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Digestibility and energy utilisation of three diets by llamas and sheep

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Summary — The aim of the study was to determine digestibility and energy utilisation of three diets: H, 100% DM chopped poor-quality natural-grassland hay; HB, 60% DM of the same hay and 40% DM of pelleted barley; S, 100% DM chopped ammonia-treated wheat straw offered at near maintenance according to a Latin square design to six adult castrated llamas and six wethers. Expressed per kg metabolic body weight (MBW), DM intakes of diets H and S were proportionally 23% and 24% lower in llamas than in sheep, respectively. Apparent digestibilities of organic matter, energy and NDF tended to be higher and apparent digestibility of ADF was higher in llamas than in sheep ($P < 0.01$). Due to large refusals of diet S, daily and circadian energy expenditures of the animals were determined by indirect calorimetry on diets H and HB only. Corrected for the same time spent standing and adjusted for the same metabolisable energy (ME) intake, daily energy expenditure was 17% lower in llamas than in sheep with diet H and was not significantly different with diet HB. Maintenance ME requirements of llamas averaged 343 and 296 kJ/kg MBW/day with diets H and HB, respectively ($P < 0.01$). The corresponding values were 412 and 317 for sheep ($P < 0.01$).

llamas / sheep / digestibility / energy metabolism / maintenance

Résumé — Digestibilité et utilisation de l'énergie de trois régimes par les lamas et les moutons. L'objectif de cette étude était de déterminer la digestibilité, la production de méthane et l'utilisation de l'énergie de trois régimes : H, 100 % de foin de prairie naturelle de mauvaise qualité ; HB, 60 % du même foin et 40 % d'orge en pellets ; S, 100 % de paille traitée à l'ammoniac offerts à un niveau proche de l'entretien selon un dispositif en carré latin à six lamas adultes castrés et six moutons castrés. Exprimées par kilo de poids métabolique (MBW), les MS ingérées avec les régimes H et S étaient 23 et 24 % plus faibles chez les lamas que chez les moutons respectivement. Les digestibilités apparentes de la matière organique et du NDF tendaient à être plus élevées mais n'étaient pas significativement différentes entre lamas et moutons. La digestibilité apparente de l'ADF était plus

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élevée chez les lamas que chez les moutons ($p < 0,01$). Les dépenses énergétiques journalières et circadiennes des animaux étaient déterminées par calorimétrie indirecte avec les régimes H et HB seulement. Les pertes d'énergie sous forme de méthane rapportées à l'énergie ingérée et digestible n'étaient pas significativement différentes entre les espèces. Pour le même temps passé debout et la même ingestion d'énergie métabolisable (EM), les dépenses énergétiques étaient 17 % plus faibles chez les lamas que chez les moutons avec le régime H et n'étaient pas significativement différentes avec le régime HB. Les besoins d'entretien des lamas étaient en moyenne de 343 et 296 kJ/d'EM/kg PM/j avec les régimes H et HB respectivement ($P < 0,01$) et ceux des moutons de 412 et 317 kJ d'EM ($p < 0,01$). Les besoins d'entretien plus faibles chez les lamas que chez les moutons observés avec le régime à faible teneur en protéines (H) pourraient résulter de l'aptitude plus grande des lamas à recycler l'urée et à éviter ainsi un déficit protéique qui peut accroître l'activité métabolique tissulaire.

lama / mouton / digestibilité / métabolisme énergétique / entretien

INTRODUCTION

From the results of 18 studies, San Martin et al (1985) showed that digestibility of organic matter (OM), neutral detergent fibre (NDF), acid detergent fibre (ADF) and crude protein (CP) were on average 2–3 percent units higher in alpacas than in sheep. Similarly, the results obtained by Hintz et al (1973), Warmington et al (1989), Cordesse et al (1992), Dulphy et al (1994) and Lemosquet et al (1996) enabled the last authors to show that the OM digestibility (OMD) of 11 diets was higher in llamas than in sheep (59.0 vs 55.6%). Camelids, especially llamas, seem therefore well adapted to the digestion of roughages. Furthermore, addition of barley (25% of DM) to a hay diet did not depress its digestibility and increased the differences in digestibility of diets between llamas and sheep (Lemosquet et al, 1996).

This ability of South American camelids to digest forage cell walls more efficiently than sheep could result from several anatomical and physiological features (Kayouli et al, 1993). The stomach of camelids is composed of three compartments instead of four in ruminants. One of the compartments, which can be considered similar to that of the rumen, includes two series of glandular sacs located on its wall and glandular cells on the ventral wall. Both produce large amounts of bicarbonates which buffer the digesta of this compartment (Rouissi, 1994). This favours the activity of micro-organisms (Jouany et Kayouli, 1989; Dulphy et al, 1994) and absorption of volatile fatty acids (Engelhart and Höller, 1982). Furthermore, the retention time of plant particles in the stomach is longer in llamas than in sheep (32 vs 25 h, on average; Dulphy et al, 1994), which increases their potential degradation through fermentation (Dulphy et al, 1994). Finally, camelids have a greater ability for recycling urea through saliva and rumen mucosa and a very low urinary urea excretion (Jouany et al, 1996). This supplies the bacteria regularly with nitrogen, favours their growth and cellulolytic activity, and makes camelids more adapted to use poor quality roughages of low protein content than other ruminants.

While the literature on the comparative digestion of camelids and ruminants is extensive, knowledge on methane production and energy utilisation is very limited; the studies included only few llamas (Schneider et al, 1974) and sometimes there were no comparisons with other ruminants (Carmean et al, 1992). The aim of the present study was, therefore, to determine digestibility, methane production and energy utilisation of three diets of very different nature and chemical composition, fed near maintenance to llamas and sheep.

MATERIALS AND METHODS

The study was carried out on six castrated llamas, aged 4 years, weighing 100.8 kg (SD 11.1) and six Texel wethers, aged 3 years and weighing 65.1 kg (SD 7.2). They were given each of the three following diets: H, 100% DM chopped poor-quality natural-grassland hay; HB, 60% of the same hay and 40% pelleted barley; and S, 100% chopped ammonia-treated wheat straw, according to a Latin square design (3 × 3) with two replicates.

Each experimental period lasted 4 weeks. During the 2-week period of transition between diets, the animals were housed in individual pens on wood shavings. Subsequently they spent 10 or 11 days in crates (llamas) or in digestibility cages (sheep) with wooden floors, and 4 or 3 days in respiration chambers. Before the beginning of the study animals were trained to these environments.

Daily rations were calculated taking into account the expected differences in OMD such that metabolisable energy intakes (MEI) would meet the estimated maintenance ME requirements (MEm) of llamas and wethers (356 kJ ME/day/kg MBW, metabolic body weight, $W^{0.75}$) (Carmean et al, 1992). They were fed in two equal meals at 9.30 h and 16.30 h. Quantities of feeds offered and refused were controlled daily during the digestibility period as well as the stay in respiration chambers. Faeces were collected over a 6-day period. Urine was not collected because of risks of losses due to the special anatomy of male llamas (Engelhardt and Schneider, 1977). The use of an urine collection apparatus (Carmean et al, 1992) could have disturbed the animals.

Bulked samples of feeds offered and of the refused material, if any, were dried at 80°C before analysis. Faeces were analysed after freeze-drying. The ash content was determined by incineration, gross energy by adiabatic calorimetry, nitrogen by a macro-Kjeldahl method, and NDF and ADF contents by the method of Van Soest and Wine (1967) (table I). Urinary energy (UE) was estimated using the following relationship established from 132 data sets with sheep fed various diets (Vermorel and Bouvier, 1978; unpublished data) :

$$UE/EI = 0.209\,CP - 0.00812\,FL + 0.0317\,ED + 0.0271$$
$$RSD = 0.0053 \quad R^2 = 0.76$$

with EI, energy intake; CP, crude protein content (g/g DM); FL, feeding level; and ED, energy digestibility. Energy expenditure (EE) of animals was determined by indirect calorimetry using two open-circuit respiration chambers (Vermorel et al, 1973). One of them was equipped for llamas and the other for sheep. Gas exchange measurements were conducted over 2 consecutive days following 1 or 2 days of readaptation to the chambers. Gas analyses were carried out both on composite samples of air leaving the chambers, collected over 23.5 h, and continuously using differential gas analysers (CO_2: 0 – 0.01; O_2: 0.21-0.20; CH_4: 0 – 0.001, Mahiak, Hamburg, Germany). All apparatuses were logged every minute. EE was computed from gas exchanges using Brouwer's relationship (1965). Because of the lack of information on urinary nitrogen excretion, the coefficient 0.99 was used to take into account the oxidative catabolism of protein (McLean, 1972).

Due to the large day-to-day variation in feed intake of some llamas, energy balances were calculated separately for each of the 2 days of measurement in the respiration chambers. As the retention time of feeds in the digestive tract was longer than 24 h, energy balances corresponding to day 1 or day 2 were calculated using the mean amounts of feeds ingested on day 0 and day 1 or on day 1 and day 2, respectively.

Each animal was connected to an electrical switch through a harness to determine its position (standing vs lying) and the energy cost of standing. Due to large between-animal differences in time spent standing, EE and energy balances were corrected for the same duration of time spent standing in order to eliminate the effect of physical activity on EE.

Table I. Chemical composition of diets (g or MJ/kg DM).

Diet	*Hay*	*Hay + barley*	*NH_3 treated straw*
Organic matter	919	915	922
Crude protein	86	105	121
NDF	678	471	730
ADF	394	256	513
Gross energy (MJ)	18.04	18.01	19.03

Statistical analyses

Results were analysed according to the following models of variance analysis (SAS, 1987). Model 1 was used for diet digestibility: $\mu + \alpha$ diet + β species + γ DMI (covariate) + δ animal (species) + diet × species + ε. The aim of this model was to test: 1) DMI as a covariate; and 2) variability due to animal nested into species and the interaction between diet and species. Model 2 was used for methane production, ME intake, EE, time spent standing, energy cost of standing, daily EE in the standing position, EE and energy retention (RE) corrected for the same time spent standing (EEc, REc): $\mu + \alpha$ diet + β species + γ animal (species) + diet × species + ε. Model 3 was used for EEc and REc adjusted for the same MEI: $\mu + \alpha$ diet + ß species + γ MEI (covariate) + δ animal (species) + diet × species + ε. Differences between adjusted means were analysed using the Student's *t*-test (Snedecor and Cochran, 1971).

RESULTS

One of the llamas had a kidney disease during the experimental period and was discarded; therefore, the number of llamas used was five. In other respects, due to a technical problem, gas exchanges of one sheep fed the HB diet could not be measured accurately.

Food intake

During the digestibility periods the ratios between DM intakes and DM expected to meet MEm requirements averaged 96.8% (SD 16.4) and 98.7% (SD 7.0) in llamas and sheep, respectively, fed diet H; in llamas they ranged from 76 to 115%. With diet S the ratios amounted to 81.6% (SD 19.9) and 100.5% (SD 10.1) in llamas and sheep, respectively, they ranged from 64 to 108% in llamas. Furthermore, during the stay in respiration chambers, refusals of straw by llamas were still greater than during the digestibility period: the ratio was only 57.6% (SD 12.7). Consequently, diet S was not used for the comparison of energy utilisation in llamas and sheep. On the contrary, there were no refusals of diet HB, and DM intakes amounted to 103.2% (SD 2.7) and 113.1% (SD 4.9) of the quantities expected to meet MEm in llamas and sheep, respectively.

DM intakes by the two species during the digestibility period were compared. They were 23% and 24% lower in llamas than in sheep with diets H and S respectively ($P < 0.001$; table II). However, they were not significantly different between species with diet HB. During the calorimetry period, DM intakes were 26% lower in llamas than in sheep with diet H ($P < 0.001$; table III). Similarly, they were not significantly different between species with diet HB.

Apparent digestibility of diets and feeds

Apparent digestibilities of DM, OM, E, NDF and ADF were analysed according to model 1 (table II). Apparent digestibilities of DM, OM and E were not significantly different between llamas and sheep. Digestibility of crude protein was not determined because of risk of pollution of faeces by urine in llamas. NDF digestibility was not significantly different between llamas and sheep with diet H and tended to be higher in llamas with diets HB and S ($P = 0.15$ and $P = 0.12$ respectively). ADF digestibility was 5%, 12% and 3% higher in llamas than in sheep with diets H, HB and S respectively ($P = 0.06$, $P = 0.01$ and $P = 0.02$). Energy digestibility of diet HB was 32% higher than that of diet H ($P < 0.001$). Assuming that ED of barley was 84%, calculated ED of hay in diet HB was 50.8% and 48.2% for llamas and sheep, respectively. These values were close to those found with diet H (48.5% and 47.5%), which suggested that at a feeding level close to maintenance there were no associative effects between barley and this poor quality hay in llamas and in sheep. In other respects, in spite of the higher cell wall content (table I), OM, E, NDF and

Table II. Dry matter intake (DMI, g/kg MBW/day) during the digestibility periods and apparent digestibilities of diets in llamas and sheep (means and SD in parentheses).

Species	*Llamas*			*Sheep*			*Statistical significance*					
number	*5*			*6*								
Diet	*H*	*HB*	*S*	*H*	*HB*	*S*	*Species*	*Diet*	*DMI (covariate)*	*Animal (species)*	*Diet × Species*	*SEM*
DMI	38.1[a]	34.4[a]	33.7[a]	49.4[b]	40.7[ab]	44.6[b]	***	*				
	(6.5)	(0.8)	(7.3)	(8.6)	(1.6)	(3.6)						
DMD	48.0[a]	64.1[c]	52.7[b]	48.1[a]	63.0[c]	52.7[ab]	NS	***	NS	***	NS	0.94
	(2.3)	(3.4)	(2.6)	(4.3)	(4.4)	(3.9)						
OMD	51.5[a]	66.9[d]	55.1[c]	50.7[a]	65.3[d]	54.6[b]	NS	***	NS	***	NS	0.84
	(2.3)	(2.9)	(2.3)	(3.9)	(4.1)	(3.9)						
ED	48.5[a]	64.1[c]	51.9[b]	47.5[a]	62.5[c]	52.3[b]	NS	***	NS	***	NS	0.91
	(1.9)	(3.3)	(2.2)	(4.6)	(4.5)	(3.5)						
NDFD	51.9[a]	54.3[a]	62.3[b]	50.3[a]	50.5[a]	61.6[b]	NS	***	NS	**	NS	1.29
	(2.1)	(4.1)	(4.7)	(4.6)	(6.8)	(2.9)						
ADFD	47.1[b]	49.1[b]	59.5[d]	44.9[a]	43.8[a]	57.6[c]	**	***	**	**	NS	1.45
	(4.4)	(4.6)	(3.6)	(7.1)	(7.5)	(0.4)						

DMD, OMD, ED, NDFD, ADFD: apparent digestibilities of DM, OM, E, NDF and ADF, respectively.
Statistical significance: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.
[a, b, c] Values with different superscripts are significantly different.

Table III. Calorimetry period: dry matter intake (DMI), gross energy intake (EI), digestible energy intake (DEI), methane energy (GE), metabolisable energy intake (MEI) (g or kJ/kg MBW/day) and metabolisability (ME% EI) of the diets (means and SD in parentheses).

Species	*Llamas*		*Sheep*		*Statistical significance*				
number	*5*		*6*	*5*					
Diet	*H*	*HB*	*H*	*HB*	*Species*	*Diet*	*Animal (species)*	*Diet × Species*	*SEM*
DMI	37.1[a]	35.1[a]	50.3[b]	39.3[a]	**	*	NS	NS	2.3
	(5.2)	(3.4)	(5.4)	(2.6)					
EI	671[a]	633[a]	909[b]	709[a]	**	*	NS	*	35.3
	(94.5)	(62)	(97)	(47)					
DEI	324[a]	407[b]	434[b]	433[b]	*	NS	NS	NS	24.3
	(52)	(39)	(77)	(29)					
GE	40.8[a]	42.3[a]	56.1[b]	52.9[b]	***	NS	NS	NS	2.4
	(6.2)	(5.7)	(5.3)	(2.4)					
GE/EI	6.1[a]	6.8[b]	6.2[a]	7.5[b]	NS	**	NS	NS	0.3
	(0.6)	(1.1)	(0.8)	(0.3)					
GE% DEI	12.6	10.5	13.4	12.2	NS	NS	NS	NS	0.8
	(1.3)	(1.7)	(2.9)	(0.7)		($P < 0.07$)			
UE/EI [1]	3.9	4.1	3.7	4.1					
MEI	257[a]	339[b]	344[b]	351[b]	*	NS	NS	NS	22.7
	(44)	(37)	(75)	(27)		($P < 0.08$)			
ME% EI	38.2[a]	53.6[b]	37.5[a]	49.6[b]	NS	***	NS	NS	1.2
	(2.0)	(2.6)	(5.0)	(2.8)					
ME% DEI	79.2[a]	83.1[b]	78.7[a]	81.0[ab]	NS	**	NS	NS	1.0
	(1.5)	(1.8)	(3.7)	(1.0)					

[1] Urinary energy: calculated values (see text). Statistical significance: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
[a b, c] Values with different superscripts are significantly different.

ADF digestibilities of the ammonia-treated straw were significantly higher than those of the poor quality hay short in crude protein ($P < 0.001$; table II). The effect of DMI as covariate on chemical compound digestibility was not significant, except for ADF ($P < 0.01$). Diet × species interaction was not significant. Animal variability nested into species was highly significant ($P < 0.01$ or $P < 0.001$).

Methane energy losses

Expressed per kg MBW, methane production was lower in llamas than in sheep (1.07 vs 1.39 L/day, $P < 0.001$). This difference could result from the lower feed intake of llamas. Indeed, if methane energy losses (GE) were related to gross energy intake (GE/EI) or to digestible energy intake (GE/DEI), there were no significant differences between llamas and sheep (table III). Finally, no clear differences in the circadian pattern of methane production appeared between the two species: methane emissions were regular and peaks of emission were associated with standing which could favour gas eructation. In other respects, GE/EI was higher with diet HB than with diet H ($P < 0.01$), probably because of the higher energy digestibility of HB diet, as GE/DEI was not significantly different between the two diets. Animal effect and diet × species interaction were not significant for GE, GE/EI and GE/DEI.

Metabolisable energy content of diets

Urinary energy losses predicted from chemical composition of the diets and feeding levels averaged 3.8% and 4.1% EI with diets H and HB, respectively (table III). The ratios between ME and gross energy were slightly but not significantly higher in llamas than in sheep and averaged 37.8% and 51.6% for diets H and HB, respectively ($P < 0.001$; table III). Similarly, the ratios between ME and DE were not significantly different between llamas and sheep and averaged 78.9% and 82.0% for diets H and HB, respectively ($P < 0.05$). ME intake of llamas expressed per kg MBW was 25% lower than that of sheep with diet H during the stay in respiration chambers ($P < 0.05$). However, there were no significant differences between llamas and sheep with diet HB. Animal effect and diet × species interaction were not significant for MEI, ME/EI and ME/DEI.

Energy expenditure of animals

Difference between gas exchanges measured either continuously or from daily composite samples averaged + 0.2% (SD 1.5), which stresses the validity of the kinetics.

Expressed per kg MBW, daily EE of llamas were 22% and 11% lower than those of sheep with diets H and HB, respectively ($P < 0.001$ and $P < 0.05$; table IV). However, ME intakes and physical activity were different between species. The time spent standing per day varied greatly between animals. It tended to be shorter in llamas than in sheep but the differences were not significant (table IV). On average llamas and sheep spent 511 min (SD 107) standing, ie, 35.5% of the day. Expressed in J/kg BW/min, the energy cost of standing (ECS) was not significantly different in llamas and in sheep with diet H and was 18% lower in llamas than in sheep with diet HB ($P < 0.05$). Expressed in kJ/kg BW/day, ECS was on average 26% lower in llamas than in sheep ($P < 0.01$). However, the percentage of ECS lying EE tended to be higher in llamas than in sheep ($P = 0.07$) and averaged 19.1% (SD 4.0). Expressed per kg MBW and per day, ECS was 25% lower in llamas than in sheep ($P < 0.05$) and averaged 6.2 and 6.9% of daily EE of llamas and sheep, respectively.

Table IV. Time spent standing (TSS), energy cost of standing (ECS), energy expenditure (EE), daily energy expenditure (DEE), retained energy (RE) and maintenance energy requirement (MEm) (means of 2 days and 5 or 6 animals, and SD in parentheses).

Species	*Llamas*		*Sheep*		*Statistical significance*					
number	*5*	*5*	*6*	*5*						
Diet	*H*	*HB*	*H*	*HB*	*Species*	*Diet*	*MEI (covariate)*	*animal (species)*	*Diet × Species*	*SEM*
TSS (I)	450	498	522	574	NS	NS	–	NS ($P = 0.07$)	NS	32
	(72)	(52)	(76)	(190)						
ECS (II)	15.1^{ab}	11.7^{a}	15.8^{b}	14.2^{b}	*	NS ($P = 0.06$)	–	*	NS	0.6
	(2.4)	(2,9)	(3,7)	(2.4)						
ECS (III)	6.8^{a}	5.6^{a}	8.4^{b}	8.4^{b}	**	NS	–	**	NS	0.5
	(1.7)	(1.3)	(2.9)	(3.8)						
ECS (IV)	21.2^{a}	17.5^{a}	23.5^{b}	27.8^{b}	*	NS	–	*	NS	1.5
	(4.8)	(4.0)	(7.5)	(7.8)						
ECS% lying EE	23.1	18.1	16.7	19.2	($P = 0.07$)	NS	–	NS	*	1.2
	(3.0)	(4.1)	(3.1)	(3.1)						
Measured DEE (IV)	313^{a}	312^{a}	404^{c}	349^{b}	***	NS	–	NS	($P = 0.07$)	12
	(19)	(23)	(31)	(36)						
Corrected DEE (V)	316^{a}	307^{a}	402^{b}	326^{a}	**	*	–	NS	*	12
	(17)	(12)	(28)	(38)						
Corrected RE (V)	-59^{a}	30^{b}	-58^{a}	25^{b}	NS	***	–	NS	NS	17
	(32)	(29)	(72)	(40)						
Adjusted DEE (VI)	338^{a}	307^{a}	395^{b}	321^{a}	*	**	*	NS	NS	10
Adjusted RE_C (VI)	-14^{b}	17^{b}	-71^{a}	2^{b}	*	**	**	NS	NS	10
MEm (IV)	343^{a}	296^{a}	412^{b}	317^{a}	**	**	–	NS	NS	14
	(14)	(11)	(30)	(50)						

(I): min/day; (II): J/kg BW/min; (III): kJ/kg BW/d; (IV): kJ/kg MBW/d; (V) corrected for the same time spent standing (511 min/day) (kJ/kg MBW/day); (VI): corrected for the same time spent standing and adjusted for the same ME intake (kJ/kg MBW/day).
Statistical significance: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.
[a, b, c] Values with different superscripts are significantly different.

In order to eliminate the effect of differences in physical activity on daily EE, these latter were corrected individually for the same time (511 min/day) spent in the standing position. Corrected daily EE (daily EEc) was proportionally 21% lower in llamas than in sheep fed diet H ($P < 0.01$) but not significantly different between the two species with diet HB. However, daily EEc increased with ME intake ($P = 0.04$). Adjusted for the same ME intake, daily EE corrected for the same physical activity was proportionally 14% lower in llamas than in sheep fed diet H ($P < 0.05$) but not significantly different between species with diet HB (table IV). Furthermore, daily EEc were significantly lower with diet HB than with diet H ($P < 0.01$).

Energy retention and maintenance energy requirements

Corrected for the same time spent standing, retained energy (REc = MEI – daily EEc) was not significantly different between species. Adjusted for the same ME intake, REc was significantly higher in llamas than in sheep fed diet H ($P = 0.02$). In other respects REc was significantly higher with diet HB than with diet H in sheep ($P = 0.001$) but not in llamas ($P < 0.15$).

Regression equations between REc and MEI (kJ/kg MBW/day) for each species and each diet were as follows:

– Llamas, diet H:

$REc = 0.685\ MEI - 235.1 \quad RSD = 11.7 \quad R^2 = 0.886$

SD 0.089 23.2

– Llamas, diet HB:

$REc = 0.738\ MEI - 223.2 \quad RSD = 18.2 \quad R^2 = 0.686$

SD 0.154 52.7

Mean efficiencies of ME utilisation near maintenance in llamas were 0.685 (SD 0.089) and 0.738 (SD 0.015) for diets H and HB, respectively. The corresponding maintenance ME requirements (MEm) of llamas were 343 (SD 14) and 296 (SD 11) kJ ME/kg MBW/day with diets H and HB, respectively.

– Sheep, diet H:

$REc = 0.861\ MEI - 354.4 \quad RSD = 27.0 \quad R^2 = 0.862$

SD 0.109 38.2

In spite of the abnormally high efficiency of ME utilisation (0.86), the maintenance ME requirement of sheep could be calculated satisfactorily because REc values were distributed below and above zero. MEm averaged 412 kJ/kg MBW/day (SD 30) with diet H. For sheep fed diet HB, there was no significant relationship between REc and MEI, probably due to the small range of MEI (CV = 7.7%). However, as REc were close for llamas and sheep fed diet HB, maintenance ME requirements of sheep offered diet HB could be estimated assuming that the efficiency of ME utilisation was the same in llamas and in sheep. Calculated MEm of sheep fed diet HB averaged 317 kJ/kg MBW/day.

DISCUSSION AND CONCLUSION

Hay and ammonia-treated straw DM intakes expressed per kg MBW or per kg body weight (BW) were significantly lower in llamas than in sheep during the digestibility periods, mainly due to large refusals by two or three of the five llamas. No clear explanations could be found for such refusals. However, DM intakes of the three or two other llamas were similar to those of sheep. As in the present study DM intakes of some llamas fed diet S were still much lower in respiration chambers than in digestibility crates, it is possible that llamas were more disturbed than sheep by these environments in spite of previous adaptation.

There were no significant differences in apparent digestiblity of DM, OM, energy and cell wall components between llamas and sheep. However, NDF and ADF digestibilities tended to be higher in llamas

than in sheep, especially with diet HB. Previous studies have shown that DM and OM digestibilities of hays were 4–5 percent units higher in llamas than in sheep. The differences mainly resulted from higher cell wall digestibility (+ 7 percent units; San Martin et al, 1985; Dulphy et al, 1994; Lemosquet et al, 1996). With mixed diets composed of hay and barley, differences amounted to 7 percent units for OM and cell wall digestibilities (Lemosquet et al, 1996). With straw based diets, differences in OM and cell wall component digestibilities ranged from 1 to 5 percent units (Warmington et al, 1989; Dulphy et al, 1994). These differences in digestibility could result from a longer retention time of feeds in llamas than in sheep due to a greater digesta content of their first two forestomachs (19.3 vs 12.7 g hay DM/kg LW before the main meal and 24.4 vs 21.0 g DM/kg LW after the main meal, (Dulphy et al, 1994).

Daily energy expenditures of llamas and sheep were corrected for the same time spent standing and adjusted for the same ME intake. Adjusted daily EE were significantly lower in llamas than in sheep, which resulted in lower maintenance ME requirements. The MEm of llamas offered diets H and HB in the respiration chambers were intermediate between those obtained with two llamas given a good quality forage diet (256, SD 11 kJ ME/kg MBW/day; Schneider et al, 1974) and with five llamas given a mixed diet (354, SD 18 kJ ME/kg MBW/day; Carmean et al, 1992). Furthermore, MEm of castrated llamas offered diet HB agreed with that of female dromedary camels offered a mixed diet composed of 66% barley grains and 33% wheat straw (296 SD 16 kJ/kg MBW/day; Guerouali et al, 1994). The efficiencies of ME utilisation for maintenance (km) were within the range predicted from diet metabolisability using Blaxter (1974) or Van Es (1975) relationships. Furthermore, differences in km (0.685 vs 0.738) and in MEm between the two diets were close to the expected differences.

The MEm of llamas and sheep fed the mixed diet (HB) were not significantly different. MEm of sheep agreed with the values obtained in balance trials with mature sheep fed various feeds at and above maintenance (317 vs 320 SD 5 kJ ME/kg MBW/day; Van Es, 1972). However, MEm of sheep fed the low protein diet (H) was one-third higher than the value obtained with the mixed diet and one-fifth higher than MEm of llamas. No technical error and no experimental bias could be found when a Latin square design was used. A possible explanation for the higher MEm of sheep could be their higher metabolic rate resulting from a deficiency in digestible protein. In fact, Fattet et al (1984) showed that fish meal supplementation of NaOH-treated barley straw with urea resulted in a reduction of MEm (496 vs 554 kJ ME kg MBW/day) in wether lambs fed near maintenance. Camelids have a greater ability to recycle urea and to reduce urinary nitrogen excretion thanks to a higher permeability of rumen mucosa and better urea resorption in the kidney (Engelhardt et al, 1984). These physiological particularities could prevent them from digestible protein deficiency and thus avoid the increase in metabolic rate and MEm with low protein forages.

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