

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

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5 **John W. Lewis<sup>1</sup>, Neil J. Morley<sup>1</sup> and Jerzy M. Behnke<sup>2</sup>**

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7 1. Department of Biological Sciences, Royal Holloway, University of London, Egham,  
8 Surrey, TW20 0EX, UK

9 2. School of Life Sciences, University Park, Nottingham, NG7 2RD, UK.

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11  
12  
13  
14 **Author for correspondence:**

15 Jerzy M Behnke, Email: [jerzy.behnke@nottingham.ac.uk](mailto:jerzy.behnke@nottingham.ac.uk)

## 16 Abstract

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

## 31 Key words:

32 *Heligmosomoides polygyrus*, *Syphacia stroma*, wood mice, *Apodemus sylvaticus*,  
33 intestinal distribution, intestine, spatial interactions

## 35 Introduction

36 The survival of parasites within hosts requires intimate fine-tuning to conditions in the site  
37 where they reside. In helminths this ranges from morphological structures required to  
38 maintain position (e.g. scoleces of cestodes, proboscis of acanthocephalans (Smyth, 1976)  
39 and the intricate surface ridges of nematodes, called crêtes; Durette-Desset, 1986), host  
40 enzyme-blocking factors (Hawley et al., 1994; Zang & Maizels, 2001) to an array of  
41 molecules that interfere with host immune effector mechanisms (Hewitson *et al.*, 2011;  
42 Whelan *et al.*, 2011). It is well established that intestinal helminths have preferred sites (niche  
43 restriction) within the intestines of their vertebrate hosts to which they are highly adapted and  
44 in which they grow, survive and reproduce optimally (Crompton 1973; Holmes, 1973;  
45 Behnke, 1974; Rohde, 1994; Sukhdeo and Bansemir, 1996), and which they locate by  
46 responding to specific environmental cues (Sukdeo, 1990; Sukhdeo and Sulhdeo, 1994). Even  
47 closely related species of nematodes co-occurring in the same host species may show niche

48 segregation, as reflected in longitudinal differences in their distribution along the intestinal  
49 tract (Sommerville, 1963), as well as radial (intestinal niches from the lumen at the centre,  
50 outwards through the mucosa, submucosa to the serosa), as recorded in the seminal paper by  
51 Schad (1963; but see also Hominick and Davey, 1973 ).

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

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

66 These two species, *H. polygyrus* and *S. stroma*, are the dominant intestinal helminths  
67 of wood mice in the British Isles and often occur in concurrent infections (Lewis, 1969;  
68 Lewis & Twigg, 1972; Behnke *et al.* 2005). Experimental studies have shown that there may  
69 be different outcomes of co-occurrence of two species that normally reside in the same  
70 location in the gut (Christensen *et al.*, 1987; Behnke *et al.*, 2001). These include one species  
71 residing more posteriorly than normal in a sub-optimal location (e.g. the cestode *Hymenolepis*  
72 *diminuta* in concurrent infections with the acanthocephalam *Moniliformis moniliformis* in  
73 rats) while the other maintains its position in its preferred location (*M. moniliformis*).  
74 *Hymenolepis diminuta* eventually outlives *M. moniliformis* in rats, and recovers its normal  
75 attachment site in the duodenum once the acanthocephalans have died from senility (Holmes,  
76 1961). Posterior shifts in the mean intestinal position of the acanthocephalans  
77 *Pomphorhynchus laevis* in the presence of *Acanthocephalus clavula*, and vis-versa, and  
78 associated change in niche width, have been reported in trout (Byrne *et al.*, 2003), and related  
79 in both cases to intensities of infection with the concurrently infecting species.

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

## 90 **Materials and Methods**

### 91 *Databases*

92 We exploited three databases based on surveys of the helminth parasites of wood mice in  
93 woodland and grassland sites in southern England. The first was conducted from January to  
94 July 1969 in the Great Wood, Virginia Water, Surrey (GPS 51.417286 - 0.567032) a flat, dry  
95 area of mainly oak and birch woodland with bracken and bramble ground flora. The second  
96 survey was conducted in September 1985 at Rogate Field Station, Rogate in Hampshire (GPS  
97 51.006610 - 0.853225) an overgrown meadow of uncut and ungrazed grasses flanked by  
98 substantial woody hedgerows, whereas the third survey in September 1987 and 1991 was  
99 undertaken in a ploughed and cultivated grassland site at Silwood Park, Ascot, Berkshire  
100 (GPS 51.411781 - 0.641590).

### 102 *Laboratory procedures*

103 Mice were captured over a period of 10 trapping nights each month using Longworth traps  
104 provided with hay and food. The maturity of males was determined by the position and size  
105 of the testes. In mature males, large testes descend into the scrotal sacs whereas males with  
106 small testes situated within the body cavity were considered juvenile and incapable of  
107 breeding, which was also confirmed by examination of the epididymis for spermatozoa. For  
108 analysis, juvenile male mice weighed between 6.9 to 18.8 gm, with a range of 19.00 to 33.4  
109 gm in mature males. In female mice, the weight of the lightest pregnant female during the  
110 period of maximum number of pregnancies was taken and mice of this particular weight and

111 above were considered to be mature ranging from 18.9 to 36.45 gm compared with 9.5 to  
112 18.5 gm in juvenile females. Prior to post-mortem examination mice were killed by exposure  
113 to chloroform-soaked cotton wool. The alimentary canal was removed and the region  
114 between the end of the stomach (at the pyloric sphincter) and beginning of the rectum, was  
115 measured and divided into three equal length sections, referred to as the anterior, middle and  
116 posterior sections of the intestine, prior to being examined for helminth parasites. Part of the  
117 posterior section incidentally contained the colon and caecum.

118

### 119 *Statistical Methods*

120 Summary statistics are presented as mean worm burdens of both *H. polygyrus* and *S.*  
121 *stroma* with standard errors of the mean (SEM). The percentage distribution of worms (PWB)  
122 was calculated in the three intestinal sections of each mouse and mean values are referred to  
123 as mean percentage of worm burden (MPWB). Mean worm burdens and the MPWB from  
124 each of the three intestinal sections were calculated from each of the three surveys. Then,  
125 following the recommendations of Zuur *et al.* (2009), some factors that may have influenced  
126 the intestinal distribution of parasites were explored using non-parametric tests in IBM-SPSS  
127 24 (Kruskal-Wallis, Mann-Whitney *U* test, and Spearman's test of correlation). In each case  
128 the value of the relevant test statistic (*H*, *U* and *r<sub>s</sub>*, respectively) and the probability (*P*) for  
129 rejecting the null hypothesis ( $\alpha = 0.05$ ) were provided. When analysing the effect of *S.*  
130 *stroma* on *H. polygyrus* data were provided on all hosts that harboured at least one individual  
131 of *H. polygyrus*, and similarly when analysing the effect of *H. polygyrus* on *S. stroma* only  
132 data from mice that harboured at least one individual of *S. stroma* were used. Finally,  
133 generalised linear models (GLMs) in R version 2.2.1 (R Core Development Team) were  
134 provided after converting the PWBs to binomial values (see Douma and Weedon (2018). Full  
135 factorial binomial GLMs were evaluated as described elsewhere (Behnke *et al.*, 2021), with  
136 sex (at two levels, males and females), age (at two levels, juveniles and mature mice), site (at  
137 three levels, three sites) and status (at two levels corresponding to mice infected only with *S.*  
138 *stroma* or concurrently with *H. polygyrus*) as explanatory factors. Minimum sufficient  
139 models were also fitted incorporating only significant main effects and 2-way interactions.  
140 From these, values of deviance (DEV) for the main effect of status, and 2-way interactions  
141 with status were provided as the principal objectives of the study.

142

## 143 Results

### 144 *Summary statistics for the combined dataset*

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

152

### 153 *Worm burdens in single and concurrently infected mice*

154 Worm burdens of *H. polygyrus* were heavier in concurrently infected compared with single  
155 infected mice (single infection =  $14.8 \pm 1.76$ ,  $n=122$ ; concurrent infection =  $21.3 \pm 2.18$ ,  
156  $n=142$ ; Mann-Whitney *U* test,  $U_{122, 142} = 10,617.5$ ,  $P=0.002$ ). However, despite the  
157 arithmetically higher intensity of infection with *S. stroma* in concurrently infected mice, for  
158 this species the difference with single-infected mice was not significant (single infection =  
159  $56.3 \pm 13.61$ ,  $n=21$ ; concurrent infection =  $81.8 \pm 11.66$ ,  $n=142$ ; Mann-Whitney *U* test,  $U_{21, 142} = 1,505.0$ ,  $P=0.9$ ).

161

### 162 *Distribution of worms in single and concurrently infected mice*

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

168 In single worm infections *S. stroma* was more or less equally distributed between the  
169 first and second thirds of the intestine, whether expressed as mean number of worms present  
170 or as MPWB (Figs. 1B and 1D, respectively), although in the latter case values were  
171 marginally higher for the middle section. However, when *H. polygyrus* was present in the  
172 anterior third of the intestine, both the mean *S. stroma* worm burden in this section (Mann-  
173 Whitney *U* test,  $U_{21, 142} = 646.0$ ,  $P<0.001$ ) and the MPWB ( $U_{21, 142} = 274.5$ ,  $P<0.001$ ) were

174 significantly lower than in single-species infections. There was a corresponding increase in  
175 the MPWB ( $U_{21, 142} = 2671.0, P < 0.001$ ) in the middle section, but an increase in worm  
176 burdens was not significant ( $U_{21, 142} = 1,817.5, P = 0.106$ ). There was also a very small increase  
177 in the number of *S. stroma* in the posterior third of the intestine in concurrently infected mice,  
178 but this was not significant (e.g. for MPWB,  $U_{21, 142} = 1,666.0, P = 0.167$ ).

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

181 Since in the presence of *H. polygyrus*, the percentage distribution of *S. stroma* altered, with a  
182 greater percentage of worms located in the middle section of the intestine, it was of interest to  
183 determine whether the extent of this posterior redistribution of *S. stroma* was dependent also  
184 on the intensity of infection with *H. polygyrus*. There was a clear dose-dependent effect, with  
185 higher *H. polygyrus* worm burdens in mice resulting in fewer *S. stroma* in the anterior section  
186 (Fig. 2; for worm burdens,  $r_s = -0.297, n = 163, P < 0.001$ ; for percentage worm burdens,  $r_s = -$   
187  $0.387, n = 163, P < 0.001$ ;) and a corresponding higher percentage now located in the middle  
188 section of the intestine ( $r_s = 0.300, n = 163, P < 0.001$ ).

#### 190 *Factors affecting the distribution of S. stroma*

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

198 The difference in MPWB of *S. stroma* in the anterior intestinal section between mice  
199 infected only with *S. stroma* and those with concurrent *H. polygyrus* infection was highly  
200 significant (GLM with binary errors, main effect of status,  $Dev_{1, 157} = 95.243, P < 0.0001$ ). This  
201 difference was not affected by host sex (for the 2-way interaction status x sex,  $Dev_{1, 148} =$   
202  $0.945, P = 0.3$ ) nor host age class (the 2-way interaction status x age  $Dev_{1, 148} = 0.391, P = 0.5$ ).  
203 However, there was a significant difference between the three field sites in the extent of the  
204 reduction in *S. stroma* in the anterior section of the intestine in concurrent infections (the 2-  
205 way interaction status x site,  $Dev_{2, 154} = 27.515, P < 0.001$ ), as shown in Table 2.

206 In contrast, in the middle section of the intestine, the percentage of *S. stroma* was  
207 higher in concurrent infections compared with mice just harbouring *S. stroma*, and this was  
208 the case in both age classes, sexes and all three sites where mice were trapped (Table 2). The  
209 difference in the MPWB of *S. stroma* in the middle section, between mice infected only with  
210 *S. stroma* and those with concurrent *H. polygyrus* was highly significant (GLM with binary  
211 errors, main effect of status,  $Dev_{1,157}=403.23, P<0.0001$ ). However, in this case there were  
212 also significant 2-way interactions with sex (for the 2-way interaction status x sex,  $Dev_{1,148}=$   
213  $4.385, P=0.036$ ), with age class (the 2-way interaction status x age,  $Dev_{1,148}= 24.039,$   
214  $P<0.0001$ ) and site (the 2-way interaction status x site,  $Dev_{2,148}= 35.52, P<0.001$ ). In each  
215 case these significant 2-way interactions arose because of variation in the extent of the  
216 difference between single and concurrently infected mice of both sexes, both age classes and  
217 from the three sites (Table 2). The key point, however, is that despite these variations in each  
218 case a greater percentage of worms accumulated in the middle section of the intestine when  
219 mice also harboured *H. polygyrus*.

220 At the Silwood Park site, mice were trapped in 1987 and 1991, although in 1987 all  
221 mice carrying *S. stroma* at this site were also infected with *H. polygyrus*, so it was not  
222 possible to test temporal variation in the extent of the redistribution of *S. stroma* in the  
223 presence of *H. polygyrus* at this site. Nevertheless, in 1991 the values for MPWB of *S. stroma*  
224 were much in line with all the other datasets referred to above. In the anterior section of the  
225 intestine in single species infections vs concurrent infections the respective values were  $42.0$   
226  $\pm 9.76\%$  and  $0.6 \pm 0.42\%$ , compared with  $56.6 \pm 9.31\%$  vs  $91.6 \pm 5.27\%$ , in the middle and  
227  $1.4 \pm 1.37$  vs  $7.8 \pm 5.20\%$  in the posterior sections.

#### 228 229 *Identification of additional helminth species in wood mice*

230 Post-mortem examination of the body cavity, alimentary canal and its offshoots  
231 confirmed the presence of five additional helminth species, including the two cestodes  
232 *Catenotaenia pusilla* (Goeze,1782) and *Hymenolepis murissylvatici* (Rudolphi, 1819)  
233 occupying the posterior intestinal section and the nematode *Aonchotheca murissylvatici*  
234 (Diesing,1851) Lopez-Neyra,1947 in the anterior section near the stomach. The larval cestode  
235 in the liver was identified as *Cysticercus Taeniae-taeniaeformis* (Batsch, 1786) and the  
236 digenean in the interlobary canals of the pancreas as *Corrigia vitta* (Dujardin, 1845). In  
237 mature mice from Great Wood, respective values for prevalence and intensity of infection



238 were 9.7% and 8.4 (*C. pusilla*), 8% and 4.0 (*H. murissylvatici*), 3.5% and 4.1 (*A.*  
239 *murissylvatici*), 2.9% and 1.0 (*Cysticercus taeniae-taeniaeformis*), 25.7% and 16.1 (*C.*  
240 *vitta*). Worm burdens of these helminth species were even lower in mice examined from  
241 Silwood Park and Rogate suggesting that these levels of infection and their location within  
242 the host, especially *C. vitta*, are unlikely to have influenced the observed interactions between  
243 *H. polygyrus* and *S. stroma* in the anterior and middle sections of the intestine.

## 245 Discussion

246 The principal findings of the present study are that in concurrent infections with *H.*  
247 *polygyrus* and *S. stroma* in wood mice, the percentage distribution of the former species  
248 along the small intestine was unaffected, while proportionally more individuals of the latter  
249 species were located more posteriorly in the middle region of the intestine. This was  
250 unexpected, since based on the occupancy of quite different niches in the intestines of their  
251 hosts, we had predicted no change in the distribution of either species. The extent of the re-  
252 distribution of *S. stroma* was highly dependent on the intensity of the *H. polygyrus* infection  
253 (i.e. the total worm burden), with relatively fewer *S. stroma* persisting in the anterior  
254 intestinal section as the intensity of *H. polygyrus* increased. Moreover, this pattern of  
255 redistribution of *S. stroma* into the middle section in concurrent infections with *H. polygyrus*  
256 was evident in both age classes and sexes of mice, and also in all three trapping sites.

257 *Heligmosomoides polygyrus* are relatively long, thin worms, which in their relaxed  
258 state appear as spring-like coils, reflecting a body shape that allow them to coil around villi in  
259 the small intestine (Durette-Desset, 1985) and preferentially in the duodenum, where in mice  
260 the villi are longer than more posteriorly (Bansemir and Sukhdeo, 1996). This gives  
261 individuals of this species, a firm holdfast on the intestinal mucosa, and it may be that this is  
262 robust enough to enable the worms to remain in the anterior part of the intestine despite the  
263 presence of other helminth species. The body shape of *S. stroma* on the other hand is much  
264 shorter and wider than *H. polygyrus* and hence unlikely to allow *S. stroma* to coil around villi.  
265 The latter species is atypical among *Syphacia* spp. in living in the anterior and middle regions  
266 of the intestine, since most of the other species of this genus live in the large intestine,  
267 including the caecum and colon of their hosts (Tenora and Mészáros, 1975). *Syphacia stroma*  
268 lives entirely in the intestinal lumen, without any evident holdfast, and therefore is more  
269 likely to lose position when competition and/or antagonistic interactions with other species

270 become an issue. Like other oxyurid species, *S. stroma* probably feeds mainly on intestinal  
271 micro-symbionts (Dunning and Wright, 1970; Adamson, 1989), the composition of which is  
272 known to change in helminth infections, and notably in the presence of *H. polygyrus*  
273 (Reynolds *et al.*, 2014; Cortés *et al.*, 2019; Lawson *et al.*, 2021). Moreover, *H. polygyrus* is  
274 known to cause marked pathophysiological changes in intestinal function (Liu, 1965; Kristan,  
275 2002; Cywińska *et al.* 2004), which may also affect the intestinal microbiome. If a  
276 redistribution of the specific intestinal microorganisms on which *S. stroma* feed does take  
277 place in the intestine of mice infected with *H. polygyrus*, this may explain why more *S.*  
278 *stroma* are located posteriorly than in concurrent infections, a hypothesis that could be tested  
279 experimentally.

280 The present study has drawn attention to the dynamic nature of the location of  
281 nematodes in the intestinal tract, a finding that is consistent with earlier studies (Stock and  
282 Holmes, 1988; Haukisalmi and Henttonen 1993). Although more individuals of *S. stroma* end  
283 up accumulating in the middle intestinal section in concurrent infections, this section is not an  
284 abnormal location for the species since in hosts that have no concurrent infections with *H.*  
285 *polygyrus*, *S. stroma* individuals are about equally distributed between the anterior and  
286 middle sections, even when the total intensity of infection is low. Therefore, in this instance  
287 competition in concurrent infections does not result in *S. stroma* having to live in a  
288 suboptimal site for feedings and reproduction. However, the test of his hypothesis would  
289 require individual worms from anterior, middle and posterior sections of the intestine to be  
290 measured and their fecundity assessed. If this interaction between the species turns out to be  
291 based upon direct competition between them, given the shift of *S. stroma* into the middle  
292 section in the presence of *H. polygyrus* and essentially no change in the distribution of *H.*  
293 *polygyrus*, *S. stroma* would appear to be the weaker competitor, as hypothesised by Holmes  
294 (1973) when two species occupy the same location in the intestine.

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

302 Finally, whilst it is clear from our results that a redistribution of *S. stroma* does occur  
1 303 in concurrent infections, the nature of the exact signal/factor that is ultimately responsible for  
2 304 *S. stroma* avoiding the anterior section of the small intestine in concurrent infections is  
3  
4 305 unknown. It is unlikely to be physical interaction between these species, but may be a  
5  
6 306 response to excretory/secretory products of *H. polygyrus*, to changes in physiology of the  
7  
8 307 mucosa in the duodenum, perhaps through components of the host's response to *H. polygyrus*,  
9  
10 308 or to an intestinal redistribution of the micro-symbionts on which *S. stroma* feed, in the  
11  
12 309 presence of *H. polygyrus*. This may be a fruitful field for further experimental investigation in  
13  
14 310 facilities where the wild host wood mice, *A. sylvaticus*, are bred and maintained in the  
15  
16 311 laboratory.  
17

18 312

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30

31 318

32  
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34  
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36  
37 321 analysed the results and all authors contributed to preparation of the manuscript and all  
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39 322 approved the submitted version.  
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439 **Table 1.** The number of mice in surveys by site, age, sex and year. This table includes only  
 440 those mice used for analysis.

441	<hr/>				
442	Factor	Virginia Water	Rogate	Silwood Park	Total
443	<hr/>				
444	Juvenile				
445	Males	37	15	10	62
446	Females	31	6	9	46
447	Total	68	21	19	108
448	Adult				
449	Males	88	5	29	122
450	Females	25	1	29	55
451	Total	113	6	58	177
452	Combined				
453	Males	125	20	39	184
454	Females	56	7	38	101
455	Total	181	27	77	285
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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 & field site ( <i>n</i> )		Anterior	Middle	Posterior
<b>Host age</b>				
<b>Single infection</b>				
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
<b>Concurrent infection</b>				
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
<b>Host sex</b>				
<b>Single infection</b>				
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
<b>Concurrent infection</b>				
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
<b>Field site</b>				
<b>Single infection</b>				
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

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Concurrent infection

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492	GWVWS	(95)	7.8 ± 1.78	90.6 ± 1.88	1.6 ± 0.73
493	RFSH	(16)	8.4 ± 2.68	91.6 ± 2.68	0
494	SPAB	(31)	10.5 ± 4.46	86.2 ± 4.66	3.3 ± 1.93
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497 **Legends for Figures**

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3 498 **Fig. 1.** The distribution of *H. polygyrus* and *S. stroma* in the anterior, middle and posterior  
4 499 sections of the small intestine in single species and concurrent infections. (A), mean worm  
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6 500 burden of *H. polygyrus* in mice with at least one *H. polygyrus* ( $n= 122$  for mice with only *H*  
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8 501 *polygyrus* and 142 for concurrently infected mice); (B), mean worm burden of *S. stroma* in  
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10 502 mice that had at least one *S. stroma* ( $n= 21$  for mice with only *S. stroma* and 142 for  
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12 503 concurrently infected mice); (C), Mean percentage of *H. polygyrus* in single and concurrently  
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14 504 infected mice; (D), Mean percentage of *S. stroma* in single and concurrently infected mice;  
15 505 Key to columns is in panel A.  
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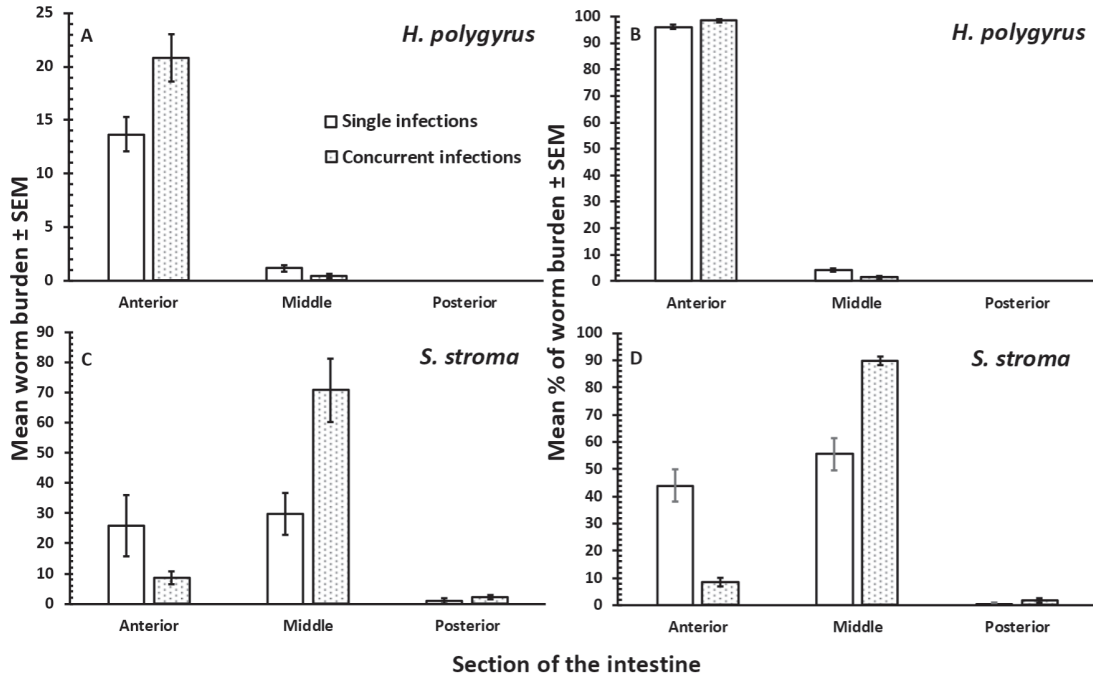
19  
20 507 **Fig. 2.** The effect of varying intensity of *H. polygyrus* on the percentage distribution of *S.*  
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22 508 *stroma* in the intestine. The figure shows the mean percentage worm burdens with *S. stroma*  
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24 509 in the anterior, middle and posterior sections of the intestine. Data are restricted to mice that  
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26 510 carried at least one *S. stroma*, and presented in infection intensity classes corresponding to no  
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28 511 *H. polygyrus* ( $n=21$ ), 1-10 *H. polygyrus* ( $n=59$ ), 11-40 *H. polygyrus* ( $n=62$ ) and more than 40  
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30 512 *H. polygyrus* ( $n=21$ ).  
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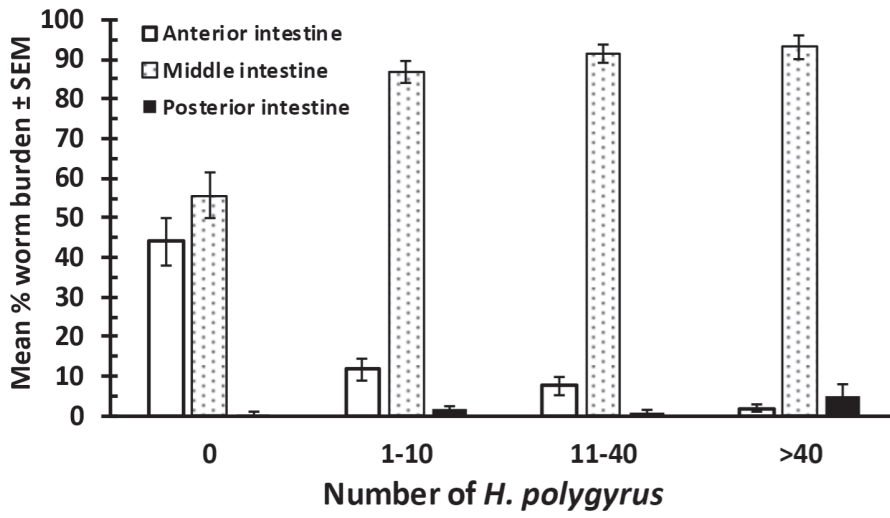
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516 **Fig. 1**



521 **Fig. 2**



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