

# Enhancing immunity to nematode parasites in pregnant and lactating sheep through nutrition and genetic selection

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## Summary

Susceptibility to infection from nematode parasites in sheep is most pronounced in young animals and in periparturient ewes. The susceptibility of young animals is a consequence of an inability to develop effective acquired immune responses to nematode parasites. In the periparturient ewe, susceptibility arises from a temporary loss of acquired immunity. Loss of immunity is associated with a rise in faecal egg counts (FEC) and this can increase the number of infective nematode larvae on a given mass of pasture. Greater pasture–larval counts will increase nematode infection of lambs. Strategies to reduce the periparturient rise in FEC will be of benefit to the ewe and to her progeny and increase animal production.

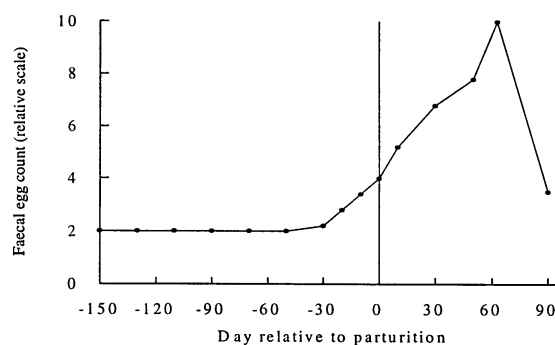
Protein requirements of young sheep and periparturient ewes are high in relation to other classes such as non-reproductive animals. Increasing the supply of protein to the intestines of young sheep has been shown to improve resistance to nematode parasites and consequently lower FEC. A similar response has been observed in the periparturient ewe. Genetic selection for increased resistance to nematode parasites has been demonstrated to reduce FEC and lower the extent of the periparturient rise. In this review, the effects of and interactions between genetic selection and nutrition on resistance to infection from nematode parasites are discussed. Given the current situation of endemic drench resistance, non-chemical approaches to control disease are of great value.

## Loss of immunity in the periparturient ewe

In sheep, a transient loss or diminution of immunity to intestinal nematode parasites begins around the time of lambing and continues for many weeks postpartum (Brunsdon 1970; O'Sullivan and Donald 1970; Connan 1976; Lloyd 1983). Loss of immunity at this time is associated with a rise in faecal egg count (FEC) and adult worm burden (O'Sullivan and Donald 1970; Donaldson *et al.* 1997) (Figure 1). This may result from

one or a combination of more than one of the following factors: increased establishment rate of incoming larvae, resumed development of arrested larvae, increased egg production by established females (fecundity) and/or decreased mortality of established adult worms (O'Sullivan and Donald 1970).

The extent to which immunity in the periparturient ewe is diminished appears to be specific to the species of nematode involved. An increase in the susceptibility of both the pregnant and lactating ewe to infection with *Trichostrongylus colubriformis* (O'Sullivan and Donald 1973; Gibbs and Barger 1986) and *Ostertagia circumcincta* (Brunsden 1970; Gibbs and Barger 1986; Jackson *et al.* 1988) has been reported but it appears that, in comparison to the non-reproductive animal, there is no loss of immunity to *Haemonchus contortus* (O'Sullivan and Donald 1973; Gibbs and Barger 1986) or *Trichostrongylus vitrinus* (Jackson *et al.* 1988). Increases in FEC and mature adult *H. contortus* numbers in the lactating ewe have been shown to be due to the resumed development of inhibited larvae rather than an increase in establishment rate of ingested larvae (Gibbs and Barger 1986). There is also evidence that the fecundity of female *T. colubriformis* and *H. contortus* increases during the periparturient period (O'Sullivan and Donald 1973).



**Figure 1** Stylised presentation of the typical pattern of faecal egg count (relative scale) of ewes during gestation and lactation. Shape of the FEC vs. time curve derived with reference to Brunsdon (1970), O'Sullivan and Donald (1970) and Kahn, Knox, Gray and Ward (unpublished).

## Causes of loss of immunity in the periparturient ewe

A number of causes for the periparturient rise (PPR) in FEC have been suggested including immunosuppression due to changes in endocrine status, reduced levels of anti-parasite IgA in the gut as a result of an increase in the transport rate of anti-parasite IgA from the gut into mammary epithelium (Jeffcoate *et al.* 1992), stress of parturition and poor nutrition.

## Endocrine changes

Endocrine-induced immunosuppression resulting from an increase in the plasma concentration of prolactin was long suspected as the principal cause for PPR (Dunsmore 1965). Prolactin was implicated in the PPR for two main reasons, the first of which was because the rise in plasma concentration of prolactin corresponds with the PPR (Dunsmore 1965). The second reason was based on experiments which involved the use of diethyl stilboestrol to artificially elevate plasma concentrations of prolactin in unbred ewes (Gibbs 1967; Salisbury and Arundel 1970). In these experiments, treated ewes exhibited a rise in FEC that was not apparent in untreated ewes.

A number of studies (Coop *et al.* 1990; Jeffcoate *et al.* 1990), however, cast doubt on the involvement of prolactin in the PPR. Coop *et al.* (1990) artificially induced a rise in plasma prolactin which was associated with mammary development and lactation in unbred ewes challenged with the abomasal parasite *O. circumcincta*. Hormone-treated ewes produced normal quantities of milk but failed to exhibit a rise in FEC. These authors also reported that the rise in FEC in twin-bearing pregnant ewes preceded any changes in plasma levels of prolactin. Jeffcoate *et al.* (1990) suppressed plasma levels of prolactin in pregnant and lactating ewes to very low levels, by treatment with bromocryptine, yet failed to demonstrate any effect on post lambing FEC following challenge with *O. circumcincta*.

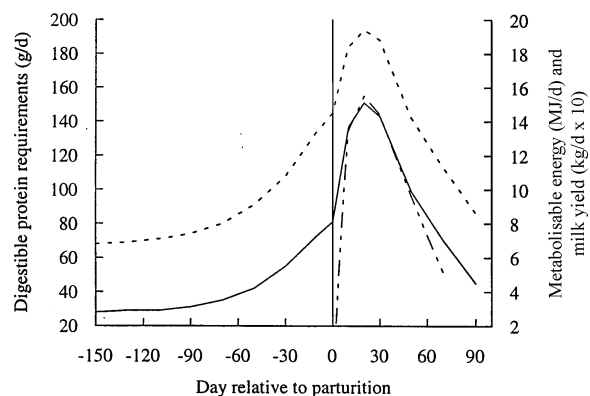
## Changes in protein and energy requirements

The PPR coincides with an increase in the nutritional requirements of the ewe due to the demands of pregnancy and lactation. Metabolisable energy (ME) requirements of a 50 kg single-bearing ewe maintaining maternal live weight and on a diet calculated to provide 11.5 MJ/kg DM increase from 6.8 MJ/d on day 1 of gestation to 13.4 MJ/d (2.0 fold increase) 2 weeks prepartum and then to 19.4 MJ/d (2.9 fold increase) 3 weeks postpartum at peak lactation (*c.* 1.5 kg/d) (Freer *et al.* 1997). Digestible protein (DP) requirements (expressed as truly digestible protein leaving the stomach, Freer *et al.* 1997) increase from 30 to 77 (2.6 fold increase) and then to 161 g/d (5.4 fold increase) over the same period (Freer *et al.* 1997; Figure 2). It is apparent that during the latter stages of pregnancy and

during lactation the requirement for DP increases at a rate greater than that for ME (Figure 2). The DP : ME requirement (g/MJ) rises from about 4.4 for the dry ewe to 5.7 two weeks prior to lambing and to 8.3 three weeks post lambing (Freer *et al.* 1997). The DP : ME requirement during late pregnancy and lactation approaches and then exceeds that able to be provided by rumen fermentation which is variable but has been estimated at *c.* 6.5 (Egan and Walker 1975). A practical means to increase the supply of DP relative to ME is to supplement animals during late pregnancy and lactation with a source of dietary protein resistant to rumen fermentation (Preston and Leng 1987).

Increased requirements for protein and ME in the periparturient ewe are complicated by changes in feed intake. The effect of pregnancy on feed intake is equivocal. Some reports suggest that there is an increase in feed intake up to 12 weeks of gestation and then a decline which is dependent on feed quality and litter size. However, others have observed a large increase in feed intake of pasture during late pregnancy (Weston 1979). In the week prior to parturition a large reduction in feed intake is commonly observed (Weston 1979). Feed intake increases during lactation, reaching a peak 6–7 weeks post lambing, when intake may have increased by up to 60% (Weston 1979).

It is important to note that the lactation-induced increase in feed intake lags behind increases in nutrient requirements associated with the rise in milk yield. In most situations the net effect of the lack of synchrony between intake and nutrient requirements is to exacerbate the increased competition for essential nutrients created by the demands of late pregnancy and lactation. It is with regard to this framework that it appears that PPR, arising from a loss in immunocompetence to nematode parasites, is exacerbated by the combination of an increased requirement for protein relative to ME and increased competition for essential nutrients experienced during late pregnancy and lactation (Donaldson 1997). Consequently, nutritional strategies that can increase the supply of DP may be expected to reduce PPR.



**Figure 2** Calculated requirements (Freer *et al.* 1997) for ME (MJ/d, dashed line) and truly digestible protein (g/d; solid line) during gestation and lactation of a 50 kg ewe maintaining maternal body weight and fed a diet providing 11.5 MJ/kg DM, and calculated milk yield (---).

## Effect of infection on the periparturient ewe

Subclinical infections with gastrointestinal (GI) parasites depress food intake in both the periparturient ewe (Leyva *et al.* 1982) and in the growing lamb (Kimambo *et al.* 1988; Kyriazakis *et al.* 1996). Periparturient ewes infected with *Ostertagia circumcincta* for 6 weeks prior to and after parturition reduced feed intake by 16% during lactation without any effect evident during pregnancy (Leyva *et al.* 1982). The magnitude of the reduction in intake is within the range of feed intake depression (6–30%) that is commonly seen in the growing lamb (Poppi *et al.* 1990).

Infection with GI parasites also causes an increased loss of endogenous proteins into the gut in the form of blood, plasma, mucin and sloughed cells from intestinal epithelium (Kimambo *et al.* 1988; Rowe *et al.* 1988; Poppi *et al.* 1990; Macrae 1993). These contribute differentially to extra protein flow at the ileum which has been calculated, in sheep infected with *T. colubriformis*, to be 20–125 g CP/d depending on the stage of infection (Poppi *et al.* 1986; Kimambo *et al.* 1988).

The efficiency of absorption of peptides and amino acids is, however, little affected by intestinal parasitism (Bown *et al.* 1984; Poppi *et al.* 1986) because absorption of peptides and amino acids can occur distal to that part of the small intestine affected (Bown *et al.* 1984). Nevertheless, because absorption of plasma proteins is not complete (Bown *et al.* 1984) some proteins of endogenous origin pass to the caecum where they will be irreversibly lost. The net result of this process is that proteins and possibly specific amino acids are diverted away from other amino acid-dependent processes such as body weight gain, wool growth and milk production. In addition the energy cost associated with the recycling of proteins lowers the gross efficiency of use of ME for energy deposition (Coop *et al.* 1982).

The comprehensive review by Barger (1982) provides abundant evidence of reduced weight gain and wool production and increased mortality associated with nematode parasite infection of sheep. Further to this, it has been shown that milk production in lactating ewes can be reduced by 17% during *O. circumcincta* infection (Leyva *et al.* 1982) and by 20–40% during *H. contortus* infection (Cobon and O'Sullivan 1992).

Resultant effects of reduced milk production on lamb survival were also substantial in these studies.

## Nutritional enhancement of immunity in the periparturient ewe

The role of nutrition in improving the resistance and production of young sheep to nematode parasites has been linked strongly to increases in the intestinal supply of digestible protein (see reviews by Coop and Holmes 1996 and van Houtert and Sykes 1996) but this response may be sheep breed (Abbott *et al.* 1985) and selection line specific (Armstrong 1995; Kahn, Knox, Gray and Ward unpublished). Reports demonstrating the importance of protein nutrition to resistance and production in the periparturient ewe are less common.

Recently, Donaldson *et al.* (1997) demonstrated that production and resistance to GI parasites in the periparturient ewe are influenced by nutritional factors in much the same way as with the growing lamb. These authors infected single and twin-bearing Coopworth ewes with *T. colubriformis* and *O. circumcincta* for the 7 weeks prior to parturition. Animals were fed diets providing two levels of ME (E1 and E2) which were calculated to promote 0 and 50 g/d gain in maternal body weight during pregnancy and –100 and 0 g/d during lactation. Within each level of ME, fishmeal was added (0 or 8%) to provide two diets calculated to supply differing levels of digestible protein. The two levels of ME and DP produced four diets viz. E1P1, E1P2, E2P1 and E2P2.

ME and DP were effective in stimulating ewe body weight gain over the 9 weeks prior to parturition but ME supply had the greatest effect. In single-bearing ewes, increasing ME intake from 10.7 to 13.2 MJ/d and DP from 94 to 110 g/d resulted in respectively 51 and 13% increases in body weight gain. Increased DP supply reduced FEC from 3 weeks prior to parturition until ewes were euthanased 6 weeks later. ME supply had a transient effect and reduced FEC in the week prior to parturition but at no other time was significant. Worm burdens of ewes, 3 weeks after parturition, fed diets calculated to provide greater amounts of DP were reduced by 87% (12,020 to 1,540) but ME supply had no effect (Table 1). The importance of DP supply, but not ME, for

**Table 1** Mean worm burden of single and twin-bearing ewes 3 weeks postpartum following 7 weeks of mixed species trickle infection.

Diet	Single-bearing			Twin-bearing		
	<i>T.colubriformis</i>	<i>O.circumcincta</i>	Total	<i>T.colubriformis</i>	<i>O.circumcincta</i>	Total
E1P1	172	6743	6915	288	11186	11474
E1P2	1	586	587	7	3390	3397
E2P1	90	9243	9333	3051	13202	16253
E2P2	3	469	472	140	3598	3738

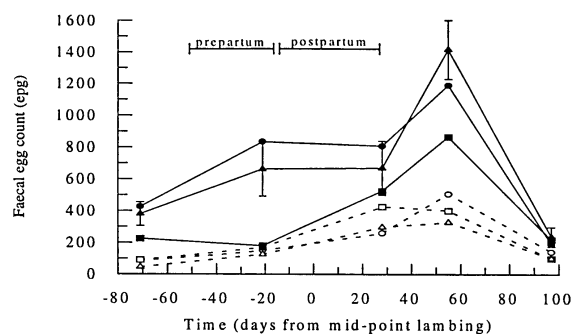
Source: Donaldson *et al.* 1997

determining resistance to GI parasites is consistent with information for the growing lamb (Bown *et al.* 1991).

It is clear from the data reported by Donaldson *et al.* (1997) that resistance to GI parasites in the periparturient ewe is sensitive to DP supply but largely unaffected by ME supply. Which components of resistance were affected by DP supply cannot be determined from the data presented. It is, however, not clear whether nutrition prior to and after parturition have the same effect on resistance, nor the effectiveness of nutritional supplementation in field situations.

To test the question of the temporal importance of protein nutrition on resistance to GI parasites we subjected 120 periparturient Merino ewes to one of three supplementation strategies viz. zero supplement, 250 g/ewe/d cottonseed meal (CSM) pellets (92% DM and 396 g CP/kg DM) fed for the 5 weeks prior to the start of parturition and 250 g/ewe/d CSM pellets fed for 6 weeks after the start of parturition. Animals were artificially infected with 9000 L<sub>3</sub> *T. colubriformis* and 3000 L<sub>3</sub> *H. contortus* prior to the trial. Larval differentiation from cultures indicated that the predominant nematode parasite throughout the trial was *T. colubriformis*. The ewes were derived from a flock that differed in its resistance to *H. contortus* (Woolaston *et al.* 1990) and were sampled from lines that have been selected for either increased resistance to *H. contortus* (R) (n = 60) or at random (C) (n = 60). Ewes from the two lines grazed in separate plots with each plot containing 5 ewes and there were 24 plots in total. Ewes were set stocked so that progeny would be exposed to larval numbers on pasture that reflected any supplement-induced differences in ewe FEC. Lambing commenced on 27 August 1998 and concluded 30 d later.

Rainfall exceeded the district long-term mean during the trial and green and total herbage mass reflected this. Mean green and total herbage mass at weeks -7, 1 and 11 (weeks relative to midpoint lambing) was 1200 kg green and 2250 kg total, 1560 kg green and



**Figure 3** Faecal egg counts (epg) (arithmetic mean  $\pm$  pooled SE) of R (open symbols and dashed lines) and C (filled symbols and solid line) Merino ewes fed either nil supplement (circle) or 250 g cottonseed meal per head daily prior to (squares) or after (triangles) the start of parturition; bars indicate periods of supplementation.

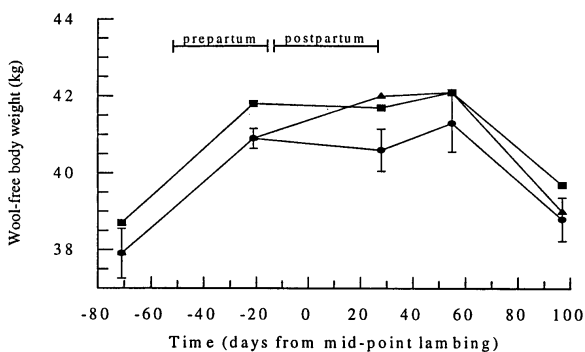
2150 kg total and 3190 kg green and 4350 kg total DM/ha respectively. These values for herbage mass result in predictions of positive maternal body weight gain throughout the trial (Freer *et al.* 1997) and suggest that a diet of pasture alone was unlikely to have caused a major limitation to animal production. Nevertheless, supplementation reduced FEC<sup>0.5</sup> with the effect reaching statistical significance ( $P = 0.05$ ) for prepartum-fed ewes 3 weeks prior to parturition (Figure 3). There appeared to be no residual effect of prepartum supplementation on FEC<sup>0.5</sup> so that at all other sampling times supplementation prior to parturition had no effect on FEC<sup>0.5</sup>. Postpartum protein supplementation had no effect on FEC<sup>0.5</sup> of both C and R ewes.

Body weight 3 weeks prior to parturition, adjusted for initial weight and weight of fleece, was increased by prepartum supplementation ( $P = 0.03$ ). There was also a suggestion ( $P = 0.08$ ) from the contrast of supplemented versus not supplemented that adjusted body weight, 4 weeks postpartum, was greatest in supplemented ewes (Figure 4).

### Genetic differences in resistance in the periparturient ewe

Resistance to infection from nematode parasites differs between sheep breeds (Courtney *et al.* 1984; Abbott *et al.* 1985; Baker 1995) and variation in resistance within flocks of the same breed can account for 85% of the total genetic variation in FEC (Woolaston and Eady 1995). Resistance to nematode parasites, as measured by FEC, is heritable with estimates from a number of studies suggesting a mean value of 0.25–0.30 (Woolaston and Eady 1995). Because FEC is a heritable trait it is possible to increase resistance to nematode parasites through selective breeding.

A number of experimental flocks that differ in their genetic capacity to resist infection from nematode



**Figure 4** Body weight (mean  $\pm$  pooled SE; adjusted for initial weight and weight of fleece) of Merino ewes fed either nil supplement (circle) or 250 g cottonseed meal per head daily prior to (squares) or after (triangles) the start of parturition; bars indicate periods of supplementation.

parasites have been established and these have been reviewed by Morris *et al.* (1995) and Woolaston and Eady (1995). Within Australian experimental flocks, selection has generally been conducted on the basis of FEC following post-weaning challenge with a single nematode species, but there are flocks where selection has followed natural mixed infection (Cummins *et al.* 1991). In New Zealand, selection has generally been conducted on the basis of FEC following post-weaning natural challenge. Using this protocol, lines selected for resistance to *H. contortus* (Albers *et al.* 1987; Woolaston *et al.* 1990), *T. colubriformis* (Windon *et al.* 1987) and mixed nematode genera (see review of Morris *et al.* 1995) have been established. Selection for or against FEC is well correlated with worm burden with resistant animals having a lower establishment rate by infective larvae and lower fecundity of established adult female nematodes (Bisset *et al.* 1991; Woolaston and Eady 1995).

Donald *et al.* (1982) investigated differences between sheep breeds in resistance to nematode parasites during the periparturient period. These authors reported that Border Leicester x Merino ewes were more resistant to *Ostertagia* infection than Merino ewes as measured by FEC and worm burdens. Selection within breed, on the basis of post weaning FEC when animals are 4–5 months of age, is successful at reducing FEC throughout the life of the animal (Gray 1991; Woolaston 1992) and selection line differences in FEC become apparent at 9–12 weeks of age (Ward *et al.* 1999). Woolaston (1992) reported that, when compared to control sheep, pre- and post-partum Merino sheep selected for increased resistance to *H. contortus* at 4–6 months of age had lower FEC and a less pronounced PPR. Although FEC of both lines increased throughout the trial, FEC of resistant animals was generally only 50% that of control animals indicating that relative differences between the lines were independent of physiological state.

The present work has reinforced these findings. Ewes from both the R and C lines exhibited a PPR that commenced prior to parturition and reached a peak some 8 weeks postpartum. Throughout gestation and lactation, FEC<sup>0.5</sup> of R ewes was significantly less (generally  $P < 0.01$ ) than that of C ewes (Figure 3). In the same experiment, FEC<sup>0.5</sup> three weeks prior to parturition was reduced in C but not in R ewes, although this difference was not statistically significant ( $P = 0.15$ ). Nevertheless, prepartum supplementation resulted in FEC<sup>0.5</sup> of C ewes approximating that of R ewes 3 weeks prior to parturition. It is possible therefore that protein supplementation prior to parturition, during periods of abundant availability of green herbage, is not effective in increasing resistance of ewes which are already expressing high levels of resistance (Figure 3).

## Conclusion

Requirements for ME and DP begin to increase around the time of parturition and rise sharply with increasing milk yield. Increases in the requirement for DP outstrip that for ME and accordingly the requirement for DP relative to ME is increased. We suggest that the increased competition for essential nutrients associated with gestation and lactation exacerbate the PPR. Donaldson *et al.* (1997) have demonstrated that increasing the supply of DP to the periparturient ewe improves production and resistance to nematode infection. Our research suggests that, in a year of abundant green herbage, prepartum protein supplementation reduces FEC of grazing ewes, during the period of feeding but that there are no residual benefits. Postpartum protein supplementation is ineffective in reducing FEC. ME appears to be ineffective in modulating resistance but, in the periparturient ewe, is most effective in promoting body weight gain.

Breeding for resistance to nematode parasites, by selection on the basis of FEC at 4–5 months of age, is effective in reducing both FEC and the magnitude of the PPR in the periparturient ewe. Interestingly, FEC of periparturient resistant ewes appears to be unaffected by protein supplementation but this may be associated with the availability of green herbage. Nevertheless, it is possible that selective breeding for disease resistance has altered the relationship commonly seen between protein supply and resistance.

Both nutritional supplementation and breeding offer opportunities to increase the resistance of ewes around the time of lambing with the benefits of reducing contamination and exposure of lambs to infection, and a possible increase in the productivity of ewes and lambs. These approaches may be independent but may also interact in important and interesting ways. At a practical level the complementary use of resistant genotypes and strategically targeted nutritional supplements offer two additional strategies for the sustainable control of nematode parasites in sheep. Further research investigating these strategies is currently in progress.

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