Interaction of parasitism and nutrition and their effects on production and clinical parameters in goats

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ABSTRACT


Weaned wether goats (n=144) approximately 6 months of age were placed in a 2×3 factorial design experiment for 5 months to test the main effects and interaction of two levels of nutrition (growth+maintenance, NUT1; twice growth+maintenance, NUT2) and three levels of Haemonchus contortus burden (0, 500 and 2000 larvae administered every 2 weeks: W0, W500 and W2000, respectively) on weight, feed intake, level of infection and packed cell volume (PCV). The rationale for the experimental design was based on the lack of information concerning the interaction between nutritional status and worm burden. Results indicated significant effects of worm burden levels on PCV, faecal egg contents (eggs per gram of feces (EPG)), actual worm numbers, feed intake and efficiency of feed utilization. Nutrition×worm burden interactions were also significant for PCV and EPG. However, the differences detected for PCV and actual worm numbers did not translate into large or consistent differences in body weight. Goats on NUT2, after an initial period, showed little difference in body weight, irrespective of worm burden. Within the NUT1 level, W0 kids weighed more than W500 or W2000 kids throughout the study. Although not statistically significant, this constitutes a trend towards an interaction between nutrition and worm burden. In both nutrition levels, there were no body weight differences between W500 and W2000 until the last 14 days. Feed intake was depressed in the first 3 months of the experiment for infected animals, but was subsequently followed by a compensatory reaction. Lower establishment rates, based on actual worm counts, were observed for the higher infection level, but in both infection levels establishment rates tended to decrease with time. Nutrition was found to be more important to counteract the consequences of a parasitic infection than to counteract the establishment of that same infection.

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INTRODUCTION

The recurring loss in productivity and profit due to parasitic infestation is a common problem for small ruminant production in most parts of the world (Gall, 1981). The literature reporting the impact of worm burden on segments of animal productivity has been considerable (Gray, 1916; Ross and Gordon, 1933; Whitlock et al., 1943; Spedding, 1952, 1954; Whitlock, 1955a,b; Gordon, 1964; Abbott et al., 1984, 1985, 1986). However, for all the extensive work produced on this topic, the primary, and almost exclusive, experimental design has been the one factor at a time approach, which does not allow the evaluation of biological interactions. Attempts by Whitlock (1949) and Stewart and Gordon (1953) lacked control of infection levels and of parasite species; furthermore, the scope of these experiments and data analyses were somewhat limited. In addition, many experiments involved very few animals which limited the statistical analysis.

The increasing utilization of computer simulation programs by all facets of the livestock industry presents the potential for more complete evaluation of the production system. However, to build such models requires not only an understanding of the interaction of biological components, but also their quantification. Blackburn et al. (1987) have designed a goat simulation model which has a parasite component. However, no existing data sets were available to evaluate the mathematical functions. Of particular interest was how nutrition and worm burden interacted to impact kid growth. The following experiment was designed to provide the needed data as well as to provide insights into the interaction of these biological components. In addition, there is a lack of experimental work dealing with the problem of haemonchosis in goats. As with sheep, those experiments performed with goats used a single-factor design and involved limited numbers of animals (Arzoun et al., 1983; Shavulimo et al., 1986; Al-Quaisy et al., 1987).

MATERIALS AND METHODS

Indigenous Brazilian wethers \((n=144)\) approximately 6 months of age were randomly allocated to six treatments of a \(2\times3\) factorial design. The design consisted of two nutrition and three infection levels. Each treatment had 32 kids assigned to it, except for the non-infected controls which had eight kids each.

The infected treatments were subdivided into four pens or subtreatments of eight animals each, based on their initial body weight, to reduce competition for feed. Upon allocation, the goats were dewormed by a combination of three different treatments alternated over a period of 2 weeks. The elimination of infection was confirmed by faecal egg counts.

Three infection levels, 0 (W0), 500 (W500) and 2000 (W2000) infective
third stage larvae were administered orally. *Haemonchus contortus* larvae were obtained from faecal cultures and stocked for 25–30 days at 7–8°C. The first infection occurred 23 days after the initiation of nutrition treatments and 38 days after the beginning of the experiment. The larvae were administered every other week for 16 weeks, totaling 4500 and 18 000 larvae for W500 and W2000, respectively. This approach was used so that infection levels would be persistent throughout the experiment.

Nutrition levels consisted of a low level which accounted for maintenance requirements and growth (NUT1), and a high nutrition level (NUT2) which was double the crude protein and energy levels of NUT1. The level fed as NUT1 was based on the mean body weight of each pen. Initially, 166 g of concentrate were fed and considered adequate to meet the minimum requirements of a 13 kg kid.

Diets were a combination of concentrate and roughage. The concentrate was 80% corn and 20% soybean bran, with a crude protein (CP) content of 19.8% and 77% digestibility (DIG). Roughage included grass hay (6.9% CP and 57.7% DIG) fed ad libitum to both treatments and for NUT2 an additional 100 g per head day\(^{-1}\) of a legume hay (20.6% CP and 60.6% DIG). The orts of all feed types were recorded to determine feed intake by difference.

Animals were confined to concrete pens for the duration of the experiment. The pens were sanitized daily to prevent extraneous sources of parasitic infection. Body weights of all animals were recorded weekly, serving as the basis for ration determination the following week. Every week, a faecal sample from each animal was collected for the determination of parasite egg contents using the method of Gordon and Whitlock (1939). Packed cell volumes (PCV) were determined every other week for a random sample of eight animals per treatment, following the methods described by Silverman et al. (1970). However, for simplicity and brevity, some of the less representative data points are omitted from some tables and figures.

The kids were serially slaughtered across the experiment so that worm establishment rates could be monitored during all phases of the experiment. The first necropsy period occurred 40 days after the initial larval inoculation, and the other three were at monthly intervals. At each necropsy, eight kids from each treatment were slaughtered, except for the controls which were all slaughtered at the end of the experiment. After slaughter, the abomasal contents were collected and then sifted using 0.062 mm filter until the flowing water became colorless. The worms were retrieved after sedimentation, fixed and then counted with the help of a microscope.

The statistical analysis performed included a wide range of techniques, from raw means to logarithmic transformations of some of the variables, residual and outlier analysis, multiple regression and generalized linear models as described by Freund et al. (1986). Weighted regression and generalized least
squares methods were used in some analyses to overcome heteroscedasticity and autocorrelation of some of the dependent variables.

The basic model was a mixed generalized linear model (Freund et al., 1986) with nutrition and worm burden levels, time periods, and pens nested within treatments as the classification variables. The mixed model included the appropriate interactions, which were tested using the appropriate error terms. Nutrition, worm burden levels and the respective interaction were tested by pens nested within treatments. Absorbing methods (Freund et al., 1986) and weighted and unweighed pen means analyses had to be used to overcome limitations of computer memory. Analyses within time periods and multiple regression models of treatment means were also used as complementary analyses. Additional and more specific details will be addressed for each variable analyzed.

RESULTS

Body weights and growth

Body weight least squares means are reported in Fig. 1, while least squares means for average daily gains are given in Table 1. Figure 2 shows the levels of statistical significance across time for main effects and interactions. To overcome heteroscedasticity, the statistical models for body weight were weighted regressions, the weights being the inverse of the variance of the respective pen or treatment. These were the weights that achieved the best variance stabilization. Adjustments for initial weight were made after weighting.

![Graph](image-url)

Fig. 1. Growth patterns of kids fed a high (NUT2) or low (NUT1) plane of nutrition and infested with 500 (W500), 2000 (W2000) or no larvae (W0).
Fig. 2. Levels of statistical significance of the main effects on body weight across time. Code for significance levels: 0, $P > 0.1$; 2, $0.05 < P < 0.1$; 4, 6 and 8, $p < 0.05$.

TABLE 1

Least squares means for average daily gain (g)

<table>
<thead>
<tr>
<th>Days 1</th>
<th>NUT1</th>
<th>NUT2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>W0</td>
<td>W500</td>
</tr>
<tr>
<td>7−21</td>
<td>93</td>
<td>35</td>
</tr>
<tr>
<td>42−49</td>
<td>48</td>
<td>-44</td>
</tr>
<tr>
<td>56−63</td>
<td>48</td>
<td>40</td>
</tr>
<tr>
<td>84−91</td>
<td>59</td>
<td>6</td>
</tr>
<tr>
<td>112−119</td>
<td>20</td>
<td>59</td>
</tr>
<tr>
<td>119−126</td>
<td>185</td>
<td>94</td>
</tr>
<tr>
<td>147−154</td>
<td>98</td>
<td>18</td>
</tr>
</tbody>
</table>

1Days of test.

Differences between nutrition levels started early in the experiment, but they were only pronounced enough to be statistically significant after 62 days. They remained statistically significant for the rest of the experiment. Final weights for NUT1 and NUT2 were 17.1 kg and 22.5 kg, respectively.

Statistically significant differences for worm burden were reached 11 days after the first inoculation and remained such for about 4 weeks, after which time the statistical significance for worm burden ceased and never again reached significance during the experiment. This was because of compensating nutritional effects which occurred for the infected kids within NUT2. Within NUT1, differences in body weight between infected and non-infected kids were always large; however, within NUT2 the impact of Haemonchus was negated after the first 4 weeks of the experiment. This reduction was the
cause of the loss of statistical significance for the main effect worm burden. It constitutes a biological interaction which was not statistically validated, but it should be noted that nutrition starts to be statistically significant at the time when worm burden ceases to be significant (Fig. 2), i.e. the interaction leads simultaneously to both phenomena, which are the reverse of each other.

The body weights of W2000 animals were not significantly different from those of W500 kids for most of the experiment, indicating that kids were able to withstand a four-fold difference in infection. During the last 3 weeks, however, the W2000 groups weighed less than the W500 goats in both NUT1 and NUT2 (0.05 < P < 0.1). This could be the result of a cumulative parasitic effect.

Pen effects were consistently significant for body weight, as expected, but never for body weight gain, indicating that differences in initial body weight did not significantly affect weight gains. A nutrition × time interaction was also found to be statistically significant (Fig. 1). Kids fed NUT2 showed continuous growth, while those fed NUT1 lost weight during the first 2 months of the experiment and then grew at a slower rate than those fed NUT2.

Feed intake

Gross feed intake data were available as daily treatment means. It was the only dependent variable for which autocorrelation was found. This was overcome by using PROC AUTOREG (Freund and Littell, 1986). Feed intake differences among worm burdens within nutrition treatments were found to be statistically significant. Owing to differences in the type of feed given goats in NUT1 and NUT2, intakes are expressed relative to the W0 treatment within nutrition level and time period (Table 2).

<p>| TABLE 2 |
| Relative intake based on intake (g kg⁻¹) |
| Days¹ | NUT1 | NUT2 |</p>
<table>
<thead>
<tr>
<th></th>
<th>W0</th>
<th>W500</th>
<th>W2000</th>
<th>W0</th>
<th>W500</th>
<th>W2000</th>
</tr>
</thead>
<tbody>
<tr>
<td>24–55</td>
<td>1.0</td>
<td>1.001</td>
<td>0.935</td>
<td>1.0</td>
<td>0.782</td>
<td>0.867</td>
</tr>
<tr>
<td>56–86</td>
<td>1.0</td>
<td>1.069</td>
<td>0.877</td>
<td>1.0</td>
<td>0.969</td>
<td>0.928</td>
</tr>
<tr>
<td>87–118</td>
<td>1.0</td>
<td>1.439</td>
<td>1.282</td>
<td>1.0</td>
<td>1.070</td>
<td>1.312</td>
</tr>
<tr>
<td>119–149</td>
<td>1.0</td>
<td>1.380</td>
<td>1.140</td>
<td>1.0</td>
<td>1.288</td>
<td>1.075</td>
</tr>
<tr>
<td>149–161</td>
<td>1.0</td>
<td>1.324</td>
<td>1.249</td>
<td>1.0</td>
<td>1.155</td>
<td>0.933</td>
</tr>
</tbody>
</table>

¹Days of test.
Efficiency of feed utilization

The efficiency of feed utilization, calculated as the ratio of weight gain to feed intake (Table 3), shows the impact of parasites on nutrient use. Analysis showed that the worm burden effect was approaching significance (0.05 < P < 0.1). Within NUT1, W0 kids consistently had higher feed efficiencies than W500 and W2000 kids (Table 3), the negative efficiency reported for NUT1–W2000 being the result of a weight loss. Within NUT2, average feed efficiencies across time are similar for W0 and W500, indicating that W500 did not have a noticeable impact on feed utilization, matching the results obtained for body weight. The efficiencies for W2000 are consistently lower, indicating that although growth was not influenced until the final stages of the experiment, these goats required additional feed to support normal growth rates. It is also interesting to note that the efficiencies of all treatment groups increased in the third time period (Table 3). These results follow trends similar to those observed by Andrews et al. (1944), Goldberg (1965) and Wilson et al. (1969).

Actual worm burden

Adult worm numbers were significantly different for worm burden levels and time, but not for nutrition and pen effects. Worm numbers were greater for the W2000 treatment, but establishment rates were usually lower (Table 4), which agrees with Dakkak (1984a). Limited numbers of immature worms were found. However, definitive conclusions regarding the phenomena of larval replacements following the inoculations may not be reached.

The W500 goats remained relatively close to the planned level of burden throughout the experiment, while the W2000 kids initially had a burden of approximately 1300 worms, and only later in the experiment did they reach the level of 2000 worms. These trends in actual worm numbers do not explain the lack of differences between the body weights of infected and non-infected goats.

<table>
<thead>
<tr>
<th>TABLE 3</th>
<th>Least squares means for efficiency of feed utilization</th>
</tr>
</thead>
<tbody>
<tr>
<td>Days</td>
<td>NUT1</td>
</tr>
<tr>
<td></td>
<td>W0</td>
</tr>
<tr>
<td>6–40</td>
<td>0.014</td>
</tr>
<tr>
<td>41–68</td>
<td>0.039</td>
</tr>
<tr>
<td>69–96</td>
<td>0.044</td>
</tr>
<tr>
<td>97–124</td>
<td>0.022</td>
</tr>
</tbody>
</table>

1 Days after the first larval administration.
TABLE 4

Least squares means for actual worm numbers and the corresponding establishment rates for the different treatments

<table>
<thead>
<tr>
<th>Days</th>
<th>W500</th>
<th></th>
<th>W2000</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NUT1</td>
<td>NUT2</td>
<td>NUT1</td>
<td>NUT2</td>
</tr>
<tr>
<td>0-40</td>
<td>405 (27%)</td>
<td>634 (42%)</td>
<td>1367 (23%)</td>
<td>1326 (22%)</td>
</tr>
<tr>
<td>41-68</td>
<td>612 (21%)</td>
<td>476 (-16%)</td>
<td>1976 (15%)</td>
<td>1373 (1%)</td>
</tr>
<tr>
<td>69-96</td>
<td>1171 (56%)</td>
<td>846 (37%)</td>
<td>1891 (-2%)</td>
<td>1894 (13%)</td>
</tr>
<tr>
<td>97-124</td>
<td>695 (-48%)</td>
<td>865 (2%)</td>
<td>2422 (13%)</td>
<td>2161 (7%)</td>
</tr>
</tbody>
</table>

1 Days after the first larval administration.
2 Actual worm numbers in the end of the interval (establishment rate occurred in the interval).

...goats within NUT2, nor do they explain the lack of differences between the body weights of W500 and W2000 kids in both nutritional treatments.

Eggs per gram of feces

No eggs were detected for both control groups, therefore they were not included in this portion of the analysis. A logarithmic transformation to normalize variances was performed before statistical analysis. Statistically significant differences were found among infection groups and time periods, but not among pens. More importantly, an interaction ($P<0.05$) between nutrition and worm burden was found (Fig. 3).

Packed cell volume

Packed cell volume values for worm burden and nutrition levels are presented in Fig. 4. Differences between nutrition, infection levels and the respective interaction were all statistically significant. As worm infection increased, PCV clearly decreased, and as nutrition improved, PCV increased. The interaction was a difference in magnitude and not an alteration in ranking.

A quadratic relationship with time was found to be statistically significant (Fig. 4). As control animals also display such a trend, it might represent an anemia associated with growth (Silverman et al., 1970). A worm burden × time interaction was also statistically significant (Fig. 4).

Mortality was very light throughout the whole experiment, with a few deaths from the lower body weight pens.
Fig. 3. Response of EPG across time (days after the first larval administration) to nutrition (low, NUT1; high, NUT2) and worm burden (no larvae, W0; 500 larvae, W500; 2000 larvae, W2000) effects.

Fig. 4. PCV patterns of kids fed a high (NUT2) or low (NUT1) plane of nutrition and infected with 500 (W500), 2000 (W2000) or no larvae (W0).

DISCUSSION

The above results indicate relationships among nutrition, infection levels and the host. The late differentiation in body weight between the two infected groups could be due to small worm size and less pathogenic ability in environments of increased competition (W2000) (Poteet and Conway, 1966; Le
Jembre et al., 1971; Pradham and Johnstone, 1972; Roberts and Swan, 1981; Dakkak, 1984a). However, the examination of hematological parameters shows a clear set of differences among treatments (Fig. 4). This indicates that the lack of differences in body weight could be attributed to physiological thresholds. Below a certain espoliation level, the goats were able to compensate for the loss without the need to mobilize additional resources or compensatory mechanisms. An alternative could be the presence of other pathogenic actions (digestive, absorption and peristaltic disturbances) not exerted at intensities proportionate with the infection levels (Dakkak, 1984b; Poppi et al., 1985, 1986).

The smaller differences in body weight between infected and non-infected goats on NUT2 indicate that these kids were better able to resist and possibly overcome the consequences of a parasitic infection. For example, at the end of the experiment NUT2–W2000 kids were only 11% lighter than control goats, while NUT1–W2000 kids were 23% below the corresponding controls. This appears to be an important biological interaction, although not statistically significant.

Examination of average daily gains (Table 1) indicates that levels of compensatory growth within NUT2 became apparent 18 days after infection. This could indicate that nutrition is more important in overcoming the consequences of a parasitic infection once it is established than to affect its establishment (Stewart and Gordon, 1953; Gordon, 1964; Goldberg, 1965; Wedrychowicz et al., 1984). Although some of these studies, as well as others cited in this discussion, deal with species other than \textit{H. contortus}, an appropriate consideration of differential pathogenic and immunologic mechanisms has to be made.

In the first 3 months of the experiment, infected kid feed intake was depressed (Table 2), which agrees with Spedding (1954), Poppi et al. (1985, 1986) and Abbott et al. (1986). However, by the fourth month of the experiment, the relative intake of infected goats surpassed that of the controls. Nowhere in the literature did we find a similar phenomenon reported, which may be due to the longer length of our experiment. This increased level of feed consumption did not translate into increased body weights, perhaps indicating that a portion of the additional nutrients consumed were utilized to compensate for parasitic burden, and/or problems of absorption resulting from a damaged mucosa.

The average relative intakes for W500 and W2000 within NUT1 were 1.24 and 1.10, respectively. Within NUT2, the same averages were 1.05 and 1.02, respectively. This indicates that higher quality diets (NUT2) provide sufficient nutrients to satiate appetite and reduce the drive for compensatory intake. Also, as worm burden increased, lower relative intakes were observed. This suggests some sort of biological threshold which depresses appetite when
worm burden is great enough (Spedding, 1954; Poppi et al., 1985, 1986; Ab- 
bott et al., 1986).

Although the nutritional effect was not statistically significant, it appeared 
to impact worm establishment. Within any given infection level, NUT1 goats 
tend to carry larger numbers of worms and achieve higher establishment rates 
than NUT2 kids (Table 4). Previous experimental results are conflicting in 
this area, for Taylor (1934), Whitlock (1949) and Abbott et al. (1985) found 
there to be differences in establishment rate caused, in part, by nutrition, while 
Stewart and Gordon (1953), Gordon (1964) and Abbott et al. (1986) did 
not show this relationship.

Establishment rates tended to decrease with time, most likely owing to pro-
tective immune responses developed in the host by earlier experimental in-
oculations (Silverman et al., 1970; Dargie and Allonby, 1975; Dakkak et al., 
1981; Kimambo et al., 1988). Nevertheless, a build-up in worm numbers oc-
curs for the W2000 kids in the last weeks of the experiment, which matches 
the trend for lower body weight.

No comparable effect of nutrition × worm burden interaction on the num-
ber of eggs per gram of feces (EPG) was found in the literature (Fig. 3). A 
possible explanation is that in environments of limited nutrition and of high 
competition for worm establishment, as in the NUT1–W2000 goats, it is likely 
that the established worms will be smaller and less able to exert their physio-
logical, reproductive and pathogenic mechanisms (Poteet and Conway, 1966; 
Le Jambre et al., 1971; Pradham and Johnstone, 1972; Roberts and Swan, 
1981; Dakkak, 1984a). This would, therefore, lead to the low level of differ-
ences observed within NUT1. The fact that the same differences were not 
found within NUT2 could be attributed to a combination of two mecha-
nisms: (1) suppression of egg-laying ability by the host’s immune defenses 
(Donald et al., 1964; Armour, 1970; Kelly, 1973; Roberts and Swan, 1981) 
when high nutritional inputs are available and low levels of infection are pre-
sent, as in NUT2–W500 kids, which closely matches the findings for body 
weights in the same treatment; (2) a lifting of such egg-laying suppression 
(Dakkak et al., 1981) caused by high levels of infection, as in the NUT2– 
W2000 goats. In the latter, with no nutritional restrictions, the worms could 
then develop to their full physiological and reproductive potential, determi-
ning the proportionate difference observed in EPG as compared to the NUT2– 
W500 goats.

No self-cure phenomena (Gordon, 1948; Dargie and Allonby, 1975) oc-
curred for either infection level (Fig. 3). When repeated infections occur, 
several types of action may take place (Gordon, 1967; Dargie and Allonby, 
1975): self-cure and protection, classical self-cure, temporary suppression of 
egg production followed by hyperinfection, and neither loss of existing infec-
tion nor establishment of new infection. Evaluating adult and immature worm 
counts, and establishment rates, it appears that in this experiment the last
option occurred, although definitive conclusions cannot be reached within the scope of this experiment.

A temporary suppression of egg production, followed by a relative hyperinfection, may have occurred for the W2000 kids in the last time periods (Table 4 and Fig. 3), coinciding exactly with the referred fall in body weight which occurred for the W2000 goats. Within W500 kids, however, the EPG data in Fig. 3 follow a quadratic relationship with time, rising to a peak and then tapering off gradually probably due to worm senescence (Whitlock et al., 1972; Roberts and Swan, 1981), perhaps associated with the development of protective immune responses of the host.

Differences in PCV among infection levels were wider in NUT1 than in NUT2 (Fig. 4), similar to the trends observed for body weight. The W2000 kids, especially within NUT1, did not raise their PCV in the last periods of the experiment, as the other treatments did (Fig. 4), and they fell below the 20% threshold of normality as indicated in Siegmund (1979). This coincides with the previously mentioned hyperinfection and fall in body weight observed for W2000 kids in the last weeks of the experiment. The level of esporiation suffered here is probably beyond a point where compensation starts to be difficult for the normal feedback mechanisms of the organism.

The results presented in this paper demonstrate the complex interactions between nutrition and parasite burden in young growing goats, and help to show how increased levels of nutrition can compensate for the detrimental effects of *H. contortus*. By evaluating the impact of these interactions on different characteristics, it was shown how these factors impacted the goats at various levels of resolution. The information generated in this study, which is biologically useful, will provide the basis for testing and evaluating a computer simulation model. By extending the data through simulation studies, the cost effectiveness of the research is greater, as is the potential impact on goat production.

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