

Enhancing life-long resistance to nematode parasites: possibilities from nutritional supplementation of recently weaned sheep

L.P. Kahn¹, M.R. Knox², S.W. Walkden–Brown¹ and J.M. Lea¹

¹ Animal Science, University of New England, Armidale NSW 2351

² CSIRO Livestock Industries, Pastoral Research Laboratory, Armidale NSW 2350

lkahn2@metz.une.edu.au

Summary

Susceptibility to infection from gastrointestinal nematode parasites in sheep is most pronounced in young animals which remain susceptible to infection well into the second year of life. The reasons for this prolonged susceptibility to nematode infection are poorly understood but may be a consequence of a number of factors such as immunological incompetence, insufficient antigenic stimulation, interrupted infection and inadequate nutrient supply. The net result of the prolonged susceptibility is greater reliance on anthelmintic control which has led to widespread anthelmintic resistance.

There are two broad strategies that can enhance resistance to nematode infection, namely manipulation of the environment or selective breeding, the latter taking 10–15 years before substantial benefits are realised. Environmental manipulations discussed in this review include nutritional supplementation and the use of forages containing condensed tannins. To be cost effective, and to have continuing effects on the epidemiology of infection, it would be useful if these parasite control options had beneficial effects that persisted beyond the period of treatment.

Evidence is presented that pastures that include the temperate legume *Lotus pedunculatus* which contains condensed tannins (CT) do not enhance resistance or resilience of weaner Merino sheep to nematode infection. In contrast, results from the same experiment indicated that when sheep grazed pastures that included *Trifolium repens*, their growth was unaffected by infection with *Trichostrongylus colubriformis*. Generalising from these results should be avoided because beneficial effects on resistance to infection from other sources of CT, including the legume *Hedysarum coronarium* (Sulla) and a semi-purified CT product, have been reported. There is also evidence that supplementation to increase the supply of digestible protein, and in some circumstances digestible energy, will enhance resistance and resilience to nematode infection during the primary infection period. This strategy is beginning to be used by graziers to assist with parasite management of the periparturient ewe.

Long-term positive effects on resistance and resilience to infection, beyond the period of supplementation, have been observed, but only on occasion, and possible reasons for this variability are discussed.

Keywords: sheep, nematodes, nutrition, resistance, resilience, immunity, long-term

Introduction

The terms resistance, immunity and resilience are commonly used to describe the response of a host to infection. These terms have been subjects of confusion, and the definitions given here are similar to those provided by Gray (1995). Resistance to infection is the ability of the animal to reduce the number of GI parasites that establish, reproduce and survive. The resistance is generally mediated by enhanced immune response, but in its broadest sense resistance may not be the result of immunological changes. Resilience is defined as the extent to which an infected animal is able to maintain production.

The failure of young sheep to develop immunity to gastrointestinal (GI) nematode parasites until well into the second year of life represents the major animal health challenge to the sheep grazing industry. The cost of GI parasites to the Australian industry has been estimated at \$220 million per annum (McLeod 1995) and this is likely to increase with the further development of resistance by parasites to anthelmintics. A number of explanations have been advanced for the slow development of immunity to GI parasites in young sheep including (i) immunological incompetence resulting in an inability of young sheep to develop effective acquired immune responses (Smith and Angus 1980); (ii) insufficient antigenic stimulation resulting from rates of natural infection being insufficient to initiate an effective immune response (Windle *et al.* 1984); (iii) interrupted infections due to anthelmintic treatment which delays or diminishes previously acquired immunity (Barger 1988); and (iv) inadequate supply of

digestible protein resulting in an inability to supply the metabolic precursors required by the immune system during parasitic infection (van Houtert *et al.* 1995).

The net effect of the failure of young Merino sheep to develop immunity is a greater reliance on anthelmintics which has hastened the natural selection of nematodes resistant to anthelmintics. In NSW, 90% of properties have GI parasites that are resistant to benzimidazole drenches, 80% to levamisole drenches and 60% to combinations of benzimidazole and levamisole (Love and Biddle 2000). In addition, 50% of properties in northern NSW have *Haemonchus contortus* resistant to closantel, and resistance to the macrocyclic lactones is also now apparent and spreading. This situation applies to other States (Rolfe 1997) and countries (Waller 1997).

The challenge to animal health researchers is to hasten and enhance the development of immunity by young sheep in a cost effective manner. Imposing the constraint of cost effectiveness requires measures that are either inexpensive or have beneficial effects over the long-term, well beyond the period during which the measure is applied. For example, Datta *et al.* (1999) demonstrated that beneficial effects on resistance, from a 9 week period of increased nutrient supply, were maintained over the next 16 months. There are a number of options available to enhance resistance which can be broadly grouped as either manipulation of the environment or selective breeding for increased resistance. Selective breeding is a powerful tool to increase resistance but the benefits of selection are not realised until many years after implementation of a program (Eady *et al.* 1997). In the interim period other strategies are required.

In this review we discuss long-term enhancement of resistance to GI parasites in young Merino sheep through environmental manipulations, such as nutritional supplementation or use of forage species containing condensed tannins.

Effects of nematode infection on young sheep

Subclinical infections with GI parasites depress food intake (Kimambo *et al.* 1988); the magnitude of the depression that is commonly seen in the growing lamb is in the range of 6–30% (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). These contribute to extra protein flow through the small intestine 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). However, because the efficiency of absorption of peptides and amino acids is little affected by intestinal parasitism (Bown *et al.* 1984; Poppi *et al.*

1986) the majority of the increase in the endogenous loss of these substances is reabsorbed, reducing losses of protein beyond the terminal ileum to 10–30 g CP/d (Poppi *et al.* 1986; Kimambo *et al.* 1988).

Nevertheless, the increased loss of protein into the gut is likely to be costly to the animal because absorption of endogenous proteins is not complete (Bown *et al.* 1984) and recycling of peptides provides an opportunity for catabolism of amino acids with associated energy requirements for peptide resynthesis. However, MacRae *et al.* (1982) found, by calorimetry, that the efficiency of use of metabolizable energy (ME) was not affected by *T. colubriformis* infection. The lack of effect of infection on energy metabolism despite a large increase in protein cycling through the gut suggests that protein synthesis in other pools within the body is reduced accordingly. In confirmation of this, Yu *et al.* (2000) and Bermingham *et al.* (2000) used isotope tracer kinetics to demonstrate that whole-body protein synthesis is unaffected by infection with *T. colubriformis*. However, Yu *et al.* (2000) demonstrated that infection with *T. colubriformis* increases leucine sequestration and oxidation in the gut by approximately 30% during weeks 5–13 of infection, and that increased usage by the gut is accompanied by a proportional reduction in the availability of amino acids for other tissues, such as skeletal muscle. This supports earlier observations (Symons and Jones 1975) that *T. colubriformis* infection reduces rates of protein synthesis in muscle and wool follicles. In a practical context, these results account for the observed effects of subclinical infections on animal production; the magnitude of the reduction in liveweight gain and wool growth varies with a number of factors, but may range from 5–30%.

Prolonged time to develop immunity

There is ample evidence from experiments with penned sheep that immunity to *T. colubriformis* (Barnes and Dobson 1993) and *H. contortus* (Coyne and Smith 1992) can be acquired by young sheep and, once acquired, can persist for weeks (*H. contortus*) to months (*T. colubriformis*) in the absence of further infection. However, development of immunity in young grazing sheep appears to be more problematic and responses to vaccination, with live irradiated (Bain 1999) or normal larvae (Kahn *et al.* unpublished), have been ineffective. In general, poor responses to vaccination have been interpreted as being a symptom of immunological incompetence of young sheep. However, Emery *et al.* (1999) have recently demonstrated that neonatal lambs are able to develop immunity to *T. colubriformis* indicating the possibility that it is the neonate, rather than the weaner, which will be more receptive to vaccination. Nevertheless, susceptibility of young grazing sheep to GI parasites remains an industry

problem and differences in the effectiveness of vaccination procedures between pen and field experiments have yet to be adequately explained. The immunological unresponsiveness of young Merino sheep to helminth infection represents a major constraint to animal production, and in the remainder of this review strategies to overcome this constraint are discussed.

Options to enhance the resistance and resilience of young sheep to internal parasites

Nutrition

It is clear from the previous discussion that infection with GI parasites diverts amino acids away from economically important functions (e.g. growth) towards survival functions associated with removal of GI parasites. It is therefore not surprising that increasing the supply of digestible protein has been demonstrated to be one of the most effective environmental means of improving growth (i.e. resilience) and hastening the development of immunity to GI parasites. Two important experiments to support this statement are discussed briefly. Bown *et al.* (1991) identified that it was the supply of digestible protein, not energy, which benefited resistance to nematode parasites. Those authors infused isoenergetic amounts of either sodium caseinate (61 g/d) or glucose (79 g/d) into the abomasum of Dorset Down x Coopworth lambs infected with *T. colubriformis*. At 6 weeks post infection there was no effect of infusate on worm burden but at 12 weeks post infection, animals receiving the infusion of protein had significantly reduced worm burdens. Increased energy supply had no effect on development of resistance. Infection reduced nitrogen (N) retention in the carcass by about 70%, but casein infusion elevated N retention to a level similar to that in uninfected control animals. Infusion of glucose also increased N retention but values were still 40% lower than for control animals.

van Houtert *et al.* (1995) reported that in Merino weaners infected with *T. colubriformis* and fed a roughage diet supplemented with either 0, 50 or 100 g/d fish meal, to increase digestible protein supply, worm burdens were unaffected by supplementation until after 10 weeks post infection. Resistance then developed most rapidly, with significant differences by 15 weeks post infection, in animals fed the largest amounts of fishmeal and most slowly for those fed none. Over the course of 20 weeks, infection reduced weight gain in unsupplemented animals by 40 g/d (60%) but supplementation at 100 g/d reduced the effect of infection to 11 g/d (11% reduction), which was not statistically different from the performance of uninfected control animals.

More recently, Kahn *et al.* (2000a) re-examined the role of energy and digestible protein (DP) in the development and expression of resistance using strategically formulated diets rather than abomasal

infusions. The basis for the re-examination of the role of energy was the recognition that while abomasal infusions of glucose increase energy supply they do not increase production rates of volatile fatty acids (VFA) which are normally associated with increased energy intake. As a consequence, abomasal infusions of glucose may not be an appropriate model to explore effects of energy supply on resistance to infection. It is possible that changes in VFA concentrations in digesta flowing from the rumen may stimulate particular effectors of immune response in the gut which are associated with increased resistance in ruminants. In support of this, Rydzynski and Dalen (1994) reported that, in mice butyrate is associated with mast cell maturation and increased histamine content which upon release translates into increased epithelial permeability. Increased permeability of gut epithelium is known to be involved in rejection responses in sheep (Steel *et al.* 1990) which is the primary mechanism for removal of established nematode parasites (Dobson *et al.* 1990).

In contrast to the findings of Bown *et al.* (1991) higher rates of digestible energy (DE) lowered burdens of *T. colubriformis* at 10 weeks post infection while the supply of DP was ineffective (Figure 1). That DP did not enhance resistance at 10 weeks post infection is consistent with a range of studies (Bown *et al.* 1991; van Houtert *et al.* 1995; Kahn *et al.* 2000b) and arises from too brief a period of differential feeding. The beneficial effects of DE on resistance to GI parasites, as opposed to the findings of Bown *et al.* (1991), suggest that changes to energy metabolism driven through changes in the production rates of VFA rather than through changes in glucose entry rates may be of greater relevance for the study of infected animals. In addition to effects on resistance, Kahn *et al.* (2000a) reported that weight gain was more responsive to DE than DP supply. Increasing DE supply by 20% resulted in a 133% increase in carcass gain while an increase of 60% in

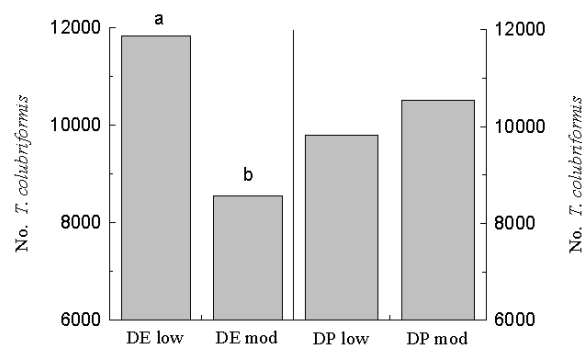


Figure 1 Mean numbers of *Trichostrongylus colubriformis* recovered from Merino weaners trickle infected with *T. colubriformis* and fed diets to provide for either a low or moderate digestible energy intake and a low or moderate digestible protein supply. a, b: difference significant ($P < 0.05$)
Note backtransformed means are presented

DP supply led to a 93% increase in carcass gain. The similarity between the findings of Bown *et al.* (1991) and Kahn *et al.* (2000a) is that in each situation the dietary conditions that most enhanced immune response were also most effective in increasing growth. These results, and others (e.g. Kahn *et al.* 2000b) where increased DP supply did not lead to a greater resistance to *T. colubriformis* infection, suggest that with young growing sheep more emphasis should be given to improved nutrition in general rather than to particular components of the diet.

Recent research has indicated that provision of non-protein nitrogen, to stimulate feed intake and increase rumen outflow of microbial protein, can also enhance the ability of infected hosts to overcome the detrimental effects of GI parasitism. In studies with young Merino sheep in pens, Knox and Steel (1999) showed that supplementation with urea of a low quality roughage diet, comprising oaten chaff plus essential minerals, reduced the detrimental effects of mixed species infection of *T. colubriformis* and *H. contortus* by reducing faecal egg output and *T. colubriformis* burden, and by increasing weight gain and wool production (Table 1). Further studies (M.R. Knox and J.W. Steel, unpublished), using a urea-molasses block supplement with a similar basal diet, indicated that production responses to supplementation in parasitised young Merino sheep arise mostly through stimulation of feed intake (Table 2). In both these studies, supplemented animals carrying mixed species infections

of GI nematode parasites showed similar or greater weight gains and wool production than their respective unsupplemented uninfected control groups. Such supplements can therefore assist sheep to overcome the detrimental effects of GI parasite infection. This response is attributed to a greater intake of the basal diet, presumably due to increased digestibility arising from enhanced rumen $\text{NH}_3\text{-N}$ levels, and the effect on microbial fermentation of available carbohydrate which results in increased post-ruminal microbial protein availability.

Condensed tannins

Condensed tannins (CT) are a component of the polyphenols present in plants and are found at greatest concentration in dicotyledons such as leguminous plants. Recently, interest in the role of pasture legumes containing CT to improve resistance to GI parasites has been investigated. Condensed tannins can affect the resistance and resilience of animals to GI nematode infections via direct or indirect mechanisms: direct effects may be mediated through tannin-nematode interactions which reduce nematode viability; indirect effects may be mediated by changes in the supply of DP, changes in amino acid supply, particularly that of threonine and methionine/cystine, changes in mineral absorption, and interactions with intestinal mucosal epithelia.

Table 1 Mean liveweight and wool production over 18 weeks of Merino weaner sheep fed *ad libitum* a basal oaten chaff diet supplemented with 0 or 3% urea and either infected or not infected with gastrointestinal nematode parasites.

Dietary treatment	Parasite treatment	Liveweight gain (g/day)	Wool production (g/day)
No urea	Nil	30 ^a	4.2 ^a
No urea	Mixed ¹	22 ^b	3.8 ^b
3% urea	Nil	50 ^c	5.3 ^c
3% urea	Mixed	39 ^d	5.3 ^c

¹ 200 *H. contortus* L₃ and 1000 *T. colubriformis* L₃ thrice weekly

Means within columns with different superscripts differ significantly ($P < 0.05$)

Table 2 Mean liveweight and wool production over 20 weeks of Merino weaner sheep fed a basal oaten chaff diet with or without access to a urea-molasses block and either infected or not infected with gastrointestinal nematode parasites.

Group	Chaff	Block	Parasite	Liveweight gain (g/day)	Wool production (g/day)
1	<i>ad libitum</i>	No	Nil	69 ^a	6.4 ^a
2	pair fed to 1	Yes	Nil	69 ^a	6.4 ^a
3	<i>ad libitum</i>	Yes	Nil	90 ^b	8.6 ^b
4	<i>ad libitum</i>	No	Mixed ¹	41 ^c	6.2 ^a
5	pair fed to 4	Yes	Mixed	39 ^c	6.0 ^a
6	<i>ad libitum</i>	Yes	Mixed	59 ^d	7.5 ^c

¹ 200 *H. contortus* L₃ and 1000 *T. colubriformis* L₃ thrice weekly

Means within columns with different superscripts differ significantly ($P < 0.05$)

There are only a limited number of CT-forages available for use in grazing systems. Of these, members of the *Lotus* genera are amongst the most promising. A recent review of the potential for CT forages to enhance resistance to GI parasites (Kahn and Diaz-Hernandez 1999) highlighted a lack of convincing information to support the notion that the CT-containing legumes *Lotus pedunculatus* and *L. corniculatus* would enhance resistance to GI parasites. In support of this conclusion are the results of a recent experiment (Kahn *et al.* 2001) with young Merino sheep that grazed grass-based pastures with either *Trifolium repens* (white clover, non-CT; c. 50% of green herbage mass) or *L. pedunculatus* cv. Maku (5.8% CT; c. 25% of green herbage mass). Animals were given a single dose of 15,000 *T. colubriformis* L₃, and faecal egg count (FEC) was measured for 10 weeks post infection (Figure 2). The FEC at 10 weeks post infection was 67% greater for animals grazed on plots with *L. pedunculatus* but differences failed to reach statistical significance; the number of *T. colubriformis* in their small intestine was, however, significantly greater ($P < 0.05$).

More promising effects on resistance have been recorded for *Hedysarum coronarium* (Sulla), a legume containing CT, Neizen *et al.* (1995) reporting a large reduction in establishment of *T. colubriformis* in sheep grazing Sulla but not those grazing *Medicago sativa* (lucerne). Such effects appear to be unrelated to DP supply which has been demonstrated to be ineffective in reducing establishment rates of infective *T. colubriformis* larvae (van Houtert *et al.* 1995).

The role of semi-purified CT products such as Quebracho tannin has also been examined. Quebracho is a commercial product extracted from several species of a South American evergreen tree and is a mixture of phenolic compounds. Butter *et al.* (2000) demonstrated that the addition of Quebracho (5% of feed dry matter) to diets low in digestible protein reduced FEC by 55% in animals trickle infected with *T. colubriformis*, but had no effect in animals fed diets high in digestible

protein. These results suggest that the beneficial effects of Quebracho were indirect and were mediated through increases in DP supply and were then most effective with animals on low protein diets. In contrast to this interpretation, Athanasiadou *et al.* (2000) studied the effects of inclusion of Quebracho at 3 and 6% of intake on lambs receiving a trickle infection with *T. colubriformis* for 11 weeks and fed a high quality diet supplying 12.6 MJ ME and 109 g DP per kg dry matter. Faecal egg counts and worm burdens were significantly lower in those lambs fed the Quebracho and the authors suggested that this was evidence of a direct anthelmintic effect acting on rates of larval establishment. The mechanisms responsible for such direct effects remain to be elucidated.

Long-term effects of nutritional supplementation on resistance and production

The evidence presented so far indicates that there are environmental factors that can be managed to enhance resistance to GI parasites but, in general, published experiments have examined effects during a single infection cycle covering the period during which treatments have been applied. Long-term benefits of these treatments (i.e. for months or years beyond the period of treatment) were discussed by Nolan (1999) but otherwise have received little attention and are extremely important to the cost effectiveness of potential treatments.

Datta *et al.* (1999) first suggested that nutritional enhancement of resistance may be retained for long periods after supplementation had ceased. Datta *et al.* (1998) fed crossbred sheep (Warridale breed: 50% Merino, 25% Border Leicester, 25% Dorset Horn; 8–9 months of age) that were trickle infected with *H. contortus*, isoenergetic (9 MJ ME/kg DM) diets with 10, 13, 16, 19 or 22% CP for 9 weeks. Crude protein content was adjusted by a reduction in barley and an increase in cottonseed meal and urea. Diets were fed *ad libitum* resulting in differences in both ME intake (c. 15% difference between 19 and 10% CP diets) and DP supply (c. 112% difference between 19 and 10% CP diets). With higher CP, feed intakes were increased, and there were significant decreases in FEC (Figure 3).

After the initial 9 week experimental period, animals were drenched to remove resident infections and grazed as a single flock. Faecal egg count and measures of productivity were recorded periodically over a 16 month period. Remarkably, the ranking of FEC observed during the initial 9 week period remained the same over the course of the experiment. Sheep fed the higher CP diets had lower FEC than those previously given the lower CP (Figure 3). In addition the weight advantage (c. 8.5 kg) generated during the period of feeding was largely (82%) maintained over the next 16 months.

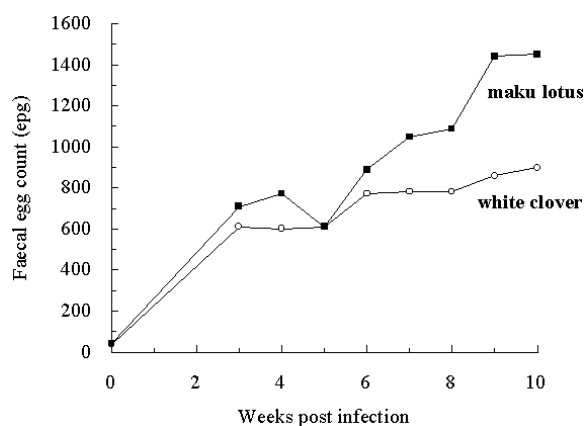


Figure 2 Mean faecal egg counts of Merino weaners after a single artificial infection with 15000 L₃ *Trichostrongylus colubriformis* and grazing pastures with either white clover (*Trifolium repens*) or *Lotus pedunculatus*, cv. Maku. Note backtransformed means are presented.

Given the importance of enhancing resistance to GI parasites over the long-term we have completed a number of related experiments which have investigated the residual value of nutritional supplementation to resistance and production and present here some preliminary findings. As part of a larger investigation, 26 Merino wether weaners (7 months of age) were exposed to natural infection from pasture; they were given individually three times each week for 7 weeks either no supplement or 140 g/d cottonseed meal pellets (90% DM; 30% CP; 20 MJ GE/kg DM; c. 50% rumen undegradable protein), and FEC was monitored weekly from week 2. Following this period, 6 animals from each group were challenged with 24,000 *T. colubriformis* L₃; FEC were determined at 3 and 4 weeks post challenge, after which animals were slaughtered to determine worm burdens. The remaining animals (7 per group), which had not received challenge infection, were drenched at the end of the supplementation period and then grazed as part of a larger flock (n = 35); FEC were determined at approximately 6 weekly intervals for the following 34 weeks. This experiment is still in progress.

Supplementation increased daily weight gain (mean $\pm$ SE) from 64 ± 9.0 to 101 ± 9.0 g/d during the 7 week period of feeding, and it reduced average FEC^{0.33} significantly ($P < 0.05$) during the 7 week experimental period prior to challenge (Figure 4). Faecal egg count following challenge was unaffected by previous supplementation; worm burden was reduced by 30% but differences were not statistically significant. Daily weight gain for the 41 week period after the start of supplementation was unaffected by the 7 weeks of feeding, 47 ± 3.1 vs. 41 ± 3.1 g/d for supplemented animals. This indicates that the initial benefit of supplementation, in terms of liveweight (1.8 kg), was lost over the 34 week period after feeding ceased, and FEC^{0.33} during that period was unaffected by that treatment (Figure 5). That supplementation did not

subsequently result in heavier weights for a considerable period is at odds with other results from our laboratory (Kahn *et al.* unpublished) and the results of Datta *et al.* (1999), perhaps because of differences between the experiments in the basal planes of nutrition at the time of supplementation. Where significant residual benefits to liveweight resulting from a short period of supplementation have been recorded the unsupplemented animals had either been losing weight or growing slowly (<30 g/d) and, as a consequence, the initial increase in liveweight resulting from supplementation was 2–3 times greater than was observed in the experiment described above.

Whereas the studies described above have used castrate male animals it is perhaps with female animals where long-term effects on resistance and production will be most valuable in Australian production systems. Kaidong Deng *et al.* (2001) are investigating the response in terms of resistance and resilience of young Merino ewes fed cottonseed meal pellets at rates of 170 or 85 g/hd/day for 10 weeks immediately after weaning. Over the 10 weeks of feeding, supplementation lowered FEC^{0.33} ($P < 0.01$) when compared to unsupplemented controls and this effect continued up to 8 weeks after supplementation ceased ($P < 0.05$) while the ewes remained in their respective experimental pasture plots. After anthelmintic treatment, at week 18, the ewes were then grazed together as one flock; FEC^{0.33} at 29, 42 and 52 weeks showed no carry-over effect of supplementation. As expected, supplementation increased liveweight gain (mean $\pm$ SE) during the feeding period (6.8 ± 0.4 , 5.9 ± 0.05 and 4.8 ± 0.4 kg for 170 g/d, 85 g/d and nil supplement, respectively) and this difference was still apparent, but to a reduced extent, 19 weeks after supplementation ceased (i.e. at week 29); the effect was not significant at 42 and 52 weeks. Fleece weight at week 31 was also increased by supplementation ($2.31 \pm .04$, 2.19 ± 0.04 and 2.12 ± 0.04 kg for 170 g/d, 85 g/d and nil supplement,

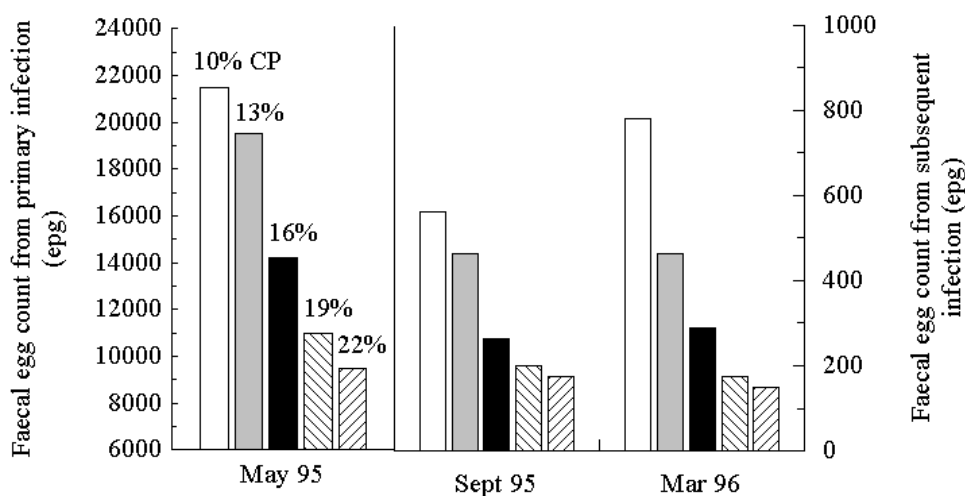


Figure 3 Faecal egg counts of Warridale weaner sheep when trickle infected with *Haemonchus contortus* and fed diets differing in crude protein content for 9 weeks until May 1995, and the counts 4 and 6 months after those treatments. Adapted from Datta *et al.* (1998, 1999).

respectively). This experiment is still in progress and the reproductive performances of these ewes during their first mating and lambing are yet to be assessed.

Conclusions

The slow development of immunity by young Merino sheep to infection from GI parasites results in animals remaining susceptible to infection until at least their second year of life. This susceptibility is a major constraint to animal production and increases reliance on anthelmintics which has led to widespread anthelmintic resistance. Nutritional supplementation will hasten the acquisition of resistance and prevent production losses due to infections but the level of success is dependent upon basal nutrient supply. With Merino sheep, the short term success (during the treatment period) and the subsequent long term success (after the treatment period and during subsequent natural infection) of supplementation appears to be predictable from the level of production of unsupplemented animals. When weight gain of unsupplemented animals is low, say <20–30 g/d, or animals are experiencing weight loss, we would predict that the effect of supplementation on resistance and resilience to infection will be apparent during the short (van Houtert *et al.* 1995; Datta *et al.* 1998) and long term (Datta *et al.* 1999); when weight gain of unsupplemented animals is moderate, say 40–60 g/d, both short and long term effects of supplementation on resistance to infection are likely to be small or non-existent (Kahn *et al.* 2000b). Effects on resilience to infection due to supplementation are likely to be apparent in the short term but may be lost over the long term.

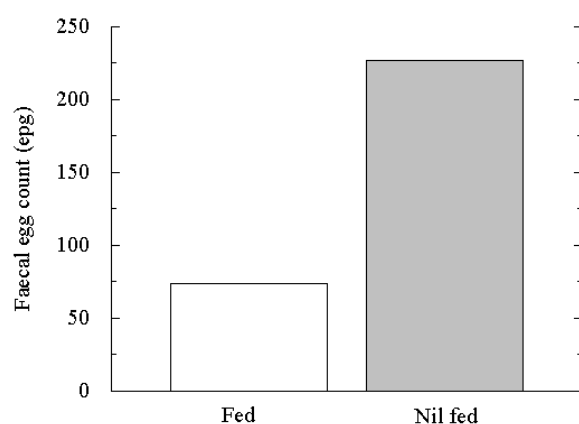


Figure 4 Mean values over weeks 3–7 for faecal egg counts of Merino weaners naturally infected and either unsupplemented or given 140 g/d cottonseed meal pellets. Note backtransformed means are presented.

This framework provides a guide for when supplementation is likely to be most effective in terms of the physiology of resistance and resilience, and in cost effectiveness. The magnitude of the initial nutritional stimulus on resistance and resilience is critical because effects will decay over time. Where supplementation is able to enhance resistance to infection and increase production over the long term, it will prove to be a cost effective parasite control option. In addition, and importantly, under such a scenario supplementation has the potential to reduce dependency on control by anthelmintics and lessen the rate of development of anthelmintic resistance.

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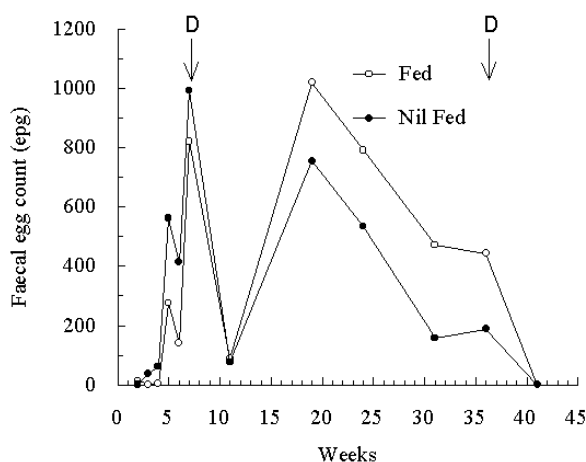


Figure 5 Mean faecal egg counts of Merino weaners naturally infected and either unsupplemented or given 140 g/d cottonseed meal pellets during weeks 0–7, and then grazed as a single unsupplemented flock for the next 34 weeks. D represents times of anthelmintic treatment. Note backtransformed means are presented.

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