Vet. Res. 35 (2004) 91–101

DOI: 10.1051/vetres:2003043

Original article

Regulation of *Teladorsagia circumcincta* and *Trichostrongylus colubriformis* worm populations by grazing sheep with differing resistance status

Lucas GRUNER[a]*, Jacques CORTET[a], Christine SAUVÉ[a], Hervé HOSTE[b]

[a] INRA, BioAgresseurs, Santé, Environnement, 37380 Nouzilly, France
[b] UMR 959 INRA-ENVT Physiopathologie Infectieuses et Parasitaires des Ruminants, 23 chemin des Capelles, 31076 Toulouse Cedex, France

(Received 7 April 2003; accepted 31 July 2003)

Abstract – In an experiment lasting 4 years, changes in the *Teladorsagia circumcincta* and *Trichostrongylus colubriformis* populations were compared in lambs and adult sheep with differing resistance statuses. Two flocks of 30 rams (resistant R and susceptible S) grazed separate pastures and 8 rams were slaughtered in the middle and at the end of each grazing season. Five groups of tracer lambs were added each year to estimate the pasture infectivity and were killed for worm counts. The availability of animals with differing resistance statuses (rams and tracer lambs) and differing levels of infection made it possible to investigate the number, size and fecundity of worms of these two species. The inflammatory response was measured in the rams by counting the globule leukocytes, mast cells and eosinophils in the fundic, pyloric and intestinal mucosa. In the tracer lambs, the daily egg production by the female worms of both species was negatively correlated with the worm burden. Worm length accounted for 60 and 70% of the variation in the number of eggs in utero for *T. circumcincta* and *T. colubriformis* respectively. Worm length was closely associated with the resistance status of the host; there were greater differences between lambs, and S and R rams for *T. colubriformis*. *T. circumcincta* worm lengths were not affected by the worm number. Globule leukocyte counts were related to the worm burdens, and mast cell counts to worm length in the R and S rams. The number, size and fecundity of the worms may well be regulated by similar mechanisms in both species, but *T. colubriformis* seemed to be more intensively regulated than *T. circumcincta*. This finding could be useful in devising more effective methods of parasite control.

sheep-nematoda / *Teladorsagia circumcincta* / *Trichostrongylus colubriformis* / population dynamics / resistance

1. INTRODUCTION

Genetic resistance to gastrointestinal nematode parasites in sheep has been demonstrated in a variety of situations after spontaneous or deliberate infection. The most convenient way of measuring resistance is the faecal egg count (FEC), the heritability of which ranges from 0.2 to 0.3 [1, 16]. These heritability values suggest that selection for increased resistance is a lengthy process and that it would take a long

* Corresponding author: gruner@tours.inra.fr

time for lower pasture contamination to lower the general level of infection of the flock. However, the FEC parameter is the outcome of complex interactions between parasite populations and their hosts. Recent findings concerning *T. circumcincta* infection have clarified the situation in sheep [13–15], showing that (i) worm length is positively associated with fecundity, (ii) worm length, and hence fecundity, decline as worm numbers increase and (iii) lambs can control worm length but not worm number. IgA secretion appears to be a major mechanism regulating worm length. Most of the data were obtained in grazing lambs drenched each month and slaughtered when six months old.

In this paper we describe the regulation of worm burdens and fecundity in grazing sheep with differing resistance statuses and history of exposure to *T. circumcincta* and to *T. colubriformis* infection. Two groups of rams selected for their resistance or susceptibility to both species grazed separate pastures over a period of four years, and susceptible young tracer lambs were added to measure pasture infection. Data were collected from rams and lambs that were slaughtered at regular intervals during the experiment. The ecological consequences of the selection for low faecal egg counts have been reported by Gruner et al. [6].

2. MATERIALS AND METHODS

2.1. Experimental design

Two flocks of 30 rams of the INRA 401 breed were selected from amongst 200 ram lambs on the basis of their low (resistant R) or high (susceptible S) faecal egg counts following two deliberate infections with a mixture comprising 12 000 *T. circumcincta* and 8 000 *T. colubriformis* infective larvae. The lambs were kept in penned conditions, and the first infection dose was given when they were 4 months old. A fenbendazole treatment was administered 33 days later and this was followed by the second infection dose after a 2-week interval. The FEC was estimated on Days 26 and 33 after each exposure to infection, and the 200 lambs were ranked according to the mean of the 4 FEC (after a square root transformation). For the four consecutive years from 1996 to 1999, these two flocks grazed separate pastures from mid April to mid November, and were housed for the winter. Each year, six to nine randomly selected rams from each flock were killed in the middle and at the end of the grazing season after being penned indoors for 3 weeks, and their worm burdens were established. In order to replace the rams that had been killed, each autumn a new group was selected at the Experimental Farm "La Sapinière" where the lambs were grazed during the autumn. More than 80% of the spontaneous natural infection consisted of *T. circumcincta* and the FEC were processed in November. As a consequence, in year 1 all the rams were 1 year old when they were turned out; in year 2, half were 1 year old and half 2 years old; in years 3 and 4, half were 1 year old, one quarter 2 years old and one quarter 3 years old. The ages of the killed rams followed the same patterns. Five groups of six 3–4 month-old lambs of the same INRA 401 breed were used each year on each pasture to estimate the level of infective larvae. They were grazed for 18 days and then slaughtered to estimate the worm burden after being penned for 3 weeks. A total of 128 rams and 240 tracer lambs were slaughtered. The details of this experiment are described in Gruner et al. [6]. All the sheep were weighed at the end of their grazing period.

2.2. Worm length and fecundity measurements

A faecal egg count was performed on the day before each sheep was necropsied. The eggs of each species were identified as described by Gruner et al. [6]. Briefly, the faeces were cooled to 4 °C after being

collected, and kept for 24 h at 10 °C and then for a further 20 h at 12 °C before the FEC. *T. circumcincta* eggs were at the embryo stage, those of *T. colubriformis* at the tadpole stage, and those of *Haemonchus contortus* (a species added during year 3) had not started to develop. At the time of necropsy, about 50 female worms of each species were sampled from each animal, fixed in Denke solution (a mixture of 15% formaldehyde, 5% acetic acid, 10% glycerin and 24% of alcohol 95%) and the length of the 25 worms measured using a camera attached to a microscope using Optimas® software (6.2 version). For each worm, the number of eggs in utero was counted. Since this was time consuming and a number of the sheep did not have enough worms, this was done on 96 rams and 56 lambs for *T. circumcincta* and on 74 rams and 75 lambs for *T. colubriformis*, respectively. These numbers were sufficiently high to permit significant statistical analysis. The daily egg excretion was estimated taking into account the faecal excretion found for this breed under penned conditions, which was 41 g per day and per kg of metabolic live weight [6]. The number of eggs produced per day per female worm was calculated as the number of eggs excreted per day divided by the number of female worms. Valid data were obtained for 116 rams and 104 lambs for *T. circumcincta* and for 103 rams and 66 lambs for *T. colubriformis,* respectively.

2.3. Mucosal cell counts

Inflammatory responses were compared in the R and S rams killed in the middle and at the end of the first two grazing seasons by counting mast cells, eosinophils and globule leukocytes in sections prepared from the pylorus, fundus and small intestine. From each site, two one-cm^2 tissue samples were serially sectioned and fixed in 10% buffered formaldehyde or Carnoy's solution respectively. The tissues were embedded in paraffin wax and then 5 µm sections were cut, mounted on slides using glycerinated albumin (BDH), and dried for 12 h at 40 °C. Six histological slides were prepared from each animal at each site. Formalin-fixed tissues were stained with Hematoxylin-Eosin to count the globule leukocytes and eosinophils. The tissues fixed in Carnoy's solution were stained with Alcian Blue/Safranin for mast cells. For each slide, the globule leukocytes, mast cells and eosinophils were counted in 10 randomly selected fields under ×400 magnification using a 10×10 calibrated grid [17].

2.4. Statistical analysis

The SAS suite of programs (SAS Institute) was used. The General Linear Model (GLM) procedure was used to carry out variance and regression analysis of egg excretion, worm length, number of eggs in utero and cell counts. The values for the worm numbers, egg output per female per day, and eggs in utero were log-transformed [log10(n + 1)]. Nearly all the cell counts were normalized after log transformation.

3. RESULTS

3.1. Worm burdens

Table I shows the geometric mean of the number of *T. circumcincta* and *T. colubriformis* harbored by rams after grazing for half of or for the whole grazing season, and by tracer lambs grazing for 18-day-periods on the R and S pastures. These numbers included the same L4 and juvenile worms, which corresponded to less than 5% of the burden. Individual variation was always high, but these data gave an indication of variables such as year, season, age (lambs or rams one year old or more), resistance status of rams (R or S) and level of exposure (from the tracer lamb data). Spring 1996 was unusual, since both pastures were heavily contaminated (about 140 and 250 million *T. circumcincta* and *T. colubriformis* eggs) as a result of being grazed by infected sheep for

Table I. Geometric mean worm burdens in rams and tracer lambs during the four grazing seasons (R = resistant, S = susceptible, trac = tracer lambs). Each number is the mean of 8 rams or 6 tracer lambs slaughtered at the end of the corresponding grazing period.

Tracer grazing period	*T. circumcincta*				*T. colubriformis*			
	S trac	S ram	R trac	R ram	S trac	S ram	R trac	R ram
Early spring 1996	10 548		6 597		9 242		4 263	
Late spring	766		1 125		933		614	
The whole spring		5 394		7 034		8 511		119
Summer	720		470		2 004		579	
Early autumn	1 337		2 375		7 042		3 332	
Late autumn	4 728		1 305		11 680		1 008	
The whole grazing season		3 120		1 064		103		3
Early spring 1997	1 150		238		7		2	
Late spring	3 201		660		14		0	
The whole spring		4 425		1 939		63		3
Summer	11 348		2 239		204		5	
Early autumn	6 702		4 494		4 987		16	
Late autumn	2 697		3 887		3 627		194	
The whole grazing season		5 106		2 933		7 881		219
Early spring 1998	4 500		1 342		47		0	
Late spring	9 806		7 484		46		6	
The whole spring		14 239		2 959		147		2
Summer	3 856		858		304		0	
Early autumn	14 538		10 214		7 666		46	
Late autumn	34 281		30 606		33 500		6	
The whole grazing season		27 000		5 670		872		4
Early spring 1999	2 681		1 814		39		2	
Late spring	5 919		8 039		103		3	
The whole spring		12 888		2 168		382		7
Summer	11 107		6 521		1 423		52	
Early autumn	9 314		6 439		15 890		1 531	
Late autumn	8 684		7 624		35 950		20 940	
The whole grazing season		4 796		2 907		2 969		15 252

several days in early April. Favorable climatic conditions permitted the two species to develop high populations in both the tracer lambs and the rams. The mean burden was always higher in the S than in the R rams, except for *T. circumcincta* in late spring 1996. In the following years, the larval populations surviving the winter were low, and infection levels were higher in the late autumn, particularly in 1998. *T. colubriformis* nearly disappeared in the R pasture grazed by R rams in years 2 and 3, but reappeared in year 4 (fall 1999), when R rams harbored high worm burdens (higher than the S rams). Very high worm burdens were observed in the tracer lambs in the late fall.

3.2. Relationships between worm burden, worm fecundity and worm length

The distribution of the parasitological variables was determined by univariate

analysis. A large range of worm numbers was observed in our set of data (from zero to more than 88 000), and so a logarithm transformation was used to normalize the data. This was however less satisfactory for *T. colubriformis* worm burdens, due to the occurrence of many nil values. Log transformation was applied to the fecundity data. The normal distribution (Wilk-shapiro normal test 0.98, $P < 0.58$) of the length of *T. circumcincta* female worms (LE) made it possible to estimate the regressions without having to transform this variable. It was difficult to normalize the length of *T. colubriformis* female worms, even when various different transformations were tried.

The daily egg production (EP) per female fell in both species as the worm burden increased in the tracer lambs, but not in the rams. The coefficient of correlation was however higher and more significant for *T. circumcincta* in tracer lambs, where the number of adult worms ranged from a few hundred to 70 000 ($r = –0.60$, $P < 0.0001$, $n = 55$ data and $r = –0.29$, $P < 0.017$, $n = 28$ for *T. circumcincta* and *T. colubriformis*, respectively).

LE alone accounted for 27% of the variation in egg production in both rams and lambs (52% in the tracer lambs alone), and 60% of the variation in the number of eggs in utero (UT) of *T. circumcincta*. The equations of the regression lines are as follows:

LogEP *T. circumcincta* = 0.29 LE – 0.94 ($P < 0.0001$, $n = 129$ rams and lambs);

LogUT *T. circumcincta* = 0.20 LE – 0.52 ($P < 0.0001$, $n = 154$ rams and lambs).

UT was negatively related to the worm burden in the tracer lambs ($r = –0.55$, $P < 0.0001$, $n = 55$); the regression was not significant in the rams, but was significantly related to LE ($r = +0.78$, $P < 0.0001$, $n = 129$).

For *T. colubriformis*, the egg production was less closely correlated with the worm burden, and not correlated at all with the length of the female worms, even though this length accounted for 70% of the variation in the number of eggs in utero in both rams and lambs. The equation of the regression line is as follows:

Log UT *T. colubriformis* = 0.18 LE + 0.10 ($P < 0.0001$, $n = 152$ rams and lambs).

In addition to these regression analyses, the relative effects of factors such as resistance status (R or S), season, year and type of host (ram or tracer lamb) were explored using the GLM procedure. For the rams, the other two factors explored were age (one year or more) and prior exposure, which was the cumulative worm count for the tracer lambs for the corresponding grazing period. The most significant models are shown in Table II. The EP of *T. circumcincta* was modulated by the resistance status: female worms in the R rams necropsied in summer produced 48 eggs per day compared with 103 to 118 in the S rams and in both the R and S rams at the end of the grazing season. The correlation with LE was by far the most important factor. Similar effects were observed in the number of eggs in utero, but again LE was by far the most obvious weighting factor. This length was greater in lambs (11.9 mm) than in rams (9.6 mm). The regression with WB (as the covariate) was not significant. The correlation of prior exposure of the rams (as the covariate) was significant only for EP ($P < 0.004$), but did not improve the model; age had no significant effect.

For *T. colubriformis*, none of the factors investigated had any significant effect on EP. Every year, the female worms were longer in the R than in the S rams, with values of 6.2 and 5.7 mm in the spring, 6.2 and 6.1 in the summer, 6 and 5.5 in the fall respectively. The worms recovered in 1996 were shorter (4.8 mm) than those found in later years (6.2 to 6.4 mm). Worms were longer in the lambs than in the rams, and the length was correlated with worm burden. In fact, the longest worms were found in the tracer lambs, irrespective of worm burden (range 9 to 43 000), and the worms were shorter in S and R rams even after they had been exposed to larvae for less

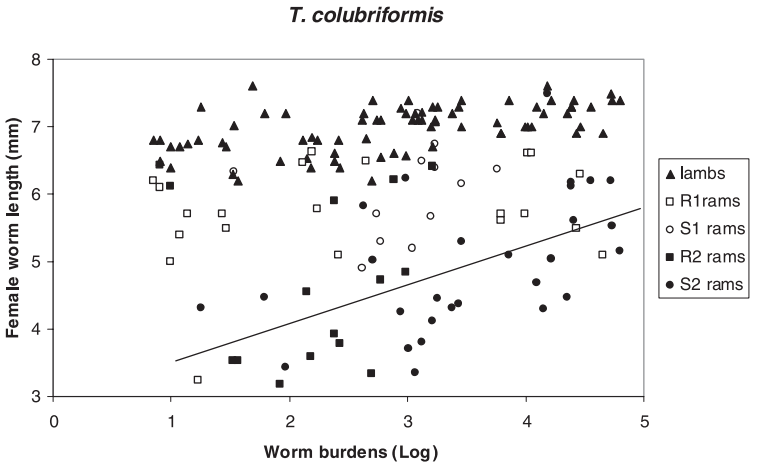

Figure 1. Female worm length in *T. colubriformis* populations from hosts with differing statuses with regards to resistance to this parasite species. (R/S = resistant or susceptible, 1 or 2 are rams exposed for a short or long time respectively to a contaminated pasture; the regression line refers only to the S2 rams.)

Table II. Variance analysis of worm length (LE) and fecundity (EP = daily egg production per female worm, UT = number of eggs in utero) in *T. circumcincta* (Tcirc) and *T. colubriformis* (Tcolu) populations (R/S status, type = rams or lambs).

Variable	Factors in the model	*P*	R^2	Samples	Means
Log EP Tcirc	R/S (season)	0.015	0.48	129 rams and lambs	
	season (year)	0.0001			
	LE Tcirc (covar.)	0.0001			
Log UT Tcirc	R/S (season)	0.026	0.65	154 rams and lambs	
	year	0.04			
	LE Tcirc (covar.)	0.0001			
LE Tcirc	Type	0.042	0.06	154 rams and lambs	9.6 mm in rams 11.9 in lambs
Log UT Tcirc	R/S (season)	0.009	0.09	154 rams and lambs	
Log UT Tcolu	R/S (season)	0.001	0.77	152 rams and lambs	
	season (year)	0.029			
	LE Tcolu	0.0001			
LE Tcolu	Type	0.0001	0.74	152 rams and lambs	5.1 mm in rams 6.7 mm in lambs
	R/S (season)	0.004			
	year	0.0001			
	WB Tcolu (covar.)	0.003			

than a month (this occurred in the spring for the S rams, and from the second year in the R rams, when no *T. colubriformis* larvae were present on the pasture, Fig. 1); the S rams had a longer period of exposure to *T. colubriformis* larvae (as did the rams

Table III. Significant regression analysis of globule leukocytes (GL) and mast cells (MC) counted in the fundus (FU), pylorus (PY) and small intestine (IN) with the parasitological variables (see Tab. II for the key to the names of the variables, WB = worm burden).

Model		*P*	R^2
Log GL FU	= – 0.33 Log WB Tcolu + 1.92	0.0006	0.31
	= – 0.85 Log WB Tcirc + 4.14	0.0013	0.28
	= – 0.51 Log EP Tcirc + 2.13	0.0155	0.13
	= – 1.35 Log UT Tcirc + 3.23	0.0035	0.13
Log GL PY	= – 1.01 Log WB Tcirc + 4.80	0.0005	0.32
	= – 0.37 Log WB Tcolu + 2.10	0.0006	0.31
	= – 0.60 Log EP Tcirc + 2.41	0.0088	0.15
Log GL IN	= – 0.33 Log WB Tcolu + 1.77	0.0035	0.24
	= – 0.66 Log WB Tcirc + 3.32	0.0367	0.13
Log MC FU	= – 0.29 LE Tcolu + 3.50	0.0015	0.42
Log MC PY	= – 0.32 LE Tcolu + 3.72	0.0076	0.32
	= – 1.21 Log UT Tcirc + 4.07	0.0024	0.25
	= – 0.24 LE Tcirc + 4.58	0.0067	0.21
	= – 0.30 log EP Tcirc + 2.74	0.0073	0.14
Log MC IN	= – 0.50 LE Tcolu + 5.21	0.0001	0.46
	= – 0.19 LE Tcirc + 4.84	0.0740	0.10

slaughtered at the end of the grazing season), and in these animals, the worms were shorter and a significant and positive correlation was detected ($r = 0.51$ for $n = 28$ S rams). Prior exposure of the rams to the parasite was correlated to UT (result not shown), but not to LE.

3.3. Relationships between mucosal cell counts and parasitological data

Log transformation was necessary to normalize most of the cell counts. The number of globule leukocytes at the three sites were inversely correlated with worm burden, egg production and the number of eggs in utero for both species (Tab. III). Mast cell counts correlated to the length of both species, and to egg production and the in utero egg count of *T. circumcincta*. There was no significant relationship with the eosinophils, even by using a similar model to that for the mast cells. These two types of cells were not correlated.

No significant differences were found between the R and S rams for the eosinophils during the 2 seasons of the first 2 years. Significant correlations were observed between the R and S rams for the globule leukocytes and mast cells (Tab. IV). The best models were those using the number of *T. circumcincta* eggs in utero as a co-variable for the globule leukocytes in the fundus and pylorus, with no co-variable in the small intestine. For the mast cells, the length of female *T. circumcincta* was a significant co-variable, not only in the pyloric region but also in the small intestine. The numbers of the various cells in R and S rams produced by the best fitting model are shown in Figure 2. Higher levels of globule leukocytes and mast cells were observed in the R rams, but only in the first year and not in the second one.

Table IV. Significant differences in the cell counts between R and S rams, according to the year (1 or 2) and the season when the rams were necropsied (summer or autumn) found by the GLM procedure (see Tab. III For the key to the names of the variables).

Variable	Factors in the model	*P*	R^2
Log GL FU	R/S (season)	0.0012	0.52
	Season (year)	0.0124	
	Log UT Tcirc (covar.)	0.0012	
Log GL PY	R/S (season)	0.0437	0.66
	Season (year)	0.0001	
	Log UT Tcirc (covar.)	0.0092	
Log GL IN	R/S (season)	0.0077	0.47
	Season (year)	0.0001	
Log MC PY	R/S (season)	0.0453	0.34
	Season(year)	0.1245	
	LE Tcirc (covar.)	0.0147	
Log MC IN	R/S (season)	0.0065	0.71
	Season (year)	0.0001	
	Log UT Tcirc (covar.)	0.0563	
Log MC IN	R/S (season)	0.0042	0.70
	Season (year)	0.0001	

4. DISCUSSION

In our experimental design, we had 1–3-year-old rams selected as being either resistant or susceptible to *T. colubriformis* and to *T. circumcincta* and 3–4 month-old, unselected and highly susceptible tracer lambs. These animals were subjected to differing infection pressures depending on the time of the year (low L3 populations at the beginning of the grazing season, more *T. colubriformis* at the end of the summer, more *T. circumcincta* in the late autumn), and on whether they were grazing pasture that had already been contaminated by R or S rams [6]. As a consequence, a large range of host-parasite relationships were explored, from lambs containing very high numbers of worms of both species in the late fall on S pasture (more than 40 000 of each species), to rams with fewer than 10 *T. colubriformis* worms, even though they had been exposed to high levels of pasture contamination. This resulted in a wide range of the number of naturally acquired worms, providing a useful dataset for exploring the effect of worm number on worm fecundity.

Daily egg production per female worm was not a precise variable, since it was a combination of three different measurements, each with its own inbuilt inaccuracies. When a low rate of infection was observed, female worm numbers were counted in all the samples but when the infection rate was higher, a 10% aliquot was counted. Only one FEC was processed on the day before necropsy, and a single measurement of this type is known to be highly variable. The amount of fresh faeces excreted by each animal was expressed per kg of metabolic live weight after being estimated in metabolic boxes with dry feed and not under natural grazing conditions [6]. Stear et al. [15] have pointed out these problems. However, apart from some aberrant values indicating

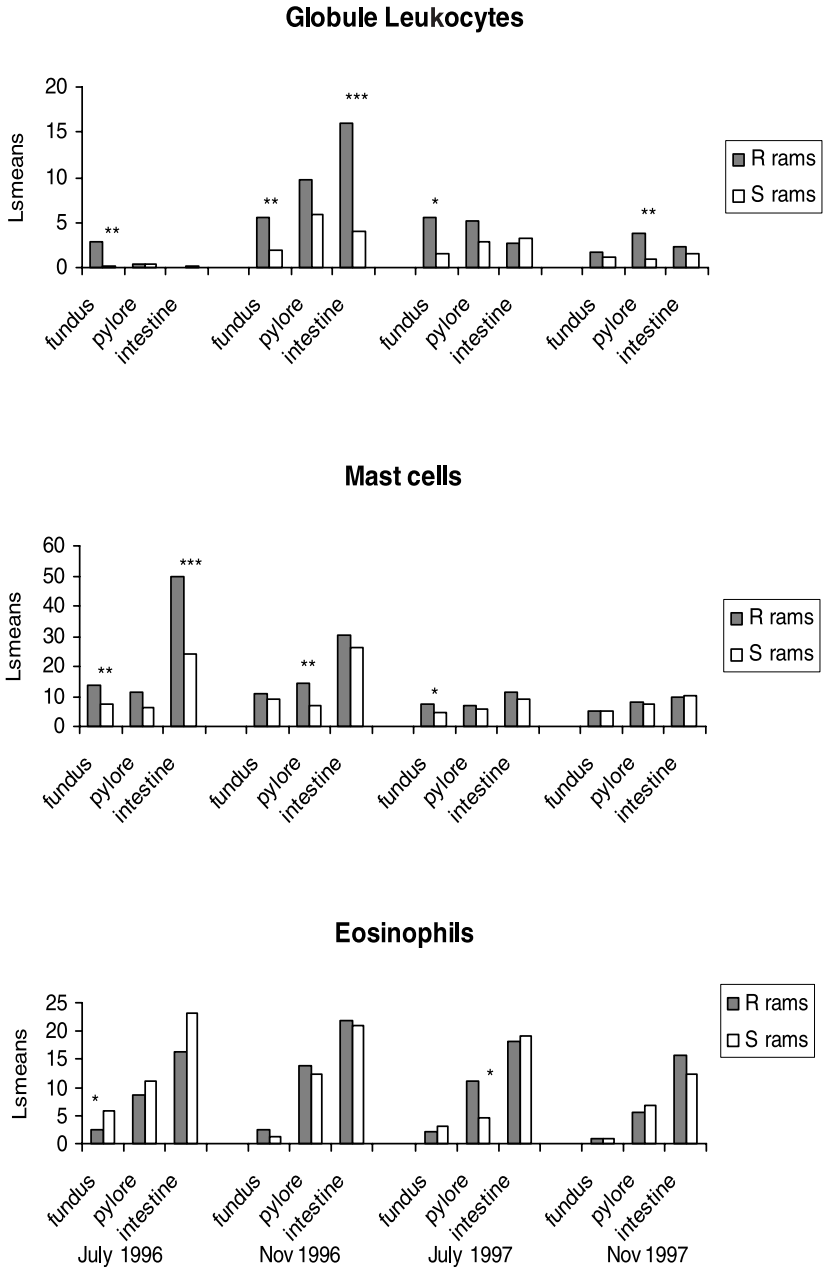

Figure 2. Mean concentrations (from the model in Tab. III) of globule leukocytes, mast cells and eosinophils in mucosal samples of the fundus, pylorus and small intestine from resistant and susceptible rams necropsied in the middle and at the end of the grazing seasons in 1996 and 1997. Differences between R and S rams were significant at $P < 0.05$ (*), < 0.01 (**) or < 0.001 (***).

more than 1 500 to 2 000 eggs per female and per day, this estimation does provide a better indicator of fecundity than simply counting the eggs in utero. On average, *T. circumcincta* females produced 3.5 times as many eggs per day as were observed in utero (107/30 in utero) versus a 14.5 fold difference for *T. colubriformis* (248/17). The latter value is close to the 262 eggs/day/female estimate of Coyne et al. for *Trichostrongylus* spp. [3]. Host factors and season had no effect on this ratio in either species. For *T. circumcincta* in tracer lambs, the egg production fell significantly when the worm number increased, whereas this was not the case in the rams. Such relationships were not observed in the *T. colubriformis* populations. As described by Stear et al. [14, 15] for the *T. circumcincta* species, the worm length was the main factor influencing egg production and the number of eggs in utero. Stear and Bishop [13] find a curvilinear relation between worm length and fecundity in *T. circumcincta*; we found a similar relationship in *T. colubriformis*, confirming the observation of Coyne et al. [3]. However, on the contrary to the findings of Coyne et al., log transformation (natural or log10) did not modify the normal distribution of this measurement. The distribution was less normal for the lengths of female *T. colubriformis,* which showed greater variability than *T. circumcincta*. *T. colubriformis* females were longer in the tracer lambs (6 to 7.5 mm), the most susceptible hosts, and this was independent of the number of worms (ranging from 6 to 44 000). Rams killed in July or on R pasture had shorter worms (between 5 and 6.5 mm), whereas those killed at the end of grazing seasons 1 and 4 had even shorter worms, but a significant positive correlation was observed with worm burdens (Fig. 1). This regulation of *T. colubriformis* differed from that of *T. circumcincta*. Ractliffe and Lejambre [10] have demonstrated for different species of Trichostrongyles from sheep and horses that the number of eggs depends on the worm growth (reflected in the length of the worms). For *Haemonchus contortus* in lambs, egg production increases with the worm burden (or rather with the total weight of the worms) [8, 11].

Some significant differences were observed between resistant and susceptible rams with regards to the mucosal inflammatory responses. The number of globule leukocytes was negatively correlated with the number of *T. circumcincta* and *T. colubriformis* worms, suggesting that this cell type plays a role in the resistance of the host [2]. This is in agreement with the results of Seaton et al. [12] and Stear et al. [14] for *T. circumcincta* in lambs more than 6 months old following experimental infections, and Douch et al. [4] for *T. colubriformis*, in the case of natural infections. Globule leukocyte counts were also negatively correlated to worm egg production and the number of eggs in utero, but only for *T. circumcincta*.

Mast cell counts in both the abomasal and the intestinal mucosa were also inversely related to the length of female worms in both resistant and susceptible rams. With *T. circumcincta*, abomasal mast cells were correlated with worm fecundity. Although the association with host resistance seems stronger for globule leukocytes, increases in mucosal mast cells have been observed in many situations corresponding to changes in the host resistance (age, physiological status, vaccination, etc.), although their precise role has not been identified [5, 7, 9]. Our findings suggest that this cell type could interfere with worm growth at least in the case of *T. circumcincta.*

Lastly, another interesting finding was the positive correlations found between the density of cells (globule leukocytes and mast cells) in the abomasal and in the intestinal mucosa, despite some differences in the timing of the development of worm species in these two organs. This observation suggests that there is a coordinated response within the digestive mucosa. Similar effects within the mucosal system have previously been reported in sheep infected with *T. colubriformis* [17]. The occurrence of similar responses in different

regions suggests the possibility of effects on worm populations located in different parts of the gastrointestinal tract.

In conclusion, this study shows the regulation in lambs and adult sheep of *T. circumcincta* and *T. colubriformis* populations and their fecundity. The same mechanisms may influence these two species, but they must be more effective in *T. colubriformis*, since the length and fecundity of the worms soon decreased with age and exposure to the parasite. These findings should be useful in trying to develop better methods for the control of trichostrongylosis in sheep.

ACKNOWLEDGEMENTS

We would like to thank C. Boizumault for her technical help in the measurements of the female worms.

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