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1 **Title:**

2 Associations between nematode larval challenge and gastrointestinal tract size that affect carcass
3 productivity in sheep

4

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19

20 **Abstract** (299 words)

21 Effects of gastrointestinal parasitism on sheep productivity are usually described using live weight
22 change, however carcass productivity is more accurately described using dressing percentage
23 (carcass weight as a proportion of live weight). This experiment had a 2x2x2 factorial design
24 whereby 10-month-old Merino wethers were fed lucerne (*Medicago sativa*) diets (fresh lucerne or
25 lucerne chaff) with 2 levels of carboxymethylcellulose (CMC) inclusion (0% or 8% CMC) and
26 nematode larval challenge (no larval challenge or 10 000 *Teladorsagia circumcincta* and 10 000
27 *Trichostrongylus colubriformis* per week). Sheep were weighed and euthanased 50 or 51 days after
28 larval challenge and CMC supplementation commenced. Weight of the carcass (hot standard
29 carcass weight) and gastrointestinal organs (full and empty) were recorded and expressed as a
30 proportion of live weight. Larval challenged sheep had a worm egg count (mean \pm standard error)
31 of 173 ± 38 eggs per gram of faeces and total worm count of $30\,237 \pm 2013$ at slaughter. Larval
32 challenged sheep had 1.3% lower dressing percentage ($p=0.048$), and 2% heavier full ($p=0.007$) and
33 1.2% heavier empty gastrointestinal tracts ($p=0.012$) compared to unchallenged sheep. There was
34 no effect of CMC inclusion or lucerne type (fresh or chaff) on gastrointestinal tract weight or
35 dressing percentage. Larval challenged sheep had 1.1% heavier full ($p<0.001$) and 0.6% heavier
36 empty ($p<0.001$) small intestines, and 0.6% heavier full ($p=0.005$) and 0.3% heavier empty
37 ($p=0.026$) large intestines compared to unchallenged sheep. Use of live weight change or other
38 measures based on live weight (eg feed conversion efficiency) to assess the impact of nematode
39 challenge in sheep may underestimate carcass productivity losses associated with larval challenge
40 in sheep even at moderate levels of larval intake and without overt clinical signs of parasitism.
41 Measurement of carcass weight and/or lean meat yield may better reflect the true economic effects
42 of parasitism in sheep.

43

44 **Keywords**

45 Sheep-nematoda, gastrointestinal, productivity, carcass

46

47 **Introduction**

48 Gastrointestinal nematode infection and the subsequent host immune response have
49 important productivity consequences for sheep meat and wool production. The impact of
50 gastrointestinal parasitism on sheep productivity is usually presented in terms of live weight
51 change, or less commonly effects on economy of nutrient utilisation by the host (Greer, 2008;
52 Sykes and Greer, 2003). Measuring changes in live weight may not accurately describe differences
53 in carcass productivity because a number of factors affect the relationship between live weight and
54 carcass weight, including body composition (particularly fatness) and weight of the gastrointestinal
55 tract contents, as well as a number of other factors such as time off feed, diet, weaning, sex, breed,
56 wool growth and the method by which carcasses are processed (Arnold and Meyer, 1988; Davis,
57 2003; Makarechian et al., 1978; Meyer, 1962; Warriss et al., 1987). The relationship between
58 carcass weight and live weight can be expressed using dressing percentage. Whilst nematode
59 infections can have important effects on protein deposition, bone size, mineral deposition,
60 gastrointestinal structure and function (Coop and Angus, 1981), the effect of nematode infections
61 on dressing percentage in lambs is not well described.

62 The experiment described herein was part of a series of studies developing a model for
63 investigating the effects of dietary soluble non-starch polysaccharides (NSP) and gastrointestinal
64 parasites on faecal consistency in ruminants (Jacobson, 2006). Dietary soluble NSP can increase
65 digesta viscosity, intestinal size, faecal moisture content and incidence of diarrhoea, and have been
66 associated with changes in the intestinal microbiota and histological mucosal structure in
67 monogastric species (Choct, 1997; Choct and Kocher, 2000; Elsenhans and Caspary, 2000;
68 McDonald et al., 2001). Diets high in soluble NSP have been associated with increased proliferation
69 of certain pathogenic bacteria in the small intestine of pigs (Pluske et al., 2002) and the
70 establishment of nematode parasites in the small intestine of mice (Sun et al., 2002). However,
71 neither the effects of soluble NSP on gastrointestinal structure and function or the interaction
72 between dietary NSP content with gastrointestinal disease agents have been studied extensively in

73 ruminants. Carboxymethylcellulose (CMC) is a purified soluble, viscous polysaccharide that has
74 been used as a model substrate to increase the viscosity of intestinal contents in pigs (Bartelt et al.,
75 2002; McDonald et al., 2001), chickens (Smits et al., 1997; van der Klis et al., 1993a; van der Klis
76 et al., 1993b) and rats (Elsenhans and Caspary, 2000; Wyatt et al., 1988).

77 The aim of this experiment was to investigate if the larval challenge with *Teladorsagia*
78 *circumcincta* and *Trichostrongylus colubriformis* or CMC affects gastrointestinal tract size and
79 dressing percentage of sheep fed lucerne (*Medicago sativa*) diets.

80

81 **Materials and methods**

82 *Animals and experimental design*

83 The experiment was approved and supervised by the Murdoch University Animal
84 Ethics Committee (permit R1032/04). Forty-eight 10-month-old Merino wethers were housed in
85 individual pens. The experiment was arranged according to a 2x2x2 factorial design with the
86 respective treatments being roughage type (“fresh” lucerne or lucerne chaff), CMC inclusion (0% or
87 8% CMC) and nematode larval challenge (larval challenge or no larval challenge). All sheep were
88 treated with an abamectin-albendazole-levamisole-closantel anthelmintic drench (Q-Drench[®],
89 Virbac) before the study commenced and fed either “fresh” lucerne or lucerne chaff for a two-day
90 introductory period. After the introductory period, sheep were stratified by live weight, allocated to
91 treatment groups and the CMC supplementation and larval dosing commenced. The experimental
92 treatment period lasted 50 days, however fresh lucerne was not available after day 21 of treatment
93 period and hence after day 21 all diets were based on lucerne chaff.

94

95 *Diets*

96 The composition and chemical analysis of the diets are outlined in Table 1. All dietary
97 treatments were fed *ad libitum* and sheep were fed daily.

98 The “fresh lucerne” diet was grown on a commercial lucerne property south of Perth,
99 Western Australia. The period between cutting and delivery ranged between 2 hours and 5 days
100 depending on weather conditions. Fresh lucerne was fed within 48 hours of arrival or loosely
101 packed into sacks and stored at 4°C for up to 3 days. There were two episodes of heavy rainfall over
102 several days that caused substantial deterioration of the quality of the standing lucerne crop
103 prompting the termination of the fresh lucerne treatment. All sheep were then fed lucerne chaff
104 from day 21 until day 50. Lucerne chaff was sourced from the same property as the fresh lucerne
105 diet.

106 Carboxymethylcellulose (CMC) diets included high viscosity CMC (1500-3000cps
107 when 1% solution at 25°C, Sigma Aldrich C-5013) that was added at a rate 8% of the total dry
108 matter content of the diet. Dry matter content of the fresh lucerne was measured by drying at 65°C
109 for at least 48 hours.

110

111 *Nematode larval challenge*

112 Sheep in the larval challenge treatment groups were dosed orally with 10 000 *Tel.*
113 *circumcincta* (Yalanbee strain, Department of Agriculture and Food Western Australia) and 10 000
114 *T. colubriformis* (Yalanbee strain, Department of Agriculture and Food Western Australia) per
115 week divided into two equal doses. The first larval dose was given on Day 0 and the last dose on
116 Day 48.

117

118 *Live weight and organ weight measurements*

119 Sheep were weighed twice weekly throughout the course of the experiment and again
120 immediately prior to euthanasia. Sheep were euthanased using a captive bolt and exsanguination on
121 days 50 and 51 of the experimental period. The viscera were removed and divided into five
122 segments: “stomachs” (reticulorumen/omasum/abomasum), “small intestine” and “large intestine”
123 (including caecum). Each segment was tied off and the full weight recorded. Empty weight of each

124 section was recorded following emptying of the contents, rinsing with water and dry blotting the
125 tissue with paper towel. Hot standard carcass weight (HSCW) was recorded based on AUS-MEAT
126 standard trim.

127

128 *Parasitological measurements*

129 Faeces were collected per rectum on 13 occasions throughout the experimental period
130 for modified McMaster worm egg count. The worm egg counts and total worm counts were
131 performed using methods described in Australian Standard Diagnostic Techniques for Animal
132 Diseases Manual (Lyndal-Murphy, 1993).

133

134 *Statistical analyses*

135 Daily dietary intake was calculated based on dry matter intake as a proportion of live
136 weight. Dressing percentage and gastrointestinal organ size were calculated based on HSCW and
137 gastrointestinal organ weight as a proportion of live weight (recorded immediately before
138 euthanasia). Statistical analyses were performed using SPSS 11.0 for Macintosh OS X (SPSS Inc,
139 Chicago, USA). The effect of experimental treatments (roughage type, CMC inclusion and larval
140 challenge) on body composition was analysed by univariate analysis of variance (ANOVA) with the
141 three treatments included as independent variables. Differences in the mean measurements between
142 treatment groups were analysed using the least squares difference post-hoc test. Relationships
143 between total worm count (excluding third stage larvae) and dressing percentage, full
144 gastrointestinal tract weight and empty gastrointestinal tract weight were analysed using Pearson
145 correlation (2-tailed significance).

146

147 **Results**

148 *Parasite establishment*

149 No strongyle worm eggs were detected in the faecal samples collected on day 1. Larval
150 establishment in the larval challenged sheep are shown in Table 2. The mean total worm count of
151 larval challenged sheep at slaughter (days 50 and 51) was $30\,237 \pm 2013$ (total worm count
152 excluding third stage larvae \pm standard error). There was no effect of roughage ($p=0.443$) or CMC
153 inclusion ($p=0.180$) on total worm count. Adult worm count (mean adult nematodes \pm standard
154 error) in larval challenged sheep was $20\,681 \pm 1575$ *T. colubriformis* and 2898 ± 549 *Tel.*
155 *circumcincta*. The mean strongyle worm egg count of larval challenged sheep at slaughter was
156 173 ± 38 eggs per gram of faeces. None of the sheep in the larval challenge groups showed overt
157 signs of parasitism such as listlessness, weight loss or persistent diarrhoea.

158

159 *Dietary intake and live weight change*

160 Mean dry matter intake, mean daily weight gain and live weight change over the course
161 of the experiment are shown in Table 3. Daily dry matter intake of sheep fed the fresh lucerne diets
162 (2.5% live weight per day) was lower compared to sheep fed lucerne chaff diets (3.0% live weight
163 per day) over the course of the experiment ($p<0.001$). After the fresh lucerne diets were
164 discontinued (from day 22 until slaughter) and all sheep were fed lucerne chaff, there was no
165 significant effect of earlier lucerne type (“fresh” or chaff fed day 1-21) on mean dry matter intake
166 ($p=0.927$). There was no effect of CMC inclusion ($p=0.196$) or larval challenge ($p=0.179$) on mean
167 dry matter intake.

168 Sheep fed the fresh lucerne diets gained more weight (23.0% increase in live weight)
169 than sheep fed lucerne chaff diets (18.5% increase in live weight, $p=0.032$) over the course of the
170 experiment. There was a trend to increased average daily gain in live weight in the unchallenged
171 sheep (151g/day) compared to the larval challenged sheep (128g/day) over the course of the
172 experiment ($p=0.062$).

173

174 *Gastrointestinal organ size and dressing percentage*

175 Gastrointestinal organ size and dressing percentage are shown in Table 3. There was no
176 significant effect of roughage, CMC inclusion or larval challenge on the size of either empty or full
177 reticulorumen-omasum-abomasum (stomachs) at slaughter. Sheep in the larval challenge groups
178 had heavier full small intestines (4.5% versus 3.4% live weight, $p<0.001$) and heavier empty small
179 intestines (1.9% versus 1.2% live weight, $p<0.001$) compared to unchallenged sheep. There was no
180 effect of roughage or CMC inclusion on full or empty small intestine weight relative to live weight,
181 but there was an interaction between roughage and larval challenge on full small intestinal weight
182 ($p=0.032$) whereby the difference between the full small intestine weight of larval challenged (4.7%
183 live weight) and unchallenged sheep (3.1% live weight) within the fresh lucerne treatments was
184 greater than the difference between larval challenged (4.3% live weight) and unchallenged (3.7%
185 live weight) sheep in the chaff treatments.

186 The larval challenged sheep had heavier full large intestines (5.0% versus 4.4% live
187 weight, $p=0.005$) and empty large intestines (2.8% versus 2.4% live weight, $p=0.026$) compared
188 with unchallenged sheep. There was no effect of CMC inclusion on full ($p=0.355$) or empty
189 ($p=0.940$) large intestine size. There was no effect of roughage type on full large intestine size
190 ($p=0.759$) but there was a trend ($p=0.066$) to heavier empty large intestine of sheep fed lucerne
191 chaff for the first 21 days (2.7% live weight) compared to sheep fed fresh lucerne in the first 21
192 days (2.4% live weight). There was also a three-way interaction between larval challenge, roughage
193 and CMC inclusion on empty large intestinal weight ($p=0.041$), whereby sheep in the fresh lucerne
194 control group (fresh lucerne/0% CMC/no larval challenge) had smaller empty large intestine (1.8%
195 live weight) compared to all other treatments except for lucerne chaff/8% CMC/unchallenged
196 group.

197 As a consequence of the changes in weight of the small and large intestines, the larval
198 challenged sheep had a lower dressing percentage (39.5%) compared to unchallenged sheep
199 (40.8%) at slaughter ($p=0.048$). There was no significant effect of roughage or CMC inclusion on
200 dressing percentage. Larval challenged sheep had heavier full gastrointestinal tracts as proportion of

201 live weight (26.0% live weight) compared to unchallenged sheep (24.0% live weight, $p=0.007$). The
202 empty gastrointestinal tracts of larval challenged sheep (9.2% live weight) were heavier than the
203 unchallenged sheep (8.0% live weight, $p=0.012$). There was no effect of roughage or CMC
204 inclusion on full or empty gastrointestinal tract size. There was no significant correlation between
205 total worm count and full ($p=0.147$) or empty ($p=0.902$) gastrointestinal tract weight as a proportion
206 of live weight or dressing percentage ($p=0.119$) in larval challenged sheep.

207

208 **Discussion**

209 The effects of parasitism on the intestinal size of sheep and consequences for carcass
210 productivity have received surprisingly little attention in the literature. Data from the present study
211 shows that larval challenge with *T. colubriformis* and *Tel. circumcineta* increased the size of the
212 gastrointestinal tract as a proportion of live weight, thereby causing a decrease in the economically
213 important measurement of dressing percentage.

214 Intestinal nematode infections have been shown to increase the size of the
215 gastrointestinal tract in guinea pigs (Symons and Jones, 1983) and in pigs (Thomsen et al., 2006).
216 *Trichuris suis* infection in pigs was associated with increased mucin staining area, crypt area and
217 crypt height but not crypt density or tunica muscularis thickness (Thomsen et al., 2006). The
218 increase in gastrointestinal tissue mass of sheep challenged with nematode larvae may be due to
219 stimulation of the local immune response (including infiltration of mucosal mast cells and globule
220 leukocytes and mucous production), and sheep selected for low worm egg count have heavier small
221 and large intestines (relative to carcass weight) compared to unselected sheep after trickle infection
222 with *T. colubriformis* and *Tel. circumcineta* (Liu et al., 2005). The genotype of the sheep may
223 therefore be expected to influence the magnitude of effect of parasite challenge on carcass
224 productivity (Greer, 2008; Liu et al., 2005) and so assessment of the effect of parasite challenge on
225 carcass productivity of sheep selected for parasite resistance using low worm egg count also
226 warrants further consideration.

227 If increased size of the gastrointestinal tract relative to live weight is shown to be a
228 consistent finding in sheep challenged and infected with *T. colubriformis* and *Tel. circumcincta*,
229 then measurements of live weight change could be expected to underestimate the impact of
230 parasitism on sheep productivity because live weight change may not fully describe the effect of
231 parasitism on carcass weight or lean meat yield. The effect of larval intake on sheep productivity in
232 general, and particularly on sheep meat productivity, therefore warrants further investigation as the
233 most important production penalties usually attributable to nematode infection and grazing of
234 pastures contaminated with nematode larvae are reductions in live weight gain, nutrient utilisation,
235 soft tissue deposition, skeletal growth, milk and wool production (Greer, 2008; Sykes, 1978, 1994).

236 The trickle larval challenge used in this experiment resulted in sub-clinical parasitic
237 infections, specifically the infected sheep continued to gain weight, intake was not significantly
238 reduced relative to non-infected sheep and there were no overt signs of parasitic disease such as ill
239 thrift, listlessness or persistent diarrhoea. The mean worm egg count of infected sheep at slaughter
240 (173 eggs per gram) was below the level at which a treatment would normally be recommended.
241 This is important because it suggests that lambs with low egg counts (<200 eggs per gram) grazing
242 pastures contaminated with larvae resulting in a larval intake of 20 000 larvae per week and
243 showing no overt signs of parasitic disease may be suffering carcass production losses due to
244 reduced efficiency of the conversion of feed to hot carcass weight. It was likely that the diversion of
245 nutrients away from carcass productivity was the result of the immune response to larval challenge
246 and was consistent with other studies showing that the acquisition and maintenance of immunity to
247 gastrointestinal parasites in sheep is a nutritionally costly process inducing a diversion of nutrients
248 from productive to immunological tissues (Greer, 2008). The exposure of the lambs to nematode
249 parasites prior to the start of the experiment was not known and so further work would be required
250 to better describe the effect of prior larval exposure (including species of nematode, size and
251 duration of larval challenge) on organ weight and dressing percentage in lambs.

252 The difference in dressing percentage observed (1.3%) in the larval challenged lambs
253 was small but significant, representing a carcass weight difference of 0.585kg for a 45kg lamb (live
254 weight) or 130g difference in carcass weight for every 10kg of lamb live weight (not held off feed).
255 Furthermore, we believe that dressing percentages of sheep in this study were underestimated
256 because sheep were not held off feed before to slaughter as would normally be the case for lambs
257 consigned for commercial slaughter. Dressing percentage would be expected to increase with
258 fasting, primarily due to decrease in the weight of gut contents and corresponding decrease in live
259 weight following feed withdrawal (Thompson et al., 1987; Warriss et al., 1987). Leanness also
260 affects dressing percentage percentages (Thompson et al., 1987). Fat score of the lambs was not
261 recorded for this experiment. Other factors that associated with differences in dressing percentage
262 are roughage content of diet, weaning, skin weight (wool length), sex and breed (Arnold and Meyer,
263 1988; Davis, 2003; Makarechian et al., 1978), although these factors were constant across all
264 treatment groups in this study. There was no effect of dietary treatments (roughage type and CMC
265 inclusion) on dressing percentage in this experiment. The differences in dressing percentage of
266 larval challenged and unchallenged sheep would be expected to be present if the lambs had been
267 held off feed for 12 hours before slaughter because there was a 1.2% live weight difference in the
268 empty gastrointestinal tract.

269 The reason for differences in the establishment of the two nematode species was not
270 tested in this experiment, but possible reasons include differences in viability of the cultured larvae,
271 differences in prior exposure to the two species or differences in the host immune response to the
272 two species (Dobson et al., 1992).

273 **Conclusion**

274 Larval challenge with *T. colubriformis* and *Tel. circumcineta* larvae increased the
275 weight of gastrointestinal tracts as a proportion of live weight in sheep compared to unchallenged
276 sheep and this was associated with a reduction in dressing percentage. The larval challenged sheep
277 had heavier small and large intestines than unchallenged sheep and this difference was observed in

278 both the full and empty weights of these organs. Use of live weight change or other measures based
279 on live weight (such as feed conversion efficiency) to assess the impact of larval challenge and
280 nematode infection may underestimate productivity losses associated with parasitism in sheep, and
281 measurement of carcass weight and/or lean meat yield may better reflect the true economic effect of
282 parasitism in sheep meat production systems.

283

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292

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- 363
- 364
- 365

Table 1: Experimental design and dietary treatments

Larval challenge (L) Roughage (R) CMC (C)	Unchallenged				Larval challenge			
	Fresh lucerne		Lucerne chaff		Fresh lucerne		Lucerne chaff	
	No CMC	8% CMC	No CMC	8% CMC	No CMC	8% CMC	No CMC	8% CMC
Sheep (n)	6	6	6	6	6	6	6	6
Nematode dosing								
<i>Tel. circumcincta</i> /week	-	-	-	-	10 000	10 000	10 000	10 000
<i>T. colubriformis</i> /week	-	-	-	-	10 000	10 000	10 000	10 000
Dietary composition (% dry matter)								
Fresh lucerne	100%	92%	-	-	100%	92%	-	-
Lucerne chaff	-	-	100%	92%	-	-	100%	92%
CMC	-	8%	-	8%	-	8%	-	8%
Calculated and chemical analysis of diet								
Mean DM	45%	46%	89%	88%	45%	46%	89%	88%
Mean ME (MJ/kg DM)	10.2	10.0	10.2	10.0	10.2	10.0	10.2	10.0
Mean CP (% DM)	25%	24%	24%	23%	25%	24%	24%	23%

Table 2: Larval establishment of nematodes in larval challenged lambs (mean \pm standard error)

	Fresh lucerne		Lucerne chaff	
	No CMC	8% CMC	No CMC	8% CMC
Adult <i>Tel. circumcincta</i>	2692 \pm 755	2367 \pm 732	3300 \pm 837	3233 \pm 1900
Adult <i>T. colubriformis</i>	20 775 \pm 3454	24 950 \pm 2477	14 350 \pm 2898	22 650 \pm 2600
Immature	883 \pm 244	550 \pm 242	925 \pm 217	1267 \pm 554
Fourth stage larvae	6733 \pm 1464	4633 \pm 812	5292 \pm 766	6350 \pm 1934
Total worm count	31 083 \pm 2997	32 500 \pm 3277	23 867 \pm 3322	33 500 \pm 5693

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Table 3: Effect of dietary treatments and larval dosing on dry matter (DM) intake, growth rate, hot standard carcass weight (HSCW) and weight of gastrointestinal organs as a proportion of live weight (Lwt) of sheep

Larval challenge (L) Roughage (R)	Non-challenged				Larval challenge				s.e.d.	ANOVA significance (p-value)						
	Fresh lucerne		Lucerne chaff		Fresh lucerne		Lucerne chaff			L	R	C	LxR	LxC	RxC	LxRxC
CMC (C)	No CMC	8% CMC	No CMC	8% CMC	No CMC	8% CMC	No CMC	8% CMC								
Mean DM intake (%/day)	2.68 ^A	2.44 ^A	3.14 ^B	3.04 ^C	2.49 ^A	2.59 ^A	2.99 ^{BC}	2.92 ^{BC}	0.04	-	***	-	-	-	-	-
Mean daily gain (g/day)	180 ^A	138 ^{AB}	139 ^{AB}	145 ^{AC}	149 ^{AC}	149 ^{AC}	91 ^B	121 ^{BC}	8.35	0.062	*	-	-	-	-	-
Lwt change (% change)	27.9 ^A	19.7 ^{BC}	20.8 ^{AB}	22.3 ^{AC}	21.9 ^{AB}	22.5 ^{AC}	13.9 ^B	16.9 ^{BC}	1.43	0.062	*	-	-	-	-	-
Dressing % (HSCW/Lwt)	40.9	41.4	40.0	41.0	38.9	40.0	39.9	39.1	0.47	*	-	-	-	-	-	-
Full gut weights (% Lwt)																
Stomachs	15.0	16.8	15.2	15.2	15.0	15.7	15.9	17.4	0.52	-	-	-	-	-	-	-
Small intestine	3.2 ^{AB}	3.1 ^A	4.1 ^{BC}	3.2 ^{AB}	4.6 ^C	4.8 ^C	4.3 ^C	4.3 ^C	0.15	***	-	-	*	-	-	-
Large intestine	4.7 ^{AB}	4.4 ^{AB}	4.5 ^{AB}	4.1 ^B	4.8 ^B	5.0 ^B	5.1 ^B	5.0 ^B	0.13	**	-	-	-	-	-	-
Gastrointestinal tract	24.8 ^{AB}	23.7 ^{AC}	24.5 ^{AB}	22.9 ^{AB}	25.7 ^{BC}	25.5 ^{AB}	25.4 ^{AB}	27.4 ^B	0.33	**	-	-	-	-	-	-
Empty gut weights (% LWt)																
Stomachs	4.2	3.8	4.7	4.2	4.9	5.0	3.7	4.6	0.32	-	-	-	-	-	-	-
Small intestine	1.2 ^A	1.2 ^A	1.4 ^{AC}	1.2 ^A	1.9 ^B	2.0 ^B	1.8 ^B	1.7 ^{BC}	0.06	***	-	-	-	-	-	-
Large intestine	1.8 ^A	2.6 ^B	2.8 ^B	2.4 ^{AB}	2.8 ^B	2.5 ^B	2.9 ^B	2.8 ^B	0.11	*	0.066	-	-	-	-	*
Gastrointestinal tract	7.7 ^{AB}	7.5 ^A	8.8 ^{AB}	7.9 ^{AB}	9.7 ^B	9.6 ^B	8.4 ^{AB}	9.1 ^{AB}	0.33	*	-	-	-	-	-	-

s.e.d. standard error of the difference

- P>0.100

* p<0.05

** p<0.01

***p<0.001