham and Schultz, 1963 ; Swanson and Hinton, 1964 ; Bath *et al.*, 1965 ; McDaniel and Legates, 1965 ; Miller *et al.*, 1967 ; Swanson, 1967 ; Hollon *et al.*, 1972 ; Rakes and Davenport, 1972 ; Lamb and Barker, 1975 ; Grieve *et al.*, 1976 ; Berglund *et al.*, 1980 ; Herland and Wiktorsson, 1982 ; Lee *et al.*, 1982 ; Fisher *et al.*, 1983 ; Lebengarts *et al.*, 1984 ; Butler-Hogg *et al.*, 1985 ; Lin *et al.*, 1985 ; Reddy and Basu, 1986 ; Ribas and Ponce de Leon, 1986 ; Heinrichs and Hargrove, 1987 ; Johnson *et al.*, 1987 ; Pikina, 1987 ; Polyakov *et al.*, 1987 ; Singh and Bath, 1987 ; Hocking *et al.*, 1988 ; Moore *et al.*, 1990 ; Akbulut *et al.*, 1993 ; Berg and Ekern, 1993 ; Grabowski *et al.*, 1993 ; Peri *et al.*, 1993 ; Andrew *et al.*, 1994 ; Dhour *et al.*, 1995 ; Groen and Vos, 1995 ; Hoffman *et al.*, 1996 ; Koenen and Groen, 1996 ; Kunzi *et al.*, 1996 ; Colburn *et al.*, 1997 ; Hoffman, 1997 ; Kertz *et al.*, 1998 ; Vacek *et al.*, 1999 ; Freetly *et al.*, 2000.

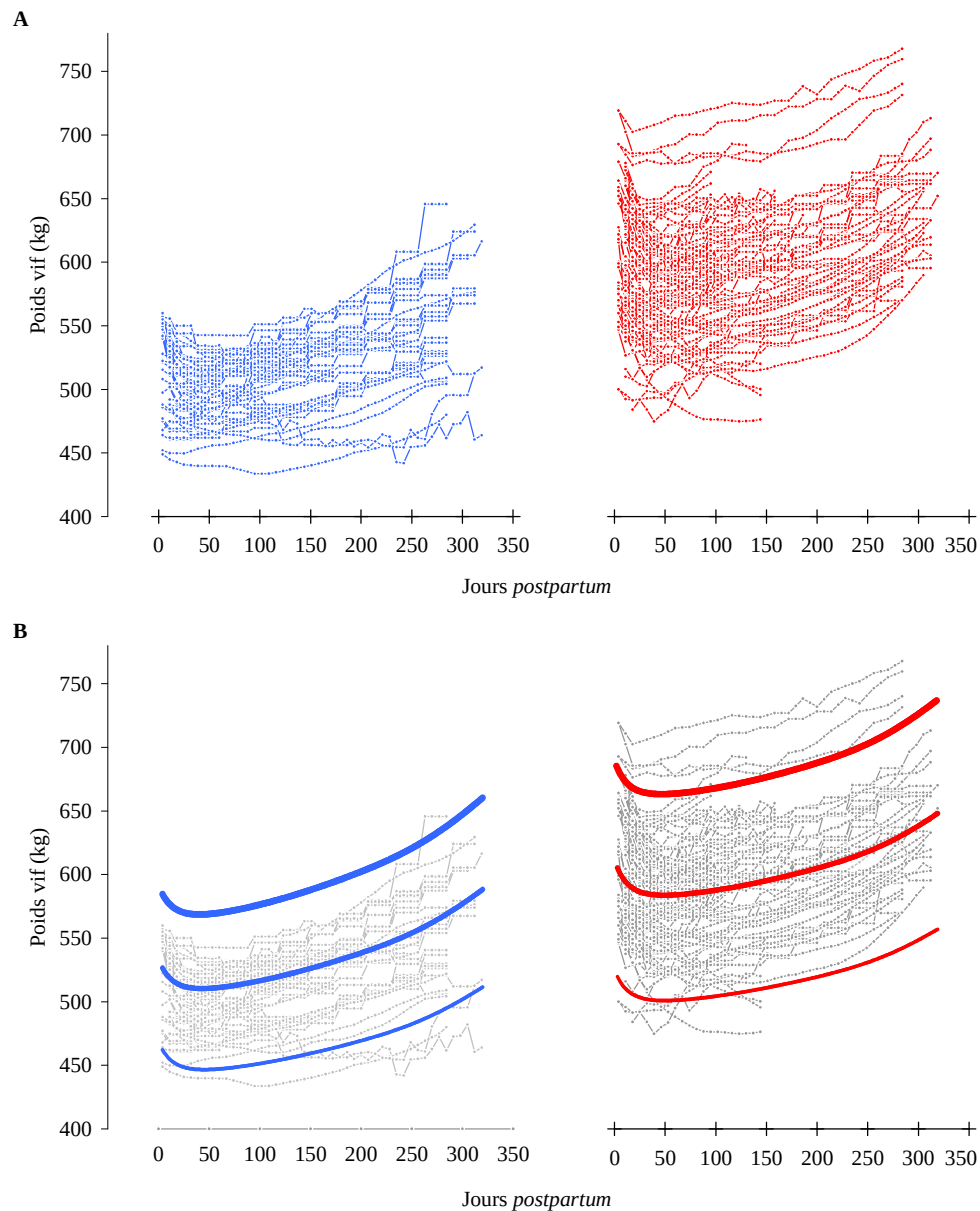


Figure 28 Évolution du poids vif *postpartum* de vaches laitières. A : Données de la littérature⁵⁴ pour des animaux primipares (*en pointillés bleus*) et multipares (*en rouge*). B : Superposition des simulations du modèle pour 3 formats à maturité (*traits d'épaisseur croissante*) et 2 rangs de lactation (*1 en bleu et 3 en rouge*).

⁵⁴ Rook and Campling, 1965 ; Mohrenweiser and Donker, 1967 ; Swanson, 1967 ; Broster *et al.*, 1969 ; Cowan, 1970 ; Decaen, 1970 ; Wiktorsson, 1971 ; Wiktorsson, 1973 ; Broster *et al.*, 1975 ; Lodge *et al.*, 1975 ; Everson *et al.*, 1976 ; Johnson, 1977 ; Vérité and Journet, 1977 ; Wohlt and Clark, 1978 ; Johnson, 1979 ; Kronfeld *et al.*, 1980 ; Garnsworthy and Topps, 1982 ; Holter *et al.*, 1982 ; Pinchasov *et al.*, 1982 ; Donker, 1983 ; Johnson, 1983 ; Krohn *et al.*, 1983 ; Llahr *et al.*, 1983 ; Holter *et al.*, 1984 ; Taylor and Leaver, 1984a ; 1984b ; DePeters, 1985 ; DePeters, 1989 ; Staples *et al.*, 1990 ; Kertz *et al.*, 1991 ; Wohlt *et al.*, 1991 ; Holter and Hayes, 1992 ; Holter *et al.*, 1993 ; Ostensen *et al.*, 1997 ; Tolkamp *et al.*, 1998 ; Soder and Holden, 1999.

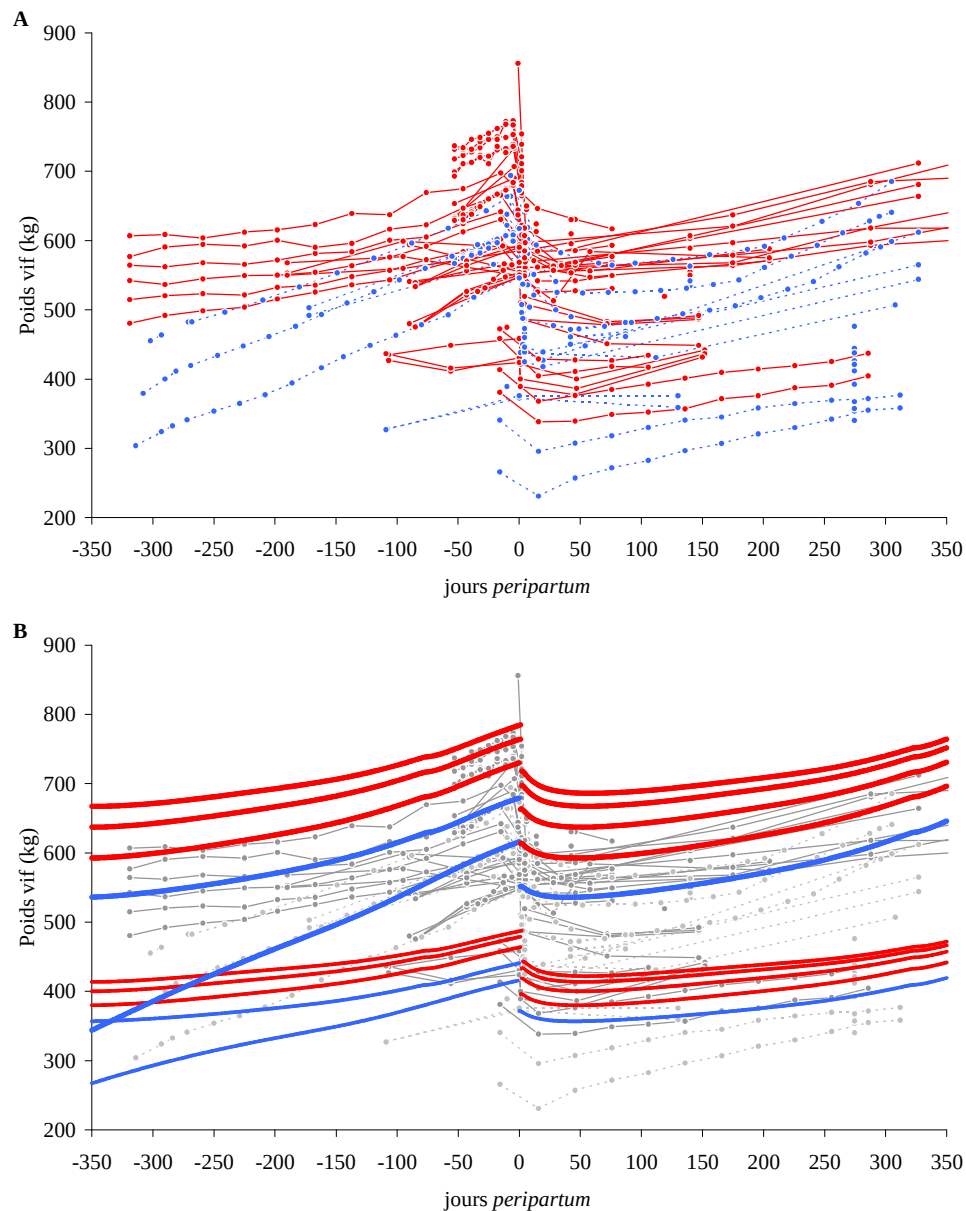


Figure 29 Évolution du poids vif *peripartum* de vaches laitières. A : Données de la littérature⁵⁵ pour des animaux primipares (*en pointillés bleus*) et multipares (*en rouge*). B : Superposition des simulations du modèle pour 2 formats à maturité (*traits fin et épais*) et 5 vêlages successifs (*rang de lactation 1 en bleu et rangs supérieurs en rouge*).

⁵⁵ Bartlett, 1926b ; Blaxter, 1944 ; Burt, 1957 ; Broster *et al.*, 1958 ; Swanson, 1960 ; Castle and Watson, 1961 ; Wickersham and Schultz, 1963 ; Swanson and Hinton, 1964 ; Hight, 1968 ; Schmidt *et al.*, 1971 ; Rakes and Davenport, 1972 ; Lamb and Barker, 1975 ; Smith *et al.*, 1978 ; Strickland and Broster, 1981 ; Bellows *et al.*, 1982 ; Macleod *et al.*, 1983 ; Gordon, 1984 ; Butler-Hogg *et al.*, 1985 ; Boisclair *et al.*, 1986 ; Taylor and leaver, 1986 ; Hocking *et al.*, 1988 ; Sieber *et al.*, 1988 ; Goehring *et al.*, 1989 ; VanSaun *et al.*, 1993 ; Berg and Ekern, 1993 ; Devir *et al.*, 1995 ; Groen and Vos, 1995 ; Grummer *et al.*, 1995a ; Peyraud *et al.*, 1996 ; Hoffman *et al.*, 1996 ; Kertz *et al.*, 1997 ; Hoffman, 1997 ; Morrison *et al.*, 1999 ; Weder *et al.*, 1999 ; Freetly *et al.*, 2000.

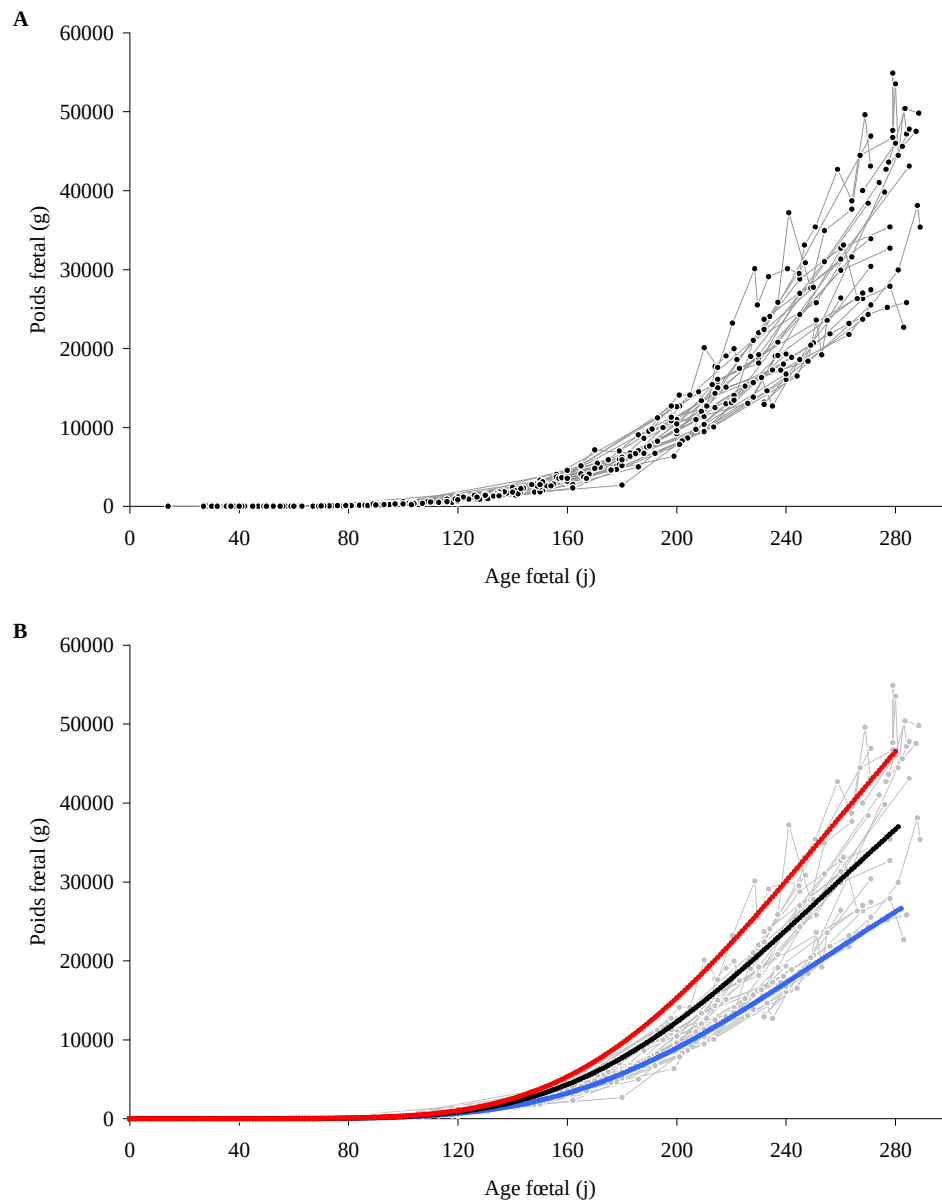


Figure 30 Croissance fœtale du veau au cours de la gestation. A. Données de la littérature⁵⁶. B. Superposition des simulations du modèle pour 3 formats à maturité.

⁵⁶ Buchem, 1909 ; Bergmann, 1921 ; Hammond, 1927 ; Esskuchen, 1931 ; Swett *et al.*, 1937 ; Hatch *et al.*, 1941 ; Winters *et al.*, 1942 ; Nichols, 1944 ; Swett *et al.*, 1948 ; Ellenberger *et al.*, 1950 ; Becker *et al.*, 1951 ; Melton *et al.*, 1951 ; Mäkelä, 1956 ; Joubert et Van Marle, 1959 ; Lyne, 1960 ; Hubbert *et al.*, 1972 ; Ferrell *et al.*, 1976 ; Eley *et al.*, 1977 ; Chew *et al.*, 1979 ; Anthony *et al.*, 1986 ; Sultan *et al.*, 1987 ; Bellows *et al.*, 1990 ; Reynolds *et al.*, 1990 ; Ferrell, 1991 ; House and Bell, 1993 ; Okano, 1994 ; Zhang *et al.*, 1999.

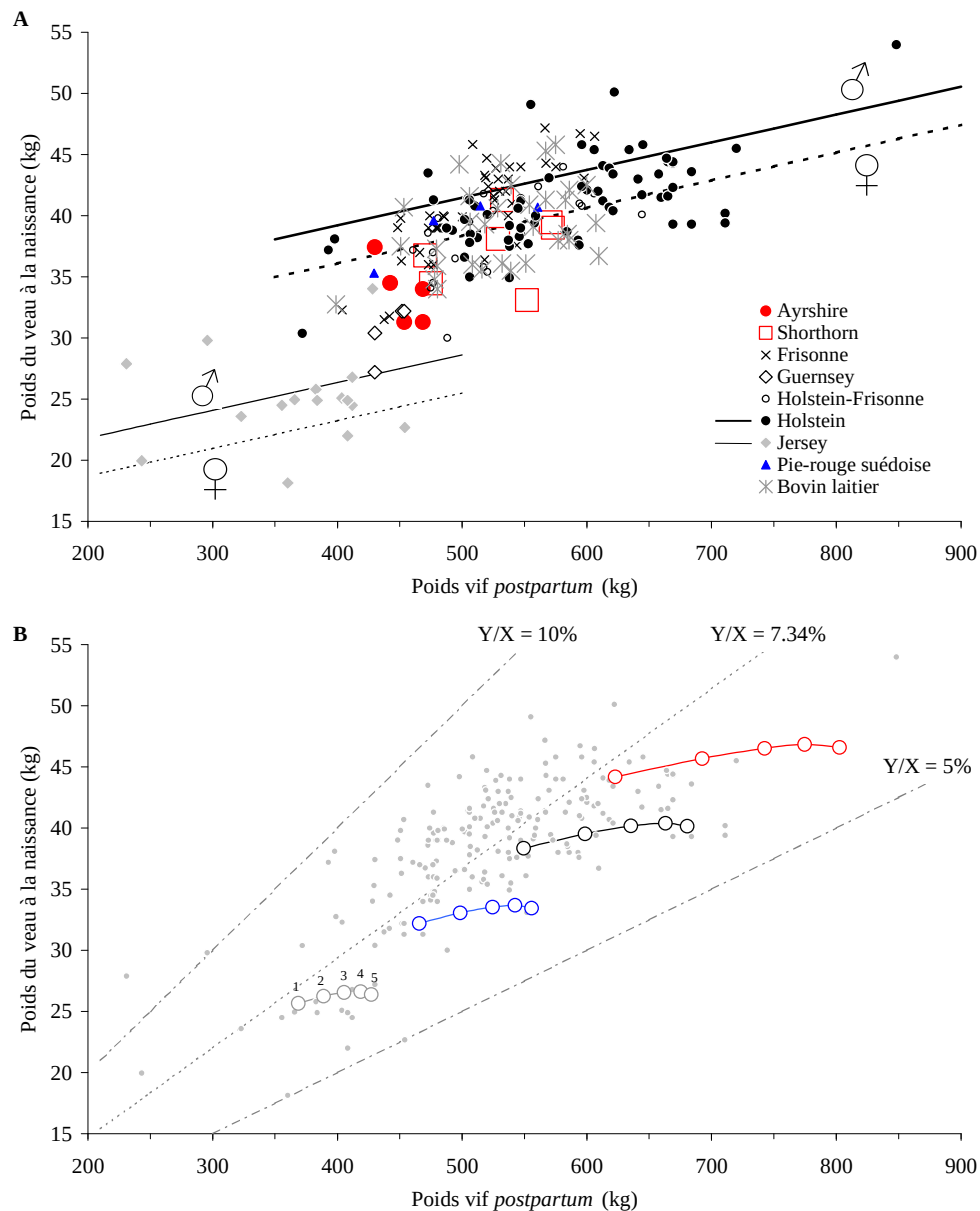


Figure 31 Relation entre poids du veau à la naissance et poids de la vache *postpartum* pour différentes races de vaches laitières (Ayrshire, Shorthorn, Frisonne, Guernsey, Holstein-Frisonne, Holstein, Jersey, Pie Rouge suédoise, Bovin laitier). A. Données de la littérature⁵⁷ et modèles linéaires synthétiques pour des veaux mâle (trait plein) et femelle (trait pointillé) de race Holstein et Jersey. B. Superposition des simulations du modèle pour 4 formats à maturité et 5 lactations successives.

⁵⁷ Eckles, 1916 ; Henry and Morrison, 1917 ; Eckles, 1919 ; Fitch *et al.*, 1924 ; Joubert and Van Marle, 1959 ; Ridler *et al.*, 1963 ; Wickersham and Schultz, 1963 ; Swanson and Hinton, 1964 ; Broster and Tuck, 1967 ; Gleeson, 1973 ; Lodge *et al.*, 1975 ; Yadava *et al.*, 1976 ; Gardner *et al.*, 1977 ; Heitzman *et al.*, 1979 ; Huth and Schmidt, 1979 ; Østergaard, 1979 ; Erb *et al.*, 1981 ; Laird *et al.*, 1981 ; Collier *et al.*, 1982 ; Holter *et al.*, 1986 ; Berglund and Philipsson, 1987 ; Stelwagen and Grieve, 1992 ; Kume and Bicoku, 1993 ; Lacasse *et al.*, 1993 ; Troccon, 1993 ; Moore, 1994 ; Troccon *et al.*, 1994 ; Kertz *et al.*, 1997 ; Hansen *et al.*, 1999 ; Negash, 1999 ; Keady *et al.*, 2001 ; Johanson and Berger, 2003.

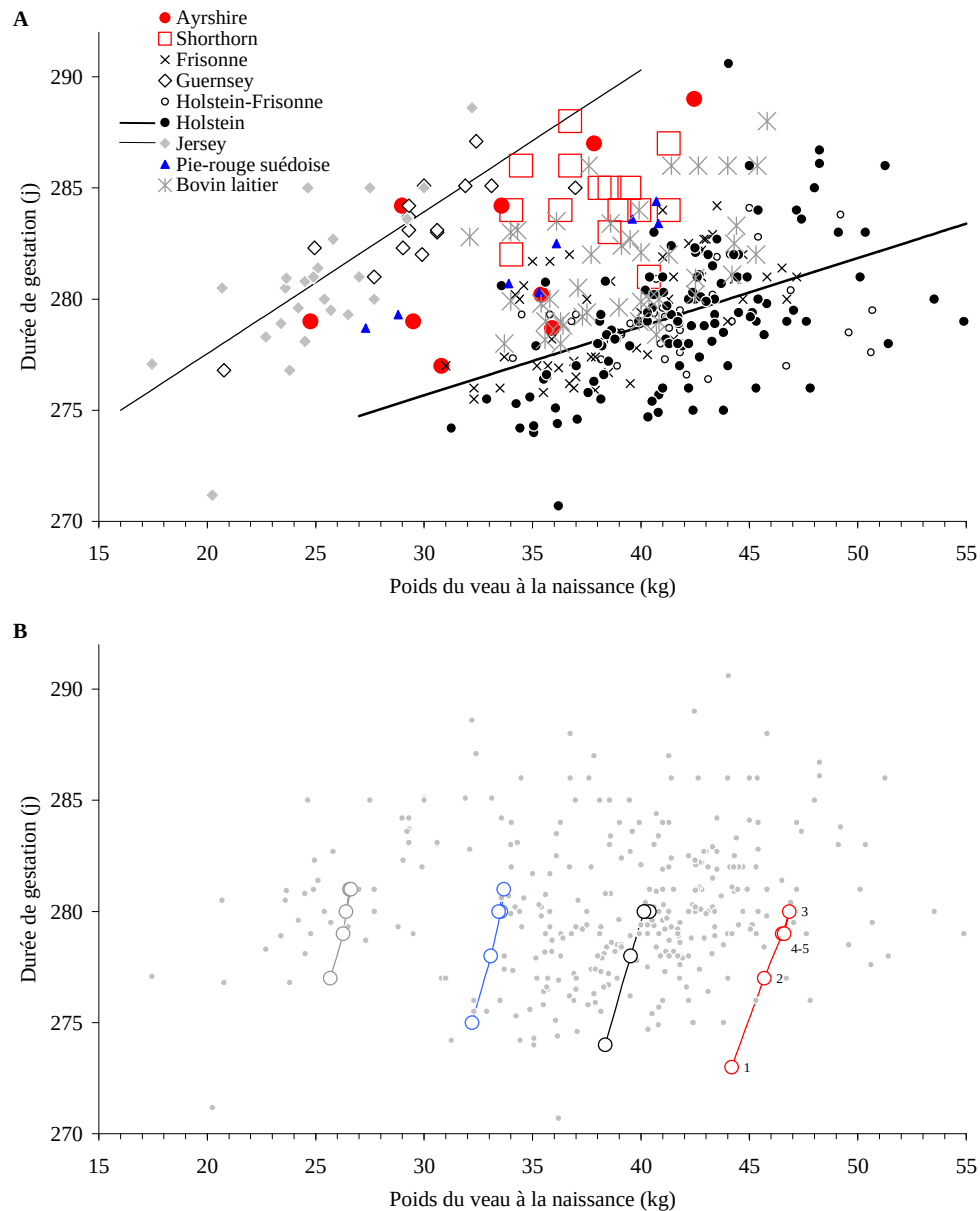


Figure 32 Relation entre durée de gestation et poids du veau à la naissance pour différentes races laitières. A. Données de la littérature⁵⁸ et modèles synthétiques (veaux ♀ et ♂, races Holstein et Jersey). B. Superposition des simulations du modèle pour 4 formats à maturité et 5 lactations successives.

⁵⁸ Eckles, 1919 ; Fitch *et al.*, 1924 ; Dinkhauser *et al.*, 1944 ; Ellenberger *et al.*, 1950 ; Brakel *et al.*, 1952 ; Davis *et al.*, 1954 ; Foote *et al.*, 1959 ; Huth, 1962 ; Ridler *et al.*, 1963 ; Andersen and Plum, 1965 ; Boyd and Hafs, 1965 ; Everett and Magee, 1965 ; Touchberry and Bereskin, 1966 ; DeTena Andreu, 1973 ; Romita, 1973 ; Beardsley *et al.*, 1974 ; Gianola and Tyler, 1974 ; Hocking, 1974 ; Koubek, 1974 ; Muller and Owens, 1974 ; Oldenbroek, 1974 ; Dijkstra *et al.*, 1975 ; Beardsley *et al.*, 1976 ; Eliya and Christensen, 1976 ; Guaragna *et al.*, 1976 ; Manrique *et al.*, 1976 ; Philipsson, 1976 ; Serrano *et al.*, 1976 ; Vos *et al.*, 1976 ; Laurijsen and Oldenbroek, 1977 ; Morgan, 1977 ; Everitt *et al.*, 1978 ; Fisher and Williams, 1978 ; Gaillard, 1978 ; Martinez *et al.*, 1978 ; Veris, 1978 ; Arbabian-Ghafouri, 1980 ; Egbunike and Togun, 1980 ; Gaillard, 1980 ; Lazarevic and Novakovic, 1980 ; Meijering, 1980 ; Chew *et al.*, 1981 ; Erb *et al.*, 1981 ; Gaillard, 1981 ; Leeuwen and Zijlstra, 1981 ; Little and Harrison, 1981b ; Gaillard, 1982 ; Das *et al.*, 1984 ; Oldenbroek, 1984 ; Bhuyan and Mishra, 1985 ; Oferrall *et al.*, 1985 ; VonKorn and Langholz, 1985 ; Holter *et al.*, 1986 ; Sang *et al.*, 1986 ; Shin *et al.*, 1986 ; Berglund and Philipsson, 1987 ; Eppard *et al.*, 1987 ; Trilk *et al.*, 1988 ; Gravert *et al.*, 1990 ; Guilbault *et al.*, 1990 ; Hagger and Hofer,

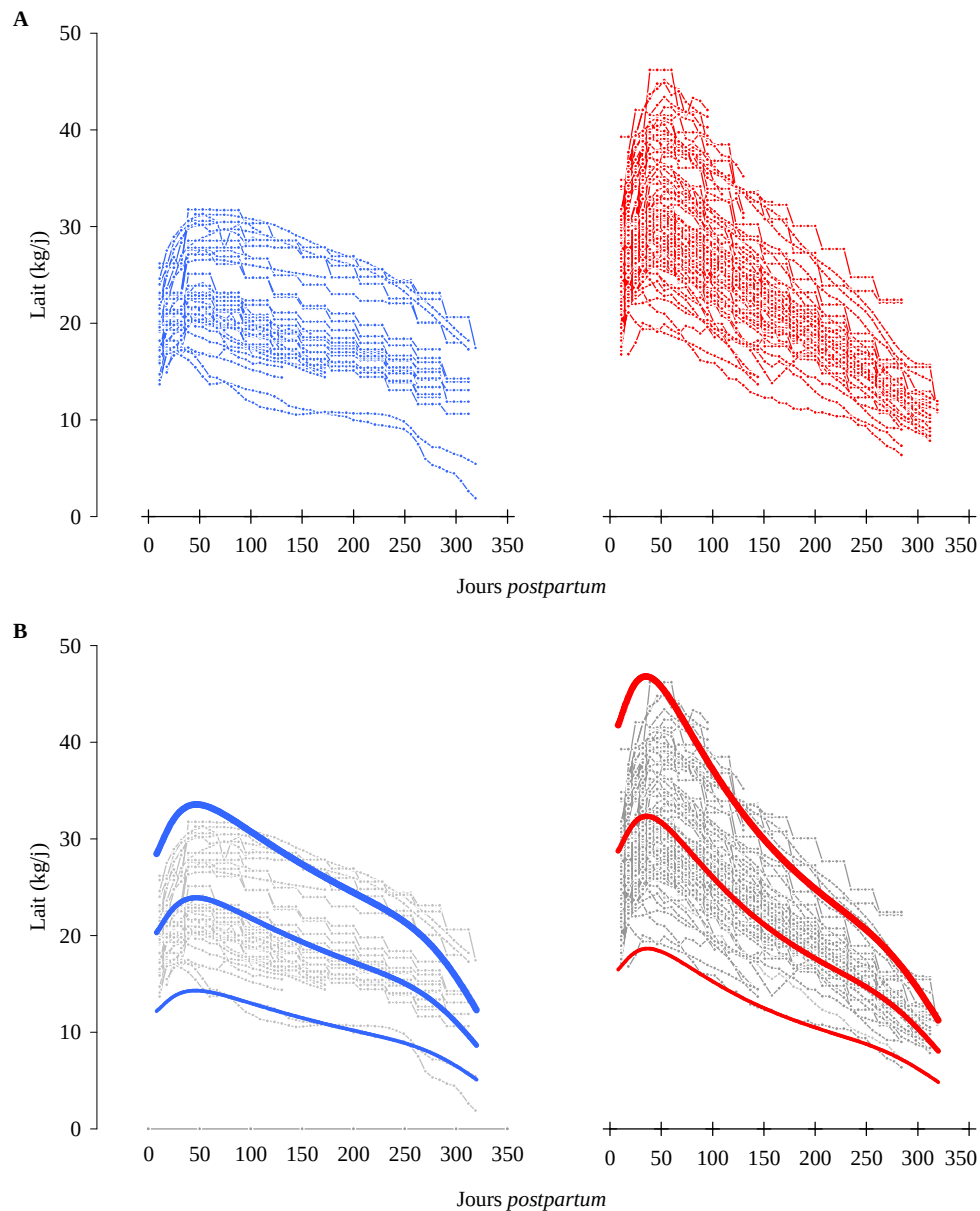


Figure 33 Évolution de la production laitière au cours de la lactation de vaches laitières. A : Données de la littérature⁵⁹ pour des animaux primipares (*en bleu*) et multipares (*en rouge*). B : Superposition des simulations du modèle pour 3 niveaux génétiques de production laitière (*traits d'épaisseur croissante*) et 2 rangs de lactation (*1 en bleu et 3 en rouge*).

1990 ; Oferrall and Ryan, 1990 ; Rooy *et al.*, 1990a ; Rooy *et al.*, 1990b ; Anonymous, 1991 ; Rémond *et al.*, 1991 ; KB-Mitteilungen, 1993 ; Troccon, 1993 ; Kojima, 1999 ; Zhang *et al.*, 1999 ; Jacobsen *et al.*, 2000 ; Perfield *et al.*, 2002 ; Johanson and Berger, 2003.

⁵⁹ Rook and Campling, 1965 ; Swanson, 1967 ; Broster *et al.*, 1969 ; Decaen, 1970 ; Broster *et al.*, 1975 ; Lodge *et al.*, 1975 ; Everson *et al.*, 1976 ; Johnson, 1977 ; Vérité and Journet, 1977 ; Wohlt and Clark, 1978 ; Johnson, 1979 ; Kronfeld *et al.*, 1980 ; Garnsworthy and Topps, 1982 ; Holter *et al.*, 1982 ; Pinchasov *et al.*, 1982 ; Donker, 1983 ; Johnson, 1983 ; Llahr *et al.*, 1983 ; Holter *et al.*, 1984 ; Taylor and Leaver, 1984a ; 1984b ; DePeters, 1985 ; DePeters, 1989 ; Staples *et al.*, 1990 ; Kertz *et al.*, 1991 ; Wohlt *et al.*, 1991 ; Holter and Hayes, 1992 ; Holter *et al.*, 1993 ; Ostensen *et al.*, 1997 ; Tolkamp *et al.*, 1998 ; Soder and Holden, 1999.

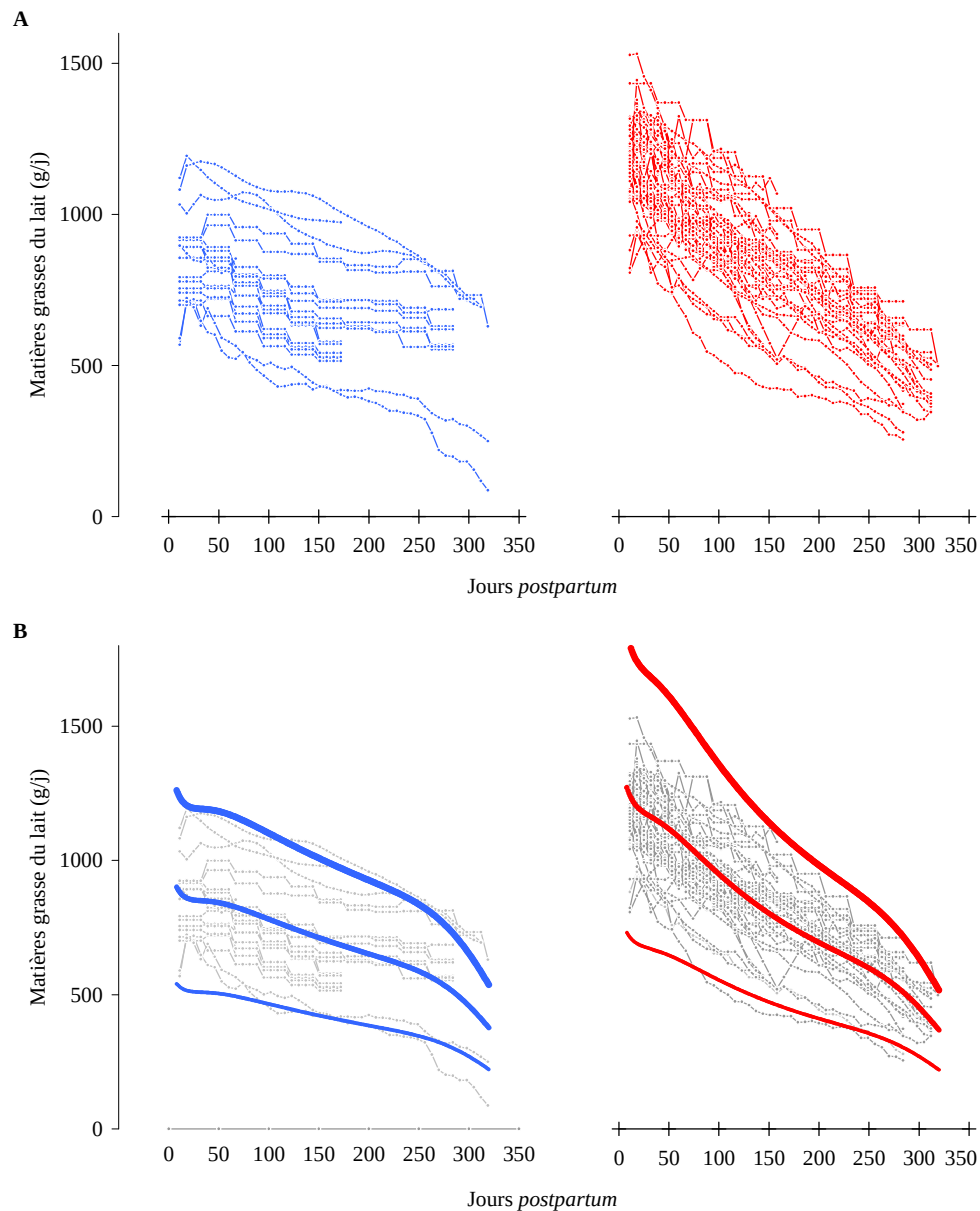


Figure 34 Évolution de la production de matières grasses du lait au cours de la lactation de vaches laitières. A : Données de la littérature⁶⁰ pour des animaux primipares (*en bleu*) et multipares (*en rouge*). B : Superposition des simulations du modèle pour 3 niveaux génétiques de production laitière (*traits d'épaisseur croissante*) et 2 rangs de lactation (*1 en bleu et 3 en rouge*).

⁶⁰ Rook and Campling, 1965 ; Swanson, 1967 ; Decaen, 1970 ; Broster *et al.*, 1975 ; Everson *et al.*, 1976 ; Johnson, 1977 ; Wohlt and Clark, 1978 ; Johnson, 1979 ; Kronfeld *et al.*, 1980 ; Donker, 1983 ; Johnson, 1983 ; DePeters, 1985 ; Staples *et al.*, 1990 ; Kertz *et al.*, 1991 ; Wohlt *et al.*, 1991 ; Holter and Hayes, 1992 ; Ostensen *et al.*, 1997 ; Tolcamp *et al.*, 1998.

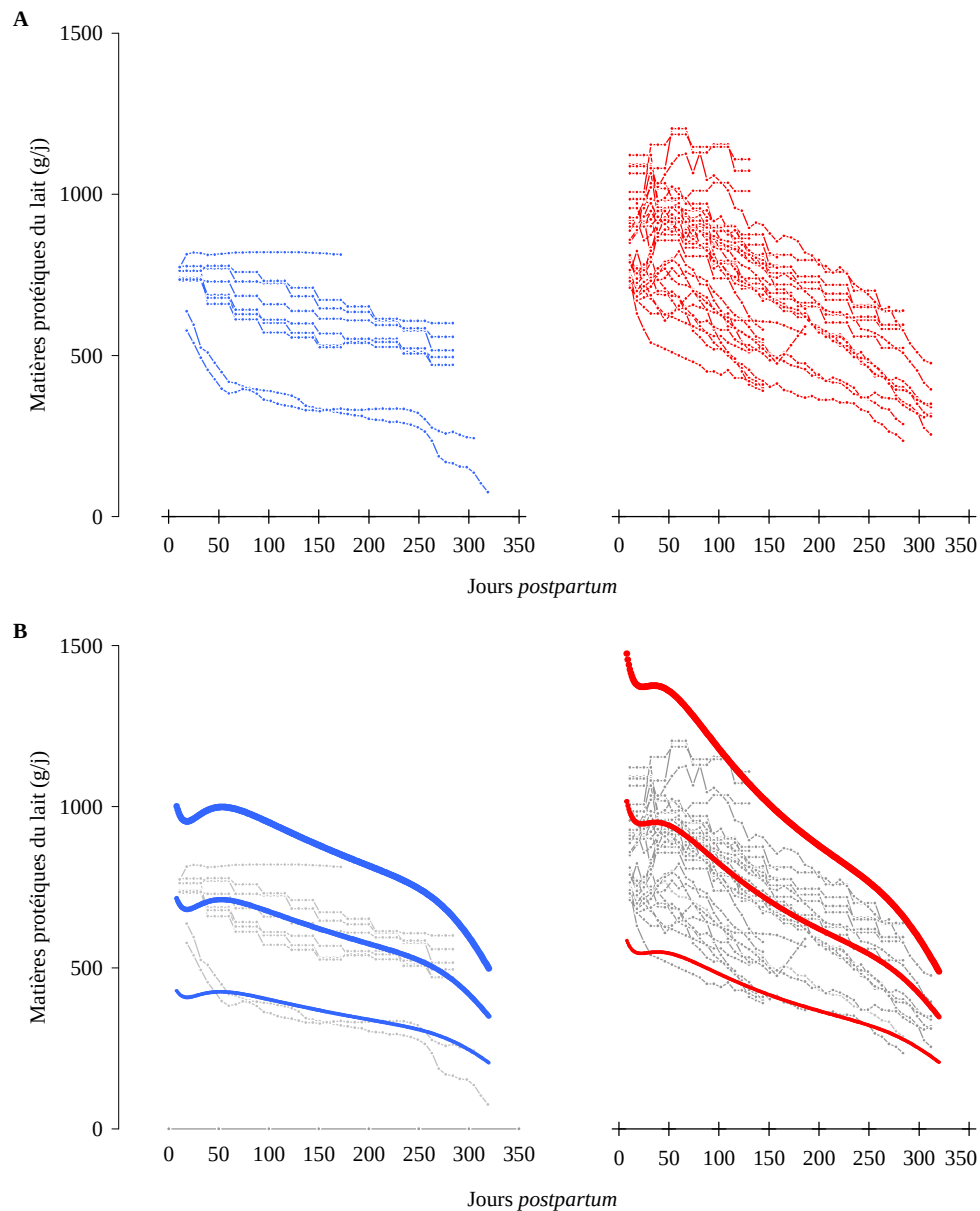


Figure 35 Évolution de la production de matières protéiques du lait au cours de la lactation de vaches laitières. A : Données de la littérature⁶¹ pour des animaux primipares (*en bleu*) et multipares (*en rouge*). B : Superposition des simulations du modèle pour 3 niveaux génétiques de production laitière (*traits d'épaisseur croissante*) et 2 rangs de lactation (*1 en bleu et 3 en rouge*).

⁶¹ Rook and Campling, 1965 ; Decaen, 1970 ; Johnson, 1977 ; Wohlt and Clark, 1978 ; Johnson, 1979 ; Kronfeld *et al.*, 1980 ; Donker, 1983 ; Johnson, 1983 ; Wohlt *et al.*, 1991 ; Ostensen *et al.*, 1997 ; Tolkamp *et al.*, 1998.

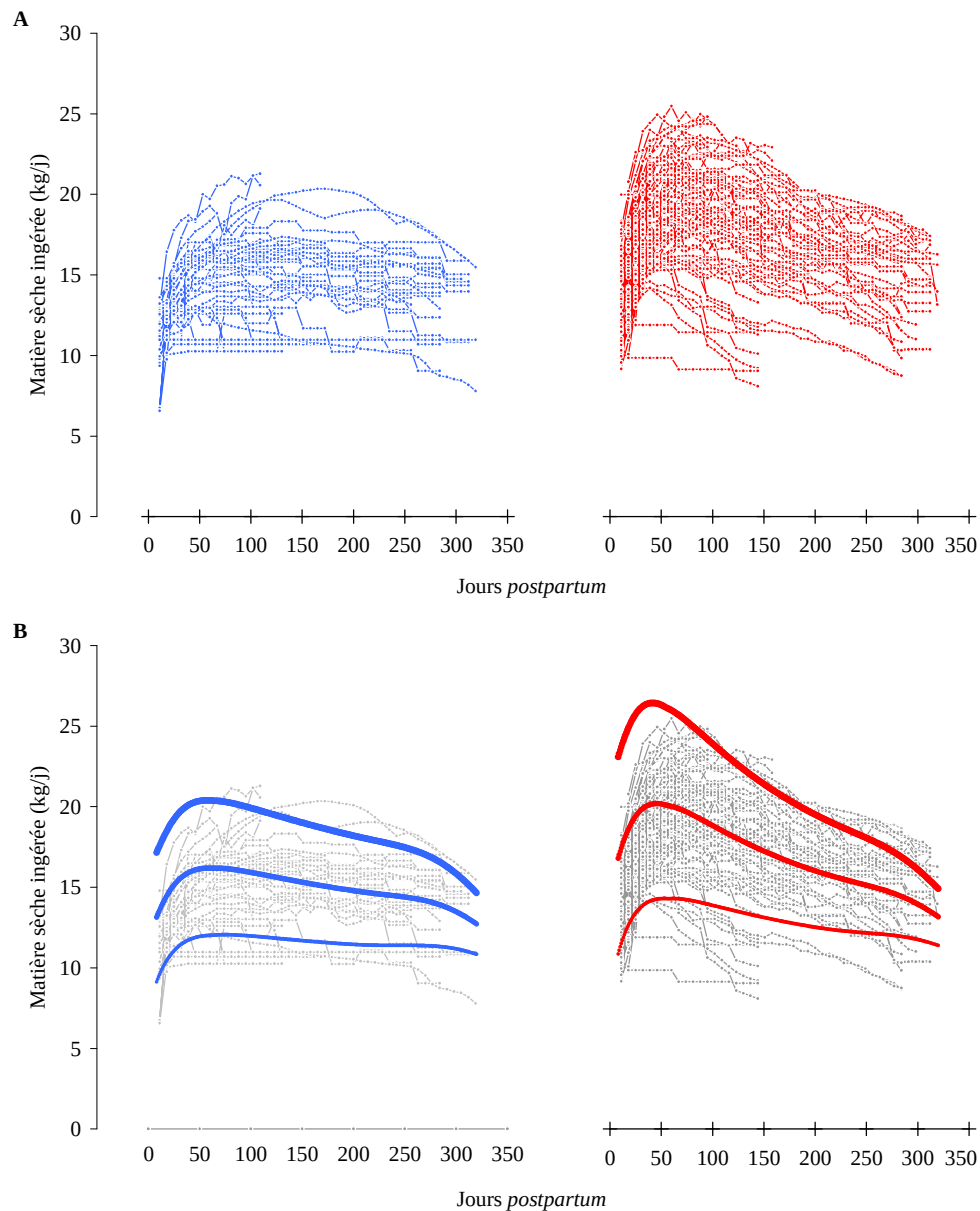


Figure 36 Évolution de la quantité de matière sèche ingérée au cours de la lactation de vaches laitières. A : Données de la littérature⁶² pour des animaux primipares (*en bleu*) et multipares (*en rouge*). B : Superposition des simulations du modèle pour 3 niveaux génétiques de production laitière (*traits d'épaisseur croissante*) et 2 rangs de lactation (*1 en bleu et 3 en rouge*).

⁶² Broster *et al.*, 1969 ; Broster *et al.*, 1975 ; Cowan, 1970 ; Decaen, 1970 ; DePeters, 1985 ; DePeters, 1989 ; Everson *et al.*, 1976 ; Garnsworthy and Topps, 1982 ; Holter *et al.*, 1982 ; Holter *et al.*, 1984 ; Holter *et al.*, 1992 ; Holter *et al.*, 1993 ; Johnson, 1977 ; Johnson, 1979 ; Johnson, 1983 ; Kertz *et al.*, 1991 ; Kronfeld *et al.*, 1980 ; Krohn *et al.*, 1983 ; Llahr *et al.*, 1983 ; Lodge *et al.*, 1975 ; Mohrenweiser and Donker, 1967 ; Ostensen *et al.*, 1997 ; Pinchasov *et al.*, 1982 ; Rook and Campling, 1965 ; Soder and Holden, 1999 ; Staples *et al.*, 1990 ; Swanson, 1967 ; Taylor and Leaver, 1984a ; 1984b ; Tolkamp *et al.*, 1998 ; Vérité and Journet, 1977 ; Wallace, 1959 ; Wiktorsson, 1971 ; Wiktorsson, 1973 ; Wohlt and Clark, 1978 ; Wohlt *et al.*, 1991.

Systemic modelling of ruminant female performance.

Application to dairy cows

The work described in this document is centred on the building of a dairy cow model. The whole model is composed of three dynamic, mechanistic and deterministic models corresponding to three different levels of representation of the cow. Each model has a specific functionality. These models, respectively denoted **teleonomic**, **energetic** and **metabolic** are linked through a hierarchical structure and are interdependent.

The teleonomic model (*cf.* II.1) consists in a representation of the animal seen as a living organism ensuring its own survival and the continuation of its species. This model is aimed at driving the energetic model. The model describes the **dynamic of the priorities** of a female mammal between functions of growth, body reserve monitoring and reproduction along its lifetime punctuated by successive reproductive cycles. This model produces a reference trajectory used to control the energetic model through two paths corresponding to homeorhesis and homeostasis. The energetic model (*cf.* II.2) consists in a representation of the animal energetic metabolism and is aimed at predicting performance. The model describes the **dynamic partitioning of energy** between flows for growth, maintenance, gestation, lactation and body reserves mobilization and storage. The model simulates milk yield and composition, foetal growth and calf birth weight, intake and changes in body mass and composition of a dairy cow throughout lifetime and during reproductive cycles. The metabolic model (*cf.* II.3) consists in a representation of the animal metabolism at the inter-organ level and is aimed at interpreting performance predicted by the energetic model as metabolites flows. The model describes the **dynamic of flows** of glucose, amino acids, acetate + butyrate, triacylglycerides and non-esterified fatty acids associated with material flows of the energetic model during lactation (milk yield, intake, body weight changes). The model simulates liver triacylglycerides and plasma metabolites contents during lactation.

The connexion between the teleonomic and energetic models is effective, but that between the energetic and metabolic models has not been formally done but only put into perspective since these two models are technically compatible. The hierarchical layout of the three models forms a consistent set proposed as a stage of work in a whole modelling project.

The introductive part of this document presents the context and the objectives. The first part of this document presents the modelling project through its stakes (*cf.* I.1), the view points adopted for the representation of the “dairy cow system” (*cf.* I.2) and the mobilized elements of knowledge (*cf.* I.3). The second part of this document concerns the presentation of the proposed whole model through the description of the three sub models : teleonomic model of priorities, energetic model of animal performance and metabolic model of metabolites pathways. The conclusive part of this document contains perspectives of improvement, extension and use of the model as well as outlooks of work.

Keywords: dairy cow ; lactation ; regulations ; teleonomic model ; energy partitioning ; metabolism.

Modélisation systémique des performances des femelles de ruminants. Application au cas de la vache laitière

Le travail de thèse décrit dans ce document s'articule autour de la construction d'un modèle de la vache laitière. Ce modèle consiste en trois modèles dynamiques, mécanistes et déterministes correspondant à des niveaux de représentation différents de la vache et présentant une fonctionnalité spécifique. Ces modèles, respectivement **téléonomique**, **énergétique** et **métabolique** s'agencent entre eux de façon hiérarchique et sont interdépendants.

Le modèle téléonomique (*cf.* Partie II.1) se situe au niveau de l'animal en tant qu'organisme vivant assurant sa survie et la pérennité de son espèce et possède une fonction de pilotage du modèle énergétique. Il s'agit d'un modèle de la **dynamique des priorités** d'une femelle entre les fonctions de croissance, de gestion des réserves corporelles et de reproduction au cours de sa vie rythmée par la succession de cycles de reproduction. Ce modèle produit une trajectoire de référence et contrôle le modèle énergétique à travers deux voies traduisant l'homéorhèse et l'homéostasie. Le modèle énergétique (*cf.* Partie II.2) se situe au niveau du métabolisme énergétique de l'animal et possède une fonction de prédiction des performances. Il s'agit d'un modèle de la **dynamique de partition de l'énergie** ingérée entre les flux de croissance, d'entretien, de gestation, de lactation et de mobilisation et stockage des réserves corporelles. Ce modèle simule la production et la composition laitière, la croissance fœtale et le poids du veau à la naissance, l'ingestion, et les variations de masse et de composition corporelle de la vache au cours de sa vie et durant les cycles gestation/lactation. Le modèle métabolique (*cf.* Partie II.3) se situe au niveau du métabolisme inter-organes et possède une fonction d'interprétation métabolique des flux de matière du modèle énergétique. Il s'agit d'un modèle de la **dynamique des flux** de glucose, d'acides aminés, d'acétate/butyrate, de propionate, de triglycérides et d'acides gras non-estérifiés conditionnés par les flux de matière du modèle énergétique au cours de la lactation (production de lait, ingestion, variations de réserves). Ce modèle simule les teneurs en triglycérides du foie et des métabolites circulants dans le plasma au cours de la lactation.

Si l'implémentation de la connexion entre les modèles téléonomique et énergétique est effective, celle entre les modèles énergétique et métabolique n'est pas formellement réalisée. Elle est ici uniquement mise en perspective dans la mesure où ces modèles sont techniquement compatibles. L'agencement hiérarchique des trois modèles forme un ensemble conceptuel cohérent présenté comme une étape de travail dans un projet global.

L'introduction de ce document positionne le contexte et les objectifs de ce travail. La première partie de ce document présente le projet de modélisation qui fonde ce travail à travers ses enjeux (*cf.* Partie I.1), les points de vue adoptés pour la représentation du « *système vache laitière* » (*cf.* Partie I.2) et les éléments de connaissances mobilisés (*cf.* Partie I.3). La deuxième partie de ce document concerne la description du modèle proposé à travers celle des trois sous-modèles qui le composent : modèle téléonomique des priorités, modèle énergétique prédictif des performances zootechniques et modèle métabolique explicatif des flux de métabolites. La conclusion de ce document contient des propositions d'amélioration, d'extension et d'utilisation du modèle ainsi que des perspectives de travail.

Mots clefs : vache laitière ; lactation ; régulations ; modèle téléonomique ; partition de l'énergie ; métabolisme.