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The effect of endoparasitism on host nutrition - the implications for nutrient manipulation

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ABSTRACT

The role of endoparasitism on host nutrition was reviewed and the opportunities for manipulation considered with emphasis on two specific nutrients for which information is becoming available-protein and copper.

The major effect of parasitism on protein metabolism is to increase the protein requirement of the host as a result of increased endogenous loss of protein rather than malabsorption per se. Protein supplementation has been shown to increase liveweight gain of infected sheep and to reduce faecal egg counts and worm burdens probably reflecting enhanced immunological competence of the host. Such rates of protein supply could be achieved in practice on temperate pastures if protein losses across the rumen could be reduced.

Liver copper levels have been shown to be depressed by parasitism in the abomasum. The effectiveness of oral copper supplements depends on their ability to increase soluble copper levels in abomasal digesta, which is reduced by nematode-induced increase in pH. Intake depression has by far the greatest effect on production loss due to endoparasitism. Evidence is emerging that the mechanism for this depression has a peripheral hormonal and central neural basis.

It was concluded that specific nutrient manipulation in plants or via supplements may enable the host to cope better with the debilitating effects of endoparasitism.

Keywords Parasites, nutrition, animal production, manipulation, specific nutrients, protein, copper, intake.

INTRODUCTION

The interaction of general level of nutrition and the ability of the animal to cope with internal parasites has long been recognized (Gibson, 1963; Dobson and Bawden, 1974; Lunn *et al.*, 1988). Some general rules have emerged indicating that better nutrition, usually defined in terms of feed digestibility or protein content of food, enables the host to cope better with the debilitating effects of parasitism. Undernutrition markedly interferes with the immunoreactivity of the host to various infections and the ability to mount effective challenges to infection can be enhanced by specific nutrient manipulation (Wan *et al.*, 1989).

In this review the quantitative significance of internal parasites on host nutrition will be assessed as will the opportunity and consequences of nutrient manipulation. Attention is directed largely to sheep and to subclinical infection for it is doubtful that nutrition other than severe undernutrition has a dominating role in the immediate removal of infestation required in clinical infection. Three specific questions need to be

answered. Can manipulation of nutrient supply alleviate the effect of the parasite on liveweight gain, contribute to immunological development of the host and influence epidemiology of parasite populations at pasture?

GENERAL EFFECTS

Subclinical infections of lambs have resulted in 40% depression in liveweight gain, 6-30% depression in food intake and little depression in feed digestibility. Wool production has been depressed up to 40% and milk production in ewes by up to 15% (Steel and Symons, 1982; Sykes, 1982). These effects to some extent are parasite species specific but depend more on the rate of larvae ingestion and the site of habitation and feeding habits of the parasite. For example, abomasal dwelling parasites (*Haemonchus contortus*, *Ostertagia circumcincta*) appear to have their major influence on the host through a depression in food intake (Rowe *et al.*, 1988; Sykes *et al.*, 1988) whilst for intestinal dwelling parasites, as well as depression in food intake, increased endogenous protein loss into the

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gastrointestinal tract occurs with consequent reduction in efficiency of energy utilisation. The latter effects are likely to be exacerbated with *Oesophagostomum* infection in the large intestine (Dobson and Bawden, 1974;) where there is no opportunity for reabsorption of the endogenous protein. Other specific effects depend on conditions created. For example elevation of abomasal pH contributed to poor Cu absorption (Bang et al., 1990a) and ingestion of blood by *Haemonchus* species eventually results in anaemia in sheep (Rowe et al., 1988).

A major consequence of chronic subclinical infection which is overlooked is the impact on overall flock productivity. Lambs take longer to reach marketable weight and if so retained compete for pasture with the hogget and ewe flocks at times when the latter require high feed allowances to achieve satisfactory liveweights for mating and summer and autumn wool production. The feed budget is compromised with detrimental effects on either or both classes of stock. Regular drenching cannot remove the effect of the parasite entirely, restoring only 10-20% of the lost growth rate (Coop, et al., 1982.; McAnulty, et al., 1982.).

An alternative approach is to generate worm free pasture by grazing areas with mature stock or alternative animal species e.g. cattle. The area of land required to support the lamb flock is such that under a typical flock structure worm free pasture is difficult to generate and maintain without compromising the development of the hogget flock or contaminating areas intended for the lamb flock (Nicol, 1986). If it were possible for lambs to graze contaminated pasture but the depression in liveweight gain alleviated through improved nutrient supply then this would have a major practical impact on the overall production system by minimising one of the major constraints on the system viz liveweight gain of lambs. At present this can only be achieved by allowing lambs only to graze pasture to a high residual dry matter or never below a height of approximately 5cm (Bown et al., 1989).

NUTRIENT MANIPULATION

The crucial questions are whether nutrient manipulation can increase the growth of parasitized animals by maintaining the supply of absorbed nutrients to productive tissues (muscle and bone) as well as providing

nutrients to allow for repair of damaged tissues (gut wall), and the immunological response of the host. The importance of protein and mineral nutrition will now be considered initially from a description of the pathophysiology of infection and from that suggestions for potential beneficial manipulations will be made. For brevity, specific examples have been chosen.

PROTEIN

The effect of parasitic infections on protein digestion and metabolism has been extensively reviewed (Dargie, 1980; Steel and Symons, 1982; Sykes, 1982; Poppi, 1986; Parkins and Holmes, 1989). In parasitism of the abomasum and small intestine there appears little or no effect on protein absorption per se. Increased endogenous loss of protein from the digestive tract can occur, most of which is reabsorbed (absorption of plasma protein is approximately 0.86). There is, as a consequence, extra flow of protein N at the ileum of up to 30g protein/day which approximates the extra N observed in the urine and/or the faeces of parasitized animals (Bown et al., 1984; Poppi et al., 1986; Rowe et al., 1988). Microbial activity in the large intestine largely influences whether the additional loss of protein from the small intestine is partitioned between absorption in the hindgut and appearance in urine or incorporation into microbes and appearance in faeces.

The consequence of this sequence is that large amounts of protein are cycled through the digestive tract which is energetically costly (Sykes, 1983). Moreover, the increase in endogenous protein (from 0-approximately 30 g protein/d) lost from the small intestine accounts chiefly for the commonly observed depression in protein retention (Roseby, 1977; Bown, 1986; Poppi et al., 1986; Kimambo et al., 1988; Rowe et al., 1988). Furthermore the partial efficiency with which absorbed protein is deposited in commercially important tissues is depressed in parasitized animals largely because protein synthesis is diverted away from muscle and bone towards repair, replacement and reaction to damage of the gut wall, mucus production and plasma or whole blood loss (Steel et al., 1980, 1982; Bown et al., 1986).

Given this scenario, the host view of parasitism is that it poses an additional nutrient demand in much the same way that lactation or foetal growth might be

viewed. Since protein absorption is not depressed to any great extent then this extra nutrient demand may be met by increasing the intestinal supply of protein through increasing food intake or the undegradable protein content of the diet. Intake is depressed in parasitized animals and its manipulation is not yet possible. Improved supply of undegradable protein may be achieved, however, by supplementation or choice of appropriate pasture species.

Support for examination of this kind of approach to limit the effect of infection was obtained recently by Abbot *et al.*, (1986, 1988) and Bown *et al.* (1986) who increased protein deposition and liveweight gain in parasitized animals to levels similar to those in control animals simply by increasing intestinal protein supply (Table 1). These results are important because they demonstrate clearly that growth in parasitized animals can be increased by specific nutrient supplementation the rationale for which was devised by a study of the pathophysiology of the parasite. We are unsure at this stage of the extent to which nutrient manipulation promoted growth simply by supplying additional nutrients above those required to maintain the alimentary tract. Alternatively nutrient manipulation may reduce the damage or loss of endogenous protein through reduction of the parasite population by enhancing the host immune response. This is difficult to assess but Bown, (1986) found that protein supplementation did not influence plasma protein loss in parasitized animals whilst Abbott *et al.*, (1988) showed that parasitized lambs on low protein diets exhibited marked hypoalbuminaemia and those on high protein diets did not. However in both these studies worm burdens and faecal egg output were depressed in protein supplemented groups suggesting enhancement of host immune response. There may well be additional long term benefits of this approach in reduced pasture contamination.

The question is whether this protein manipulation can be achieved practically. The estimated duodenal crude protein supply per kilogram of digestible organic matter in the experiments of Abbott *et al.*, (1986, 1988) and Bown *et al.* (1986) and that which is currently supplied from pasture in New Zealand (Cruickshank *et al.*, 1985) are given in Table 2. Pasture supplies a nutrient ratio similar to that used in the basal diets of the above experiments but if they are to supply protein at

TABLE 1 Liveweight gain in parasitized (P) and control (C) lambs consuming diets varying in protein content.

Parasite	Liveweight gain (g/d)		Protein content of diet (g/kg)
	C	P	
<i>H. contortus</i> (1)	47	27	88
	88	84	169
<i>T. colubriformis</i> (2)	95	37	118
	-	82	150

(1) Abbott *et al.* (1988); (2) Bown *et al.* (1986)

rates similar to the supplemented diets protein supply to the intestines needs to be higher. However pasture has the potential to supply high protein/energy ratios in absorbed nutrients if the losses of protein across the rumen could be minimized (Table 2) with potential benefits for the animal to cope with parasitism.

TABLE 2 Duodenal crude protein supply per kilogram digestible organic matter (g DUCP/kg DOM) estimated from diets used by Abbott *et al.* (1988) and Bown *et al.* (1986) (see Table 1) and that which is supplied from or could potentially be supplied from common NZ pastures (Cruickshank *et al.*, 1985).

	Abbott <i>et al.</i>	Bown <i>et al.</i>		
Basal diet (g DUCP/kg DOM)	218	190		
Supplemented diet (g DUCP/kg DOM)	295	250		
Supply from pasture species	Lucerne	White clover	Ryegrass	Prairie grass
Duodenal CP supply (g DUCP/kg DOM)	224	225	195	215
Potential duodenal CP supply (g DUCP/kg DOM)*	430	380	340	280

* assuming no losses of protein in digesta passage across the rumen.

A factor arising from examination of the protein transactions and the response to protein supplementation is the extent to which total protein is involved or whether it is a response to a specific amino acid. Wool break and depressed wool growth are observed in parasitized animals (Barger *et al.*, 1973; Leyva *et al.*, 1982) and S amino acids are the first limiting amino acids for wool synthesis and lamb growth. Of the extra endogenous protein leaving the small intestine, plasma protein appears to account for a maximum of only 30% because 86% is reabsorbed (Bown *et al.*, 1984). The rest must come from mucus and sloughed epithelial cells. Mucus, a glycoprotein, is high in cysteine and appears to be poorly absorbed in the small intestine (Lindsay *et al.*, 1980). Parasitized animals may therefore have a higher demand for S amino acids than uninfected animals and it is possible that the responses observed by Abbott *et al.* (1986, 1988) and Bown *et al.* (1986) may be largely due to these amino acids. However Barger *et al.* (1973) could not eliminate the depression in wool growth of parasitized animals by infusion of 2 g cysteine/day but observed that resistant animals appeared to grow less wool which suggested that the partitioning of S amino acids was different in these animals.

Another feature of the S amino acids is their involvement in the leukotrienes, a class of compounds synthesized from arachidonic acid and involved in the ability of the host to impede larval development through smooth muscle contraction and paralysis of larvae (Douch *et al.*, 1983). Kimambo and MacRae (1988) demonstrated that resistant animals had a substance present in mucus from the abomasum and intestines and in ileal digesta which reduced motility of larvae. The leukotrienes have a number of cysteine residues in their structure. It is not known if leukotriene production is influenced by supply of S amino acids but the possible association between leukotriene and mucus production, worm burdens and protein supplied to the intestines deserves investigation.

The importance of identifying the role of individual amino acids is that it may be easier to manipulate their supply than that of total protein. For example, protected sources of amino acids are now available and protein fractions of high cysteine content and low rumen degradability have been identified in plants and there is speculation that genetic engineering may enable

their transfer into economically important species (Spencer *et al.*, 1988).

MINERALS

Of the major minerals studied (Ca, P, Mg), P absorption appears most affected by parasitism of the small intestine (Wilson and Field, 1983; Poppi *et al.*, 1985; Bown *et al.*, 1989). Parasitized animals show reduced bone formation, low plasma P levels, reduced salivary P secretion and low apparent absorption of P from the small intestine. Induced P deficiency may be responsible for the depression of food intake in parasitism. However, unlike the situation with protein it appears unlikely that enhancement of dietary P will increase P available to the tissues because ability to absorb P is impaired by infection (Wilson and Field, 1983). However, Coop and Field (1983) were able to increase liveweight gain of parasitized animals by increasing the P content of the diet from 1.88 to 2.75 g P/kg DM. Worm burdens at slaughter after 14 weeks of infection were about 11000 and 1250 larvae on the low and high P diets respectively, suggesting an effect of P status on the hosts immune response in this experiment.

The interaction of trace elements and parasitism has not been extensively studied despite the fact that both are major causes of ill-thrift on farms. Much work has been of a qualitative nature or inconclusive. For Cu there are some recent quantitative data and this element is used as the example here. Copper is absorbed from the small intestine and animals grazing contaminated pasture have been shown to have lower liver Cu levels than contemporary animals drenched with anthelmintic (Andrew *et al.*, 1971). Bang *et al.* (1990a) observed that elevated abomasal pH was associated with reduced net uptake of Cu in the liver of lambs infected with *Ostertagia circumcincta*. In a Cu deficient area this would exacerbate any ill thrift associated with the mineral deficiency. These authors supplemented infected animals orally with copper oxide wire particles (COWP), a recommended method of Cu supplementation. Release of Cu and uptake of Cu by the liver was halved in infected animals and the effect was directly related to the abomasal pH induced by parasite infection. They postulated that the elevated abomasal pH caused by this parasite interrupted Cu solubilization.

Copper has been recognised for some time to

have anthelmintic properties (Hall and Foster, 1918; Gordon, 1939). The effectiveness of Cu against major parasite species has recently been demonstrated by Bang *et al.*, (1990b). These authors dosed lambs with COWP prior to parasite infection and found a 96% reduction in the worm burden of *Haemonchus contortus* whilst a 56% reduction occurred with *Ostertagia circumcincta* and no depression occurred with *Trichostrongylus colubriformis*. The implications of such findings are to urge caution in interpreting weight gain response to copper treatment simply as alleviation of Cu deficiency, particularly in areas where *H. contortus* and *O. circumcincta* are significant species and to ask whether in areas of known Cu deficiency or marginality it may be safe to incorporate Cu into pulsatile controlled release devices as both anthelmintic and Cu supplement. Much further work is required. The extent of anthelmintic activity will reflect the ability to increase soluble Cu concentration in digesta and the susceptibility of the helminth species to Cu toxicity. The former will be diminished in pathogenic infections in which abomasal pH has been previously elevated by infection and a sophisticated combination of anthelmintic may be needed to allow utilisation of this phenomenon. The rapid development of drug resistance to conventional anthelmintics may require such novel approaches to extend anthelmintic effectiveness.

INTAKE

By far the most significant effect of parasitism on the host is a depression in food intake. The extent is dependent on the numbers of larvae ingested and the helminth species (Steel *et al.*, 1980, 1982; Sykes *et al.*, 1988) but can be as great as 30% even in subclinical infection. That it is dependent on some physical presence or action of the worm can be deduced by the observations that intake increases in parasitized lambs as they develop immunity and show self cure (Steel *et al.*, 1980, 1982) and that, on anthelmintic drenching, intake increases within a week (Fox *et al.*, 1989a; R.A. Dynes unpublished data).

There is a paucity of data on the mechanism of this depression in intake (Symons, 1985) and most work has concentrated on hormonal disruption. Symons (1985) demonstrated increased plasma CCK levels with a bioassay technique and linked the known satiety

effect of CCK to the parasite induced anorexia of *T. colubriformis*. However the role of CCK in anorexia in sheep is not well established and Dynes *et al.*, (1990) using specific antagonists to peripheral CCK receptors were not able to increase intake of parasitized animals. It is possible that CCK may still be involved centrally with elevation occurring by stimulation of other pathways.

With abomasal infection by *Ostertagia ostertagi* in calves, depression in food intake was closely associated with elevated plasma gastrin and pepsinogen, the pattern of change reflecting the time course for worm development and mucosal damage (Fox *et al.*, 1989a, b). Depression of appetite was reversed on anthelmintic drenching. Use of omeprazole to raise plasma gastrin caused a depression in food intake (Fox *et al.*, 1989c) but in these types of experiments the reverse procedure of antagonizing the hormone and elevating intake needs to be performed to clearly implicate that pathway and provide practical means of increasing intake. Immunisation of animals against the target hormone may well be a long term practical strategy.

Recently Dynes *et al.*, (1990) have examined the eating patterns of parasitized and control animals. The major difference was not the pattern of eating associated with initiation and cessation of meals but rather the rate at which food was consumed during the eating periods. They postulated that hunger rather than satiety was involved and that the effect of parasitic damage to the intestines on peripheral or central opioid release or action should be considered. They were able to increase intake in parasitized animals by blocking the satiety role of the ventromedial hypothalamus (VMH) through the diazepam receptor indicating that if the opioid axis is involved its action is modified by signals arising from the VMH.

Understanding of the mechanism of intake depression is still in its infancy but alleviating the depression has major potential benefits for the host by markedly increasing nutrient supply.

EPIDEMIOLOGY

Any potential strategies for alleviating the depression in performance of chronic subclinical infection must take a wider view of the management of the farm, particularly with regard to altered feed demand curves and

epidemiology of the parasite population.

Increasing the protein/energy ratio of absorbed nutrients has resulted in reduced faecal egg output and worm burdens and some suggestion of an enhancement in the onset of immunity (Abbott *et al.*, 1986, 1988; Bown *et al.*, 1986). If such manipulations were employed in spring then it would be expected to result in a reduction in larval contamination of pasture and a depression in the autumn rise of larvae on pasture. Thus it is complementary with other strategies used to reduce pasture larval contamination.

CONCLUSIONS

It may be concluded that manipulation of specific nutrients markedly influences the ability of the host to cope with a chronic subclinical infection. Specific nutrient manipulation is possible through supplementation or manipulation of nutrient content of plants. The interaction of nutrition with immunological development of the host has major implications for any future control measures.

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