Effect of nutritional level on the onset of puberty in the Sardi ewe lamb: relationships with FSH, GH and Leptin

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Effet du niveau nutritionnel sur la puberté et la variation de la FSH, GH et la leptine chez l'agnelle Sardi.

Résumé

Le but de ce travail est d'étudier l'effet d'une restriction alimentaire suivie d'une réalimentation et la possibilité d'une croissance compensatoire, sur la puberté et sur les événements endocrines apparentés chez la femelle Sardi. Trente agnelles Sardi âgées de 205 jours et ayant un poids de 22±1,2 kg ont été divisées en 3 groupes : HH nourri avec un régime haut (500 g de paille et du concentré industriel ad libitum), LL avec un régime bas (500 g de paille et 200 g de concentré industriel) et LH avec le régime bas pendant 2 mois suivi d'un régime de niveau supérieur pendant 4 mois. L'essai a commencé le premier juillet et s'est arrêté au 30 décembre. Les échantillons de sang ont été prélevés trois fois par semaine pour les dosages de la progestérone, FSH, GH et leptine. Une différence significative du taux de croissance entre les deux groupes (haut et bas) a été observée. Toutefois, le gain quotidien moyen est resté au dessous de 100 g/d. Après la période de restriction, l'apport illimité de concentrés (groupe LH) assure une croissance soutenue des agnelles mais seulement légèrement supérieure en moyenne à celle des agnelles du groupe HH (89 g/animal/jour de GMQ contre 84). Ces résultats ne permettent qu'une croissance compensatrice partielle et variable. Dans le groupe HH, l'entrée en activité sexuelle est très compacte. Les premiers cycles normaux se manifestent en moyenne 9 jours seulement après le premier cycle ovarien et les premières chaleurs sont déjà présentes en moyenne 7 jours après les premières activités ovariennes. Ces intervalles très courts s'expliquent par le fait que pour 8 des 10 agnelles, la première activité cyclique est directement accompagnée des premières chaleurs. La restriction alimentaire (groupe LL) qui freine la croissance des agnelles a pour effet d'empêcher leur entrée en activité cyclique ovarienne et comportementale. Par contre, dans le groupe LH, l'apparition des premiers cycles et des chaleurs chez toutes les agnelles est fortement retardée (plus de 50 jours) par rapport au groupe HH alors qu'aucune différence significative, en ce qui concerne le poids vif au moment du démarrage de l'activité reproductrice, n'est observée entre ces deux groupes. Avant la première ovulation, une augmentation dans le niveau de FSH est observée pendant que le niveau de GH diminue avec une corrélation négative significative entre ces hormones. Aucune relation significative n'a été trouvée entre l'entrée en activité ovarienne et le niveau de Leptine. De la même manière, il n'y avait pas de corrélation entre le niveau de leptine et le poids ou le gain moyen quotidien. Une corrélation positive entre la concentration de GH et le gain moyen quotidien a été notée dans les différents groupes ($P < 0,05$) tandis qu'aucune relation n'a été détectée entre les concentrations de FSH et le gain moyen quotidien. Nos résultats démontrent une fois encore l'importance du développement corporel des agnelles pour l'âge de la puberté. Une réalimentation ad libitum suite à une période de forte restriction permet une reprise effective de la croissance ainsi que l'initiation de l'activité reproductrice dès la première année chez toutes les agnelles. Par ailleurs, nos analyses indiquent que les concentrations plasmatiques de la FSH ne sont pas affectées par la restriction alimentaire. Les profils de la leptine laissent penser à la présence d'autres métabolites, plus importants que la variation de la Leptine, pour informer l'axe hypothalamo-reproducteur de l'état nutritionnel de l'agnelle.

Mots-clés *: Agnelle, nutrition, coissance, GH, FSH, leptin, puperté*

تأثير مستوى التغذية على حلول فترة البلوغ عند الخروفة من سلالة السردي و ما يتعلق بها من أحداث هرمونية

ملـخص

تهدف هذه الدراسة إلى تقييم إمكانية النمو الاستدراكي بتغذية متوازنة بعد فترة من التغذية الناقصة عند الخروفة، ومدى تأثيرها على حلول فترة البلوغ الجنسي وما يتعلق بها من أحداث هرمونية. أجريت الدراسة على ثلاثين خروفة من صنف السردي، حيث قسمت إلى ثلاث مجموعات HH : بمستوى تغذية عالي، LL بمستوى تغذية ضعيف وLH بمستوى تغذية ضعيف لمدة شهرين متبوع بمستوى تغذية عالي لمدة أربعة أشهر. تكونت وجبة الغذاء الضعيفة من 500 غ من التبن و 200 غ من العلف المركز، في الوقت الذي كان العلف المركز غير محدود في الوجبة العالية. بدأت التجربة في شهر يوليوز حيث كان عمر الخروفات حوالي سبعة أشهر وانتهت في آخر شهر دجنبر. عينات من الدم كان تؤخذ ثلاث مرات في الأسبوع للقيام بتحاليل العناصر التالية : الجسفرون: P4، الهرمون المحفز للجريبات: FSH، هرمون النمو: GH و leptin.

أظهرت النتائج أن الفرق في سرعة النمو خلال فترتي الغذاء الضعيف والغذاء العالي كان ملموسا. إلا أن سرعة النمو لم تتعدى 100 غ / اليوم. ولم يكن هناك أي نمو استدراكي للخروفات اللواتي كان عندهن نقص في التغذية خلال الفترة الأولى و غذاء كامل خلال الفترة الثانية.

حلول مرحلة البلوغ ارتبط أساسا بالوزن الحي حيث أن جميع الخروفات و صلن لمرحلة البلوغ عند وزن متوسط يتراوح ما بين 31,4 ± 0,7 و 29 ± 1,2 كلغ عند كل من المجموعتين HH و LH على التوالي، وكانت مجموعة HH أثقل نسبيا ($P<0,05$) . قبل أول عملية الإباضة، يلاحظ عموما ارتفاع في نسبة FSH في الدم في الوقت الذي تنخفض فيه نسبة GH في علاقة سلبية محسوسة بين الهرمونين.

أما بالنسبة لمادة leptin، لم تكن هناك أية علاقة محسوسة بين فترة البلوغ ونسبة هذه المادة في الدم، كما أنه لم تكن هناك أية علاقةايجابية بين نسبة GH في الدم وسرعة النمو عند كل المجموعات ($P<0,05$)، ولم تكن هناك أية علاقة بين نسبة FSH و سرعة النمو.

الكلمات المفتاح : الخروفة، سلالة السردي، فترة البلوغ، مستوى التغذية، هرمونات

Abstract

The aim of this study was to investigate the possibility of a compensatory growth following starving and re-feeding of ewe lambs, the effects on puberty onset and the related endocrine events in Sardi sheep. Thirty ewe lambs born in autumn were assigned to 3 groups: HH fed a high-level diet, LL a low-level diet and LH a low-level diet during 2 months followed with a high level diet during 4 months. The low-level diet consisted of straw (500g) and concentrate (200g) while in high-level diet the concentrate was fed ad libitum. The assay started on July 1st when the lambs were 7 months of age and finished on December 30th. Blood samples were taken thrice a week for progesterone, FSH, GH and Leptin assays.

The main results showed a significant difference between growth rates of ewe lambs on low or high diet but the average daily gain remained low 87 ± 9 g/d. There was a partial compensatory growth in fasted-refed lambs. The onset of puberty was mainly related to the live-weight in all ewe lambs. Thus, the average live weight at puberty was 31.4 ±0.7 kg and 29.8 ± 1.2 kg in HH and LH groups respectively ($P<0.05$). Before the first ovulation, an increase in FSH plasma level is observed while GH level decreases with a significant negative correlation between these hormones. At both the individual and the group level, no significant relationship was found between the age at puberty and the plasma Leptin levels. Likewise, there was no correlation between plasma Leptin levels and live weight or average daily gain. A positive correlation between GH concentration and average daily gain was noted in the different groups ($P < 0.05$) whereas no relationship was detected between FSH concentrations and average daily gain.

These results confirm the importance of body development on the appearance of puberty, and raise the possibility of a compensatory growth in ewe lamb. Elsewhere, FSH concentrations were not significantly altered by feed restriction. The observed absence of a relationship between the age at puberty and the plasma Leptin levels may reflect the presence of another metabolite, besides than Leptin that signals nutritional status to the reproductive axis of the ewe lamb.

Key-words: : Ewe lamb, nutrition, growth, GH, FSH, leptin, puberty

Introduction

In many African countries, sheep breeding experiences irregular climatic conditions and feed quality and availability fluctuations. Periods of severe undernourishment can coincide with critical phases of animal development or reproduction. This situation is observed in the case of Sardi breed, located in the central part of Morocco. This rain fed region is characterized by harsh soil and climatic conditions. Under this context, lambs show very limited growth rate and a delayed puberty and therefore low breeding performances (I'Anson et al., 1991; Hamidallah et al., 2004).

Subsequent to an improvement of the nutritional status, a compensatory growth could alleviate this situation. This well-known phenomenon indicates that, in good nutritional conditions following a feed restriction, some animals may be able to show an average daily gain higher than animals regularly fed with high level diets (Ryan, 1990).

Relationships between age at puberty, nutrition and the mechanisms of reproduction are strongly dependent upon hormonal status, mainly the gonadotrophic axis. The growth hormone (GH) also plays a crucial role by activating sexual maturation in monkey (Wilson et al., 1988). At last, Leptin is also involved in this mechanism through its relation to body energy (Ahima et al., 1996; Barash et al., 1996; Chehab et al., 1996). In cattle and sheep, dietary energy restriction suppresses episodic release of LH (Schillo, 1992). Other authors reported that nutritional flushing alters blood concentration of some reproductive and metabolic hormones (Forcada et al., 2006). Indicators could be an increase in insulin and Leptin concentration and a decrease in growth hormone leading to lower oestradiol concentration in the blood. The consequence of these actions is a reduced negative feedback on the hypothalamic-pituitary system and an increased FSH secretion that leads to the stimulation of folliculogenesis (Scaramuzi et al., 2006)

The objective of this investigation is to evaluate the effects of feed restriction and nutritional conditions on the ovarian activity and onset of puberty in Sardi ewe lambs. In order to document the hormonal dynamics involved in such conditions, FSH, GH and Leptin levels were monitored.

Materials and Methods

The experiment was conducted in the Regional Agronomic Research Center of Settat (Morocco) with 30 Sardi ewe-lambs born in November – December. Ewe lambs, all born as singleton and weaned at an average age of 114 days, were raised in traditional management conditions until the beginning of the experiment, on July 1st with an average age and weight of 205 days and 22 kg, respectively. After weaning, a vasectomized ram was introduced in the group to avoid any subsequent "ram effect".

Animals were randomly assigned to 3 groups. Two groups (L for Low) received a basic feeding designed to cover their theoretical maintenance requirements, i.e. 500 g of wheat straw and 200 g of a commercial mixed feed during 2 months (Period 1). The

third (H for High) received wheat straw and a concentrate feed ad libitum estimated to 1 kg per day and per ewe lamb. On a dry matter basis, the concentrate contains 12% protein, 2% fat, 9% cellulose, 0.55% phosphorus, 1% calcium, and vitamins (A : 500000 IU, D3 : 75000 IU, E : 1000 IU). At the end of the first period and for four months thereafter (Period 2), one out of the two restricted groups and the H group continued to receive the same diet they were assigned to (groups LL and HH) whereas the last received the mixed feed ad libitum (group LH) after one week transition period.

Lamb's live weight was recorded at birth, at weaning and at every 2 weeks until the end of the experiment. Sexual behavior of ewes was monitored for heat detection, using a vasectomized ram with a marking system twice per day.

Blood sampling was performed thrice a week by jugular venipuncture into 10-ml vacuumed heparinized tubes (Venoject, heparin-Li). Samples were immediately centrifuged at 2500 x g at 4°C for 15 min and the plasma stored frozen (-20°C) until assayed for plasma Follicle-Stimulating Hormone (FSH), Progesterone (P4), Growth Hormone (GH) and Leptin by radio-immunoassay. FSH, P4 and GH were determined using the techniques described by Bister (1980) and Sticker et al. (1995). Leptin was measured with a method adapted from a specific RIA technique for the ovine Leptin developed by Chilliard et al. (2000). Intra- and inter-assay coefficients of variation and assay sensitivities were 6.8 %, 10.1 % and 0.05 ng/ml for P4; 7 %, 11 % and 0.14 ng/ml for FSH; 8 %, 11 % and 0.5 ng/ml for GH and 14.3 %, 7.2 % and 0.6 ng/ml for Leptin respectively.

Plasma P4 level > 1 ng/ml is a reliable indicator for an active corpus luteum and is related to a cyclic ovarian activity (Boulanouar et al., 1995). Puberty attainment was determined according to various criteria: the beginning of the ovarian activity (first increase of P4 > 1 ng/ml), the beginning of the normal ovarian activity (cycles of 16-17 days with P4 >1 ng/ml), the appearance of first heat and first normal cycle accompanied with estrus (Abba, 2005).

Statistical analyses

Statistical analyses were performed using SAS for Windows, version 8.2 (SAS, 1987). Analysis of variance was used to detect differences among the different groups and means were separated by the Least Significant Difference (LSD) test. A t-Student test was performed to calculate the significance of the correlations (R2). Significant levels for all analyses were set at $p < 0.05$.

Results

Animal performance

Live weight changes in the 3 groups are depicted in figure 1 and the main growth features are given in Table 1. At the end of this study, ewe lambs in HH group weighted 37.4 ± 0.5 kg. A temporary decrease in average daily gain (ADG) is observed in this

group at the beginning of the second period; this could be explained by perturbations of the animals in the transition period which lead to a slightly lower ADG in the second period ($P < 0.05$). In the LL group, the ADG was 18 g/d overall the experiment, but the growth pattern showed a great animal to animal variability (-2.5 kg to +7 kg). In the LH group, a small (24 g/d) and steady ADG was observed during the first period. During the second period, the LW in the LH group gains were slightly but not significantly higher than those of the HH group. A large animal to animal variation was observed during this period (4 to 12.5 kg of total live weight gain) and only part of the animals showed a compensatory growth.

Reproduction performance

In the HH group, all ewe lambs showed ovarian activity (P4≥1ng/ml) during the experiment with cycles being immediately normal in most of the cases (Table 2). In the LL group, no normal cyclic activity was observed through the experiment. Ewe lambs from the LH group, expressed normal cyclic activity by the end of the study except in one ewe lamb, which showed a low growth rate (4 kg) during the second period of the experiment. In both groups, cyclic estrous activity was established soon after the first ovulation (8 to 10 days after the first cycle).

The ewe lamb in the HH group, reached puberty at 320 ±18 days of age and an average weight of 31.4± 0.7 kg with 9 out of the 10 ewes showing, the first normal ovarian cycle accompanied with heat. In the LL group, no ovarian activity was observed in spite of an average age of 404 days at the end of experiment. However, the average LW of these ewe lambs was only 24.8 ± 2.7 kg.

In the LH group, the average age at puberty was (372 ± 9), 51 days later than the one of the HH group whereas, differences between the two groups are lower for LW.

Hormonal profiles

Figure 2 depicts average evolution of the plasma FSH concentration in the 3 groups. It was similar in the 3 groups at the beginning and at the end of the trial. A transient increase in the levels is observed in LL and LH groups during the second period and lead to significant difference with the HH group ($P < 0.05$) for 30 days.

Figure 3 shows the average plasma GH concentrations in each group. Due to high individual variations, no significant difference was detected. However, the values of the HH group seem to be lower than those of the other groups at the end of the first period and the beginning of the second one. A positive correlation between the GH concentrations and ADG was observed in the different groups ($P < 0.05$), but no relation was detected between FSH concentrations and ADG.

Average plasma Leptin concentrations are presented in figure 4 in the three groups. A transient increase is observed in the LH group in the beginning of the second period (*ad libitum* feeding) but values decrease thereafter in a similar way than in the other groups.

There is no correlation between plasma Leptin and live weight or ADG, whereas at the end of the trial a positive correlation between LW and Leptin was noted .

In ewe lambs reaching puberty, the average levels of FSH, GH and Leptin before and after the day of the first P4 secretion related to an ovarian activity were calculated (figure 5). It shows that the first normal ovarian cycle follows a period of increased FSH secretion and decreased GH plasma levels while Leptin concentrations remained unaffected.

Discussion

This experiment was designed to study the effects of the nutritional level on puberty onset and the related endocrine events in Sardi ewe lamb. After a conventional feeding until the age of 205 days and at a weight of 22 kg, the unrestricted concentrate feeding during the 6 following months (HH group) resulted in a daily average gain of 95.5g, which reflects the rustic character of this breed.

The objective to cover maintenance needs in LL group was reached since only very modest weight gains (less than 20 g/animal/day) were observed.

In the LH group, restricted during 2 months and feed *ad libitum* during 4 months, no significant compensatory growth was observed (89 g/animal/day against 84 for the HH group). This low difference between groups is due to the fact that in the LH group, large animal to animal variations are observed; some lambs showing poor growth recovery as oposed to the others. These results show that, as indicated by other authors (MacManus et al., 1972; Barash et al., 1979; Thornton et al., 1979), the compensatory growth can be total, partial or even null. The last case scould stem from a delay in the digestive system development resulting in insufficient levels of ingestion (Ryan et al., 1993).

The initiation of the reproductive activity at puberty is followed by the cyclic secretion of progesterone and by expression of heat. It can be very variable according to individuals, e.g. short or long cycles with low progesteronemia, normal cycles with progesteronemia higher than 1 ng/ml but without estrous behaviour, or normal cycle directly accompanied with heat. In this regard, our results are in agreement with those of other authors (Fitzgerald & Butler, 1978; Foster et al., 1979). What is remarkable enough in the present study is the very short time (8 to 10 days) between the first ovarian activity and the full expression of puberty.

Results of this experiment confirm those of others (Lindsay et al., 1993) showing that the live weight and then the body development of ewes is the major factor triggering puberty. This weight is of 30 kg (for an average adult weight of 45 kg) and it is reached at 10-11 months of age in the HH group and 50 days later in the LH group. In the LL group, however, no ewe lamb reached the puberty at 400 days, but the average LW was then only 25 kg. The negative effect of under-nourishment on reproduction mechanisms was also shown in the Barabarine breed (Lassoued, 1991; Lassoued et al., 1998).

Interestingly, patterns of plasma FSH concentrations don't match, in the present experiment, with those of progesterone secreted by the ovary, when analyses are performed on the basis of the timing in the experiment. The average FSH concentration change is the same in the 3 groups: low values until the end of September and an increase and fluctuations thereafter. But when the analysis is done with values centered on the day of the first P4 increase related to a *Corpus luteum* (CL) activity, an increased FSH secretion is shown within the 10 days before the expected ovulation.

In this analysis, a decrease in the GH levels is observed, while an increase has been reported at puberty in other studies, owing to the stimulating effect of sexual steroids (Mauras et al., 1990; Giustine et al., 1997). It would be the result of a feed-back effect between FSH and GH reported when exogenous GH is injected in an attempt to modify the ovarian activity (Perrad et al., 1996).

Other authors reported a stimulating effect of undernourishment on GH secretion, especially in the cow (Yambayamba et al., 1996; Hornick et al., 2000), probably through a reduction of hypothalamic secretion of somatostatin (Vance et al., 1992) or by a process of energy saving (Ortigues et Durand, 1995). It may explain the increase in GH secretion observed in the LL group. Other studies reported similar results (Barash et al., 1996; Wester et al., 1995). The higher level of GH could be associated with the disappearance of the resistance to the GH observed during the period of food restriction, allowing thus the development of a hypersomatotropic state during the ingestion of large amounts of energy and proteins. This elevated concentration of plasma GH could exercise a lipolytic activity during the compensatory growth phase, characterized by a metabolism continuing to adjust to a shortage of feed supply. But in the LH group, a similar increase of plasma GH concentrations is temporally observed with higher values than those of the HH group yet fed in the same way.

Leptin is an adipocyte-derived protein that has been shown to vary directly with body mass index and percentage of body fat (Prolo et al., 1998; Chilliard et al., 2000). Our results in this experiment indicate that plasma Leptin concentrations underwent a similar evolution in the 3 groups of Sardi ewe lambs. However, during the first period of the experiment, Leptin concentrations were higher in the HH group than in the two other groups. MacManus and Fitzgerald (2000) reported that young mares with low body fat also had lower Leptin concentration than older and fatter mares. In the beginning of October, values decreased in the 3 groups and were stabilized at the same level. The lower Leptin levels in LL and LH groups in the first period were expected, according to Chilliard et al. (1999) showing that feed restriction decreases leptinemia, as well as insulinemia (Saladin et al., 1995). The concomitant reduction of the leptinemia in the 3 groups in early October indicates that the photoperiod could play a role in these mechanisms. Chilliard et al. (1999) observed that Melatonin injections (simulating short photoperiod days) decreased the leptinemia in the rat. Fitzgerald and Mac Manus (1999) also reported a profound seasonal variation in Leptin concentration in mares with ave-

rage concentration decreasing from October to December. On the other hand, the absence of a change in Leptin levels when puberty approached in ewe lambs of the HH and LH groups does not corroborate the involvment of the Leptin in this process, contrarily to the observations in mice (Ahima et al., 1997; Barash et al., 1998). These authors reported that Leptin constitutes one of many factors involved in mechanisms initiating puberty. Nevertheless, the Leptin levels are related with LW in growing lambs at the end of the trial; this confirms the observations of Bister et al. (2004) showing that the relationship between Leptin secretion and the body weight is significant only when the evolution of the live weight is positive.

Conclusion

Unrestricted concentrate feeding allows a sustained growth of the ewe lambs (less than 100 g/d at the beginning and 85 g/d at the end of the trial), while the restriction allows only a very low growth (15 g/d). In the LH group, first restricted, then fed *ad libitum*, a compensatory growth was observed in some individuals only.

The continuous feed restriction prevents all ovarian activity and behavioral demonstration throughout the experiment, the ewe lambs being then at an age of more than 404 days.

The results confirm that the body development is a predominant factor in triggering puberty mechanisms.

In the present study a correlation between GH concentrations and ADG was observed in the different groups, but no difference was detected in FSH concentrations.

Although Leptin concentrations were low in LL and LH groups and higher in HH group in the beginning of the experiment, there is a wide animal to animal variation of its concentration in well-fed ewe lambs, indicating that other factors may determine Leptin concentration in good body condition. One of these factors may be lamb growth rate; a minimal ADG seems to be necessary to stimulate the Leptin secretion in relation with live weight.

Acknowledgements

The authors would like to thank Ms F. Gaboun for her assistance in data analysis and Dr. Derqaoui L. and Boukhliq R. for reading of the manuscript. The study was co-funded through a collaborative project supported by the Belgian Academic Cooperation for Development.

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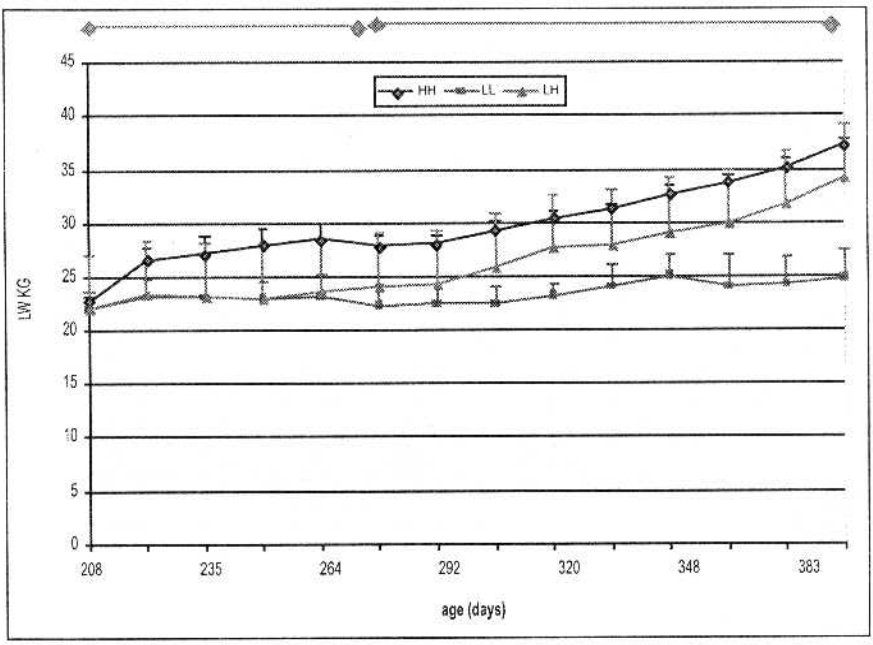

Figure 1. Average live weights (kg) of ewe lambs during the experimental period

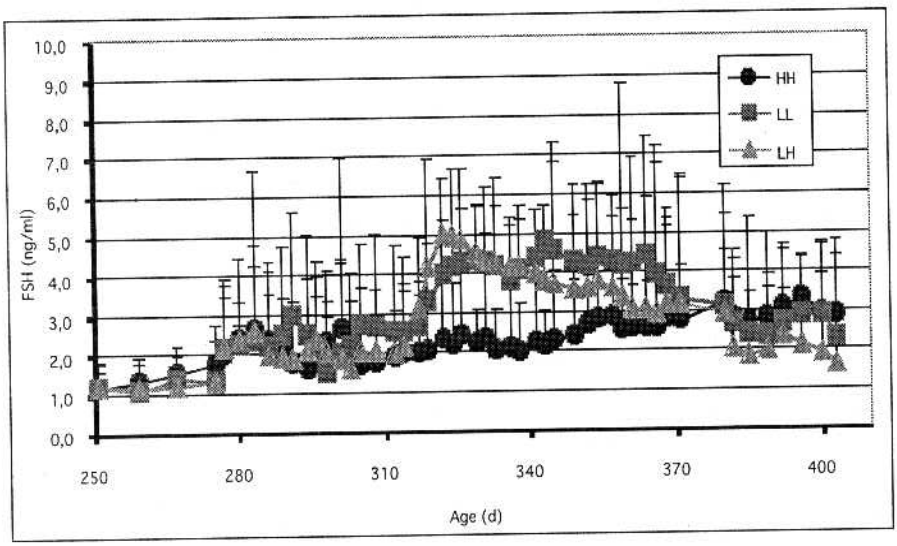

Figure 2. Evolution of FSH plasma concentrations in ewe-lambs fed ad libitum (H) or restricted (L) diets.

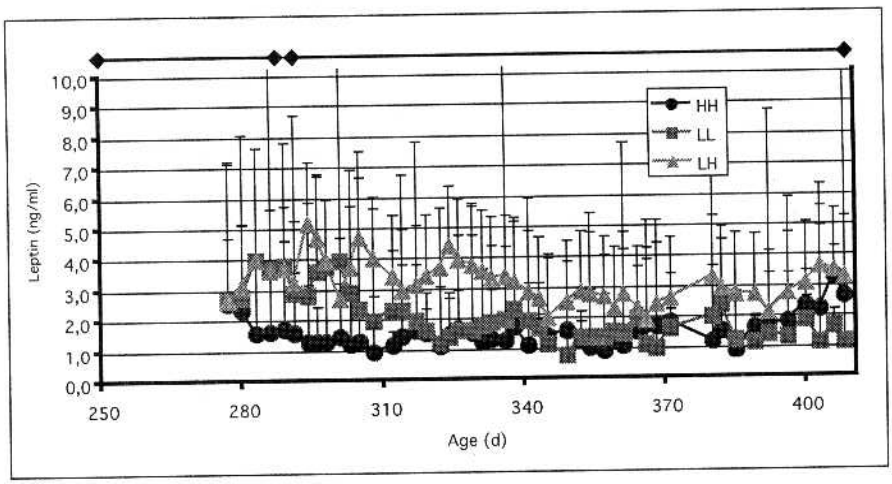

Figure 3. Evolution of plasma GH concentrations in ewe-lambs fed ad libitum (H) or restricted (L) diets.

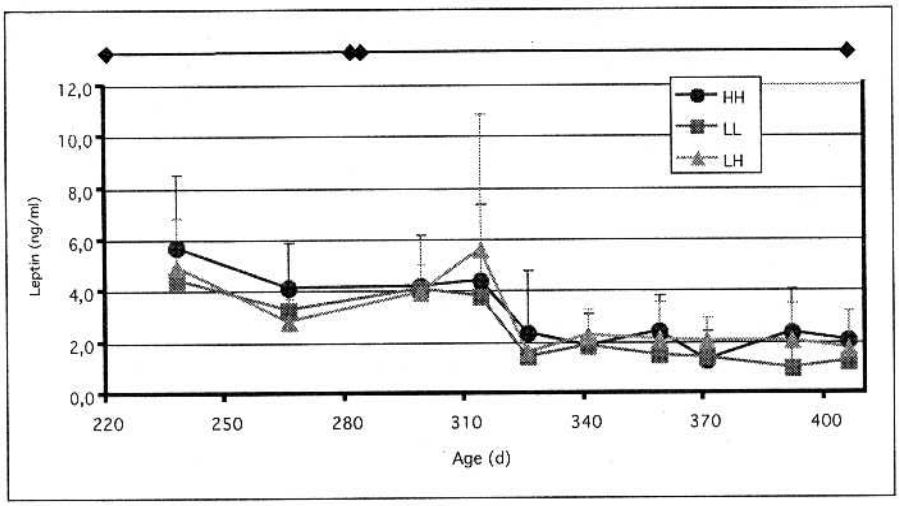

Figure 4. Evolution of plasma Leptin concentrations in ewe-lambs fed ad libitum (H) or restricted (L) diets.

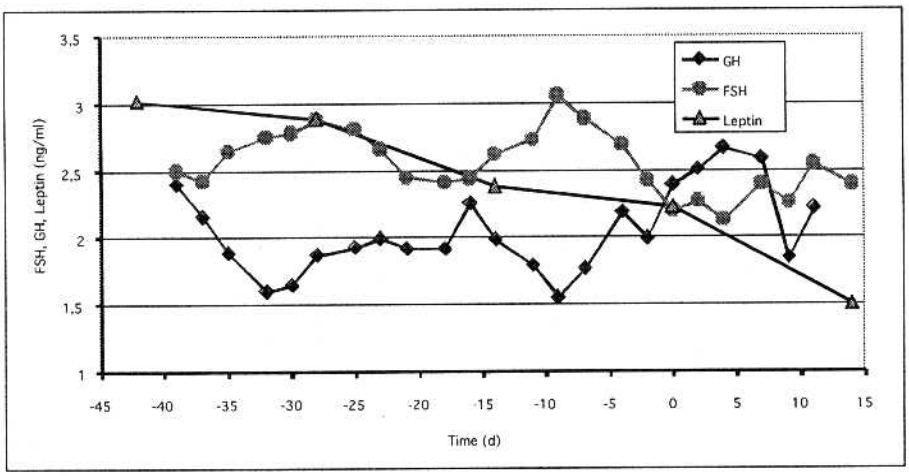

Figure 5. Average plasma levels of FSH, GH and Leptin centered on the day of first luteal activity (P4 > 1ng/ml) for all the ewe lambs reaching puberty during the experiment.

Table 1. Animal performance of ewe-lambs fed an ad libitum or a restricted diet, or subjected to a period a feed restriction (P1) before realimentation (P2).

Parameter		HH	L	H
Live weight (kg)	Initial	22.8 ± 0,4	22.0 ± 1,6	21.6 ±1.6
	Transition	28.6 ± 1,3[a]	23.1 ± 2,2[b]	23.0 ± 1.5[b]
	End	37.4 ± 0,5[a]	24.8 ± 2,7[b]	33.3 ± 3.3[c]
ADG (g/d)	P1	107 ± 20[a]	16 ± 20[b]	24 ± 12[b]
	P2	84 ± 10[a]	21 ± 15[b]	89 ± 24[a]

Within the same parameter and line, means with different letters differ significantly (P<0.05)

Table 2. Reproductive performance of ewe-lambs fed an ad libitum (H) or a restricted (L) diet.

Parameters	HH	LL	LH
Number of ewe lambs attaining puberty	10/10	0/10	9/10
1st ovarian cycle			
Age (j)[1]	320 ± 18		372 ± 9
LW (kg)[1]	30.4 ± 0,5		28.9 ± 1.3
1st heat			
Age (j)	327 ± 13		379 ± 13
LW (kg)	30.7 ± 0.3		29.8 ± 1.3
1st normal cycle with heat			
Age (j)	329 ± 18		380 ± 14
LW (kg)	31.4 ± 0.7		29.8 ± 1.2

[1] Age and live weight in the LH group are calculated for the ewe lambs that reached puberty