The processes influencing the distribution of parasitic nematodes among naturally infected lambs

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SUMMARY

The impact of mixed, nematode infection upon a group of animals will depend upon the number of nematodes present, how they are distributed among hosts and whether individuals that are heavily parasitized with one species are more likely to be heavily parasitized with other species. A survey of over 500 six-month-old, Scottish Blackface lambs from a single farm in Southwest Strathclyde identified 7 different categories of nematodes in the abomasum and small intestine. There were considerable differences among years and among nematodes in the prevalence and mean intensity of infection. *Ostertagia circumcincta* was present in nearly all lambs and judged by prevalence and intensity is one of the most successful of all parasitic nematodes. Each category of nematodes had a skewed distribution; most animals had relatively few worms but a small proportion had many worms. The variances of the number of nematodes in each category were approximately equal to the square of the mean. The counts of adult *O. circumcincta* followed a negative binomial distribution, but the negative binomial distribution did not provide a good description of the observed values for the other species. These other species had a lower prevalence and possibly some sheep were not exposed to infection. There was no significant genetic variation among lambs in the number of nematodes present and therefore the differences among these lambs were unlikely to be a consequence of genetic differences in host susceptibility. Lambs with increased numbers of one species were more likely to be have increased numbers of the other species, but the correlations were weak and may reflect covariation in exposure to different parasites.

Key words: sheep, Nematoda, *Ostertagia circumcincta*, distribution, negative binomial.

INTRODUCTION

The abomasal nematode *Ostertagia* (*Teladorsagia*) *circumcincta* is a major constraint on efficient sheep production in temperate areas of the world. There has been considerable effort put into understanding the interaction between this parasite and sheep and it is now one of the best understood of all host–parasite relationships (Grenfell *et al.* 1995; Stear *et al.* 1997*a*).

One area where information is lacking concerns the distribution of worms among naturally infected animals. Yet the impact of infection upon a flock of sheep will depend not only upon the number of nematodes present but also how they are distributed among sheep. In addition, the relationships among the number of different species of nematodes present in the host will influence the pathogenicity. If animals with higher than average numbers of one species also have higher than average numbers of all species, the impact on the heavily infected animals would be more severe.

Barger (1984, 1985) reported that the distribution of worms from 4 different species followed a negative binomial distribution in 3-month-old Merino lambs in Australia. There were strong positive correlations among different species, i.e. sheep with high numbers of one species had high numbers of the other species. Hoste & Cabaret (1992) used principal component analysis to demonstrate that there were also positive associations among nematodes in sheep from both France and Morocco. However, there is little published information for temperate areas where a different set of nematode species exist, or about the variation among different years in the prevalence, intensity or distribution of nematodes.

The aims of this paper are to describe and, where possible, to explain the distribution of nematodes among lambs, in a temperate climate over 4 consecutive years.

MATERIALS AND METHODS

Animals

All sheep were from a commercial, upland farm in

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Table 1. Prevalence (%) of the different parasites found in naturally infected lambs

	1992 ($n = 109$)	1993 ($n = 100$)	1994 ($n = 153$)	1995 ($n = 152$)
Ostertagia circumcincta	100	100	99	100
Trichostrongylus axei	0	6	1	30
Haemonchus contortus	0	0	0	9
Cooperia spp.	29	71	61	89
Trichostrongylus vitrinus	58	28	29	70
Nematodirus spp	65	63	19	55
Bunostomum trigonocephalum	1	0	0	0

Southwest Strathclyde and all husbandry procedures followed standard, commercial practice. The sheep were all straightbred Scottish Blackface. The lambs were born in a 2 or 3 week period in late April to early May. Within 1 week of lambing the ewes and lambs were moved onto 1 of 3 fields close to the farmhouse. At 3 or 4 months of age the lambs were separated from their mothers and moved onto the largest of the 3 fields. All lambs were given a broad spectrum anthelmintic (albendazole sulphoxide) according to the manufacturers' recommendations every 4 weeks from 4 to 20 weeks of age. This anthelmintic is effective against the nematodes that were present (McKellar & Scott, 1990). The efficacy of the drug on this farm was assessed by faecal egg count reduction tests and was consistently greater than 95 %. Six or 7 weeks after the final anthelmintic treatment, the lambs were slaughtered at the local abattoir.

Necropsy

Standard parasitological procedures were used to identify and count all nematodes present in the small intestine and abomasum (Armour, Jarrett & Jennings, 1966). The abomasum and small intestine were washed separately and the number of worms present in a 2 % sample of the washing fluid was multiplied by 50 to estimate the worm burden. The large intestine was not studied. Since the pre-patent period for all common large intestinal species exceeds 4 weeks, these species would be unable to reproduce because of the frequency of anthelmintic treatment. In addition, larval cultures in 1990 and 1991 of faecal samples from animals on the same farm did not reveal any large intestinal species. Over 530 sheep were sampled but due to missing records only 514 were used in this study.

Statistical analyses

The univariate procedure on SAS (SAS Institute, Cary, North Carolina) was used to estimate the prevalence, mean intensity and variance for each species in each year. The GLM procedure (SAS) was used to estimate the regression of variance on the mean: the 'noint' option was used to omit the intercept parameter from the model. The parameters of the negative binomial distribution were estimated by maximum likelihood procedures using the GENSTAT package (Lawes Agricultural Trust); the number of worms counted in the 2 % aliquot was used rather than the estimated total. The correlation procedure (SAS) was used to estimate Pearson product moment correlations on log-transformed data. One was added to each observation to avoid problems with values of zero. Sire variance components were estimated from general linear mixed models with the mixed procedure (SAS). A separate model was used for each category of parasite. The models fitted sire and dam as random effects, sex, type of birth (single or twin), and field nested within year as fixed effects. The heritability was estimated as 4 times the sire variance component divided by the phenotypic variance (Falconer & Mackay, 1996).

RESULTS

The nematodes counted were divided into 7 categories. Three species came from the abomasum: *O. circumcincta*, *Trichostrongylus axei* and *Haemonchus contortus*. Four categories came from the small intestine: *Cooperia* spp., *Trichostrongylus vitrinus*, *Nematodirus* spp. and *Bunostomum trigonocephalum*.

There was considerable variation in the prevalence of these nematodes (Table 1). *O. circumcincta* was present in nearly all (513 of 514) sheep examined. *B. trigonocephalum* was present in only 1 animal and *T. axei* and *H. vitrinus* and *Nematodirus* spp.) were present in some sheep every year but there was considerable variation in prevalence. For example, the prevalence of *Cooperia* spp. varied from a low of 29 % in 1992 to a high of 89 % in 1995.

There was also considerable variation in the mean intensity of infection among the different nematodes and among years (Table 2). The most prevalent species were also the most numerous. *O. circumcincta*

Table 2. The mean intensity of infection (arithmetic mean counts of larvae and adult nematodes) among naturally infected lambs

	1992 ($n = 109$)	1993 ($n = 100$)	1994 ($n = 153$)	1995 ($n = 152$)
Ostertagia circumcincta	12936·3	3405·5	2301·0	6274·0
Trichostrongylus axei	0	67·5	1·3	361·9
Haemonchus contortus	0	0	0	17·1
Cooperia spp.	83·9	388·0	561·8	4369·1
Trichostrongylus vitrinus	255·5	116·0	257·0	1022·0
Nematodirus spp.	230·7	455·5	119·6	295·4
Bunostomum trigonocephalum	0·9	0	0	0

Table 3. The variance of nematode numbers among naturally infected lambs

	1992 ($n = 109$)	1993 ($n = 100$)	1994 ($n = 153$)	1995 ($n = 152$)
Ostertagia circumcincta	100860000	6937116	4518042	26103244
Trichostrongylus axei	0	143049	129·9	130993
Haemonchus contortus	0	0	0	10268
Cooperia spp.	35087	299198	879812	27336720
Trichostrongylus vitrinus	133858	135449	353124	2484726
Nematodirus spp.	67172	384853	148518	207793
Bunostomum trigonocephalum	91·7	0	0	0

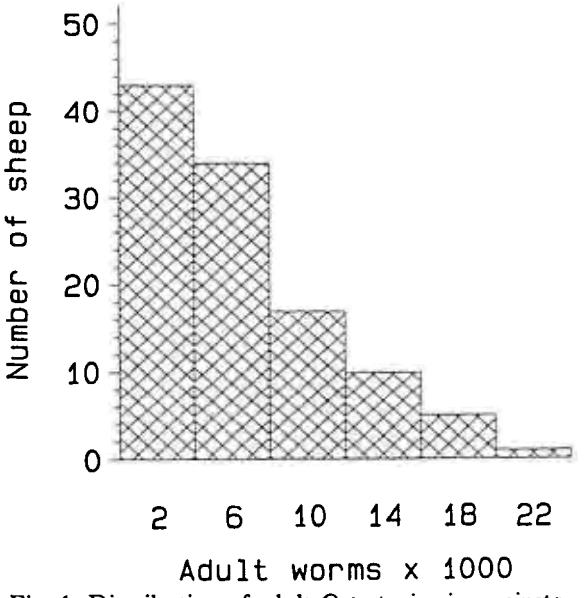

Fig. 1. Distribution of adult *Ostertagia circumcincta* among naturally infected lambs. All lambs were born in a 2-week period during late April, 1992 and necropsied 6 months later. The values on the x-axis represent the mid-points of the groups.

accounted for 74% of all nematodes recovered over the 4 years but there was considerable variation among different years: 96% of all nematodes counted in 1992 were *O. circumcincta*, 77% in 1993, 71% in 1994 but only 51% in 1995. The mean number of *O. circumcincta* ranged from a high of almost 13000 in 1992 to a low of only 2300 in 1994. Other species also showed considerable variation in the mean intensity of infection. For example, the mean number of *Cooperia* spp. per lamb ranged from a low of under 100 in 1992 to a high of over 4300 in 1995. The differences in intensity were related to the changes in prevalence (29% in 1992 and 89% in 1995). However, even considering only infected animals there was considerable variation in the mean intensity of infection. The mean number per infected lamb ranged from 286 *Cooperia* in 1992 up to 4883 *Cooperia* in 1995.

The variances were considerably greater than the arithmetic means for all species at all times (Table 3). There was a very strong relationship between the mean and the variance across years. For *O. circumcincta* the regression of the variance on the mean fitted the equation: variance = $(\text{mean})^{1.95 \pm 0.01}$ ($P < 0.0001$; $r^2 > 0.99$). For *Cooperia* spp. the regression equation was variance = $(\text{mean})^{2.13 \pm 0.06}$ ($P < 0.0001$; $r^2 > 0.99$). The regression equation for *T. vitrinus* was variance = $(\text{mean})^{2.30 \pm 0.09}$ ($P < 0.0001$; $r^2 > 0.99$). For *Nematodirus* spp. the relationship was: variance = $(\text{mean})^{2.18 \pm 0.09}$ ($P = 0.0002$; $r^2 > 0.99$).

The distribution of each category of nematode was positively skewed; most individuals had relatively few worms but a small number had very high counts. Figure 1 illustrates the skewed distribution of adult *O. circumcincta* among lambs in 1992. Table 4 provides further information on the distribution of adult *O. circumcincta*. The number of adults showed less variation among years than the total numbers of

Table 4. The number of adult *Ostertagia circumcincta* among lambs that had been naturally infected

	1992 ($n = 109$)	1993 ($n = 100$)	1994 ($n = 153$)	1995 ($n = 152$)
Mean number of adult worms	6570	2778		2992
Ratio of larvae (L4+L5) to adults	0·97	0·23	0·49	1·10
Sex ratio (males/females)	0·71	0·75	0·70	0·76
The negative binomial distribution parameter k	1·90	1·79	1·63	1·90
Standard error of k	0·24	0·24	0·17	0·20

Table 5. The correlation between the numbers of worms from the different species

Trichostrongylus axei	0			
Cooperia spp.	0·10*	0·19***		
Trichostrongylus vitrinus	0·32***	0·16***	0·18***	
Nematodirus spp.	0·27***	0·09*	0·17***	0·24***
	Ostertagia circumcincta	*Trichostrongylus axei*	*Cooperia* spp.	*Trichostrongylus vitrinus*

*$P < 0.05$; ***$P < 0.001$

this species. This was due to the greater proportion of larvae in years of heavier infection. The sex ratio indicated that there were fewer males than females in each year. Nonetheless, after pooling sexes there was a good fit ($P > 0.05$) to the negative binomial distribution. The values of k, an inverse measure of aggregation, were slightly higher in years with a greater mean intensity of infection but the values were not significantly different from year to year.

Although the data were positively skewed, the number of adult *Cooperia* spp., *T. axei*, *T. vitrinus* and *Nematodirus* spp., did not, in general, fit a negative binomial distribution. The 3 exceptions were the number of *Nematodirus* spp. in 1993 ($k = 0.339 \pm 0.057$), the number of *Nematodirus* spp. in 1994 ($k = 0.060 \pm 0.012$) and the number of *Cooperia* spp. in 1992 ($k = 0.137 \pm 0.012$).

Table 5 provides the Pearson product moment correlation coefficients that were calculated from the log-transformed distributions. The 2 species that were very rare on this farm have been omitted. All the correlations were positive and statistically significant at the 5% level or lower except for the correlation between the 2 species (*O. circumcincta* and *T. axei*) in the abomasum. The correlations within each year also gave similar patterns (data not shown).

The additive genetic contribution to the variation among lambs in worm numbers was examined by mixed model analysis of variance. In all cases the sire component was either non-estimable (*T. axei* and *B. trigonocephalum*) or not significant ($P > 0.05$). Therefore there is no evidence in these data that genetic variation in the host influences variation in nematode numbers. In contrast, the same model indicated a very strong heritability of 0·62 ($P < 0.05$) for the mean length of adult female *O. circumcincta*. This very high heritability indicates that the most important source of variation among sheep in the average length of their adult *O. circumcincta* is due to genes of the host. This high heritability for worm length also suggests that the failure to demonstrate heritable variation in worm numbers is not due to an unusual host population.

DISCUSSION

The analyses have shown that there was considerable variation among years and among different categories of nematodes in the prevalence, intensity and variance of nematode infection. The variance had a close, curvilinear relationship with the mean. The distribution of adult *O. circumcincta* followed a negative binomial distribution, although this was not due to genetic variation among lambs. The distribution of adult nematodes for the other species did not, in general, follow negative binomial distributions. There were weak but significant positive correlations among most species in the numbers present in the host.

The high prevalence and intensity of *O. circumcincta* in these sheep is in remarkable contrast to most species of parasitic nematode which seldom achieve such high values (Shaw & Dobson, 1995). Indeed, if the values obtained from these sheep are representative of other sheep in temperate areas, then *O. circumcincta* should be considered as one of the most successful of all parasitic nematodes. The

explanation for its success may not lie in its egg production because it does not appear more fecund than other nematodes of sheep in temperate areas, although definitive data are lacking. It does, however, survive better on pasture and within infected animals than many other species (Stear *et al.* 1997*a*).

Shaw & Dobson (1995) suggested that nematodes in farmed ruminants occur at high densities because relatively large host populations are kept at artificially high densities. This may be true although feral sheep on St Kilda also experience high intensities of nematode infection (Gulland, 1992). In both cases, the hosts are unable to migrate to less heavily contaminated pastures. Possibly, the ambulatory and migratory behaviour of many herbivores has evolved to increase access to food and to reduce the intensity of nematode infection. In any event, the high density of host populations does not, in itself, explain why *O. circumcincta* is more successful than other contemporary species.

Such high levels of infection with *O. circumcincta* can have severe effects on the growth and survival of sheep. The pathogenicity of infection depends upon the condition of the host and its diet (Coop & Holmes, 1996) as well as upon the number of worms and their mean size (Stear, Park & Bishop, 1995*b*). Moderate, experimental infection can reduce growth rates by about a third (Coop *et al.* 1985). The sheep in this study and additional sheep from the same farm were used to estimate the genetic correlation between growth rate and faecal egg count (Bishop *et al.* 1996). The correlation was negative; lambs with genetic (breeding) values for low growth rate had breeding values for high egg counts. The genetic correlation was also very strong (0·8), which suggests that most of the genetic variation in the growth rate of grazing lambs is due to genetic variation in the ability of hosts to control the growth and fecundity of worms (Stear *et al.* 1997*b*). A separate study in feral sheep on St Kilda demonstrated that those animals that survived population crashes were less heavily parasitised than those that died (Gulland, 1992).

Taylor's power law (Taylor, 1961) provided a good description of the relationship between the variance and the mean number of nematodes. The power coefficient can also be used to estimate the optimal transformation prior to parametric analysis; when the coefficient is 2 a logarithmic transformation is appropriate. Our results are compatible with the widespread use of logarithmic transformations. However, the regression equation may provide a biased estimate of the slope of y on x when both variables are subject to error (Boag, Hackett & Topham, 1992; Sokal & Rohlf, 1995) but there is no agreement on the best method to avoid this bias (Sokal & Rohlf, 1995).

The negative binomial distribution provided a good description of the observed distribution of the number of adult *O. circumcincta* in different lambs. The inverse index of dispersion (k) is influenced by the mean intensity of infection (Bliss & Owen, 1958; Grenfell *et al.* 1995) and caution is needed in comparing distributions with different mean intensities. Our k values are slightly, but not significantly, higher than those reported by Barger (1985). The higher k values in our study may reflect higher mean intensities or real differences between the study populations.

The negative binomial distribution did not provide a good description of the observed values for the other species. This result contrasts with Barger (1985) who found a good fit for worm counts of the genera *Haemonchus*, *Ostertagia*, *Nematodirus* spp. and *Trichostrongylus* in the intestine. Interestingly, *O. circumcincta* was the most prevalent species in our study and the prevalence of the other species was lower than in the study of Barger (1985); only the distributions of the most prevalent nematodes appear compatible with the negative binomial distribution. Therefore, differences in prevalence could be responsible for the deviations from the negative binomial distribution. Grass will become contaminated as larvae migrate from faecal pellets. Most pellets will contain eggs from the highly prevalent species, but only some pellets will contain larvae from the less prevalent species. Therefore lambs will experience greater heterogeneity in exposure to the less prevalent species. Certainly, those categories that did not conform to a negative binomial distribution had a greater than expected proportion of sheep with zero values.

Alternatively or additionally, male lambs have more nematodes than females (data not shown). If the distribution of parasites follows a negative binomial distribution in both males and females, then the distribution when males and females are combined will not conform to a negative binomial (Grafen & Woolhouse, 1993). Similar arguments apply to the distribution of male and female parasites. If the numbers of male and female parasites are unequal, and if each sex conforms to a negative binomial distribution, then the combined data will only conform to a negative binomial if the two sexes have equal variance to mean ratios (Grafen & Woolhouse, 1993). These are very stringent conditions. Possibly, many parasite distributions conform only approximately to a negative binomial distribution but the deviation from a negative binomial was only apparent in our data because we examined a large, homogeneous data set.

The distribution of parasitic nematodes in their hosts will, in principle, be due to 4 sources of variation: variation in exposure to infection, variation in resistance to infection, measurement error and associations among parasites, especially competition. Boag, Topham & Webster (1989) have demonstrated that faeces and infective larvae are not

randomly distributed on pasture and, therefore, there could be considerable variation among sheep in exposure to infection. As the heritability of nematode numbers was not significantly different from zero, genetic differences among lambs in resistance to infection are not likely to play a major role in generating the observed distributions.

Measurement error exists for all nematode counts, but there is no reason to believe that it is higher in this survey than in other comparable studies. Measurement error can be systematic or random. Systematic errors, such as inadequate mixing prior to sampling and counting an aliquot, would produce positive associations among all the different species from the same organ. The absence of any correlation between the number of *T. axei* and *O. circumcincta* argues against, at least some types of, systematic error playing an important role. Random error is inevitable when 2% aliquots are counted. This will superimpose a Poisson distribution over the underlying true distribution of worms among lambs.

The other source of variation will be positive or negative associations among worm species. The positive correlations observed among most species in this study may merely reflect differences in exposure to infection. The distribution of infective larvae on pasture means that a mouthful of grass containing 1 species of infective larvae is likely to contain infective larvae of other species. The absence of any association between *O. circumcincta* and *T. axei* may be because the tendency of co-exposure to produce a positive association is balanced by the negative effects of competition for food or space in the abomasum. The apparent absence of competition among the small intestinal species may be a consequence their occurrence at different sites within the intestine (Urquhart *et al.* 1996).

The correlations among the numbers of nematodes from the different species were much lower than those reported by Barger (1984). The development of resistance to *O. circumcincta* develops in 2 stages. Lambs in their first grazing season develop anti-parasite IgA and this appears to be the major mechanism controlling worm length and fecundity (Stear *et al.* 1995*a*). However, only older animals can control worm numbers, possibly by immediate hypersensitivity reactions against incoming larvae (McCririe *et al.* 1997). As the heritability of worm numbers was not significantly different from zero, resistance to the other species of nematodes in sheep may also develop in 2 stages. The lower correlations among different species in our lambs compared to the Australian study could be due to greater heterogeneity among lambs in exposure to different nematodes. The higher prevalence of multiple infection in the Australian study would reduce heterogeneity in coexposure as faecal contamination of grass would be more likely to produce a mixed infection.

In conclusion, a survey of nematodes in the abomasum and small intestine of 6-month-old, Scottish Blackface lambs from a single farm in Southwest Strathclyde identified 7 different categories of nematodes. *O. circumcincta* was present in nearly all lambs and judged by prevalence and intensity must be considered a very successful species. The variances of the parasite distributions over years were greater than the mean and followed Taylor's power law. The power coefficients were consistent with the logarithmic transformation of worm numbers prior to parametric analysis. Only the counts of adult *O. circumcincta* followed a negative binomial distribution. The negative binomial distribution did not provide a good description of the observed values for the other species.

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