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The adaptation of domestic ruminants to environmental constraints under extensive conditions

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Abstract — The dietary energy requirements for maintenance of suckling ruminants typically account for more than 75% of the animals total annual energy requirements and are influenced by animal size and productive potential. Consequently, it is the maintenance requirement of a ruminant animal in relation to feed intake that will primarily determine the success with which it adapts to its nutritional environment. In the case of the female ruminant, it is energy intake above maintenance that influences her ability to grow and conceive; and to partition nutrients towards the developing conceptus and suckling young. Emerging evidence suggests that the ability of the female ruminant to do the latter may have implications for the lifetime performance and fertility of her offspring. The legacy of undernutrition in utero for the performance of future generations, however, remains to be determined. Within a nutritional environment, factors such as ambience and herbage availability and quality can be manipulated at key stages of the animals reproductive life and annual breeding cycle so as to alleviate some of the difficulties of genotype selection. Ways and means by which this can be achieved are discussed. © Elsevier/Inra

extensification / ruminants / genotype / nutrition / reproduction

Résumé — L'adaptation des ruminants domestiques aux contraintes environnementales en conditions d'extensification. Les besoins d'entretien des ruminants menés en système allaitant correspondent à plus de 75 % des besoins énergétiques totaux avec des variations selon la taille de l'animal et son potentiel de production. De ce fait ce sont ses besoins d'entretien (*et sa capacité d'ingestion*) qui vont en premier lieu déterminer la réussite de son adaptation à son milieu nutritionnel. Dans le cas de la femelle cela va d'abord influencer sur son aptitude à croître et à concevoir ; puis si nécessaire, à orienter les nutriments vers le développement du conceptus et l'allaitement du jeune. Des résultats récents semblent indiquer que la capacité de la femelle à l'allaitement peut avoir des effets sur la performance et la fertilité de sa progéniture. En revanche, un effet rémanent de la sous-nutri-

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tion in utero sur les performances des générations suivantes reste encore à déterminer. Pour un même environnement nutritionnel, plusieurs facteurs tels que la qualité et/ou la disponibilité des fourrages peuvent être modulés à des périodes clés du cycle de production et de la vie reproductive pour aplâner certaines difficultés inhérentes au choix des races. Les voies et moyens d'y arriver sont discutés.
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extensification / ruminants / génotype / nutrition / reproduction

1. INTRODUCTION

Under most extensive systems of ruminant livestock production breeding animals spend their lives in the thermal and nutritional environment in which they are born and this determines the degree to which they achieve their productive potential. Environmental conditions within the European continent range from being hot and arid to being cold and wet, and at each of these two extremes forage availability will be limiting. The effects of low levels of nutrition on animal growth and development can be experienced from an early age. Indeed, through its effects on the growth and development of foetal tissue and organs, nutrition can influence adult performance. These early programming effects will continue to influence animal performance through puberty and adolescence, and into adulthood. The success with which a ruminant adapts to its nutritional environment will depend to a large extent on the requirements for maintenance and productive purposes of the biological type in question relative to the quantity, quality and seasonal distribution of available nutrients. In the case of the female ruminant this success will determine her reproductive competence and hence biological efficiency.

This paper is concerned with examining how different biological types of ruminant adapt to their nutritional environment during early life; and the consequences that this might have on animal performance in later life. After identifying the nutritional requirements of ruminants under extensive conditions, and how these are influenced by genotype, season and herbage quality, this paper

will consider the factors that influence herbage intake, and hence the ability of ruminants to meet their requirements. The final section of the paper considers the consequences of nutritional environment on animal performance.

2. ANIMAL REQUIREMENTS UNDER EXTENSIVE CONDITIONS

2.1. Effect of biological type

The proportion of the annual dietary energy requirements of suckling ruminants required for maintenance is typically around 75% of the total for a beef cow [24, 61] and for single and twin-bearing ewes it is 80 and 73% respectively. Much effort has, therefore, been devoted to quantifying the maintenance requirements of such animals. A positive relationship is known to exist between the genetic potential for production (growth and/or milk production) and maintenance requirements with commonly accepted values for the metabolisable energy (ME) requirements for maintenance (ME_m) in thermoneutral conditions of between 0.40–0.55 MJ $ME \cdot kg^{-1} Wt^{0.75}$ for dry beef cows; 0.50–0.65 MJ $ME \cdot kg^{-1} Wt^{0.75}$ for lactating beef cows; and up to 0.77 MJ $ME \cdot kg^{-1} Wt^{0.75}$ for lactating dairy cows [86]. Commonly accepted values for ME_m in sheep vary from 0.4 to 0.8 MJ $ME \cdot kg^{-1} Wt^{0.75}$. Such ranges are related to differences in body composition and the size and metabolic rate of the visceral organs [24, 77]. In cattle, ME_m allowances may need to be increased by 10–50% to meet the requirements of locomotion in difficult terrain and by slightly

higher proportions for sheep in similar circumstances [6].

2.2. Effect of season and climate

Seasonal variations in requirements for energy for general maintenance purposes and the achievement of live weight stability in cattle are considered to be mainly due to seasonal variation in body composition [48] rather than seasonal variation in thermoneutral maintenance energy requirements [9]. General energy expenditure is also closely associated with animal activity, which tends to be greater in the summer than in the winter, at least in deer [73].

Our understanding of the thermal requirements of ruminants in temperate climates is sufficiently detailed to allow us to accurately predict the effects of climate on the performance of dairy cows, beef cows and growing calves using mathematical models [16]. One model [15] predicts sensible heat loss from the parameters air temperature, wind speed, net radiation and rainfall, and has been used to quantify the benefits of different types of shelter, including housing, shelter belts and woodlands. For example, the model predicts that in cold (5 °C), wet (5 mm rain per day) and windy (wind velocity of 9 m/s) conditions a non-pregnant, lactating cow would require 104 MJ ME/day to maintain constant body weight and that this value would not be reduced by housing. In contrast, the food energy requirements of a non-pregnant, non-lactating cow would increase proportionately by 0.31 (72 versus 55 MJ ME/day) if it was kept outside rather than housed in the same conditions. The increase in metabolic heat production associated with the increased level of ME intake necessary to support lactation enables lactating animals to be more tolerant to adverse climatic conditions. Thus, animals may remain productive in such circumstances, but this will depend on the provision of adequate levels of food energy during the period of adversity. This conclusion is support-

ed by recent evidence from Sweden, where growing cattle fed outside during the winter achieved similar growth rates (533 g/day) to their contemporaries that were fed indoors (553 g/day) on the same diet [65].

2.3. Effect of forage quality

In extensive conditions most, if not all, the requirements for energy and other nutrients must be supplied by naturally occurring grass or conserved forage. Therefore, the requirements of the ruminant animal will be influenced by factors that influence herbage availability and quality in addition to those associated with animal species and breed type.

It is recognised that the efficiency of utilisation of dietary energy for maintenance, growth and lactation depends on diet quality (metabolisability; ME/GE; [6, 42]). Metabolisable energy is utilised less efficiently in low quality diets and so forage availability must be adjusted accordingly. Until recently, however, a fixed value (0.133) for the efficiency of utilisation of ME for conceptus growth (k_c) has been used, so that the metabolisable energy requirements of pregnant ruminants, particularly those carrying two or three fetuses, have been poorly estimated. Although not perhaps significant in terms of the animals total annual energy requirements, inadequate provision of metabolisable energy during gestation can have serious consequences for the viability and performance of the dam and offspring (see section 4.3). There is now evidence from sheep studies that k_c is positively correlated with the energy density (M/D) of the diet [38, 66]. In order to illustrate its significance, this finding is applied to cattle to predict the effect of diet quality on the requirements for ME during gestation. A 550 kg non-lactating, single-bearing beef cow (genetic potential mature weight of 750 kg), which experiences zero maternal (i.e., excluding the conceptus) live-weight change, fed a diet with an M/D of 7.4 MJ·kg⁻¹ DM

(0.6 UFL·kg⁻¹ DM; late cut hay) would require 33% more ME than an equivalent cow fed a diet with an M/D of 12.9 MJ·kg⁻¹ DM (1.1 UFL·kg⁻¹ DM) in pregnancy to week 40 of gestation. It is clear, therefore, that the quality of forage, i.e., its metabolisability, has a large effect on the efficiency of energy utilisation for all the functions of ruminant animals and, hence, on their energy requirements.

3. HERBAGE INTAKE UNDER EXTENSIVE CONDITIONS

Under extensive grazing conditions intake is primarily limited by herbage availability and digestibility. Ruminants can compensate for low herbage availability, to a certain extent, by increasing the time spent grazing, but such activity has a cost. For example, cattle in the study of Holloway et al. [36] required about three times the amount of forage dry matter per kg live weight in order to achieve similar growth rates to those animals managed under intensive grazing conditions. Animals cannot compensate, however, for low herbage digestibility which affects both the energy available for use by the animal per kg DM intake and the intake of herbage DM. For cattle fed hay based diets, it has been predicted that every 1% decrease in the organic matter digestibility reduces intake by 33g/100 kg live weight [63].

For a given ruminant species, the animal related factors known to influence voluntary food intake (VFI) include genotype, size, age, body-condition score, physiological state and milk production [26, 43]. The VFI of dairy females is known to be 10% higher than that of beef females of the same weight [5]. Among beef breeds Limousins have a relatively low intake capacity [29] which is similar to that of the Belgian Blue [32]. VFI calculated from several trials where diets were based on forages was shown to be allometrically related to live weight (coefficient = 0.9; [5, 78]), and to

increase more quickly than their maintenance requirements expressed on a metabolic live weight basis. Thus, for animals differing in size, the largest may have an advantage in ad libitum feeding systems.

In the breeding cow, voluntary food intake is minimal just before parturition then increases rapidly to reach a maximum during the second month of lactation. Primiparous cows, however, have lower VFIs than adult cows (by 8% to 12% after adjustments are made for differences in size and milk production), but such differences are not so obvious in ewes. A strong relationship exists between VFI and milk production in high performing ruminants [22], and milk yield is often used as a predictor of intake in dairy cows and ewes [11, 23]. This relationship is not so strong, however, among low producing ruminants [41].

4. ANIMAL PERFORMANCE UNDER EXTENSIVE CONDITIONS

4.1. Attainment of mature body size and body composition

Working with four beef cow genotypes that differed in terms of their potential mature size and milk production, Sinclair et al. [74] demonstrated that young, growing cows adjust their weight, body composition and milk yield to that which can be supported by the prevailing level of annual energy intake. Morris et al. [54] also reported that young cows (1 to 5 years of age) were lighter (by 9%) than others of the same genotype when managed on the least favourable of three locations. However, permanent stunting in growth is unlikely to have occurred in animals in either study; rather these animals would have attained a steady-state body weight, since Taylor et al. [76] observed that all but the most severely food restricted heifers in their study resumed growth when realimented after 5 to 7 years of age and reached live weights approaching those of non feed restricted heifers. Little is known

about the body composition of such animals, but maintenance efficiency was not significantly affected in that study. In studies where the nutritional environment during early life has failed to influence mature size (e.g., [79]), cows were exposed to bulls continuously and culling for reproductive failure was not practised. Therefore, these animals were able to gain weight and conceive at some later point.

4.2. Seasonal changes in body composition and milk yield

There are recognisable and quantifiable effects of season on changes in body composition [64], growth rate [4] and milk yield [46] among the different ruminant species. Growth rates, for example, are greater under long days than under short days for both lambs [27, 28] and calves [4, 55], and milk yields are also known to vary seasonally, with the highest yields occurring during the long days of summer [25]. Such effects arise from a complex interaction between food availability and quality, VFI [51], basal metabolic rate [10] and nutrient partitioning.

Important differences between genotype and sex in the ability to respond to seasonal cues are known to exist both in cattle and sheep. For example, sheep genotypes selected for hill conditions at northern latitudes tend to exhibit greater seasonal patterns in VFI and, to a lesser extent, maintenance metabolic rate than genotypes recognised as being less seasonal in their reproductive behaviour and managed at lower altitudes [40]. At zero weight change mature non-pregnant and non-lactating beef cows lose body protein during the summer while gaining body fat, which is later mobilised during the winter and spring while body protein is being accreted [49]. Similar observations have been made in sheep [7]. Ball et al. [7] however, observed important differences between the two sexes. The seasonal oscillation in fat and protein weight was not only greater for rams than for ewes

in that study but was also out of phase by 3.5 months. This phase shift was also observed by Laurenz et al. [49] between the two genotypes of cow in their study. Angus cows accreted body protein, on average, 3 months later than Simmental cows, during the spring. However, although the biological significance of these observations is apparent, the practical significance is not. More work is required to determine if the differences observed between genotypes in the studies cited above confer any selection advantage for extensive conditions.

4.3. Early performance and later achievement

4.3.1. Attainment of puberty

The optimal age of first calving in order to maximise lifetime performance and profit margins for most dairy and beef cows is considered to be around 24 months [35, 50]. Lifetime productivity of ewes can also be increased by introducing them to the breeding flock as pubertal lambs in the first breeding season [21]. The achievement of such production targets is dependent on the onset of puberty which varies considerably between genotypes [53] and is influenced by pre-pubertal plane of nutrition [2], diet composition [68], and season [2, 69].

In cattle, *Bos indicus* genotypes tend to be older, heavier and taller at the onset of puberty than *Bos taurus* genotypes. Martin et al. [53] reported significant genetic variation among *Bos taurus* genotypes both within and between breeds for age at puberty. Breeds selected for dual purpose characteristics (e.g., Brown Swiss and Simmental) reach puberty earlier than breeds selected purely for growth and carcass characteristics (e.g., Charolais, Limousin and Hereford). In general, between beef breeds fast growing and late maturing breeds reach puberty later than slow growing and early maturing breeds. The overall heritability for onset of puberty among beef cattle, however,

is high (at around 0.4); and age at puberty tends to be lower among crossbreds than among pure-breds.

Studies investigating the effects of nutrition on the attainment of puberty have been largely confined to those concerned with feeding level, growth rate and body weight and composition. In general, animals that are fed high planes of nutrition and grow rapidly during early life attain puberty earlier and at heavier weights than animals that are not fed so well. Both energy and protein restriction delayed the onset of puberty in ewe lambs in the study of Boulanouar et al. [13], but these authors concluded that weight gain was probably more important than type of dietary restriction in determining age at puberty. However, considerable variation in age, size and body composition at puberty exist both within and between breeds of cattle and sheep [67, 70].

In practice nutritional effects are confounded by season of birth in ways which make the results of many experiments difficult to interpret. Autumn born calves reach puberty earlier than spring born calves, but they tend to exhibit a bimodal pattern in the onset of puberty [69]. Heifers born during the early autumn period, particularly those with a genetic propensity to attain puberty at early ages, will do so during the following summer, whereas those born during the late autumn and early winter period, and have the genetic propensity to attain puberty at older ages, often do not attain puberty until the following spring. Melatonin receptors have been identified in foetal tissues as early as day 30 of gestation in both sheep [33] and deer [81], and may be instrumental in mediating the prenatal photoperiodic effects on postnatal reproductive maturation reported in these two species by Helliwell et al. [34] and Adam et al. [1]. The importance of such effects under ambient light is uncertain however, since they may be modified by post-natal photoperiodic changes.

4.3.2. Milk yield potential

The development of optimum feeding strategies for the management of replacement heifers and ewe lambs is complicated by the fact that the high planes of nutrition that favour the onset of puberty during the rearing period have a negative effect on mammary development and subsequent milk yields [70, 71]. The relevance of this problem under extensive systems and indeed in single-suckled calf production systems, where the emphasis is on the total weight of calf weaned per cow kept in the herd rather than on the milk produced, has been questioned [44]. Although the growth rate and weaning weight of calves were reduced when heifers gained more than 0.55 kg per day from 2 to 8 months of age, the early attainment of puberty and improved fertility meant that, over a three year period, the total weight of weaned calf produced was greater for these animals.

4.3.3. Reproductive potential

The early attainment of puberty allows young ruminants to experience at least two to three oestrous cycles before mating, thus ensuring high levels of fertility to first service [17], and a high proportion of heifers delivering offspring within two years and ewe lambs within one year of birth. Low planes of nutrition during foetal and early post-natal life, however, in addition to delaying the onset of puberty and conception, can have longer term repercussions which extend late into adult life to influence the reproductive performance of the animal [31]. Recently, Borwick et al. [12] presented evidence that maternal undernutrition during the first nine weeks of pregnancy in sheep can delay the normal process of oocyte degradation and postpone the arrest of ovarian meiotic activity in female foetuses at day 62 of gestation, with possible consequences for oocyte number and reproductive performance in adult life. The effects of undernutrition during foetal and early

post-natal life maybe confounded by plane of nutrition during adult life to further reduce fertility [30].

4.3.4. Compensatory growth

A characteristic feature of extensive systems of livestock production is the seasonal pattern of herbage availability and the associated seasonal pattern of live-weight change. For unweaned young stock, such seasonal shifts in nutrient intake and growth are buffered, to some extent, by the consumption of milk from the dam. The effectiveness of this buffer, however, is limited by the milk producing capability of the dam. In single suckled calf production systems, milk yields are known to vary between breeds and to be influenced by such factors as parity and plane of nutrition, resulting in small (8 to 12%) but significant differences in calf performance from birth to weaning [60, 74]. Provided nutrient intake and calf growth rates are not unduly compromised during the first 4 months of life [58], most production systems will provide ample opportunity for compensatory growth in later life.

Compensatory growth is normally expressed over a relatively short period of time (typically 4 to 8 weeks on spring pasture), and arises as a consequence of increased VFI [39], reduced maintenance energy requirements [45] and increased efficiency of energy and protein utilisation [18]. Early body-weight gains following restriction comprise increased proportions of protein and water and a reduced proportion of fat, which is then followed by a period in which gains consist of an increased proportion of fat, such that eventually, body weight and composition of restricted animals returns to that of non-restricted animals [83]. The precise timing of these events and the composition of live-weight change both during and after compensation will, however, be dependent on genotype (early versus late maturing), sex and stage of maturity; and could be influenced by seasonal factors (section 4.2.)

in ways which currently have not been fully investigated. What is known, however, is that compensatory growth in weaned suckled calves can be supported by a wide range of vegetation types [82].

Knowledge of the timing and extent of compensatory growth in peri-pubertal female ruminants can be used to overcome problems of impaired mammary growth and development (section 4.3.2.) which result as a consequence of rapidly growing ruminants striving to attain puberty at an early age (section 4.3.1) in order to maximise subsequent reproductive potential (section 4.3.3; [19, 59, 85]).

4.4. Reproductive performance

4.4.1. Genotype \times environment interactions

Due to the competing demands of maintenance, pregnancy, lactation and maternal growth, heifers calving for the first time at between 2 to 3 years of age frequently have longer calving intervals over their first two parities than mature cows [52]. When young heifers are introduced to very poor nutritional environments, the resultant delays in onset of puberty and age at first calving are frequently carried into late adulthood [80]. Important interactions between the nutritional environment and genotype are likely to occur in such circumstances. Large and/or milky genotypes have the greatest requirements and so, consequently, may become thinner and less fertile than small and relatively less milky genotypes [54]. The literature in this area, however, is inconclusive. Working exclusively with mature cows, Nugent et al. [57] observed that low levels of annual energy intake (equivalent to average daily intakes of $650 \text{ kJ ME} \cdot \text{kg}^{-1} \text{ Wt}^{0.75}$) had less of a detrimental effect on the interval from calving to first ovulation for relatively large and milky genotypes (Gelbvieh and Simmental) than for relatively large and non-milky genotypes (Limousin and Cha-

rolais). Sinclair et al. [75] offered 705 and 820 kJ ME·day⁻¹·kg⁻¹ Wt^{0.75} (0.06 and 0.07 UFL·day⁻¹·kg⁻¹ Wt^{0.75}) to young first and second parity cows in their study, and observed that the large and non-milky genotype (Charolais) had longer intervals from calving to first ovulation and lower conception rates compared to the large and milky genotype (Simmental). Other studies conducted in France [20, 37, 62] lend support to the idea that important genotype × nutritional environment interactions exist particularly among primiparous cows. It would seem that genotypes selected for large mature size and very lean growth characteristics maybe less fertile and more sensitive to fluctuations in dietary energy intake than those selected for 'dual purpose' characteristics.

4.4.2. Control of ovulation

In domestic ruminants nutritional status is known to influence both the ability of the animal to ovulate and the number of ovulations. In cattle the effects of nutritional status are largely constrained to the achievement of ovulation, whereas, in sheep nutritional status can also influence the number of ovulations.

It can take several months for an ovarian follicle that leaves the primordial pool to reach the point whereby it undergoes terminal maturation and ovulates. Consequently, dietary restriction 6 months prior to ovulation in sheep has been shown to influence ovulation rate [56]. Long term effects of nutrition on the reproductive axis can also operate by altering body tissue reserves (mainly lipid) during the peri-ovulatory period, so influencing the general availability and equilibrium of metabolic fuels during this time. Body lipid reserves are highly correlated with ovulation rate in a number of species but there has been much debate in the literature as to whether or not body fat has any direct role in regulating ovulation [14]. Interest in the role of body fat in controlling ovulation was rekindled recently with the possible role of leptin, that

is secreted from adipose tissue during lipogenesis, in regulating gonadotrophin secretion and gonadal activity [8].

Short term improvements in nutritional status can be very effective in improving ovulation rate in sheep, particularly those that are in relatively poor body condition as a consequence of being managed under extensive systems of production. Nottle et al. [56] observed a significant increase in ovulation rate in those ewes whose nutrition had been restricted 6 months prior to ovulation when their diet was supplemented with lupin grain (a legume high in digestible energy and protein). Adams et al. [3] hypothesised that the acute effects of nutrition may act to disrupt the tight feedback mechanisms that control ovulation rate so giving a rapid response. In practice, the ability of animals managed under extensive conditions to respond in such a manner will be dependent on the provision of good quality grass or supplementary feed during this key stage of the animals annual reproductive cycle.

4.4.3. Post-partum anoestrus

There are well established relationships for beef cows between the effects of pre- and post-partum nutrition, the interval from calving to first ovulation and the resumption of oestrous cycles of regular length [72]. Although pre- and post-partum nutrition are known to interact with one another to determine the interval from calving to first ovulation [84], pre-partum nutrition is generally considered to be more important than post-partum nutrition in this regard, particularly in primiparous cows. In heifers the negative effects of low energy intakes during the pre-partum period cannot be completely abolished by very high levels of dietary energy during the early post-partum period [47]. Working with first and second parity cows, Sinclair et al. [75] demonstrated that the interval from calving to first ovulation increased with live-weight loss during the first month post partum only in thin cows

that were mobilising relatively large quantities of lean body tissue.

5. CONCLUSIONS

The process by which a ruminant animal adapts to its nutritional environment begins very early in life, prior to fertilisation and during the period of gametogenesis. The success with which a given species adapts to its nutritional environment will depend on the requirements for maintenance and growth of the genotype in question relative to that nutritional environment. This will influence body composition, and in the case of the breeding female, the ability to conceive and to partition nutrients towards the developing conceptus and suckling young. Certain genotypes are more sensitive to photoperiodic effects on VFI, nutrient partitioning and reproduction than others, and there is evidence that such effects may have their origin during early foetal life. Hence, in an era when agricultural production systems are becoming more extensive, judicious genotype selection for the more marginal ruminant livestock producing areas of Europe will be essential.

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