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Spatial interactions between two nematode species along the intestine of the wood mouse *Apodemus sylvaticus* from woodland and grassland sites in southern England

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Abstract

The distributions of the nematode parasites *Heligmosomoides polygyrus* and *Syphacia stroma* were quantified in three equal-length sections along the intestine of wood mice (*Apodemus sylvaticus*) trapped in three different locations in the south of England. The distribution of *H. polygyrus* did not change in the presence of *S. stroma*, this species being largely confined to the anterior third of the intestine, whether *S. stroma* was or was not present. However, while in single infections with *S. stroma*, worms were equally distributed in the anterior and middle sections of the intestine, in the presence of *H. polygyrus*, a higher percentage of worms was located in the middle section. This was a dose-dependent response by *S. stroma* to increasing worm burdens with *H. polygyrus*, and even relatively low intensities of infection with *H. polygyrus* (e.g. ≤10 worms) were sufficient to cause a posterior redistribution of *S. stroma* into the middle section. A similar posterior shift in the percentage distribution of *S. stroma* in the intestine was evident in juvenile and mature mice of both sexes, and in mice from all three study sites. The ecological significance of these results is discussed.

Introduction

The survival of parasites within hosts requires intimate fine-tuning to conditions in the site where they reside. In helminths this ranges from morphological structures required to maintain position (e.g. scoleces of cestodes, probosces of acanthocephalans (Smyth, 1976) and the intricate surface ridges of nematodes, called crêtes (Durette-Desset, 1985)), host enzyme-blocking factors (Hawley *et al.*, 1994; Zang & Maizels, 2001) to an array of molecules that interfere with host immune effector mechanisms (Hewitson *et al.*, 2011; Whelan *et al.*, 2012). It is well established that intestinal helminths have preferred sites (niche restriction) within the intestines of their vertebrate hosts to which they are highly adapted and in which they grow, survive and reproduce optimally (Crompton, 1973; Holmes, 1973; Behnke, 1974; Rohde, 1994; Sukhdeo & Bansemir, 1996), and which they locate by responding to specific environmental cues (Sukhdeo, 1990; Sukhdeo & Sukhdeo, 1994). Even closely related species of nematodes co-occurring in the same host species may show niche segregation, as reflected in longitudinal differences in their distribution along the intestinal tract (Sommerville, 1963), as well as radial (intestinal niches from the lumen at the centre, outwards through the mucosa, submucosa to the serosa), as recorded in the seminal paper by Schad (1963; but see also Hominick & Davey, 1973).

The trichostrongyloid nematode *Heligmosomoides polygyrus* of Eurasian wood mice (*Apodemus sylvaticus*, also referred to as the long-tailed field mouse) aggregates in the anterior sections of the small intestine (Panter, 1969; Lewis & Bryant, 1976; Beckett & Pike, 1980). The long coil-like shape of this species (previously known as *Nematospiroides dubius*; Behnke *et al.*, 1991) enables worms to coil around and between the villi especially those located in the duodenum and the anterior jejunum of the small intestine (Bansemir & Sukhdeo, 1996). Here the worms feed on enterocytes of the villi (Bansemir & Sukhdeo, 1994).

In contrast, the oxyuroid nematode *Syphacia stroma* is an entirely lumen-dwelling species and, like most oxyuroids, feeds on symbiotic intestinal microorganisms and also on gut contents (Dunning & Wright, 1970; Adamson, 1989). *Syphacia stroma* lives in the anterior portion of the small intestine, but is less site specific in that worms can often be found further along the small intestine, especially in heavy infections. Moreover, patent female worms migrate through the small and large intestines to deposit their eggs on the external perianal region of the host (Lewis, 1969).

These two species, *H. polygyrus* and *S. stroma*, are the dominant intestinal helminths of wood mice in the British Isles and often occur in concurrent infections (Lewis, 1969; Lewis & Twigg, 1972; Behnke *et al.*, 2005). Experimental studies have shown that there may be

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different outcomes of co-occurrence of two species that normally reside in the same location in the gut (Christensen *et al.*, 1987; Behnke *et al.*, 2001). These include one species residing more posteriorly than normal in a sub-optimal location (e.g. the cestode *Hymenolepis diminuta* in concurrent infections with the acanthocephalan *Moniliformis moniliformis* in rats), while the other maintains its position in its preferred location (*M. moniliformis*). *Hymenolepis diminuta* eventually outlives *M. moniliformis* in rats, and recovers its normal attachment site in the duodenum once the acanthocephalans have died from senility (Holmes, 1961). Posterior shifts in the mean intestinal position of the acanthocephalans *Pomphorhynchus laevis* in the presence of *Acanthocephalus clavula*, and *vice versa*, and associated change in niche width, have been reported in trout (Byrne *et al.*, 2003), and related in both cases to intensities of infection with the concurrently infecting species.

While such interactions between competing helminths in the intestine are well known from experimental infections, there are fewer records from naturally infected wild rodents (Stock & Holmes, 1988; Haukisalmi & Henttonen, 1993). In the present study, we have exploited three datasets, from three different sites in the south of England, in which the occurrence of intestinal helminths in wood mice was quantified separately in each third of the length of the intestine. Given the quite different strategies of *H. polygyrus* and *S. stroma* for survival in the intestine, and their different food resources, we test the null hypothesis that co-occurrence should make no difference to their distribution along the small intestine of wood mice.

Materials and methods

Databases

We exploited three databases based on surveys of the helminth parasites of wood mice in woodland and grassland sites in southern England. The first was conducted from January to July 1969 in the Great Wood, Virginia Water, Surrey (GPS 51.417286–0.567032) – a flat, dry area of mainly oak and birch woodland with bracken and bramble ground flora. The second survey was conducted in September 1985 at Rogate Field Station, Rogate in Hampshire (GPS 51.006610–0.853225) – an overgrown meadow of uncut and ungrazed grasses flanked by substantial woody hedgerows. The third survey was carried out in September 1987 and 1991 and was undertaken in a ploughed and cultivated grassland site at Silwood Park, Ascot, Berkshire (GPS 51.411781–0.641590).

Laboratory procedures

Mice were captured over a period of ten trapping nights each month using Longworth traps provided with hay and food. The maturity of males was determined by the position and size of the testes. In mature males, large testes descend into the scrotal sacs whereas males with small testes situated within the body cavity were considered juvenile and incapable of breeding, which was also confirmed by examination of the epididymis for spermatozoa. For analysis, juvenile male mice weighed between 6.9 and 18.8 gm, with a range of 19.00 to 33.4 gm in mature males. In female mice, the weight of the lightest pregnant female during the period of maximum number of pregnancies was taken and mice of this particular weight and above were considered to be mature ranging from 18.9 to 36.45 gm compared with 9.5–18.5 gm in juvenile females. Prior to post-mortem examination mice were killed by exposure to chloroform-soaked cotton wool. The alimentary canal was removed and the region between the end of the stomach (at the pyloric sphincter) and beginning of the rectum, was measured and divided into three equal length sections, referred to as the anterior, middle and posterior sections of the intestine, prior to being examined for helminth parasites. Part of the posterior section incidentally contained the colon and caecum.

Statistical methods

Summary statistics are presented as mean worm burdens of both *H. polygyrus* and *S. stroma* with standard errors of the mean (SEM). The percentage distribution of worms (PWB) was calculated in the three intestinal sections of each mouse and mean values are referred to as mean percentage of worm burden (MPWB). Mean worm burdens and the MPWB from each of the three intestinal sections were calculated from each of the three surveys. Then, following the recommendations of Zuur *et al.* (2009), some factors that may have influenced the intestinal distribution of parasites were explored using non-parametric tests in IBM-SPSS 24 (1 New Orchard Road, Armonk, New York 10504-1722, USA) (Kruskal–Wallis, Mann–Whitney *U* test and Spearman's test of correlation). In each case the value of the relevant test statistic (*H*, *U* and r_s, respectively) and the probability (*P*) for rejecting the null hypothesis ($\alpha = 0.05$) were provided. When analysing the effect of *S. stroma* on *H. polygyrus*, data were provided on all hosts that harboured at least one individual of *H. polygyrus*, and similarly when analysing the effect of *H. polygyrus* on *S. stroma*, only data from mice that harboured at least one individual of *S. stroma* were used. Finally, generalized linear models (GLMs) in R version 2.2.1 (R Core Development Team, the R Foundation for Statistical Computing) were provided after converting the PWBs to binomial values (see Douma & Weedon, 2018). Full factorial binomial GLMs were evaluated as described elsewhere (Behnke *et al.*, 2021), with sex (at two levels, males and females), age (at two levels, juveniles and mature mice), site (at three levels, three sites) and status (at two levels corresponding to mice infected only with *S. stroma* or concurrently with *H. polygyrus*) as explanatory factors. Minimum sufficient models were also fitted incorporating only significant main effects and two-way interactions. From these, values of deviance (*DEV*) for the main effect of status, and two-way interactions with status were provided as the principal objectives of the study.

Results

Summary statistics for the combined dataset

The database included 290 records of individual mice, but five mice that were not infected with either *H. polygyryus* or *S. stroma* were excluded. Of the 285 mice that carried at least one individual of *H. polygyrus* or *S. stroma*, 181 were from the Virginia Water site, 27 from Rogate and 77 from Silwood Park (table 1). Among these mice, 264 (92.6%) carried *H. polygyrus*, 163 (57.2%) *S. stroma* and 142 (49.8%) had both species. The intensity of infection with *H. polygyrus* (all mice infected with this species) was 18.3 ± 1.44 ($n = 264$) and with *S. stroma*, 78.5 ± 10.32 ($n = 163$).

Worm burdens in single and concurrently infected mice

Worm burdens of *H. polygyrus* were heavier in concurrently infected compared with single infected mice (single infection =

Table 1. The number of mice in surveys by site, age, sex and year. This table includes only those mice used for analysis.

Factor	Virginia Water	Rogate	Silwood Park	Total
Juvenile				
Males	37	15	10	62
Females	31	6	9	46
Total	68	21	19	108
Adult				
Males	88	5	29	122
Females	25	1	29	55
Total	113	6	58	177
Combined				
Males	125	20	39	184
Females	56	7	38	101
Total	181	27	77	285

14.8 ± 1.76, $n = 122$; concurrent infection = 21.3 ± 2.18, $n = 142$; Mann–Whitney U test, $U_{122,142} = 10{,}617.5$, $P = 0.002$). However, despite the arithmetically higher intensity of infection with *S. stroma* in concurrently infected mice, for this species the difference with single-infected mice was not significant (single infection = 56.3 ± 13.61, $n = 21$; concurrent infection = 81.8 ± 11.66, $n = 142$; Mann–Whitney U test, $U_{21,142} = 1{,}505.0$, $P = 0.9$).

Distribution of worms in single and concurrently infected mice

Heligmosomoides polygyrus was largely confined to the anterior third of the intestine, with heavier worm burdens overall occurring in concurrently infected mice (fig. 1A). When worm burdens for each mouse were expressed as the percentage present in each third of the intestine, the presence of *S. stroma* made no difference to the distribution of *H. polygyrus* (fig. 1B).

In single worm infections, *S. stroma* was more or less equally distributed between the first and second thirds of the intestine, whether expressed as mean number of worms present or as MPWB (fig. 1C, D, respectively), although in the latter case values were marginally higher for the middle section. However, when *H. polygrus* was present in the anterior third of the intestine, both the mean *S. stroma* worm burden in this section (Mann–Whitney U test, $U_{21,142} = 646.0$, $P < 0.001$) and the MPWB ($U_{21,142} = 274.5$, $P < 0.001$) were significantly lower than in single-species infections. There was a corresponding increase in the MPWB ($U_{21,142} = 2671.0$, $P < 0.001$) in the middle section, but an increase in worm burdens was not significant ($U_{21,142} = 1{,}817.5$, $P = 0.106$). There was also a very small increase in the number of *S. stroma* in the posterior third of the intestine in concurrently infected mice, but this was not significant (e.g. for MPWB, $U_{21,142} = 1{,}666.0$, $P = 0.167$).

The effect of varying intensities of H. polygyrus on the distribution of S. stroma

Since in the presence of *H. polygyrus* the percentage distribution of *S. stroma* altered, with a greater percentage of worms located in the middle section of the intestine, it was of interest to determine whether the extent of this posterior redistribution of *S. stroma* was dependent also on the intensity of infection with *H. polygyrus*. There was a clear dose-dependent effect, with higher *H. polygyrus* worm burdens in mice resulting in fewer *S. stroma* in the anterior section (fig. 2; for worm burdens, $r_s = -0.297$, $n = 163$, $P < 0.001$; for percentage worm burdens, $r_s = -0.387$, $n = 163$, $P < 0.001$;) and a corresponding higher percentage now located in the middle section of the intestine ($r_s = 0.300$, $n = 163$, $P < 0.001$) (fig. 2).

Factors affecting the distribution of S. stroma

Datasets used for this analysis included four variables that may have affected the distribution of *S. stroma* in single and concurrent infections – that is, host age and sex, the trapping site and, in the case of mice trapped in Silwood Park, the years in which mice were captured (i.e. in 1987 and 1991). Data in table 2 show that although there were some relatively minor variations, irrespective of host age, sex or site of capture, in all cases the percentage of *S. stroma* in the anterior intestinal section was smaller when mice were also concurrently infected with *H. polygyrus*.

The difference in MPWB of *S. stroma* in the anterior intestinal section between mice infected only with *S. stroma* and those with concurrent *H. polygyrus* infection was highly significant (GLM with binary errors, main effect of status, $Dev_{1,157} = 95.243$, $P < 0.0001$). This difference was not affected by host sex (for the two-way interaction status × sex, $Dev_{1,148} = 0.945$, $P = 0.3$) nor host age class (the two-way interaction status × age $Dev_{1,148} = 0.391$, $P = 0.5$). However, there was a significant difference between the three field sites in the extent of the reduction in *S. stroma* in the anterior section of the intestine in concurrent infections (the two-way interaction status × site, $Dev_{2,154} = 27.515$, $P < 0.001$), as shown in table 2.

In contrast, in the middle section of the intestine, the percentage of *S. stroma* was higher in concurrent infections compared with mice just harbouring *S. stroma*, and this was the case in both age classes, sexes and all three sites where mice were trapped (table 2). The difference in the MPWB of *S. stroma* in the middle section, between mice infected only with *S. stroma* and those with concurrent *H. polygyrus*, was highly significant (GLM with binary errors, main effect of status, $Dev_{1,157} = 403.23$, $P < 0.0001$). However, in this case there were also significant two-way interactions with sex (for the two-way interaction status × sex, $Dev_{1,148} = 4.385$, $P = 0.036$), with age class (the two-way interaction status × age, $Dev_{1,148} = 24.039$, $P < 0.0001$) and site (the two-way interaction status × site, $Dev_{2,148} = 35.52$, $P < 0.001$). In each case, these significant two-way interactions arose because of variation in the extent of the difference between single and concurrently infected mice of both sexes, both age classes and from the three sites (table 2). The key point, however, is that despite these variations in each case a greater percentage of worms accumulated in the middle section of the intestine when mice also harboured *H. polygurus*.

At the Silwood Park site, mice were trapped in 1987 and 1991, although in 1987 all mice carrying *S. stroma* at this site were also infected with *H. polygyrus*, so it was not possible to test temporal variation in the extent of the redistribution of *S. stroma* in the presence of *H. polygyrus* at this site. Nevertheless, in 1991 the values for MPWB of *S. stroma* were much in line with all the other datasets referred to above. In the anterior section of the intestine in single species infections vs. concurrent infections the respective values were 42.0 ± 9.76% and 0.6 ± 0.42%, compared with 56.6 ± 9.31% vs. 91.6 ± 5.27%, in the middle and 1.4 ± 1.37 vs. 7.8 ± 5.20% in the posterior sections.

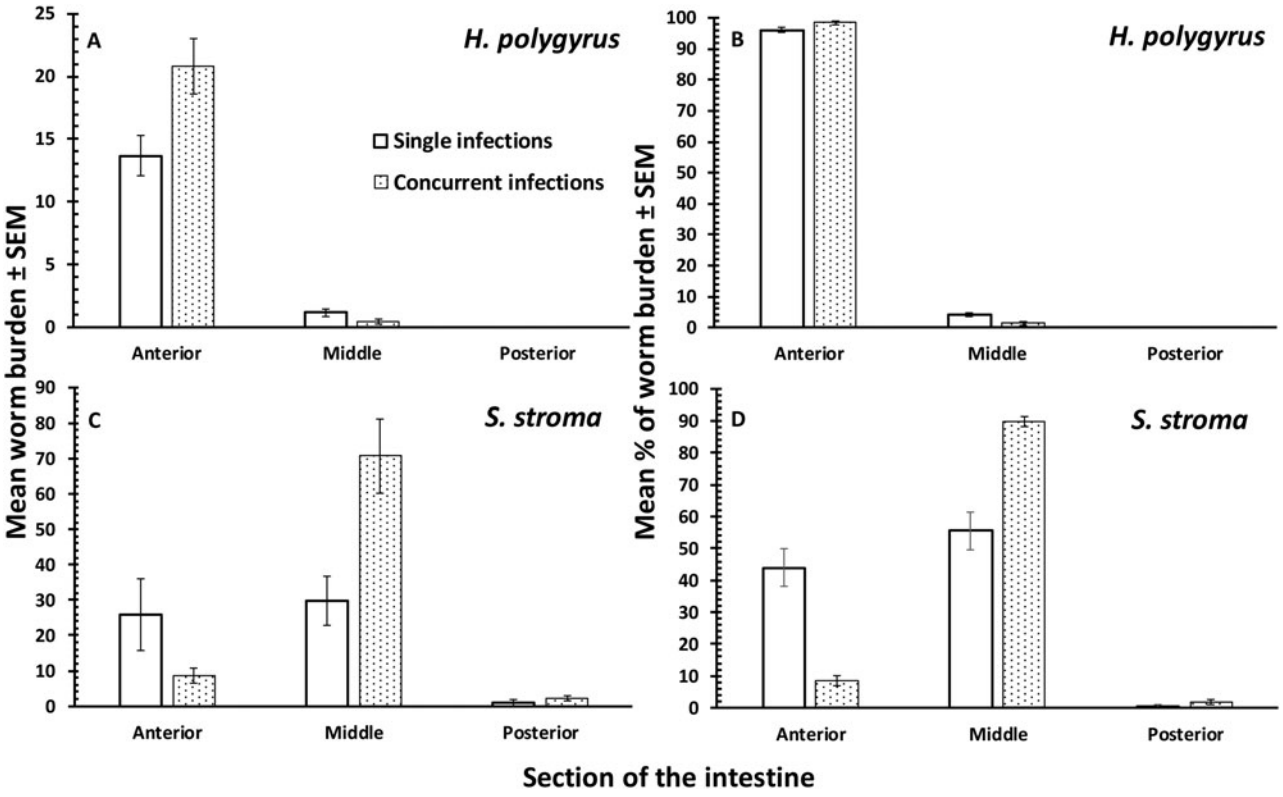

Fig. 1. The distribution of *H. polygyrus* and *S. stroma* in the anterior, middle and posterior sections of the small intestine in single species and concurrent infections. (A) Mean worm burden of *H. polygyryus* in mice with at least one *H. polygyrus* ($n = 122$ for mice with only *H. polygyrus* and 142 for concurrently infected mice); (C) mean worm burden of *S. stroma* in mice that had at least one *S. stroma* ($n = 21$ for mice with only *S. stroma* and 142 for concurrently infected mice); (B) mean percentage of *H. polygyrus* in single and concurrently infected mice; (D) mean percentage of *S. stroma* in single and concurrently infected mice. Key to columns is provided in panel (A).

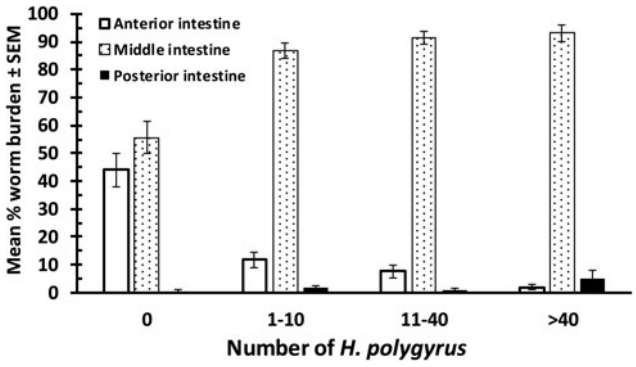

Fig. 2. The effect of varying intensity of *H. polygyrus* on the percentage distribution of *S. stroma* in the intestine. The figure shows the mean percentage worm burdens with *S. stroma* in the anterior, middle and posterior sections of the intestine. Data are restricted to mice that carried at least one *S. stroma*, and presented in infection intensity classes corresponding to no *H. polygyrus* ($n = 21$), 1–10 *H. polygyrus* ($n = 59$), 11–40 *H. polygyrus* ($n = 62$) and more than 40 *H. polygyrus* ($n = 21$).

Identification of additional helminth species in wood mice

Post-mortem examination of the body cavity, alimentary canal and its offshoots confirmed the presence of five additional helminth species, including the two cestodes *Catenotaenia pusilla* (Goeze, 1782) and *Hymenolepis murissyvatici* (Rudolphi, 1819) occupying the posterior intestinal section and the nematode *Aonchotheca murissylvatici* (Diesing, 1851) Lopez-Neyra, 1947 in the anterior section near the stomach. The larval cestode in the liver was identified as Cysticercus *Taeniae-taeniaeform*is (Batsch, 1786) and the digenean in the interlobary canals of the pancreas as *Corrigia vitta* (Dujardin, 1845). In mature mice from Great Wood, respective values for prevalence and intensity of infection were 9.7% and 8.4 (*C. pusilla*), 8% and 4.0 (*H. murissylvatici*), 3.5% and 4.1 (*A. murissylvatici*), 2.9% and 1.0 (Cysticercus *T.-taeniaeformis*) and 25.7% and 16.1 (*C. vitta*). Worm burdens of these helminth species were even lower in mice examined from Silwood Park and Rogate, suggesting that these levels of infection and their location within the host, especially *C. vitta*, are unlikely to have influenced the observed interactions between *H. polygyrus* and *S. stroma* in the anterior and middle sections of the intestine.

Discussion

The principal findings of the present study are that in concurrent infections with *H. polygyrus* and *S. stroma* in wood mice, the percentage distribution of the former species along the small intestine was unaffected, while proportionally more individuals of the latter species were located more posteriorly in the middle region of the intestine. This was unexpected, since based on the occupancy of quite different niches in the intestines of their hosts, we had predicted no change in the distribution of either species. The extent of the redistribution of *S. stroma* was highly dependent on the intensity of the *H. polygyrus* infection (i.e. the total worm burden), with relatively fewer *S. stroma* persisting in the anterior intestinal section as the intensity of *H. polygyrus*

Table 2. The distribution of *S. stroma* (mean percentage of worm burden) in the anterior, middle and posterior sections of the intestine in single species and concurrent infections in wood mice by host age and sex, and trapping site (Great Wood, Virginia Water, Surrey (GWVWS), Rogate Field Station, Hampshire (RFSH) and Silwood Park, Ascot, Berkshire (SPAB)).

	Section of the intestine		
Host age, sex and field site (*n*)	Anterior	Middle	Posterior
Host age			
Single infection			
Juveniles (13)	51.6 ± 7.16	48.4 ± 7.16	0
Mature mice (8)	31.6 ± 8.85	67.0 ± 8.59	1.4 ± 1.37
Concurrent infection			
Juvenile (39)	11.8 ± 3.86	86.0 ± 4.04	2.1 ± 1.65
Mature mice (103)	7.2 ± 1.58	91.2 ± 1.66	1.6 ± 0.64
Host sex			
Single infection			
Males (11)	40.0 ± 8.07	59.0 ± 7.82	1.0 ± 1.00
Females (10)	48.4 ± 8.72	51.6 ± 8.72	0
Concurrent infection			
Males (105)	8.3 ± 1.72	89.8 ± 1.85	1.9 ± 0.84
Females (37)	8.9 ± 3.51	89.8 ± 3.52	1.3 ± 0.63
Field site			
Single infection			
GWVWS (10)	39.4 ± 9.02	60.6 ± 9.02	0
RFSH (3)	64.6 ± 5.65	35.4 ± 5.65	0
SPAB (8)	42.0 ± 9.76	56.6 ± 9.31	1.4 ± 1.37
Concurrent infection			
GWVWS (95)	7.8 ± 1.78	90.6 ± 1.88	1.6 ± 0.73
RFSH (16)	8.4 ± 2.68	91.6 ± 2.68	0
SPAB (31)	10.5 ± 4.46	86.2 ± 4.66	3.3 ± 1.93

increased. Moreover, this pattern of redistribution of *S. stroma* into the middle section in concurrent infections with *H. polygyrus* was evident in both age classes and sexes of mice, and also in all three trapping sites.

Heligmosomoides polygyrus are relatively long, thin worms, which in their relaxed state appear as spring-like coils, reflecting a body shape that allows them to coil around villi in the small intestine (Durette-Desset, 1985) and preferentially in the duodenum, where in mice the villi are longer than more posteriorly (Bansemir & Sukhdeo, 1996). This gives individuals of this species a firm holdfast on the intestinal mucosa, and it may be that this is robust enough to enable the worms to remain in the anterior part of the intestine despite the presence of other helminth species. The body shape of *S. stroma* on the other hand is much shorter and wider than *H. polygrus* and, hence, unlikely to allow *S. stroma* to coil around villi. The latter species is atypical among *Syphacia* spp. in living in the anterior and middle regions of the intestine, since most of the other species of this genus live in the large intestine, including the caecum and colon of their hosts (Tenora & Mészáros, 1975). *Syphacia stroma* lives entirely in the intestinal lumen, without any evident holdfast, and, therefore, is more likely to lose position when competition and/or antagonistic interactions with other species become an issue. Like other oxyuroid species, *S. stroma* probably feeds mainly on intestinal micro-symbionts (Dunning & Wright, 1970; Adamson, 1989), the composition of which is known to change in helminth infections, and notably in the presence of *H. polygyrus* (Reynolds *et al.*, 2014; Cortés *et al.*, 2019; Lawson *et al.*, 2021). Moreover, *H. polygyrus* is known to cause marked pathophysiological changes in intestinal function (Liu, 1965; Kristan, 2002; Cywińska *et al.*, 2004), which may also affect the intestinal microbiome. If a redistribution of the specific intestinal microorganisms on which *S. stroma* feed does take place in the intestine of mice infected with *H. polygyrus*, this may explain why more *S. stroma* are located posteriorly than in concurrent infections, a hypothesis that could be tested experimentally.

The present study has drawn attention to the dynamic nature of the location of nematodes in the intestinal tract, a finding that is consistent with earlier studies (Stock & Holmes, 1988; Haukisalmi & Henttonen, 1993). Although more individuals of *S. stroma* end up accumulating in the middle intestinal section in concurrent infections, this section is not an abnormal location for the species since in hosts that have no concurrent infections with *H. polygyrus*, *S. stroma* individuals are about equally distributed between the anterior and middle sections, even when the total intensity of infection is low. Therefore, in this instance, competition in concurrent infections does not result in *S. stroma* having to live in a suboptimal site for feedings and reproduction. However, the test of his hypothesis would require individual worms from anterior, middle and posterior sections of the intestine to be measured and their fecundity assessed. If this interaction between the species turns out to be based upon direct competition between them, given the shift of *S. stroma* into the middle section in the presence of *H. polygyrus* and essentially no change in the distribution of *H. polygyrus*, *S. stroma* would appear to be the weaker competitor, as hypothesized by Holmes (1973) when two species occupy the same location in the intestine.

Although prevalence and abundance of *H. polygyrus* and *S. stroma* can be significantly affected by host age (Behnke *et al.*, 1999), this variable did not influence the prevailing pattern of reduced *S. stroma* distribution in the anterior intestine when concurrently infected with *H. polygyrus*. This result is unsurprising, as the effects of host age on parasite occurrence have been related to increasing opportunity for older mice to have contact with free-living transmission stages (Behnke *et al.*, 1999), a variable unlikely to affect the intestinal distribution of *S. stroma*.

Finally, whilst it is clear from our results that a redistribution of *S. stroma* does occur in concurrent infections, the nature of the exact signal/factor that is ultimately responsible for *S. stroma* avoiding the anterior section of the small intestine in concurrent infections is unknown. It is unlikely to be physical interaction between these species, but may be a response to excretory/secretory products of *H. polygyrus*, to changes in physiology of the mucosa in the duodenum, perhaps through components of the host's response to *H. polygyrus*, or to an intestinal redistribution of the micro-symbionts on which *S. stroma* feed, in the presence of *H. polygyrus*. This may be a fruitful field for further experimental investigation in facilities where the wild host wood mice, *A. sylvaticus*, are bred and maintained in the laboratory.

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