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Nutrition effects on fertility in small ruminants with an emphasis on Mediterranean sheep breeding systems

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SUMMARY - The aim of this presentation is to review some aspects of nutrient utilization in small ruminants that can affect the reproductive efficiency of females, i.e., oestrous activity, ovulation and embryo survival. Nutrition affects reproduction through short- (<10 days, i.e., "immediate nutrient effect"), and long-term effects ("static", i.e., mediated through body condition; "static and dynamic", i.e., confounded effects of body condition and body weight gain). Body condition affects the onset of anoestrus, the resumption of post-weaning estrus if photoperiod is favourable, and ovulation rate. The positive effect of "flushing", i.e., supply of energy and protein in excess of requirements for body maintenance, on ovulation rate, is mediated, at least partly, through glucose, amino acid and insulin metabolism. The efficiency of "flushing" may be impaired by decreased feed intake at pasture, especially if it consists in cereal grain. The "static" effects on ovulation rate are mediated through modulation of follicular atresia, whereas "immediate nutrient effects" seem to affect the rate of maturation immediately before ovulation of potentially ovulatory follicles. Provision of excess dietary protein during a few days prior to mating is a potential way to improve fecundity, but effects vary according to source of protein. Too generous a provision or an acute deficit of energy, and overfatting of ewes, reduce progesterone concentration in blood and embryo survival during the first stages of pregnancy. Therefore, "flushing" must be limited to the pre-mating period, which implies synchronization of oestrus.

Key words: Sheep, goats, nutrition, reproduction, ovulation rate.

RESUME - *"Effets de la nutrition sur la fertilité chez des petits ruminants en particulier dans les systèmes méditerranéens d'élevage d'ovins". L'objectif de cette présentation est de passer en revue quelques aspects de l'utilisation des nutriments chez les petits ruminants, qui peuvent affecter l'efficacité reproductive des femelle, par exemple l'activité d'oestrus, l'ovulation et la survie de l'embryon. La nutrition affecte la reproduction au travers d'effets à court terme (<10 jours, c'est-à-dire effet immédiat des nutriments) et d'effets à long terme (statiques, c'est-à-dire au travers de l'état corporel ; statiques et dynamiques, c'est-à-dire les effets confondus de l'état corporel et du gain de poids corporel). L'état corporel affecte le déclenchement de l'anoestrus, la reprise de l'oestrus post-sevrage si la photopériode est favorable, et le taux d'ovulation. L'effet positif du "flushing", c'est-à-dire l'apport de plus d'énergie et de protéine qu'il n'en faut pour les besoins de l'entretien corporel, sur le taux d'ovulation, se fait au travers, du moins partiellement, du métabolisme du glucose, des acides aminés et de l'insuline. L'efficacité du "flushing" peut être compromise par une diminution de l'ingestion alimentaire sur pâturages, spécialement si elle consiste en graines de céréales. Les effets "statiques" sur le taux d'ovulation se font au travers de la modulation de l'atrésie folliculaire, tandis que les "effets immédiats des nutriments" semblent affecter le taux de maturation immédiatement avant l'ovulation des follicules potentiellement ovulatoires. L'apport d'un surplus de protéine alimentaire pendant quelques jours avant l'accouplement est une manière puissante d'augmenter la fécondité, mais les effets varient selon la source de protéine. Un apport trop libéral ou un déficit aigu d'énergie, et un engraissement excessif des brebis, réduit la concentration en progestérone dans le sang et la survie embryonnaire pendant les premières étapes de la gestation. Par conséquent, le "flushing" doit être limité à la période pré-accouplement, ce qui implique une synchronisation de l'oestrus.*

Mots-clés : *Ovins, caprins, nutrition, reproduction, taux d'ovulation.*

Introduction

Small ruminant husbandry in Mediterranean and semi-arid areas is characterized by phases of under- and over-nutrition ("phased nutrition"). Nutrient supply and individual body condition vary widely within a flock and between months of the year, affecting both separately and co-jointly reproduction in small ruminants. We have adopted the classification of nutritional effects on the reproductive performance of female small ruminants described by Smith and Stewart (1990): (i) the effect of body weight (BW) and body condition (BC) is termed "static" effect (in contrast with "dynamic"), i.e., induced by different levels of stable metabolism, if BW, BC, or better, body composition have been kept steady at least 3 weeks before estrus; (ii) changes in BW or BC occurring during 3 weeks before estrus, that affect reproduction, are termed "dynamic" effects and (iii) "immediate nutrient" effects represent shifts in nutrient supply less than 10 days before the studied estrus. This represents a longer period than described by Smith and Stewart (1990), e.g., 4-6 days, in order to include effects exerted during a greater portion of the late luteal phase preceding ovulation, which is critical for follicular development.

In the last 20 years, the development of total intragastric nutrition has allowed to study the efficiency of different VFA combinations for productive processes in ruminants (reviewed by Orskov, 1991). The *in situ* "Dacron bags" technique has allowed to evaluate easily the availability of nutrients for ruminal *vs* intestinal absorption (examples: Tagari *et al.,* 1995, for amino acids; Sauvant *et al.,* 1994, for starch), and to formulate diets in which carbohydrate and protein ruminal degradabilities vary. These new methods lay a basis for better understanding of the effects of the availability of nutrients, particularly glucose and amino acids (AA), during short periods before mating ("immediate nutrient effect"). In addition, the alkane method has enabled to assess easily feed intake and digestibility in grazing animals, which makes research in nutrition more relevant to most farm situations (Mayes *et al.*, 1995).

The main methodological problem that we face when addressing the nutrition x reproduction interface is to weigh the concurrent and mixed effects on reproduction of "static", "dynamic" and "immediate nutrient" components. The effects of body condition at mating and body gain before mating are often confounded (see for example the study on goats by Henniawati and Fletcher, 1986; Fig. 1). When enough feed is available, thin animals eat more than fatter counterparts, therefore, the "static" effect of BC is confounded with a "dynamic" effect of BC on appetite (see for example Molle *et al.*, 1995), or with "immediate nutrient effect" if measurements are made during short periods before mating. Nutritional effects, belonging to both the "dynamic" or "immediate nutrient" effects are shared in common by males and females (Martin and Walkden-Brown, 1995). Therefore, these effects on females may well be mediated through the "male effect", and be partly confounded with it. This is the case in numerous studies involving "flushing" of ewes with a supplement and monitoring effects on females when males are also present in the flock as a component of an estrus synchronization procedure, and have free access to the same supplement (for example, Torre *et al.*, 1991; Landau *et al.*, 1996). A second methodological problem is confounding the effects of pre- and post-mating nutrition: the same treatment that increases ovulation rate (OR), such as liberal allowance of crude protein provided by soyabean-meal (Molle *et al.*, in preparation) may be deleterious to embryo survival, therefore, effects will be masked if effects are not measured on due time. Non-invasive ultrasound procedures now allow to evaluate accurately effects on OR and embryo survival (Schrick *et al.*, 1993).

Recent reviews have been published on the nutritional "dynamic and static" (Forcada *et al.*, 1994a) and "immediate nutrient" (Forcada *et al.*, 1994b) effects on different reproductive characters in sheep. The aim of this presentation is to further highlight metabolic aspects of the relations between nutrition and reproduction under Mediterranean condition. It is anticipated that better identification of "static", "dynamic and static" and "immediate nutrient" effects on estrous activity and OR will be of great help to translate scientific information into common feeding practices.

Static and dynamic effects on estrus activity and ovulation rate

The length of seasonal anoestrus seems to be related with BC: the onset of anoestrus was found to be earlier in Rasa Aragonesa ewes in medium to high condition, compared with low condition. (Rondon *et al.*, 1996). The appearance of oestrus post-partum seems to be affected more by photoperiod than by nutrition (Bocquier *et al.*, 1993). "Static" and "static and dynamic" effects of nutrition on reproductive performance of Mediterranean sheep are presented in Table 1. Body condition (Abecia *et al.*, 1991; Dapoza *et al.*, 1995; Rondon *et al.*, 1996), or the amount of body fat, assessed by deuterium dilution (Abecia *et al.*, 1995), did not seem to affect significantly the resumption of cyclic activity in Aragonesa ewes that lambed in spring, under unfavourable photo-period. In a study with Prealpes ewes (Bocquier *et al.*, 1993), under favourable day-length (autumn), the shortest duration of anovulatory period post-partum was achieved in ewes that gained 1 kg body lipids during the first month post-partum, and seemingly varied according to a quadratic pattern. In this study, the effect of body condition gain was stronger than the effect of BC ("static"), but both were confounded in a "static-dynamic" effect. The sward height of raygrass, continuously grazed by milking Sarda ewes for approximately 70 days until day 20 before mating, that resulted in greater BW and BC, i.e., a "static" effect, did not affect the date of mating at the onset of the estrus season (Molle *et al.*, 1996). Excessive rate of fat accumulation had deleterious effects on the oestrous activity of Prealpes ewes (Bocquier *et al.*, 1993). In studies carried out in non-Mediterranean sheep, low BC and severe under-nutrition (confounded effects, reviewed by Rhind, 1993), as well as excessive BC (Rhind *et al.*, 1984; West *et al.*, 1991) had deleterious effects on oestrous activity.

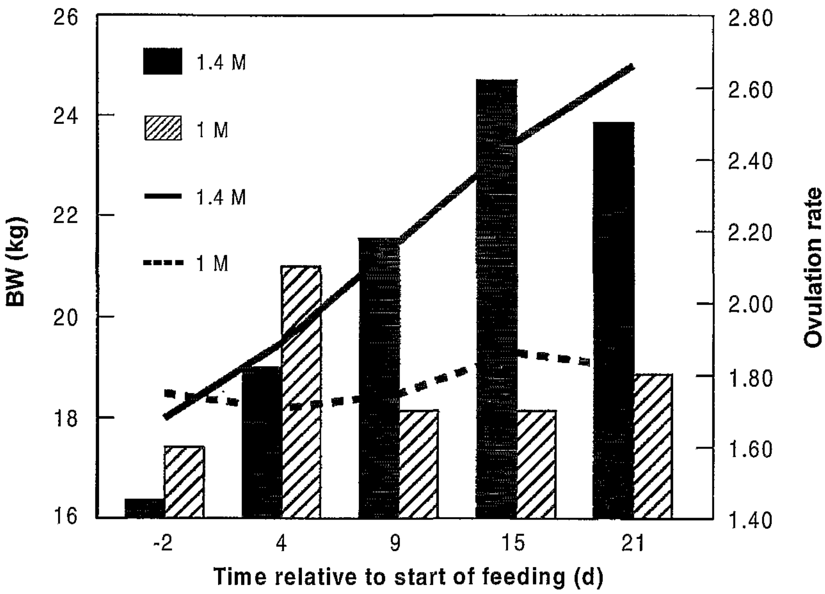

Fig. 1. The body weight (BW, kg, in lines) and ovulation rate (Bars) in goats, that were fed at maintenance level (1 M) or 1.4 maintenance level (1.4 M), relative to days elapsed from initiation of dietary treatment; after Henniawati and Fletcher (1986).

Body condition and flushing may enhance conception rate, ovulation rate, or both simultaneously. Body condition and flushing (confounded effects) were reported to increase OR at the onset of oestrus in Rasa Aragonesa (Abecia *et al.*, 1995; Dapoza *et al.*, 1995) but not affect prolificacy in Ripollesa, ewes, mated at the onset of the estrous season (Torre *et al.*, 1991). However, the conception rate of Ripollesa ewes was quadratically affected by BC (Torre *et al.*, 1991). Residual effects of nutrition during mid-lactation were evidenced in Sarda ewes mated on a mature pasture. In particular herbage availability monitored by measuring sward height paralleled ovulation rate (Molle *et al.*, 1995), and corn supplementation (Molle *et al.*, in preparation) showed a similar effect on prolificacy.

No negative effect of over-condition on reproduction seems to have been documented in goats, as it has been in sheep. The appearance and continuation of oestrous activity of goats are less dependent on nutrition than OR: in British Saanen and Toggenburg thin goats, severe energy deprivation (25% of allowance for maintenance) during 19 days before a synchronized estrus did not significantly affect the proportion of goats coming into oestrus, but did decrease OR, and timing of ovulation was delayed (Mani *et al.*, 1992). In small prolific Indonesian goats, which gained body weight at 30 g/d before mating, OR increased asymptotically when BW increased linearly from 18 to 25 kg (Henniawati and Fletcher, 1986; Fig. 1). Unfortunately, "static and dynamic", and "immediate nutrient" effects on OR were confounded in this study.

Table 1. A summary of "static" and "static and dynamic" nutritional effects on the reproductive performance of sheep under Mediterranean conditions

Authors	Sheep breed	Seasonal conditions at mating	Days from lambing	Effect measured	Parameter monitored	Result
Rondon *et al.* (1996)	Aragonesa No grazing	June	>150 d	Body condition	Onset of anoestrus End of seasonal anoestrus	Significant NS
Bocquier *et al.* (1993)	Prealpes Grazing	Short days Long days	>60 d >60 d	Body lipid change Body lipid change	Resumption of oestrus " " "	∪ quadratic NS
Abecia *et al.* (1991)	Aragonesa No grazing	August	ND	Static effect of BC	Resumption of oestrus Ovulation rate	NS Significant
Dapoza *et al.* (1995)	Aragonesa No grazing	July-August	90-130 d	Static effect of BC Static+ dynamic BC gain Static effect of body lipids Body lipid gain	Post-weaning oestrous activity and ovulation rate	Significant interaction of nutrition and BC on *ovulation rate; and* Δ BC on ovulation rate.
Abecia *et al.* (1995)	Aragonesa No grazing	July-August	>90	BW, BC, body lipids	Resumption of oestrus	NS
Torre *et al.* (1995)	Ripollesa Grazing	April-June	>150 d	Static effect of BC Static + dynamic	Conception rate Prolificacy	∩ quadratic NS
Molle *et al.* (1995)	Sarda Grazing	June-July	>150 d	Static effect of previous sward height (30, 60, 90 mm)	Ovulation rate Litter size	Positive 90>60, 30 NS
				Dynamic, high-energy diets High protein *vs* low protein	Ovulation rate Litter size	High-pro.>low-pro. NS
Molle *et al.* (unpublished)	Sarda Grazing	June-July	>150 d	Corn supplementation at mid-lactation Sward height (30, 60, 90 mm) at mid-lactation	Conception rate Litter size Conception rate Litter size	Significant NS NS Significant

ND: Non determined; NS: Non significant

In the most intensive systems, goats are involved in dairy systems where they are mated at the climax of the estrous season, and they have plenty of time to reconstitute body reserves, which insures reproductive performance that is close to the potential of the breed. However, in some Mediterranean systems, goats are kept for meat only or milked for a short period, and they are occasionally mated more than once a year. In such systems, mating may occur when body condition is less than optimal. Research is needed to clarify the relationships between BC and reproductive performance in Mediterranean meat-goats.

Immediate nutrient effects on ovulation rate

Feedstuffs used to stimulate OR may be classified as belonging to the "protein-type" or the "energy-type". Both of them are rich in energy (>2.9 Mcal ME/kg DM), but those belonging to the "protein-type" have also elevated concentrations of Crude Protein (>20% CP, DM basis).

Which nutrients?

Increased glucose availability (Teleni *et al.,* 1989) is one of the "immediate nutrient" effects on ovulation rate. Glucose entry rate explained 63% of the variation in the OR of ewes that were infused with glucose, formaldehyde-treated casein, or were supplemented with lupin grain (Rowe, 1986). An interaction of treatment x day of cycle in the same ewes was demonstrated by Leury *et al.* (1986), suggesting that phenomena linked with oestrous cycle may be related with changes in glucose metabolism. Glucose availability in sheep is increased if dietary starch is allowed to reach the small intestine (Janes *et al.,* 1985). Diets that were associated with increased glucose entry rate, probably through higher intestinal absorption (Landau *et al.*, 1992), were also associated with increased OR in Israeli crossbred ewes bearing the Booroola gene for fertility, but not in ewes that were not bearing the gene (Landau *et al.,* 1995a).

Numerous studies that report on the positive effect of protein-rich supplements on the ovulation rate of ewes have been reviewed by Smith (1988) and more recently by Rhind (1993). Some results derived from Mediterranean studies are shown in Table 2. Providing excess dietary CP by feeding 500-750 g/day of lupin grain during 5-8 days before the anticipated oestrus, i.e., beginning in mid-luteal phase, increased OR (Smith, 1988; Smith and Stewart, 1990), but feeding an iso-nitrogenous amount of formaldehyde-treated casein failed to do so (Teleni *et al.,* 1989). A "threshold" effect of total CP intake (310 g/day; Smith, 1988) or digestible protein intake (125 g/day; pooled by Smith and Stewart, 1990) was identified in studies carried out on Merino sheep. The increase in OR was correlated positively with the change in concentrations of AA, particularly the branched chain amino acids (BCAA), in the plasma (Waghorn *et al.,* 1990). Infusions of BCAA increased OR in ewes (Downing *et al.*, 1995a). Differences were noted in the dynamics of follicles of ewes supplemented with iso-nitrogenous amounts (330 g/d of CP) of corn gluten meal, characterized by low ruminal degradability and high BCAA content and soybean meal, characterized by high ruminal degradability and low BCAA content: follicles in the latter group exhibited faster rate of development that resulted in earlier ovulation (Landau *et al.*, 1996).

Feeding calcium soaps of long chain fatty acids (Ca LCFA), a non-glucogenic feedstuff, was claimed to increase litter size in non-grazing Manchega, but not in grazing Ripollesa ewes mated in summer (Table 2) (Casals *et al.*, 1991).

Interaction between body condition and immediate nutrient effect on ovulation rate

Pearse *et al.* (1994) recorded no interaction between BC and "immediate nutrient effect", implemented by lupin grain supplementation, on OR in Merino ewes, which suggests that short-term flushing may be useful to improve reproductive performance in ewes of all body conditions.

Table 2. A summary of short and medium term nutritional effects on reproductive performance in Mediterranean breeds of sheep

Authors	Sheep breed and management	Seasonal conditions at mating	Days from lambing	Effect measured	Parameter monitored	Result
Landau *et al.* (1995a)	Booroola x Assaf, non-grazing	May	Approx. 90 d	22 d comparison of corn starches differing in ruminal degradability	Ovulation rate	Significant in F-gene bearing animals
Casals *et al.* (1991)	Manchega, non-grazing 15 d flushing with Ca-LCFA	Summer	ND	15 day flushing with Ca-LCFA	Litter size	Significant
	Ripollesa, grazing 15 d flushing with Ca-LCFA	Summer	ND	15 day flushing with Ca-LCFA or barley	Litter size	NS
Molle *et al.* (submitted)	Sarda, grazing 7 *vs* 14 d flushing	June	>150 d	Duration of flushing with soyabean meal	Ovulation rate Litter size	Significant effect of flushing NS
Leibovitch *et al.* (1995)	Assaf, non-grazing	December	Approx. 90 d	7 d flushing with soyabean meal	Conception rate Litter size	NS Significant
Landau *et al.* (1995b)	Assaf	December	Approx. 90 d	7 day flushing with soyabean meal or corn gluten meal	Conception rate Litter size	NS Significant

ND: Non determined; NS: Non significant

Timing and duration of supplementation

In an review of "energy" *vs* "protein" effects on OR based on 6 Australian studies, Smith and Stewart (1990) established that OR is increased following 6 days feeding of a "protein-type" supplement (generally, supplied by using lupin grain). In contrast, a time lag of 3 weeks is needed for cereal grain, a typical "energy-type" supplement, to affect OR in Merino ewes. An interesting exception is the case of glucose infusions that increased OR in 9 days (Teleni *et al.*, 1989). In these studies, at the exception of the latter, feed intake was not quantitatively defined: group feed offer was quantified but refusals, if any, were not weighed. Our data show that in Sarda ewes, offered 270 g/d of soybean meal while grazing on a mature pasture, were willing to consume only 220 g/day. A similar observation was made by Teleni *et al.* (1989). In addition, no attempt was made to evaluate the individual feed intake on critical days before mating. Our data with Sarda ewes (Molle *et al.*, 1995) provide an simple explanation to the lag phenomenon: corn grain depressed feed intake from pasture to such extent that energy intake was identical in ewes supplemented with corn and unsupplemented controls. Only after 3 weeks did feed intake at pasture recover in the corn-supplemented ewes, which coincides with the lag period described by Smith and Stewart (1990). In opposition, soybean meal slightly depressed herbage intake, which resulted in greater ovulation rate, subsequent to greater intake of protein and energy by these ewes. Many failures in detecting a "flushing" effect in spring are probably the result of depressed intake at pasture: an example is the lack of effect of 'flushing' with barley grain during 2 weeks before mating on the conception rate and prolificacy of Ripollesa ewes (Casals *et al.*, 1991; Torre *et al.*, 1991). Similar information is not available for goats, but a comparison of corn and soybean meal for goats fed *Pistacia lentiscus* and *Quercus calliprinos* shows that browse intake is depressed much more by corn that by soyabean-meal (Gilboa *et al.*, 1996).

Increase in OR was achieved after 6 days of supplementation with 750 g/d of lupin grain (reviewed by Smith and Stewart, 1990). The critical period for success was identified as days 8 to 5 before ovulation, and feeding lupins on days 4 to 1 before ovulation had, if any, a negative effect on OR (Stewart and Oldham, 1986). A recent study with Sarda ewes shows that a trend for greater OR is obtained with supplementation of soyabean-meal for 14 days, compared with 7 days before mating (Molle *et al.*, submitted). Because adaptation to supplements takes a few days, it may be advisable that flushing be commenced 2-3 days before day -8, relative to expected date of ovulation. Finally, contrarily to the traditional long-term flushing with energy-rich feedstuffs, short-term high-protein flushing increases fecundity in high yielding dairy ewes, even if liberally supplemented with concentrates all-year-round (Leibovitch and Livne, 1995). However, supplying protein in great excess may be hazardous: when ewes were given 330 g/d of protein, mainly from soybean meal during 7 days before a synchronized estrus, conception rate and litter size tended to be decreased in Israeli dairy ewes, when compared with iso-nitrogenous and iso-energetic amounts of a corn-gluten meal and corn grain mixture (Landau *et al.*, 1995b).

Mechanisms for nutritional effects on ovulation rate

Nutrition can affect OR by two possible pathways. The first one is action on the gonadotrophic axis, the second being direct action on the ovary. A number of strategies modulating recruitment or selection can be expected to yield a high OR: (i) high recruitment and unaltered selection; (ii) high recruitment and reduced selection; or (iii) unaltered recruitment and reduced selection. In each of the latter two cases, fewer follicles would undergo atresia (Driancourt and Fry, 1988). The recent development of ovarian ultra-sononography in ewes (Schrick *et al.*, 1993) may help to elucidate which of these strategies is used when ovulation rate is increased from 1 to 2 or more.

Effect of body condition, feed intake and nutrients on follicular dynamics

In studies reviewed by Rhind (1993), greater numbers of big follicles were present and more follicles were oestrogenic, i.e., potentially ovulatory, in high-condition, compared with low-condition animals. This means that less follicles become atretic and greater numbers of potentially ovulatory follicles are present at luteal regression in high-condition animals. In contrast, feed intake did not affect the number of potentially ovulatory follicles, measured a few hours before ovulation but rather, the proportion of them which was induced to mature and ovulate. We have recently shown that ewes fed iso-nitrogenous amounts of corn gluten- and soybean meal, differing in BCAA content and ruminal degradability differed in the dynamics of follicles disappearing from the ovary after a $PGF_{2\alpha}$ injection (Landau *et al.*, 1996) (Fig. 2). Feed restriction delays standing oestrus and probably ovulation, in goats, (Mani *et al.*, 1992). It is not known if thin ewes, in which only one single, large, estrogenic and potentially ovulatory follicle is present, or ewes from breeds in which follicular dominance exist, are likely to benefit from increased availability of nutrients. We also do not know what, in fat ewes, in which several potentially ovulatory follicles are found, impairs the shedding of multiple ova.

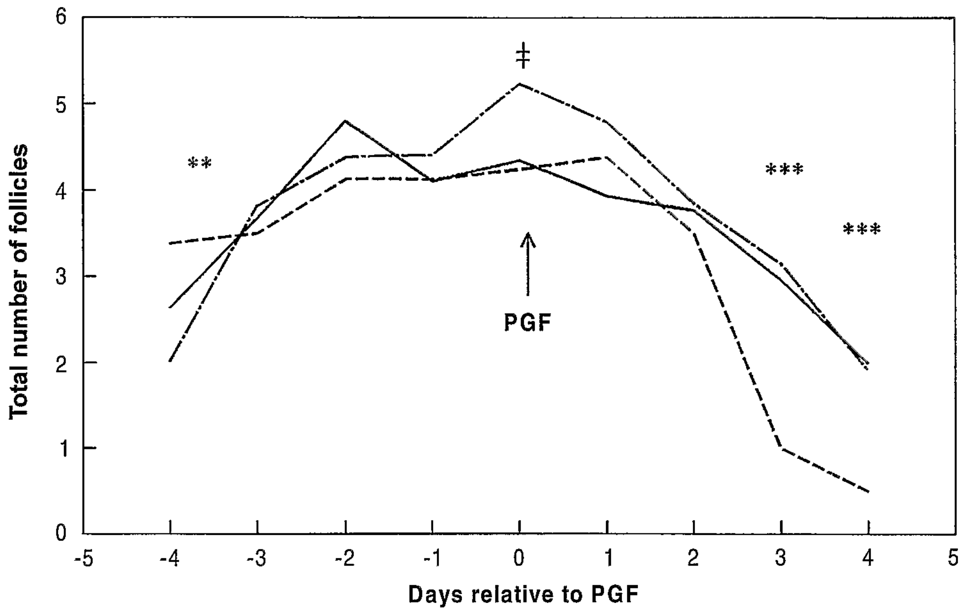

Fig. 2. Total number of follicles ≥2 mm in diameter in the ovaries of ewes fed diets with ground corn grain (GC, ——), soybean meal (SBM, ------) or corn gluten meal and corn grain (CGM-GC, — - —). Data are least square means. Asterisks depict time points at which ewes fed SBM had a higher (**P<0.01) or lower (‡P<0.08) number of total follicles, compared with CGM only; and lower (***P<0.001) number of total follicles than ewes in the other groups; after Landau *et al.* (1996).

Dietary protein, glucose and ovulation rate

Energy restriction is known to suppress the increase in LH pulsatile secretion that is necessary for growth of ovarian follicles in the pre-ovulatory stage in sheep. Infusions of glucose and AA either alone or in combination maintain a high level of LH in ovariectomized lambs subjected to restricted feeding (Schillo, 1992). In male goats, the frequency of LH pulses is related with dietary protein content (Walkden-Brown *et al.,* 1994). Using Merino rams, Boukhliq *et al.* (1996) have shown that after 10 days of supplementation with 750 g/d of lupine grain, LH pulse frequency and FSH concentration in plasma were increased. Concomitantly, the insulin concentration in both plasma and cerebrospinal fluid was increased, and glucose concentration was increased in cerebrospinal fluid, but not in plasma. These evidences suggest that nutritional effects on gonadotrophin secretion may be mediated by glucose and/or insulin at the brain level. However, the effect of short term infusions of glucose to rams increased LH pulse in males in some studies (reviewed by Martin and Walkden-Brown, 1995) but failed to do so in others (Boukhliq *et al.*, 1996), probably because no effort were made to neutralize glucose x insulin feed-backs by using eu-glycemic or eu-insulinemic clamps. The metabolisms of glucose and most of AA are linked via gluconeogenesis and/or by their respective ability to trigger insulin secretion. Therefore, identification of their respective abilities to affect LH involves considerable methodological complications, including multi-clamped infusions. However, the implication of individual AA, such as tyrosine (TYR), in the reproduction of small ruminants may well be worth being investigated: acute administration of TYR increases litter size in rats and pigs, induces oestrus and follicular growth in acyclic cows, and increases LH pulse frequency in lambs (reviewed by Schillo, 1992).

The effect of nutrient supply on the gonadotropic axis may result from high concentration of NADPH-dependent hepatic mixed function oxydases (MFO) in the liver. High MFO's result in increased steroid metabolism and in the secretion of more gonadotropins following negative feedback, which causes increased OR (Thomas *et al.,* 1987). Diets, characterized by high-glucose-C recycling (Landau *et al.,* 1992), generate high amounts of NADPH (Russell and Young, 1990), and promote high OR in ewes (Landau *et al.,* 1995a). Ewes treated with progestagens recycle more glucose and synthesize more glucose from propionate (Wilson, 1984). This suggests that high levels of progesterone synthesis and clearance during the luteal phase may enhance OR by increasing glucose availability. Studies reviewed by Orskov (1991) show, on one hand, that body protein is oxidized in fasting animals to provide glucose precursors, as evidenced by urinary nitrogen excretion, but provision of VFA to supply 20-30% of energy required for maintenance reduces nitrogen excretion to basal levels, suggesting glucose shortage is unlikely to happen in "non-productive" animals. On the other hand, glucose recycling, a glucose sparing mechanism (Russell and Young, 1990), exists in goats in situations of glucose-deprivation as well as of glucose abundance (Stangassinger and Gieseke, 1986). This suggests that even "non-productive" ruminants may exhibit phases of high glucose demand, possibly associated with reproductive requirements.

BCAA, insulin and ovulation rate

The infusion of a BCAA mixture (Leucine, Isoleucine and Valine) increases the ovulation rate of ewes, when administered during the late luteal phase (Downing *et al.*, 1995a). Because the main source of amino acids of ewes fed rumen degradable protein is microbial, and is relatively poor in BCAA (Merchen and Titgemeyer, 1992), it is possible to increase the duodenal flow, and hence the absorption of BCAA, by using feedstuffs rich in BCAA and of low ruminal degradability, such as corn gluten meal (Tagari *et al.,* 1995). There are several possible mechanisms by which BCAA could increase ovulation rate. First, on the basis of the data of Downing *et al.* (1995a), direct effects of changes in plasma concentration of BCAA on ovarian function cannot be excluded. Because BCAA are not glucogenic AA, their effect on OR is unlikely to be mediated by higher availability of glucose following increased gluconeogenesis.

A different mode of action of BCAA on ovarian function may involve insulin secretion; leucine is the most effective amino acid in stimulating insulin secretion in sheep (Kuhara *et al.,* 1991), half of it escapes first-pass removal by the liver and has a critical role in the regulation of muscular protein catabolism (Lobley, 1992). Elevated concentrations of plasma insulin were noted in sheep infused with BCAA (Kuhara *et al.*, 1991), or fed excess dietary protein from soybean-meal (Molle *et al.,* 1995), lupin grain (Downing *et al.*, 1995b), and corn gluten meal (Landau *et al.*, 1996), but not urea (Madibela *et al.,* 1995). A role for insulin is backed by the recent findings that peripheral insulin concentration is cyclic in cows (Schrick *et al.,* 1992) and peaks on the day of estrus in ewes (Landau *et al.*, 1996). Infusions of insulin increased the ovulation rate of adult (Hinch and Roelofs, 1986), but not of young ewes (Beam and Holcombe, 1992).

Other nutritionally driven hormonal effects affect ovulation

The present review stresses on relationship between insulin and reproduction, but other hormones, related or not to insulin, are also implicated. Evidences for a role of IGF1 on LH secretion begin to accumulate (Khalid and Haresign, 1996). Another scope of the nutrition x reproduction interface will appear if large-scale use of recombinant growth-hormone (rGH) is cleared as a routine managerial tool for dairy animals: rGH affects follicular dynamics and can enhance the development of ovarian follicles during the gonadotrophin-dependent stages (Gong *et al.*, 1996).

Embryo survival

The missing link between oocytes and embryos is fertilization. No studies on the effect of female nutrition on sperm transport and ova fertilization seem to have been carried out, to our knowledge.

The effect of nutrition on embryo survival is limited as recently reviewed by Abecia and Rhind (1994) and by Hanrahan (1994). According to the latter review, only 10% of the probability of embryo survival can be explained by changes in feeding levels within the range 0.5-1.5 x maintenance requirement. However extreme body conditions and abrupt changes in the feeding level after mating were shown to lower embryo survival. The effect of nutrition on embryo survival has been claimed to be linked with peripheral progesterone concentration. High post-mating nutrition results in reduced progesterone levels and elevated embryo losses (Parr *et al.,* 1987). Nutrition effects on progesterone seem to be mediated by effects on LH (Rhind *et al.*, 1989). Both under-fed and over-fed sheep exhibit low post-mating progesterone level, but the progesterone response to LH injection is greater in sheep fed at 0.5 maintenance level than in counterparts fed at 1.5 maintenance level (Rhind *et al.,* 1989). However, the significance of peripheral progesterone is now being re-assessed, because it does not reflect the concentration of progesterone in the ovarian blood vessels. Continuation of flushing after mating seems to be deleterious for embryo survival (Molle *et al.*, in preparation). High post-mating nutrition was beneficial to survival of triple embryos only, and was otherwise deleterious to conception rate in sheep (West *et al.,* 1991). Severe energy deprivation of goats through third month of pregnancy was associated with increased embryo loss (Mani *et al.,* 1992).

When ewes are fed excess rumen degradable protein during the pre-ovulatory period, liquids flushed from the reproductive tract are rich in ammonia and urea. Ova that are collected from such ewes metabolize more glucose and are more advanced in their development, but their viability is decreased, compared with ova from ewes fed at maintenance level without extra-protein allowance (Madibela *et al.,* 1995). Therefore, an interaction between allowance and source of protein during the pre-ovulatory period on follicular and embryonic development may exist.

Ewes grazing pasture that contain estrogenic clover have reduced reproductive performance attributed to reduced sperm transport, causing a reduction in the proportion of eggs fertilized, and decreased embryo survival. The same effects have been claimed to be caused by selenium deficiency (see review by Wilmut *et al.*, 1986).

Conclusions

The profitability of small ruminant breeding in most parts of the world is derived from their ability to exploit harsh environments and survive periods of nutritional deficiency (phased nutrition). In Mediterranean production systems, periods of nutritional abundance generally coincide with lactation, whereas mating takes place when nutritional resources are limited. As a result, reproductive performance is lower than allowed by the theoretical potential of the breed for number of parameters including number of ewes mated until a scheduled date, ovulation rate and prolificacy. The integration of recent methodological advances in nutrition (for example, Dacron bags and infusion methods) and reproduction (ultrasound methods) research provide an opportunity to monitor the short term effects of nutrients on follicular development. This approach seems compatible with existing production systems based on phased nutrition. It can be assumed that significant improvement of reproduction performance can be achieved if the information concerning nutrient effects on the hormonal milieu and ovarian response is translated into short-term feeding practices.

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