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Breed dependent nutritional sensitivity of periparturient relaxation of immunity to nematode parasites in sheep

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Abstract. Periparturient relaxation of immunity (PPRI) to parasites is sensitive to metabolizable protein (MP) scarcity and varies between sheep breeds. This paper compares resistance to *Teladorsagia circumcincta* in Scottish Blackface (BF) and Mule (MU) ewes under two MP feeding regimes. We hypothesized that if the degree of PPRI is caused by nutrition alone, then its sensitivity to MP scarcity will not differ between breeds when feeding is adjusted for between-breed differences in MP demand. Twin-rearing BF and MU ewes, trickle infected with 10,000 infective larvae three times a week, were fed at either 0.8 (LP) or 1.3 (HP) times their estimated MP requirements. Breed and feeding treatment independently affected ewe body weight loss and litter weight gain during lactation, which were higher for MU than BF ewes. Similarly, litter daily weight gain was higher for HP ewes than LP ewes. However, breed and feeding treatment interacted on faecal egg counts (FEC) and plasma pepsinogen during lactation; LP feeding resulted in higher FEC and plasma pepsinogen than HP feeding in MU but not in BF ewes. The higher degree of resistance to parasites of LP-BF ewes relative to LP-MU ewes, in the presence of similar effects of MP scarcity on performance in both breeds, may suggest that Scottish Blackface ewes could be genetically more resistant to nematode parasite infection than Mule ewes.

Keywords. Sheep – Metabolizable protein – *Teladorsagia circumcincta* – Faecal egg counts.

Baisse de l'immunité face aux parasites nématodes pendant le péri-partum des brebis, liée à une sensibilité nutritionnelle sous la dépendance de la race

Résumé. La baisse de l'immunité pendant la période péri-partum (PPRI) face aux parasites est un phénomène sensible à un faible apport en protéine métabolisable (MP) et varie selon les races ovines. Cet article compare la résistance à *Teladorsagia circumcincta* chez des brebis de races Scottish Blackface (BF) et Mule (MU) soumises à deux régimes alimentaires différents en termes de MP. L'hypothèse était que si le degré de PPRI est causé par la seule nutrition, sa sensibilité à un faible apport en MP ne différera pas entre races lorsque l'alimentation est ajustée pour les différences inter-races de besoins en MP. Les brebis BF et MU élevant des agneaux doubles, infectées en continu avec 10.000 larves pathogènes trois fois par semaine, recevaient soit 0,8 fois (LP) soit 1,3 fois (HP) leurs besoins estimés en MP. La race et le traitement alimentaire ont affecté indépendamment la perte de poids corporel des brebis et le gain de poids de la portée pendant la lactation, qui ont été plus élevés pour les brebis MU que pour les brebis BF. De même, le gain de poids quotidien de la portée a été plus élevé pour les brebis HP que pour les brebis LP. Toutefois, la race et le traitement alimentaire ont interagi sur les dénombrements d'œufs fécaux (FEC) et les valeurs plasmatiques du pepsinogène durant la lactation; l'alimentation LP a résulté en FEC et valeurs plasmatiques du pepsinogène plus élevés que l'alimentation HP chez les brebis MU mais pas chez les brebis BF. Le plus fort degré de résistance aux parasites chez les brebis LP-BF par rapport aux brebis LP-MU, en présence d'effets similaires de faible apport de MP sur les performances des deux races, semble suggérer que les brebis Scottish Blackface pourraient être génétiquement plus résistantes à l'infection par parasites nématodes que les brebis Mule.

Mots-clés. Brebis – Protéine métabolisable – *Teladorsagia circumcincta* – Dénombrements d'œufs fécaux.

I – Introduction

Periparturient relaxation of immunity (PPRI) plays an important role in the epidemiology of gastrointestinal nematode parasite infections. It has long been recognized that it is associated with an increased nematode egg excretion from ewes into pastures, which can be a main source of infection for their immunologically naïve lambs (Heath and Michel, 1969). More recently, it has been suggested that the degree of PPRI to gastrointestinal nematode parasites is sensitive to metabolisable protein (MP) scarcity (Coop and Kyriazakis, 1999). Indeed, many studies have shown that periparturient protein supplementation at times of MP scarcity decreases faecal egg counts (FEC) and reduces worm burdens in ewes (Kyriazakis and Houdijk, 2006; Sykes and Kyriazakis, 2008).

The degree of PPRI also considerably varies between small ruminant breeds (Houdijk, 2008). For example, under *ad libitum* feeding, Scottish Blackface ewes had a lower degree of PPRI than Greyface ewes (Zaralis *et al.*, 2009). Likewise, under natural grazing conditions, Horro ewes have a higher degree of PPRI than Menz ewes (Tembely *et al.*, 1998). It has been suggested that such between-breed variation in PPRI may not necessarily be associated with genetic resistance *per se*, but could have a nutritional basis, due to variation in nutrient scarcity arising from between-breed differences in nutrient demand (Houdijk, 2008). Indeed, the higher susceptibility of Greyface and Horro ewes in comparison to Blackface and Menz ewes may be related to their higher nutrient demand resulting from their increased productivity (Zaralis *et al.*, 2009; Mukasa-Mugerwa *et al.*, 2000). This view is consistent with a large body of evidence showing that a lower nutritional demand arising from rearing single rather than multiple lambs and/or kids consistently reduces the degree of PPRI in small ruminants (Houdijk, 2008). Here, we have designed an experiment to test the hypothesis that if the aforementioned between-breed variation in PPRI has a nutritional basis only, then its sensitivity to MP scarcity would not differ between breeds when feeding is adjusted for between-breed differences in MP demand.

II – Materials and methods

This experiment was conducted in the lambing season of the year 2009 at Scottish Agricultural College, Edinburgh, UK.

1. Animals, diets and infection

Thirty-six Scottish Blackface ewes (BF) and 36 Mule ewes (MU) all scanned for twin-pregnancy, all 4 to 5 years old, with mean body weight (\pm SE) of 57.6 ± 0.70 kg and 69.1 ± 0.73 kg, respectively, at day₋₅₆ (day₀ was expected mean parturition date), were housed individually. Initial body condition score was similar for both breeds (2.6 ± 0.09). At day₋₂₃, ewes in each breed were randomly allocated to either a low (LP) or high (HP) MP feeding treatment, calculated to supply 0.8 or 1.3 their estimated MP requirements, respectively. The feeds were offered in order to restrict metabolizable energy (ME) intake at 0.9 times their estimated ME requirement. Using AFRC recommendations (1993) for the estimation of ME and MP requirements, we assumed a litter birth weight of 6.6 kg for BF and 10.3 kg for MU, no maternal body weight gain during late pregnancy and 10.2 g MP per day for wool growth. For lactating ewes, we assumed daily milk yields of 2.4, 2.6, 2.8 and 2.8 kg for BF ewes, and 3.0, 3.3, 3.6 and 3.6 kg for MU ewes in week 1, 2, 3 and 4 of lactation respectively. Furthermore, a 10.2 g MP per day for wool growth for both breeds and a body weight loss of 80 and 100 g per day was assumed for BF and MU, respectively (Houdijk *et al.*, 2006; Houdijk *et al.*, 2001; Peart 1970). Daily allowance was composed of $\sim 1/3$ of medium quality hay and $\sim 2/3$ barley-based concentrates during both pregnancy and lactation. Differences in dietary MP supply were achieved mainly through including xylose-treated soybean meal at the expense of partially alkaline treated straw, whilst diets were kept iso-energetic through varying the barley to fat ratio. The ewes

were treated at housing with levamisole (Levacide, Norbrook, Newry, UK) and ivermectin (Oramec, Merial, Harlow, UK) to clear any resident worms, and subsequently infected with 10,000 infective larvae of the abomasal nematode parasite *Teladorsagia circumcincta*. This infective dose was administered three days a week on a Mon-Wed-Fri basis from day₋₄₁ onwards.

2. Measurements and statistics

The ewes were weighed at day₋₅₆ and then weekly from day₋₄₂ onwards, as well as within 12 h of parturition. The lambs were weighed within 12 h after birth and weekly afterwards. The body condition of the ewes was scored regularly, by lumbar palpation on a 0 to 5 scale to an accuracy of a quarter. Faecal egg counts (FEC, expressed as eggs per gram of fresh faecal sample (epg)), was monitored twice a week from day₋₂₃ to day₃₂ according to a modified floatation method (Christie and Jackson, 1982). The ewes were fed restrictedly, and refusals were not expected. However, whenever refusals did occur, they were collected and weighed twice a week and dried. Blood samples were taken from the jugular vein of the ewes into heparinised vacutainers immediately before infection (day₋₄₁), prior to the start of the feeding treatments (day₋₂₆), and during the periparturient period (day₁₁, day₋₃, day₇ and day₂₅). The plasma samples were analyzed for plasma urea (mmol/l), plasma pepsinogen (expressed in $\text{iu} \times 1000$ per liter as μl) and plasma albumin (g/l) concentration.

Ewe FEC were transformed via $\log(\text{FEC}+1)$ for statistical analyses and backtransformed means (with 95% confidence intervals) were reported. Average daily gain was estimated by linear regression. Ewe and litter body weight, FEC and plasma constituents were analyzed using Restricted Maximum Likelihood (REML) 2 x 2 factorial analysis of variance (ANOVA) with power block model to account for repeated measures. Ewe parturition body weight, litter birth weight as well as ewe and litter average daily gain were analyzed using a 2 x 2 factorial ANOVA with initial ewe body weight (day₋₅₆) as a covariate.

III – Results

1. Feed intake, ewe performance and plasma proteins

During both pregnancy and lactation, feeding treatment and the interaction between breed and feeding treatment did not affect achieved DM intake and estimated ME intake ($P=0.05$). Achieved MP intake differed between the LP and HP ewes, while the interaction with breed indicated that this difference was larger for the MU ewes than for the BF ewes.

Figures 1a and 1b show effects of breed and feeding treatment on ewe and litter body weight, respectively. Ewe body weight increased over time for both breeds during late pregnancy ($P<0.001$) and this increase was larger for HP ewes than for LP ewes ($P=0.015$), resulting in heavier post parturition body weight for HP ewes compared to LP ewes (58.7 vs 57.1 kg; SED: 0.68 kg; $P=0.025$). During lactation, time interacted with breed and with feeding treatment on body weight, reflected in differential effects on body weight loss; MU ewes had a higher rate of body weight loss than BF ewes (174 vs 111 g/d; SED 18.6 g/d; $P=0.001$), whilst HP ewes had a higher rate of body weight loss than LP ewes (165 vs 121 g/d; SED 18.6 g/d; $P=0.023$). Body condition score was similar at day₋₂₈ (2.43 ± 0.065). By day₋₁₄, condition score was lower for LP ewes than HP ewes (2.35 vs 2.46; SED 0.064; $P=0.093$), and reduced further over time ($P<0.001$) to an average 2.08 and 2.21 for LP and HP ewes, respectively, during lactation (SED 0.047; $P=0.008$). MU ewes had a higher condition score than BF ewes during pregnancy (2.48 vs 2.31; SED 0.064; $P=0.024$) and lactation (2.18 vs 2.10; SED 0.048; $P=0.094$). Interaction effects on ewe performance were not significant.

Feeding treatment and breed interacted for litter birth weight ($P=0.008$). As such, HP litters were heavier at birth than LP litters in MU ewes only (Fig. 1b). Time and breed ($P<0.001$), and time and

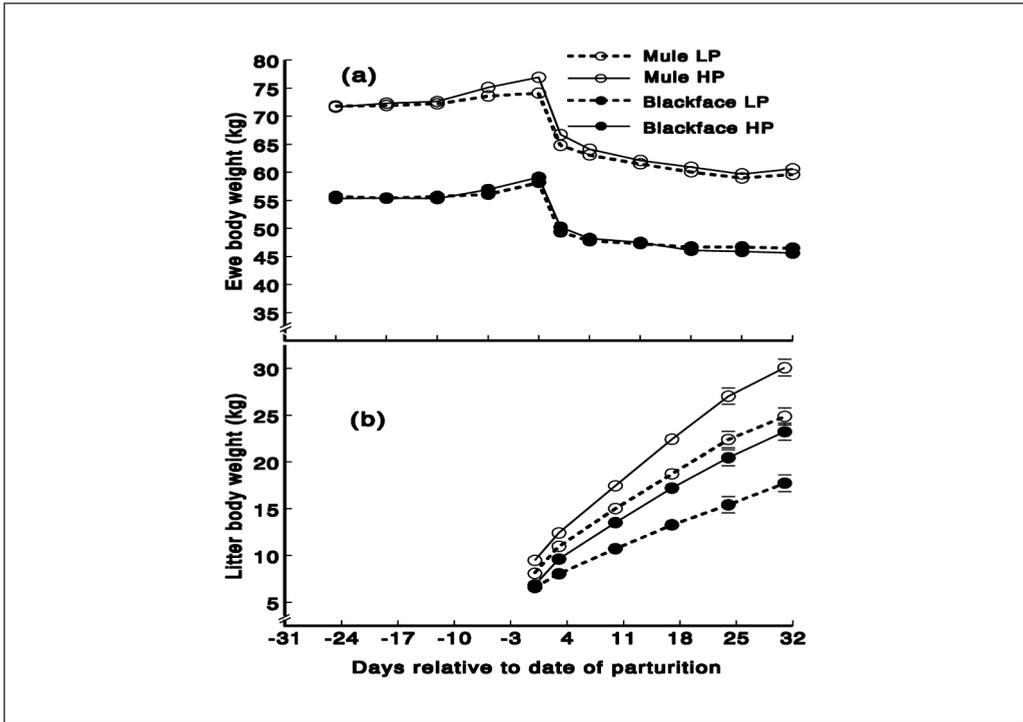


Fig. 1. Ewe body weight (a) and litter body weight (b) of Mule and Blackface ewes fed 0.8 (LP) or 1.3 (HP) times their estimated MP requirement during late pregnancy and early lactation.

feeding treatment ($P < 0.001$) interacted on litter body weight (Fig. 1b). This was reflected in differences in average daily gain; MU litters grew faster than BF litters (615 vs 444 g/day; SED 15.1 g/day; $P < 0.001$), whilst HP litters grew faster than LP litters (616 vs 453 g/day; SED 15.1 g/day; $P < 0.001$).

Figures 2a and 2b show effects of breed and feeding treatment on plasma albumin and urea, respectively. Mean pre-infection plasma urea was significantly higher for BF than MU ($P = 0.014$), whereas plasma albumin was significantly higher for MU ewes than BF ewes ($P = 0.029$). These differences disappeared by day₂₆ once the background levels were included as a covariate in the model. However, throughout the periparturient period, both plasma urea and albumin were higher for HP ewes than LP ewes ($P < 0.001$), with no effect of breed or interaction between breed and feeding treatment with time.

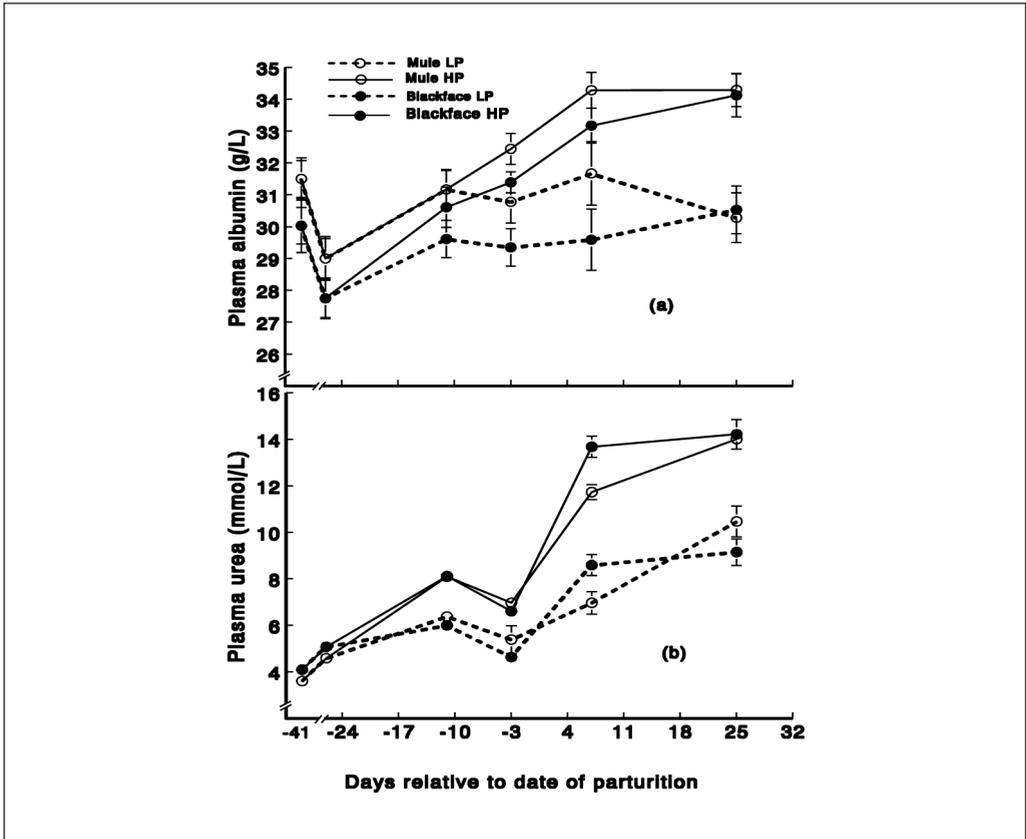


Fig. 2. Plasma albumin (a) and urea (b) of Mule and Blackface ewes fed 0.8 (LP) or 1.3 (HP) times their estimated MP requirement during late pregnancy and early lactation.

2. Ewe faecal egg counts and plasma pepsinogen

Figures 3a and 3b show effects of breed and feeding treatment on ewe FEC and plasma pepsinogen, respectively. During late pregnancy, FEC increased over time ($P < 0.001$) whilst none of the interaction effects were significant on FEC ($P > 0.10$). BF ewes had lower FEC than MU ewes ($P = 0.018$), whilst LP ewes had higher FEC than HP ewes ($P = 0.08$). However, during lactation, breed and feeding treatment interacted on FEC ($P = 0.05$). The LP feeding treatment increased FEC in MU ewes ($P < 0.001$) but not in BF ewes ($P = 0.581$).

Mean pre-infection plasma pepsinogen was higher for the MU ewes than the BF ewes (383 vs 319; SED 29.4 $\mu\text{u/l}$; $P = 0.033$) and increased following infection ($P < 0.001$). In the last two weeks of pregnancy, however, plasma pepsinogen was lower for MU than BF (1466 vs 1140; SED 166 $\mu\text{u/l}$; $P = 0.023$), with no effects of feeding treatment or breed x feeding treatment interaction. However, during lactation, breed and feeding treatment interacted on plasma pepsinogen ($P = 0.025$); LP ewes had higher pepsinogen levels than HP ewes for MU ewes only.

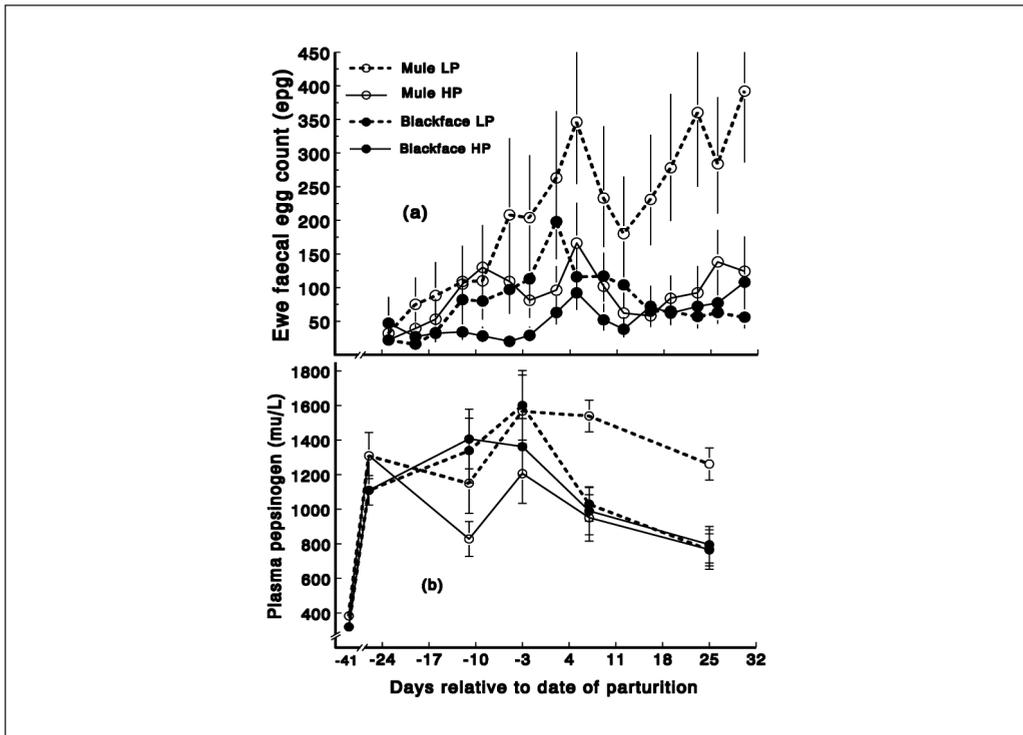


Fig. 3. Back-transformed mean faecal egg count (with 95% confidence interval) (a) and mean plasma pepsinogen (with SE) (b) of Mule and Blackface ewes fed 0.8 (LP) or 1.3 (HP) times their estimated MP requirement during late pregnancy and early lactation.

IV – Discussion

The lower litter weight gain in both LP-MU and LP-BF ewes relative to their HP counterparts indicates that the LP feeding treatment resulted, as intended, in a higher degree of MP scarcity than the HP feeding treatment. The absence of a feeding treatment x breed interaction on litter weight gain supports the view that the degree of MP scarcity achieved for both breeds was similar. The higher body weight loss in HP ewes compared to LP ewes during lactation, which was also observed in an earlier study (Houdijk *et al.*, 2000), may have arisen from a higher degree of body fat mobilization to sustain the higher level of milk production at the restricted levels of ME intake.

The elevated FEC and pepsinogen levels for the LP-MU ewes compared to the HP-MU ewes is consistent with a large body of evidence supporting the view that the degree of PPRI is sensitive to MP scarcity, as reviewed recently (Kyriazakis and Houdijk, 2006; Sykes and Kyriazakis, 2008). The increased levels of plasma pepsinogen would indicate that MP scarcity in the MU ewes led to reduced ability to maintain abomasal mucosal integrity (Houdijk *et al.*, 2003). Since it has been suggested that abomasal permeability correlates with worm burdens (Simpson, 2000), the higher levels of plasma pepsinogen in the LP-MU ewes may indicate a larger adult worm burden compared to their HP counterparts.

The aforementioned effects of MP scarcity on pepsinogen and FEC were not observed for the BF ewes. Zaralis *et al.* (2009) observed similar effects when assessing the effects of protein supple-

mentation on parasitism in *ad libitum* fed Greyface and Blackface ewes. However, because both breeds in that study displayed a similar intake of the low protein basal food, the degree of MP scarcity in the Blackface ewes would have been smaller than in the Greyface ewes. Such a difference in degree of MP scarcity could have led to the observed lower FEC in the Blackface ewes in that study (Houdijk *et al.*, 2003). In the current experiment, this confounding effect of breed and MP scarcity was accounted for through restricted feeding relative to breed-dependant MP requirements. Since this resulted in the same degree of MP scarcity between the breeds used, the lower level of FEC in the Blackface ewes could suggest that variation in PPRI between Blackface and Mule ewes may also arise from differences in genetic resistance, and that moderate MP scarcity would not increase the degree of PPRI in genetically more resistant ewes. In support of the latter, it has indeed been observed that in contrast to their randomly-bred counterparts, MP scarcity does not increase periparturient FEC in ewes genetically selected for low FEC (Kahn *et al.*, 2003).

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