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**A dynamic model incorporating dietary protein for predicting liveweight gain of parasitised grazing lambs**

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**ABSTRACT**

Internal parasites are one of the major constraints to liveweight gain (LWG) in young grazing ruminants. However, even in parasite-free animals, diets low in crude protein can constrain LWG from values expected on the basis of metabolisable energy intake alone. We investigate the impact of protein supplementation in overcoming reduced growth rates of parasitised animals. This was done via a dynamic model which assumes increased maintenance requirements (immune requirements, increased cell turnover and mucous production) in parasitised animals. A key output from the model is LWG over an extended grazing period. We calibrated and validated the model using published data from an indoor feeding experiment in which trickle-infected lambs were fed for 20 weeks on three diets providing different amounts of metabolisable protein. The mean liveweight and worm burden predicted from the model compared well with experimental data. Such models will prove useful in designing supplementation strategies for grazing lambs where anthelmintic control of parasites is not a management option.

**Keywords:** modelling; liveweight gain; parasites; dietary protein.

**INTRODUCTION**

Internal parasites are a major constraint to production in grazing ruminants (Vlassoff *et al.*, 2001). In parasitised animals both pasture intake and the efficiency with which nutrients are used is decreased (Sykes & Coop, 1976; Sykes & Coop, 1977). Anthelmintics can be successful in restoring some of the lost production, but they have no effect on the majority of the parasite population, which is present in the faeces or the pasture as eggs and immature larval stages (Vlassoff *et al.*, 2001). Where anthelmintics cannot be used due to farm status *(e.g.* organic), or anthelmintic resistance, then strategic supplementation may be an option.

The complex relationship between larval challenge, host immune response, adult parasite burden and liveweight gain (LWG) has recently been addressed in a dynamic model (Louie *et al.*, 2007). Such a model may have an important role in evaluating supplementation options. However, this model uses metabolisable energy (ME) only in determining LWG, and some nutritional studies have shown that increased protein supply might be more important than ME in enabling the animal to cope with the debilitating effects of parasites (Bown *et al.*, 1991; Yu *et al.*, 2000). Indoor feeding trials with parasitised lambs have indicated that dietary supplementation with rumen undegradable protein can alleviate much of the decrease in LWG associated with the parasites (Van Houtert *et al.*, 1995; Bown *et al.*, 1991).

The model in (Louie *et al.*, 2007) indirectly accounted for the extra protein requirement imposed by the parasites by increasing the ME required for the protein synthesis. In order to build a model which can assist in designing supplementation strategies to overcome the effects of parasites on LWG of grazing lambs, the supply of metabolisable protein (MP) in the diet and additional protein requirements due to parasitism need to be made explicit. This was achieved by modifying standard equations in AFRC (1993) and SCA (1990) to take account of the additional protein requirements and appending these to the model in (Louie *et al.*, 2007). This updated model was then calibrated and validated using results from an indoor feeding trial in sheep (Van Houtert *et al.*, 1995).

**METHODS**

The following procedure was used to determine LWG in the model of Louie *et al.*, 2007:

1. Fix initial animal age, liveweight and dry matter intake.
2. Using only ME of the feed, the equations in SCA (1990) were used to calculate the expected LWG for the animal by subtracting ME requirements for maintenance and grazing activity, allocating the remainder to growth.
3. The liveweight was updated and steps 1 and 2 continued for the chosen duration of grazing.

The LWG calculated in step 2 will have a protein component. To account for protein
explicitly we need to quantify this and compare with the protein supplied in the feed. The additional steps required are:

4. From the LWG in step 2 calculate the protein requirement (SCA, 1990, equation 1.36A, p 43).
5. Using the concepts of protein degradability summarised in AFRC (1993), calculate the MP supplied in the feed and compare with the requirement in step 4.

With feeds very low in crude protein, degradability or both, the MP supplied from step 5 was usually less than MP required from step 4. In this case MP rather than ME is the limiting factor determining LWG.

Modification to account for parasites

In the model of Louie et al. (2007), parasites have three effects on the values calculated in steps 2 and 3 of the above procedure. The first is an additional cost of energy required for maintenance, which accounted for protein synthesis involved in increased cell turnover and mucous production. This was modelled by reducing the efficiency of use of ME for maintenance ($k_{\text{main}}$) with increasing worm burden. The second effect was to reduce the feed intake of the infected host animal, with the reduction again assumed dependent on the individual worm burden. The final effect was to reduce the efficiency with which any excess ME was used for growth ($k_g$). All three effects were assumed to vary amongst the hosts by allowing individual values for $k_{\text{main}}$, $k_g$ and the parameter controlling reduction of feed intake. This modelled the individual variability observed in groups, with more parasite-resistant hosts suffering less reduction in these parameter values than their less parasite-resistant cohorts at the same worm burden. The model outputs were for individual animals but for comparison with experimental data the mean values were often used.

Protein requirement for ME-predicted LWG

For young, growing animals protein will be required to replenish that incurred in urinary and faecal endogenous losses (EUP, EFP respectively), dermal loss in cattle or wool growth in sheep, plus the amount directly needed for accretion of tissues resulting from the LWG predicted from ME considerations. This last quantity is determined by

\[ \text{PROTEIN in LWG (g/kg EBG)} = \frac{212 - 4R - (140 - 4R)/[1 + \exp(-6(P - 0.4))]}}{\text{EBG (g/d)}} \times \left(\frac{4SRW^{0.75}}{1}\right) \tag{1} \]

where

\[ R = \text{EBG (g/d)}/(4SRW^{0.75}) - 1 \]

as given in SCA (1990, p 43, equation 1.36A). Here EBG is the empty body gain, $W$ the current weight and $SRW$ the standard reference weight of the animal.

To obtain the total metabolisable protein intake required for young growing lambs the components for growth, endogenous urine and faecal losses and wool growth are summed and then divided by an efficiency factor of 0.7. (SCA 1990, p102)

\[ \text{MP required (g/d)} = \left(\text{PROTEIN in LWG + EUP + EFP + WOOL}\right)/0.7 \tag{3} \]

Protein supply using protein degradability from AFRC (1993)

In the AFRC protein system the yield $y$ (g/MJ FME) of microbial crude protein (MCP) is related to the level of feeding and determined by AFRC, 1993 equation (34), p16. FME is fermentable metabolisable energy and is that portion of the ME which can be utilised by the rumen microbes. It is related to ME by AFRC, 1993 equation (5), p48. If DMI is dry matter intake of the feed in kg DM/d then the supply of microbial crude protein is given by:

\[ \text{MCP (g/d)} = y \times \text{DMI} \times [\text{FME}] \tag{4} \]

This calculation assumes that MCP is not limited by the supply of ammonia and amino acids, but is limited by the FME required to incorporate ammonia and amino acids into MCP. If the feed is low in crude protein or contains large amounts of rumen-protected protein then the yield of MCP may be less. The SCA protein system is not as clear in how to deal with varying crude protein (CP) and protein degradability. In the AFRC protein system the degradable part of the feed is partitioned into quickly degraded protein (QDP) and slowly degraded protein (SDP). In order to calculate effective rumen degradable protein (ERDP), which is a measure of the total N supply that is actually captured and utilised by the rumen microbes for growth and synthetic purposes, we assume the effective degradability $p$ (AFRC, 1993 equation (26), p12) and the cold water extracted fraction $a$ (AFRC, 1993 equation (27), p13) of the feed total CP is known. Then ERDP may be simply calculated from:

\[ \text{ERDP} = (p - 0.2 \times a) \times \text{CP} \tag{5} \]

This calculation establishes the supply of protein to the rumen available for microbial metabolism, based on the assumption that MCP could also be limited by the supply of ammonia.
and amino acids. Thus, the MCP available for digestion is the lesser of ERDP (equation 5) and the value calculated from FME in equation (4). The AFRC system clarifies the role of protein degradability in determining the amount of MCP available for digestion by making this either ERDP or FME-limited. The amount of undegradable protein is that which is neither quickly nor slowly degraded

\[ UDP = CP - (QDP + SDP) \]  

(6)

and the fraction of undegraded dietary protein that is apparently digested (DUDP) in the small intestine increases with crude protein of the feed according to (SCA, 1990, equation 2.15, p98)

\[ DUDP/UDP = (0.455CP - 14.65)/100 \]  

(7)

The metabolisable protein available from the feed is given by the sum of that provided by the rumen microbes and the amount which escapes degradation

\[ \text{MP supplied (g/d)} = 0.56\text{MCP} + \text{DUDP} \]  

(8)

The adequacy of the MP supply is judged by comparing the value from equation (8) with the MP required from equation (3).

Effect of Parasitism

We include the effect of parasites on protein utilisation by including an additional requirement to account for the protein sequestered by the gastro-intestinal tract for its maintenance and local immune response (Sykes & Greer, 2003). Estimates of the increase for sheep dosed with 2500 *Trichostrongylus colubriformis* L3 per day range from 42—150% of the usual endogenous protein-N lost to the gastro-intestinal tract (Poppi et al., 1986). In equation (3) we introduced another term which increases protein requirement according to the lamb’s worm burden. This was assumed to increase linearly for small worm burden and then plateau as worm burden became very large.

\[ \text{PIPR (g/d)} = \frac{140\text{WB}}{\text{WB} + (3 \times 10^4)} \]  

(9)

where PIPR is the parasite-induced protein requirement, WB the current worm burden of the animal, the plateau level of extra protein required is 140 g/d for extremely large worm burden, and the protein required was half this maximal value when the worm burden was $3 \times 10^4$. The plateau level of 140 g/d was derived by assuming an additional parasite requirement of 150% of the 95 g/d endogenous protein-N lost to the gastro-intestinal tract in non-infected animals. (Lindsay et al., 1980)

Procedure when MP supply fails to meet MP requirement for LWG

It was previously noted that for feeds very low in CP or degradability, protein might be a limiting factor in determining LWG. Because parasites are assumed to increase MP requirements, infected animals would be more likely to suffer a greater protein-limited constraint on their LWG. Thus pasture which might not be protein-limiting for LWG in parasite-free animals may become so for infected animals. When MP is a constraint on growth we need a procedure to determine the protein-limited LWG. If we assume that endogenous losses, wool growth and extra protein required for parasites have priority for MP, then the protein-limited LWG will be determined by the amount of MP remaining after these demands have been satisfied. Thus the amount of MP available for LWG can be calculated from:

\[ \text{PROTLWG} = \text{(MP supplied} \times 0.7) - [\text{EUP} + \text{EFP} + \text{WOOL} + \text{PIPR}] \]  

(10)

Using SCA 1990, equation 1.36A, p 43 which gives the protein required for weight gain we can derive the following equation to solve for $l$, the protein-limited LWG in kg/d:

\[ 0.92[\frac{212 - 4R - (140 - 4R)}{1 + \exp(-6|P - 0.4|)}] = \text{PROTLWG} \]  

(11)

where as before $R = \frac{920l}{4\text{(SRW)}^{0.75}} - 1$

and the factor of 920 converts LWG in kg/d to empty body gain in g/d. The quadratic equation (11) for $l$ yields two solutions and we choose the positive one. By solving this equation at every time step as we update the animal’s liveweight we can investigate a long-term grazing scenario.

RESULTS

This simulation for 3 month old lambs fed indoors with protein supplement was done as a direct comparison with the feeding trial of Van Houtrert et al., (1995). Cumulative LWG predicted from the model over the 24 week experimental period which started on day -28 are shown in Figure 1.

The mean worm burdens are shown in Figure 2. Under all three levels of supplementation there was a rapid increase to a peak which occurred approximately 10 weeks after dosing began and then a more gradual decline towards the end of the trial period.
Figure 1: Cumulative LWG in lambs fed indoors on chopped oaten hay and three different levels of supplementation with fishmeal (FM0, FM50, FM100 = 0, 50 and 100 g/d respectively). Experimental data are shown as circles (FM0), triangles (FM50) and squares (FM100). Model outputs are shown as solid lines (FM0), dotted lines (FM50) and dashed lines (FM100).

Figure 2: Mean worm burden of each supplemented group of lambs fed indoors on chopped oaten hay and three different levels of supplementation with fishmeal (FM0, FM50, FM100 = 0, 50 and 100 g/d respectively) dosed with 3000 L3 *T. colubriformis* per week. Experimental data are shown as circles (FM0), triangles (FM50) and squares (FM100). Model outputs are shown as solid lines (FM0), dotted lines (FM50) and dashed lines (FM100).
DISCUSSION

The model assumed that parasitism increased protein requirements and consequently the demand for MP. The increased requirement meant that less MP would be available for LWG. The LWG achieved was based on comparing supply of MP through diet and MP required by the animal. When MP supply matched or exceeded requirement the LWG was given by step 3 of the procedure in the Methods section. If MP supply was inadequate then LWG was determined from solving the quadratic equation (11).

The model assumed worm burden reduced host appetite although in the literature (Sykes & Greer 2003; Poppi et al., 1990) appetite depression was more usually linked to level of L3 intake. However, studies in which removal of worms with anthelmintic resulted in rapid restoration of appetite (Kyriazakis et al., 1996) suggest the dependence on worm burden is correct. In the feeding trial of Van Houtert (1995) the reduced feed intake with infection and no supplement was reversed when supplement was given.

In order to achieve the final mean LWG of 9.7 kg for the unsupplemented group of non-infected lambs (Van Houtert et al., 1995), a CP content of at least 12% in the base feed needed to be used in the model. This was higher than the value of 7% for oaten hay sprayed with urea recorded by those authors. By also fixing the effective protein degradability at 0.8 and the cold water extracted fraction of CP, a, at 0.25 the modelled cumulative LWG was then very close to 9.7 kg. The model gave a smaller final value for the 50 g/d supplementation of 12.9 kg LWG compared to the experimental value of 14.6 kg. However, the values for the 100 g/d supplementation of 15.6 kg (model) and 15.4 kg (experiment) were in very good agreement.

In Figure 1B the preceding liveweight comparisons were repeated with an L3 trickle infection of 3000 T. colubriformis per week. The model parameters controlling establishment and mortality of worms (Louie et al., 2007) were calibrated for the no-supplement group of Van Houtert et al. (1995). Validation of the model was then carried out by comparison with the two supplemented groups. This led to lower values in modelled LWG for the supplemented groups than was observed in the experiment, with final LWG of 8.6 kg and 11.4 kg for 50 and 100 g/d supplement respectively, compared with measured values of 12.0 kg and 13.7 kg. One possible reason for this discrepancy was evident when we compared the worm burden from the model with the experimental values. Although the overall trend agreed with Van Houtert et al. (1995), there were differences in the timing and value of the peak values. In the model, worm burden affects LWG not only through an increased protein requirement but also by reducing feed intake. The differences in modelled worm burden evident in Figure 2 manifest as differences in modelled LWG in Figure 1B. However, although the measured worm burden showed even larger differences after peaking at 10 weeks, with those lambs receiving 100 g/d supplement having almost zero worm burden at 20 weeks, these differences do not appear to be reflected in the measured LWG.

If the worm burdens can be modelled more accurately then this framework should provide a foundation for more realistic grazing simulations to be run, identifying the amount of rumen undegradable protein to be supplied in order to achieve a specified target LWG under different degrees of parasite infection.

CONCLUSIONS

A model which includes an extra protein requirement due to parasitism has been calibrated and validated against the results obtained in an indoor feeding trial. This model can help in designing supplementation schemes for grazing lambs outdoors. This will be essential on farms where anthelmintic use is restricted or not a possible control option.

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