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Helminth parasites of the wood mouse *Apodemus sylvaticus* in Southern England: levels of infection, species richness and interactions between species

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Research Paper

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Abstract

Helminth parasites of the wood mouse, *Apodemus sylvaticus* ($n = 440$), were surveyed in five localities, comprising woodland and grassland sites, in Southern England. Seven species of helminths were identified, among which *Heligmosomoides polygyrus* and *Syphacia stroma* were dominant (prevalence = 79.1% and 54.1%, respectively). Less common species were the trematode *Corrigia vitta* (14.8%), cestodes *Catenotaenia pusilla* (8.4%), *Hydatigera taeniaeformis* (4.1%) and *Microsomacanthus crenata* (3.4%) and the nematode *Aonchotheca murissylvatici* (0.2%). Differences in prevalences between localities were found for *H. polygyrus*, *H. taeniaeformis* and *M. crenata* and in abundances of *H. polygyrus*, *S. stroma* and *C. vitta*. Age-dependent increases in both parameters were identified among species and for helminth species richness. The only species to show significant host sex bias was *S. stroma* with prevalence values being higher in male mice. A number of different methods for exploiting raw data, and data corrected for significant confounding factors, were used to determine whether there were significant associations (prevalence) between species or quantitative interactions (abundance). The strongest evidence for a positive association was shown in concurrent infections with the trematode *C. vitta* and the cestode *C. pusilla* (significant in the whole dataset and evident in each locality, both sexes and both age classes). The abundance of *C. pusilla* was also higher in mice with *C. vitta* and vice versa. Overall, however, there was little support for associations or quantitative interactions between species, especially after data had been corrected for significant extrinsic/intrinsic factors, and we conclude that the helminths of wood mice in these communities are largely non-interactive and hence, perhaps better referred to as assemblages.

Dedication

In deep sorrow, we dedicate this paper to the memory of the primary author, who sadly passed away as the manuscript was being resubmitted to the *Journal of Helminthology*. Professor John Lewis was the inspiration for this, and many other studies in the field, and was one of the pioneers of helminth ecology in wild rodents. Despite his serious illness throughout the year, John participated in all stages of analysis and completion of this manuscript.

Introduction

Helminths of the wood mouse, *Apodemus sylvaticus*, have been studied extensively in host populations throughout mainland Europe (Tenora, 2004; Tenora *et al.*, 1977; Mészáros & Murai, 1979; Genov, 1984; Feliu *et al.*, 1997; Galán-Puchades *et al.*, 1998; Milazzo *et al.*, 2005; Eira *et al.*, 2006; Miljević *et al.*, 2022) and the British Isles, the first comprehensive study in the latter region being undertaken by Elton *et al.* (1931) in *A. sylvaticus* and also the bank vole, *Myodes* (*Clethrionomys) glareolus britannicus* (Miller) from Bagley Wood near Oxford. Elton and his co-workers studied seasonal variation in infection levels, but the biology of hosts and parasites were treated separately as the life histories of parasites were then unknown. Apart from the work of Thomas (1953), James (1954), Sharpe (1964), Lewis (1964, 1968), Lewis & Twigg (1972) and Lewis & Bryant (1976), it is surprising that few studies of this nature, demonstrating predictable features of infracommunities and component communities, were made in the British Isles between 1953 and 1976. Nevertheless, these and subsequent studies on the population dynamics of helminth parasites in wild and laboratory rodents (Scott & Lewis, 1987) have shown that highly predictable intrinsic and extrinsic factors have a profound effect on parasite burdens and also species richness within these communities.

Arguably, the most important extrinsic factor has been shown to be the geographical locality in which mice are trapped. Helminth infracommunities of wood mice, as well as those of other rodents, for example, bank voles, are known to differ between host subpopulations living in close proximity to one another but in different localities, among habitats that are ecologically very similar, as well as among those that differ radically (Kisielewska, 1970a, b; Montgomery & Montgomery, 1989; Abu-Madi *et al.*, 1998, 2000; Behnke *et al.*, 2001; Bordes *et al.*, 2012; Grzybek et al., 2015a; Loxton *et al.*, 2017; Babayan *et al.*, 2018; Sweeny *et al.*, 2021a). Moreover, some authors have even observed differences in the distribution of rodent pathogens between subpopulations trapped in different areas of a discrete locality (leptospirosis in Twigg *et al.*, 1968; helminth infracommunities in Lewis & Twigg, 1972; Krasowska, 1974). Lewis (1968) clearly showed that *Apodemus sylvaticus* sampled from Skomer Island off the Pembrokeshire coast in West Wales were primarily and heavily infected with *Syphacia stroma* in juvenile and mature mice (mean values of 123.2 and 238.7, respectively), which appeared to prevent establishment of the more frequent and dominant nematode *Heligmosomoides polygyrus* occurring in mainland mice. Seasonal changes in helminth burdens are also well recognized, although most such studies have been conducted over very short time spans, usually just 1–2 years (Lewis, 1968; Langley & Fairley, 1982; O'Sullivan *et al.*, 1984; Montgomery & Montgomery, 1988, 1989, 1990; Gregory, 1992; Abu-Madi *et al.*, 1998, 2000; Behnke *et al.*, 1999). More recently, attention has shifted to perturbation experiments in wild mice (Ferrari *et al.*, 2004; Pederson & Grieves, 2008; Knowles *et al.*, 2013; Pederson & Antonovics, 2013) and to monitoring long-term changes (Grzybek et al., 2015a: Behnke *et al.*, 2019, 2021; Sweeny *et al.*, 2021a; Hayward *et al.*, 2022; Wood *et al.*, 2023) Both approaches have revealed remarkable stability of some helminth species, usually the core species, as well as marked fluctuations in others reflecting between year cycles and responses to perturbation, temporally declining worm burdens, as well as complete loss and acquisition of new species.

Perhaps intuitively, we might expect intrinsic factors to play a major role in determining parasite burdens but few such factors have emerged as critical. Host age ranks highly among those intrinsic factors that are consistently reported as having a marked influence on parasite burdens (Elton *et al.*, 1931; Kisielewska, 1971; Montgomery & Montgomery, 1988, 1989; Abu-Madi *et al.*, 1998; Behnke *et al.*, 1999; Loxton *et al.*, 2016, 2017). In studies where the age of mice was assessed and the mice were subsequently allocated to different age classes, helminth species richness has been found to increase significantly with increasing host age (Montgomery & Montgomery, 1989; Sáez-Durán *et al.*, 2021). The same has been found for the worm burdens of some, but not all individual helminth species (Behnke *et al.*, 1999). Helminth burdens accumulate with age because most species form chronic infections by employing effective strategies for evading host immunity (Behnke *et al.*, 1992; Maizels *et al.*, 2004). Nevertheless, some studies have reported convex age-prevalence and age-abundance curves indicative of increasing age-dependent loss of worms from hosts, likely from acquired immunity to infection or increased mortality and loss of heavily infected aging hosts (Elton *et al.*, 1931; Pascala & Dobson, 1984; Gregory *et al.*, 1992; Vandegrift & Hudson, 2009a).

The second most often-assessed intrinsic factor is host sex, but while differences between the sexes in susceptibility and resistance to infections in mammals are generally well established (Poulin, 1996a; Zuk & McKean, 1996; Moore & Wilson, 2002), studies based on wild rodents have been less consistent in this respect (Behnke *et al.*, 1999; Bordes *et al.*, 2012). While male-biased helminth burdens in rodents have been reported in some studies (Lewis, 1968; Lewis & Twigg, 1972; Gregory *et al.*, 1990), other studies have failed to find any evidence for sex-bias (Abu-Madi *et al.*, 1998; Ferrari *et al.*, 2004; Lo & Shaner, 2015; Babayan *et al.*, 2018), and some have reported female bias (Grzybek *et al.*, 2015b; Miljević *et al.*, 2022). Generally, sexual dimorphism in helminth burdens appears to be extremely context dependent (i.e. often seasonal, varying between years and locality specific; Abu-Madi *et al.*, 1998, 2000; Behnke *et al.*, 1999; Sáez-Durán *et al.*, 2021; Sweeny *et al.*, 2021a). Despite this, evidence has been provided through a perturbation study that male mice (*Apodemus flavicollis*) are more important than females in driving *H. polygyrus* infections in host populations (Ferrari *et al.*, 2004, 2007; see also Luong *et al.*, 2009, for a similar outcome in *Peromyscus leucopus* infected wih *Pterygodermatites peromysci*). Finally, some recent studies have also considered factors such as host weight, as a proxy for age but possibly reflective of body condition (Vandegrift *et al.*, 2008; Sweeny *et al.*, 2021a; Miljević *et al.*, 2022), availability of food (Vandegrift & Hudson, 2009b; Sweeny *et al.*, 2021b) and reproductive status (Sweeny *et al.*, 2021a), also often with context dependent effects on/relationships with parasite prevalence and abundance.

Compared with helminth species richness and diversity of wood mice from continental Europe (Feliu *et al.*, 1997; Fuentes *et al.*, 2004; Milazzo *et al.*, 2005; Eira *et al.*, 2006; Bordes, 2012), those from localities in the British Isles have been found to be severely depauperate (Sharpe, 1964; Lewis, 1968; Abu-Madi *et al.*, 2000), likely a legacy of their isolation since the late Quaternary about half a million years ago (Gupta *et al.*, 2017). Although all helminth species recorded in wood mice from the British Isles have also been recorded in various geographical localities throughout the European mainland, many of those found abroad have never been recorded in wood mice from the British Isles, for example, *Mastophorus muris*, *Rictularia proni* and *Heligmosomum* spp.

Nevertheless, in host populations carrying several different helminth species, occupying overlapping sites in the intestine and characterized by shared features of their life cycles, modes of nutrition, effects on host physiology, immune system etc., we might expect to see some evidence of interactions between species (Haukisalmi & Henttonen, 1998; Behnke *et al.*, 2005, 2009; Poulin, 2005). Interactions between species, resulting in positive or negative changes in the abundance of concurrently residing species and co-occurrence of species suggesting interdependence, are expected features of animal communities (Margolis *et al.*, 1982; Morin, 2011), but often these have proved difficult to identify and verify quantitatively with appropriate statistical support (Behnke *et al.*, 2005; Poulin, 2005). For this reason, parasitologists have often preferred to refer to parasite assemblages, rather than communities (Poulin, 2007, 2019; Levy *et al.*, 2021).

At the level of interactions between species, we have recently shown that the two dominant helminth species of wood mice in the British Isles appear to interact in the host intestine such that in concurrent infections, *S. stroma* worms are encountered more posteriorly when the anterior of the intestine is also occupied by *H. polygyrus* (Lewis *et al.*, 2021). Moreover, some evidence for associations between helminth species influencing the likelihood of being infected and for interactions that result in worm burdens being affected, has also been provided for helminth

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species of wood mice based on destructive sampling in cross-sectional and yearly repeated surveys (Montgomery & Montgomery, 1990; Behnke *et al.*, 2005). However, such studies have been criticized as unreliable for a variety of reasons (Knowles *et al.*, 2013), and repeated non-invasive sampling of marked hosts has been proposed as a more robust approach for quantifying associations and interactions between species (Fenton *et al.*, 2014; Sweeny et al., 2021a).

Despite the limitations of cross-sectional studies, if associations and/or interactions exist between parasites infecting a host species, some evidence of these should be apparent in large scale destructive sampling. In the present study the helminth burdens of five populations of wood mice from Southern England, comprising 440 animals in total, were sampled at various times over a period of 25 years (1965–1989). First, we provide a quantitative analysis of the factors that significantly influenced prevalence and abundance of helminth species in order to identify confounding effects that need to be taken into account when seeking evidence for associations/interactions between species. Then, we seek evidence for associations between species at the level of prevalence and for quantitative interactions affecting worm burdens.

Materials and methods

Databases

This analysis uses existing datasets based on surveys of the helminth parasites of wood mice collected from woodland and grassland sites in Southern England in early autumn months (late August to late October). Parts of these datasets have been utilized in earlier papers (Lewis & Twigg, 1972; Lewis *et al.*, 2021), but have not been analysed as extensively, nor with the same objectives, as reported herein. Three woodland sites were located north of Virginia Water, Surrey, and include: the Great Wood (Global Positioning System (GPS) 51.417286 – 0.567032) a flat, dry area of mainly oak and birch woodland with bracken and bramble ground flora sampled in 1965, 1968 and 1969, Alderhurst (GPS 51.41877, −0.56872), an area made up of copses and strips of deciduous woodland and brambles separated by small areas of grassland, sampled in 1966–67, 1982 and 1985–1989, and Ulverscroft (GPS 51.4189, −0.57077), an area of mixed woodland and brambles surrounding a cultivated grassland area with domestic buildings, sampled in 1987. These woodland sites are within one mile of each other but separated by a road and a stream. Great Wood is on the valley floor and Alderhurst is on the upper slope of the valley. A stream separates the two sites. Soil moisture content/water drainage is possibly different between these two sites. Ulverscroft is at the top of the valley separated from the other sites by a road and domestic buildings along the road. Grassland sites were at Rogate Field Station, Rogate in Hampshire (GPS 51.006610 – 0.853225; more than 30 miles distant from Great Wood), an overgrown meadow of uncut and ungrazed grasses flanked by substantial woody hedgerows, sampled in 1982, 1985–86 and 1988; and at Silwood Park, Ascot, Berkshire (GPS 51.411781 – 0.641590, approximately five miles distant from Great Wood), a ploughed and cultivated grassland site sampled in 1987 and 1989.

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 to 18.8 g with a range of 19.00 to 33.4 g 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 g compared with 9.5 to 18.5 g in juvenile females. Prior to post-mortem examination mice were killed by exposure to chloroform-soaked cotton wool. The alimentary canal and associated organs (liver, pancreas, kidneys and bladder) were removed and examined for helminths.

Nomenclature

We refer to *Microsomacanthus crenata* (= *Hymenolepis murisylvatici* (Rudolphi, 1819) = *Variolepis crenata* (Goeze, 1782)), since Prokopic (1967) synonymized *H. murissylvatici* with *Passerilepis crenata*, followed by reallocation of the species to the genus *Microsomacanthus* (Khalil *et al.*, 1994). We also refer to *Aonchotheca murissylvatici* (= *Capillaria murissylvatici* (Diesing, 1851) following Moravec (1982) and to *Hydatigera taeniaeformis* (=*Taenia taeniaeformis* (Batsch, 1786) Lamarck, 1816) following Nakao *et al.*, 2013 and Lavikainen *et al.*, 2016, but see also Verster, 1969.

Statistical analysis

For data subsets, prevalence values (% of mice infected with helminth species referred to) are given with 95% confidence limits (CL_{95}) in the text and 95% confidence intervals (CI_{95}) illustrated in figures, and calculated in bespoke software based on the tables of Rohlf & Sokal (1995). For quantitative data (i.e. abundance as reflected in worm burdens), mean values ± standard error of the mean (SEM) are provided and we refer to abundance as defined by Margolis *et al.* (1982) and Bush *et al.* (1997), and derived for all mice in a data subset, including those uninfected by the parasite in question.

Prevalences were analysed using maximum likelihood techniques based on log-linear analysis of contingency tables in the software package IBM SPSS (version 28). Full factorial models included sex (two levels, male and female mice), age (two levels, juvenile and mature mice), geographical locality (five levels, five sites as specified above) and presence/absence of infection (hereafter referred to as INFECTION) with the parasite being investigated. This approach is based on categorical values of factors of interest, which are used not only to fit hierarchical log-linear models to multidimensional cross-tabulations using an iterative proportional-fitting algorithm but also to detect associations between factors, one of which is INFECTION. Multi-factorial models were fitted as described previously (Abu-Madi *et al.*, 2016), beginning with the full factorial model. Then, by employing the backward selection procedure in SPSS, we simplified the model until only significant terms remained. For each level of analysis in turn, beginning with the most complex model, involving all possible main effects and interactions, those combinations that did not contribute significantly to explaining variation in the data were eliminated in a stepwise fashion beginning with the highest level interaction (backward selection procedure). A minimum sufficient model was then obtained, for which the likelihood ratio of Chi-square was not significant, indicating that the

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model was sufficient in explaining the data. The importance of each term in interactions involving INFECTION in the final model was assessed by the probability that its exclusion would alter the model significantly and these values are given in the text, assessed by a likelihood ratio test between models with and without each term of interest.

For quantitative data we first fitted full factorial generalized linear statistical models in R (version 4.1.0, R Core Development Team), testing models that were based on negative binomial or Poisson error structures, as relevant. Full factorial models as specified in the text were then simplified by a step-wise deletion of non-significant terms until only significant main effects and interactions, and also main effects that were components of interactions but not significant in their own right, remained (minimum sufficient models referred to as MSM). The significance of each of the remaining terms was then assessed by comparison of models with and without that effect. Values of likelihood ratios (*LR*) for models based on negative binomial errors and deviances (*Dev*) for models with Poisson errors are provided. These procedures are fully described by Behnke *et al.* (2021).

In some cases we used the model selection procedure in R comparing all relevant models with different combinations of variables by the corrected Akaike information criterion (AICc; Burnham & Anderson, 2002), and using the AICcmodavg package in R. For these we provide AICcWt values (=total amount of predictive power provided by the full set of models contained in the model referred to), AICcDelta values (difference in AIC score between the model referred to and the best model) and ER values (evidence ratio which is a measure of how much more likely the best model is compared to the model being referred to) (Symonds & Moussalli (2011). We also used the covariance distribution test described by Haukisalmi & Henttonen (1998), compared species density distributions to the null model of Janovy *et al.* (1995), both using our bespoke software, and in some cases implemented the non-parametric Spearman's test of correlation, Kruskal–Wallis and Mann–Whitney *U* tests in IBM SPSS.

Results

Summary statistics for mice and helminth species in the combined dataset

The dataset comprised records for 440 wood mice, of which 62.0% were males and 38% females. Overall, there were more mature mice (65.9%) compared with juveniles (34.1%), and although there was a mature host bias among both sexes, this was more marked among male mice with 29.7% being juveniles and 70.3% mature mice, whereas among females 41.3% were juveniles and 58.7% were mature (for host sex × age, $\chi^2_1 = 6.2$, $P = 0.013$). The majority of mice were trapped from the Great Wood (58.2%) and Alderhurst (23.0%) compared with Rogate (7.5%), Silwood (9.3%) and Ulverscroft (2.0%). The proportion of juvenile to mature mice varied significantly between sites (locality × age, $\chi^2_4 = 33.8$, $P < 0.001$), and to a lesser degree between male and female mice (locality × sex $\chi^2_4 = 9.9$, $P = 0.042$).

Seven helminth species were recorded overall (table 1), with 407 (92.5%) of the mice being infected with at least one of these species. The most prevalent were *H. polygyrus* and *S. stroma*, with the capillariid *A. murissylvatici* being the rarest and recorded in just one mouse. The oxyurid nematode *S. stroma* showed the highest mean worm burden with a maximum of 1174 being recorded. Up to 94.2% of 28,540 helminths recovered were nematodes with *S. stroma* accounting for 73.7% of helminths and 78.3% of nematodes. *Heligmosomoides polygyrus* accounted for 20.5% of helminths and 21.7% of nematodes, while other helminths were rarer.

Prevalence of helminth species

Although there was no significant difference in the prevalence of *H. polygyrus* between the sexes (table 2; sex × INFECTION, $\chi^2_1 = 0.061$, $P = 0.81$) or between juvenile and mature mice (age × INFECTION, $\chi^2_1 = 1.90$, $P = 0.168$), there was a significant but weak interaction between these two factors (age × sex × INFECTION, $\chi^2_1 = 4.47$, $P = 0.034$). Prevalence was higher among mature male mice compared with juveniles (83.3% [74.82–89.48] and 71.6% [59.27–81.67], respectively) but lower among mature female mice compared with juveniles (75.5% [61.78–85.74] and 81.2% [70.58–88.63], respectively). With host age and sex taken into account, there was a highly significant effect of locality ($\chi^2_4 = 15.94$, $P = 0.003$), with prevalence being high at Ulverscroft and the Great Wood, but relatively lower in mice from Rogate (table 2). Prevalence values of *S. stroma* varied significantly between the sexes (table 2, higher in male mice; for sex × INFECTION, $\chi^2_1 = 8.55$, $P = 0.003$) and prevalence was higher in mature mice (table 2; for age × INFECTION, $\chi^2_1 = 6.31$, $P = 0.012$) However, *S. stroma* prevalence values did not vary between mice from the five localities (locality × INFECTION, $\chi^2_4 = 2.31$, $P = 0.68$).

Table 1. Prevalence and abundance of helminth species in the combined data set with a host sample of 440.

	Prevalence		Abundance		
Species	(%)	CL_{95}[a]	Mean	Standard error of the mean	Maximum [b]
Heligmosomoides polygyrus	79.1	73.37–84.00	13.3	1.05	219
Syphacia stroma	54.1	47.61–60.57	47.8	6.05	1174
Corrigia vitta	14.8	10.69–19.96	2.3	0.46	132
Catenotaenia pusilla	8.4	5.44–12.79	1.1	0.32	79
Hydatigera taeniaeformis	4.1	2.09–7.47	0.089	0.043	18
Microsomacanthus crenata	3.4	1.66–6.62	0.29	0.108	26
Aonchotheca murissylvatici	0.2	0.05–2.04	0.009	0.009	4

[a]95% confidence limits.
[b]maximum worm burden.

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Table 2. Prevalence of helminth species by host sex, age and geographical locality.

Factor and level	*n*	*Heligmosomoides polygyrus*		*Syphacia stroma*		*Corrigia vitta*		*Catenotaenia pusilla*		*Hydatigera taeniaeformis*		*Microsomacanthus crenata*	
		%	CI_{95}	%	CI_{95}	%	CI_{95}	%	CI_{95}	%	CI_{95}	%	CI_{95}
Sex													
Males	273	**79.9**	75.48–83.61	**60.1**	55.05–64.92	**14.7**	11.40–18.57	**7.3**	5.07–10.42	**3.7**	2.15–6.05	**4.0**	2.43–6.50
Females	167	**77.8**	69.47–84.42	**44.3**	35.68–53.33	**15.0**	9.44–22.47	**10.2**	5.81–16.84	**4.8**	2.08–10.25	**2.4**	0.68–7.02
Age													
Juveniles	150	**76.0**	68.05–82.59	**44.7**	36.52–53.17	**10.0**	5.88–16.17	**6.0**	3.03–11.28	**5.3**	2.57–10.52	**0.7**	0.08–3.93
Mature	290	**80.7**	76.23–84.48	**59.0**	53.80–64.01	**17.2**	13.60–21.55	**9.7**	6.96–13.19	**3.4**	1.96–5.88	**4.8**	3.03–7.56
Geographical locality													
Great Wood	256	**84.4**	80.51–87.64	**57.0**	52.15–61.79	**17.2**	13.74–21.23	**7.4**	5.21–10.43	**2.0**	0.97–3.87	**1.2**	0.47–2.82
Alderhurst	101	**73.3**	66.59–79.08	**49.5**	42.46–56.54	**12.9**	8.81–18.31	**11.9**	7.94–17.11	**10.9**	7.07–16.07	**6.9**	4.09–11.37
Rogate	33	**57.6**	42.87–71.27	**51.5**	36.83–66.11	**9.1**	3.29–21.09	**3.0**	0.39–12.95	**6.1**	1.59–17.34	**3.0**	0.39–12.95
Silwood	41	**75.6**	59.32–87.20	**51.2**	35.01–67.10	**12.2**	4.69–26.58	**12.2**	4.69–26.58	**0**	0–9.50	**9.8**	3.21–23.90
Ulverscroft	9	**88.9**	55.66–99.43	**44.4**	16.88–74.86	**0**	0–32.33	**0**	0–32.33	**0**	0–32.33	**0**	0–32.33

The trematode *Corrigia vitta* showed very similar prevalences among the sexes (table 2, sex × INFECTION, $\chi^2_1 = 0.19$, $P = 0.66$) and between localities (locality × INFECTION, $\chi^2_4 = 5.21$, $P = 0.27$), but significantly higher among mature relative to juvenile mice (age × INFECTION, $\chi^2_1 = 4.35$, $P = 0.037$). Prevalence values of the cestode *Catenotaenia pusilla* were not significantly different between sexes (sex × INFECTION, $\chi^2_1 = 1.452$, $P = 0.23$), age classes (age × INFECTION, $\chi^2_1 = 1.81$, $P = 0.18$) nor localities (locality × INFECTION, $\chi^2_4 = 4.14$, $P = 0.39$). However, it is noteworthy that none of the nine mice sampled from Ulverscroft were infected with this cestode species, nor with any trematode species.

Prevalence values of *H. taeniaeformis* were lower than those of the above-mentioned species and this larval cestode was absent from the mice caught at both Ulverscroft and Silwood (table 2; locality × INFECTION, $\chi^2_4 = 16.511$, $P = 0.002$). There was no independent effect of either sex ($\chi^2_1 = 0.33$, $P = 0.57$) or age ($\chi^2_1 = 0.86$, $P = 0.35$), but there was a significant interaction between these factors and the prevalence of *H. taeniaeformis* ($\chi^2_1 = 4.432$, $P = 0.035$). This interaction arose because prevalence was higher among juvenile compared with mature males (7.4% [2.85–16.76] and 2.1% [0.43–7.19], respectively) whereas among female mice, prevalence was lower among juveniles (2.9% [0.63–9.68] and 6.1% [1.77–16.65], respectively. *Microsomacanthus crenata* was the least prevalent cestode species overall but was most prevalent among mice from Silwood (table 2; locality × INFECTION, $\chi^2_4 = 9.722$, $P = 0.045$), and among mature mice (age × INFECTION, $\chi^2_1 = 4.225$, $P = 0.040$). Prevalences were not significantly different between the sexes (sex × INFECTION, $\chi^2_1 = 1.36$, $P = 0.24$).

Abundance of helminth species

Quantitative analyses were only appropriate for *H. polygyrus*, *S. stroma* and *C. vitta*, each of which occurred in more than 10% of the wood mouse population, although *C. pusilla* had an overall prevalence of 8.4%. Mean abundances of *H. polygyrus* infections varied significantly between host ages, (table 3) being higher in mature mice (generalized linear model (GLM) with negative binomial errors, $LR_{1,433} = 18.876$, $P < 0.0001$) and also between sites with the highest abundance in mice from Great Wood, and the lowest in those from Alderhurst ($LR_{4,433} = 17.839$, $P = 0.0013$). There was also a significant two-way interaction (locality × sex; $LR_{4,429} = 11.793$, $P = 0.019$) arising from a higher, although differing abundance of *H. polygyrus* in male mice compared with females from Ulverscroft, Silwood, Alderhurst and Great Wood. The reverse occurred in Rogate where abundance was greater in female mice (fig. 1A).

The abundance of *S. stroma* was significantly higher in mature mice (table 3; GLM with negative binomial errors, $LR_{1,434} = 3.880$, $P = 0.049$) and differed significantly between sites ($LR_{4,434} = 11.876$, $P = 0.018$), being higher among mice from Great Wood and Rogate and lowest among those from Ulverscroft. Model selection favoured one that also included the two-way interaction between site and age (fig. 1B), although this was just the wrong side of the cut-off for significance in the deletion approach ($LR_{4,430} = 8.913$, $P = 0.063$). Abundance did not vary significantly between the sexes ($LR_{1,433} = 0.69$, $P = 0.41$).

The only factor affecting the abundance of *C. vitta* was locality (table 3; GLM with negative binomial errors, $LR_{4,435} = 17.247$, $P = 0.0017$). This species was most abundant among mice from Great Wood, and totally absent in those from Ulverscroft. Although present in the other three sites, abundances were low compared with mice from Great Wood. In contrast, the abundance of *C.*

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Table 3. Abundance (mean worm burden) of helminth species by host sex, age and geographical locality.

Factor and level	*n*	*Heligmosomoides polygyrus*		*Syphacia stroma*		*Corrigia vitta*		*Catenotaenia pusilla*		*Hydatigera taeniaeformis*		*Microsomacanthus crenata*	
		Mean ± SEM		Mean ± SEM		Mean ± SEM		Mean ± SEM		Mean ± SEM		Mean ± SEM	
Sex													
Males	273	**14.3**	1.34	**54.5**	8.62	**2.14**	0.468	**0.76**	0.344	**0.04**	0.015	**0.30**	0.134
Females	167	**11.6**	1.70	**36.9**	7.41	**2.55**	0.957	**1.71**	0.631	**0.16**	0.110	**0.27**	0.180
Age													
Juveniles	150	**8.4**	1.29	**29.9**	6.39	**1.81**	0.551	**0.32**	0.130	**0.07**	0.026	**0.01**	0.007
Mature	290	**15.8**	1.43	**57.1**	8.52	**2.54**	0.645	**1.53**	0.481	**0.10**	0.064	**0.43**	0.163
Geographical locality													
Great Wood	256	**15.8**	1.57	**60.1**	9.33	**3.55**	0.779	**1.19**	0.450	**0.02**	0.009	**0.02**	0.013
Alderhurst	101	**8.2**	0.99	**21.3**	5.04	**0.82**	0.321	**1.47**	0.775	**0.32**	0.183	**0.67**	0.363
Rogate	33	**15.0**	4.98	**66.2**	27.30	**0.21**	0.155	**0.03**	0.030	**0.06**	0.042	**0.73**	0.727
Silwood	41	**9.3**	2.38	**29.6**	10.89	**0.24**	0.115	**0.98**	0.581	**0**	0	**0.71**	0.424
Ulverscroft	9	**11.0**	4.99	**9.0**	5.58	**0**	0	**0**	0	**0**	0	**0**	0

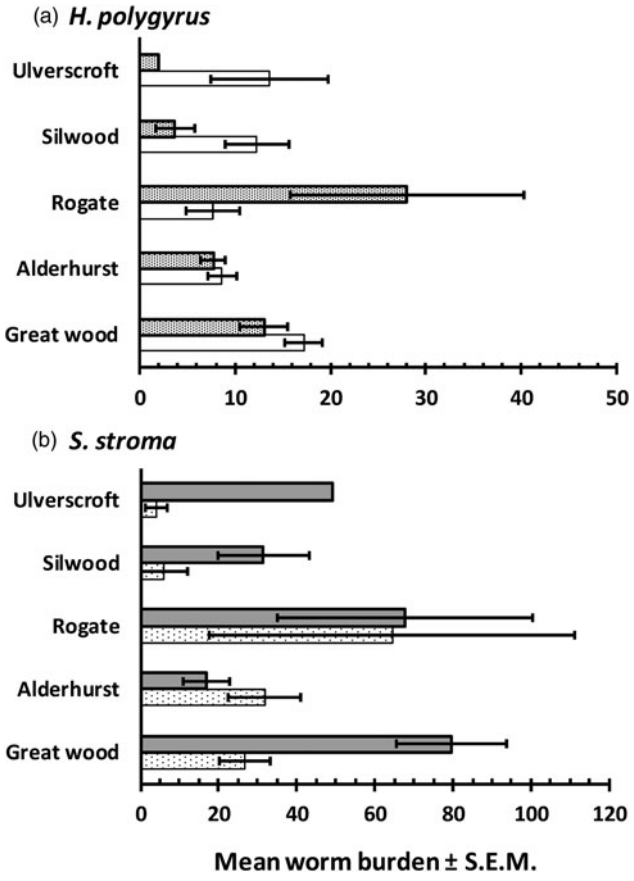

Fig. 1. Two-way interactions between factors affecting the abundance of *Heligmosomoides polygyrys* (A, locality × host sex; females in filled columns and males in open columns; *n* for Ulverscroft, Silwood, Rogate, Alderhurst and Great Wood females = 2, 14, 12, 50 and 89, respectively, and for males = 7, 27, 21, 51 and 167, respectively) and *Syphacia stroma* (B, locality × host age; mature mice in filled columns and juveniles in open columns; *n* for sites as above and mature mice = 1, 38, 18, 71 and 162, respectively, and for juveniles = 8, 3, 15, 30 and 94, respectively).

pusilla only differed significantly between the two age classes (table 3; $LR_{1,438} = 4.360$, $P = 0.037$).

Helminth species richness and species density distribution

The mean helminth species richness (mean number of helminth species per host) in male and female mice was very similar (males

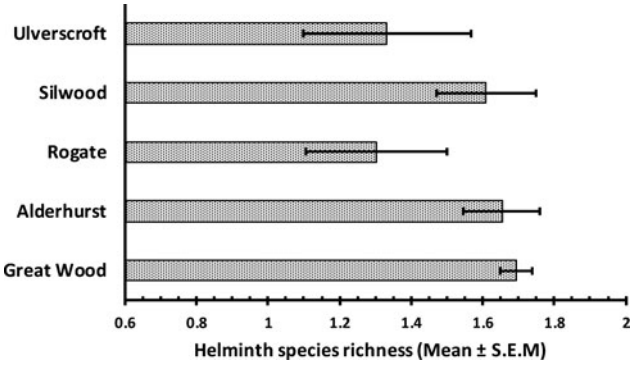

Fig. 2. Mean helminth species richness by site (*n* for Ulverscroft, Silwood, Rogate, Alderhurst and Great Wood females = 9, 41, 33, 101 and 256, respectively).

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= 1.70 ± 0.052 and females = 1.55 ± 0.068), although species richness was higher among mature (1.75 ± 0.050) compared with juvenile mice (1.43 ± 0.070) (GLM with Poisson errors, $Dev_{1,438}$ = 6.54, P = 0.011). Species richness by site (fig. 2) showed very close values for mice from Silwood, Alderhurst and Great Wood, but somewhat lower for those from Ulverscroft and Rogate. There was on the other hand no significant difference between sites ($Dev_{4,433}$ = 3.05, P = 0.549).

The majority of mice harboured two species of helminths (43.6%), and the second most frequent category included mice with just one species (fig. 3). At this level in the combined dataset, the species density distribution (i.e. the distribution of data subsets comprising number of mice with no helminth species, one helminth species, two helminth species etc. following Janovy *et al.*, 1995) conformed well (χ^2_5 = 9.66, P = 0.086) to predictions of the null model of Janovy *et al.* (1995), suggesting no marked interactions between species in this dataset. We also examined species density distributions of mice from four of the study sites including Great Wood (χ^2_4 = 6.59, P = 0.16), Silwood (χ^2_3 = 0.60, P = 0.90) and Alderhurst (χ^2_5 = 8.63, P = 0.125) independently. All mice conformed well to the model, except those from Rogate (χ^2_3 = 8.16, P = 0.043) where there was a significant difference between observed numbers and those expected from the null model. At Rogate there were more uninfected hosts and those with four species than expected, but fewer than expected with a single or three helminth species.

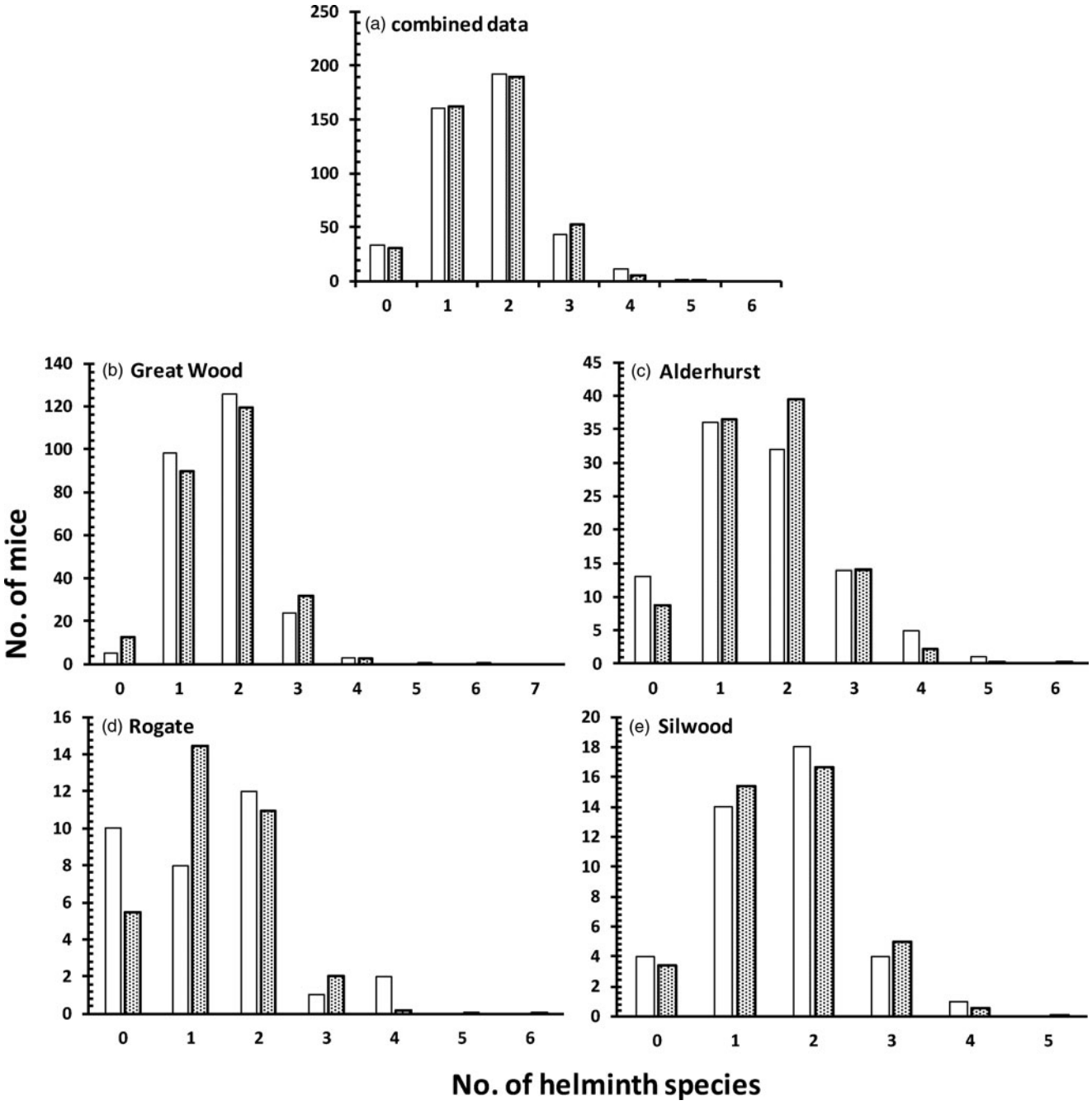

Fig. 3. Helminth species richness in the combined dataset and in four of the study sites (observed, open columns). The expected values (filled columns) are from the null model for ecologically significant interactions of Janovy *et al.* (1995) and are based on prevalences of individual species.

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Associations based on the presence/absence of helminth species

H. polygyrus

Since *H. polygrus* and *S. stroma* were the species with the highest prevalences we first fitted models with these two species, taking into account both intrinsic (age and sex) and extrinsic (geographical locality) factors. There was no independent association of these two species ($\chi^2_1 = 0.032$, $P = 0.86$), but there was a significant association of these species with locality ($\chi^2_4 = 15.88$, $P = 0.003$). The prevalence of *S. stroma* was higher in mice without *H. polygyrus* among those trapped in Great Wood (fig. 4A), but the situation was reversed in Rogate, and there was essentially no difference in prevalence in mice from Alderhurst and Silwood.

Although prevalence of *C. vitta* was numerically higher among mice with *H. polygyrus* (15.8% [12.05–20.37]) compared to those without (10.9% [4.80–22.02]), this was not a significant difference ($\chi^2_1 = 1.50$, $P = 0.22$), and neither was there any evidence of significant associations of both species confounded by intrinsic and extrinsic factors. Similarly there was no direct association between *H. polygyrus* and *C. pusilla* (prevalence of *C. pusilla* in mice with *H. polygyrus* = 8.9% [6.16–12.77] and without 6.5% [2.12–16.58]; ($\chi^2_1 = 0.57$, $P = 0.45$)). However, there was a significant association between these species in a model with host age (age × presence/absence of *H. polygyrus* × presence/absence of *C. pusilla*, $\chi^2_1 =$ 4.74, $P = 0.030$). There were no cases of *C. pusilla* among juvenile mice without *H. polygyrus* (prevalence = 0% [0.00–8.59]), but prevalence was 10.7% [5.58–18.94] among mature mice without *H. polygyrus*. Conversely, in mice infected with *H. polygyrus* prevalences were similar both in juvenile (7.9% [4.70–12.92]) and mature mice (9.4% [6.97–12.54]).

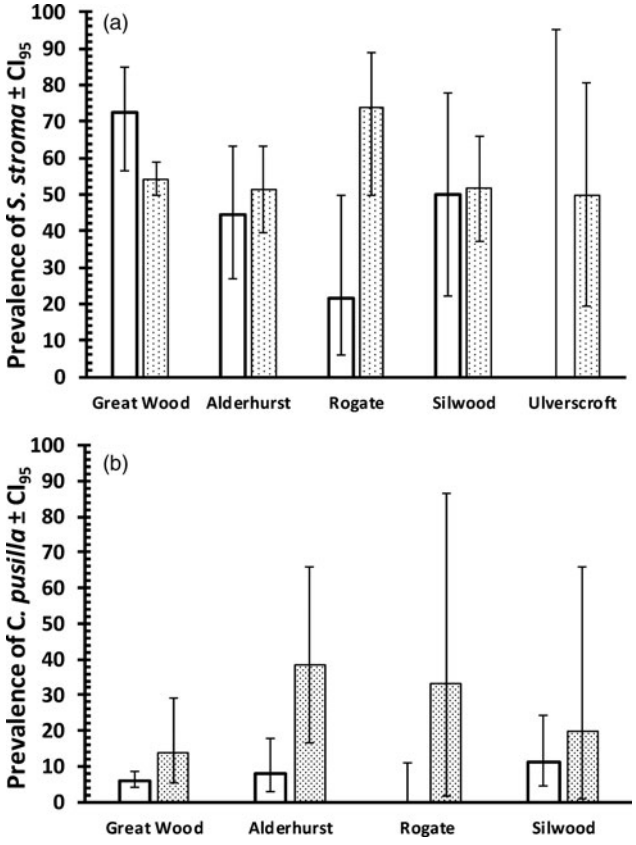

Fig. 4. Locality-dependent association of *Syphacia stroma* with *Heligmosomoides polygyrus* (A, open columns, *H. polygyrus* absent [*n* for Ulverscroft, Silwood, Rogate, Alderhurst and Great wood = 8, 31, 19, 74 and 216, respectively]; filled columns, *H. polygyrus* present, [*n* = 1, 10, 14, 27 and 40, respectively]) and *Catenotaenia pusilla* with *Corrigia vitta* (B, open columns *C. vitta* absent [Silwood, Rogate, Alderhurst and Great wood *n* = 36, 30, 88 and 212, respectively]; filled in columns *C. vitta* present [*n* = 5, 3, 13 and 44, respectively]).

S. stroma and *C. vitta*

Prevalences of *C. vitta* were virtually identical in mice with (14.7% [11.63–18.37]) and without *S. stroma* (14.9% [11.94–18.25]; $\chi^2_1 =$ 0.002, $P = 0.97$), and these were not influenced significantly by other factors. Similar trends were evident for *S. stroma* and *C. pusilla* (prevalences of *C. pusilla* =9.1% [6.81–12.14] with *S. stroma* and 9.2% [4.90–16.20] without *S. stroma*; $\chi^2_1 < 0.001$, $P = 0.99$).

One of the strongest associations between species in the dataset was between the presence/absence of *C. vitta* and *C. pusilla*. In mice without *C. vitta*, the prevalence of *C. pusilla* was 6.4% [4.04–9.94], although if mice were infected with *C. vitta*, prevalence increased to 20.0% [12.21–30.41]. With other factors such as host sex, age and locality taken into account, this was also a significant effect and independent of other fitted factors ($\chi^2_1 =$ 10.583, $P = 0.001$). The bias for higher prevalences of *C. pusilla* in the presence of *C. vitta* was not only evident in both sexes (males without *C. vitta* = 6.0% [4.09–8.67], with *C. vitta* = 15.0% [6.43–30.04]; females without *C. vitta* = 7.0% [3.84–12.51], with *C. vitta* = 28.0% [13.37–47.97]) but also in both age classes (juveniles without *C. vitta* = 4.4% [2.03–9.03], with *C. vitta* = 20.0% [5.69–46.57]; mature mice without *C. vitta* = 7.5% [5.32–10.42], with *C. vitta* = 20.0% [10.06–32.36]), and in all four sites where mice were infected with these species (Fig 4B).

Associations based on quantitative (abundance) data

Analysis of quantitative data was largely restricted to four species (*H. polygyrus*, *S. stroma*, *C. vitta* and *C. pusilla*) which had overall prevalences exceeding 8%. If species interact negatively to lower worm burdens in one species when both are present, or positively if one species lowers the host's resistance to the second species, we might expect to see a difference in the mean worm burden of one species in the presence or absence of another. To test this in the presence or absence of species 1, we calculated the mean worm burden of species 2, first for data restricted to all mice that carried species 2, and then to all the 440 mice in the study (table 4). Only in four cases was a significant difference between mice with and without species 1 evident. In data restricted to mice carrying *H. polygyrus*, mean worm burdens were significantly higher in mice also carrying *S. stroma* (Mann–Whitney $U_{159,189} = 17{,}851$, $P = 0.002$). This was also the case when the test was repeated on all mice (Mann–Whitney $U_{202,238} = 27{,}031.5$, $P = 0.024$). Furthermore, in the full dataset the mean worm burden of *C. pusilla* was higher in the presence of *C. vitta* (Mann–Whitney $U_{375,65} = 13{,}785.5$, $n = 440$, $P < 0.001$) and conversely the worm burden of *C. vitta* was higher in the presence of *C. pusilla* (Mann–Whitney $U_{403,37} = 9007.5$, $n = 440$, $P < 0.001$).

Covariance of helminth species with and without subset groups

The analyses above did not take into account possible variations between data subsets, such as geographical localities, age classes, sexes, and to repeat the analyses on each subgroup would entail

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Table 4. Mean worm burdens of species 2 (in all mice carrying that species and in all the mice in the study) in mice with or without species 1.

	Species 1											
	Only mice infected with species 2						All mice					
Species 1	Absent			Present			Absent			Present		
Species 2	*n*	Mean	SEM*	*n*	Mean	SEM	*n*	Mean	SEM	*n*	Mean	SEM
Heligmosomoides polygyrus												
Syphacia stroma	49	129.5	30.72	189	77.7	10.46	92	69.0	17.64	348	42.2	6.04
Corrigia vitta	10	20.7	12.89	55	14.6	2.10	92	2.3	1.5	348	2.3	0.44
Catenotaenia pusilla	6	19.8	10.84	31	12.1	3.29	92	1.3	0.83	348	1.1	0.34
S. stroma												
H. polygyrus	159	13.3	1.59	189	19.7	1.88a	202	10.5	1.31	238	15.6	1.58a
C. vitta	30	18.9	5.05	35	12.6	2.16	202	2.8	0.88	238	1.9	0.43
C. pusilla	17	15.9	5.18	20	11.2	4.10	202	1.3	0.53	238	0.9	0.39
C. vitta												
H. polygyrus	293	16.0	1.30	55	21.0	3.99	375	12.5	1.07	65	17.8	3.5
S. stroma	203	88.3	10.76	35	88.6	35.12	375	47.8	6.25	65	47.7	19.58
C. pusilla	24	16.3	4.40	13	7.8	4.09	375	1.0	0.35	65	1.6	0.88a
C. pusilla												
H. polygyrus	317	16.7	1.34	31	17.5	3.51	403	13.2	1.11	37	14.6	3.12
S. stroma	218	89.5	11.21	20	75.9	26.75	403	48.4	6.45	37	41.0	15.62
C. vitta	52	16.3	2.99	13	12.3	5.35	403	2.1	0.47	37	4.3	2.08a

[a]Significantly different. See text for details.
* indicating standard error of the mean.

extensive Bonferroni corrections to the cut-off for significance. Instead we implemented the covariance distribution method described by Haukisalmi & Henttonen (1998), using bespoke software. Based on log $(x + 1)$ transformed data and 1000 randomizations, the strongest covariance (0.192) was between *H. polygyrus* and *S. stroma*, but this was just the wrong side of the cut-off for significance in the whole dataset ($P = 0.058$), and hence significance was lost when the subset grouping was taken into account ($P = 0.661$). Covariance between *C. vitta* and *C. pusilla* (0.0466) was weaker but significant in the whole dataset ($P = 0.050$), and also lost significance when subset grouping was taken into account ($P = 0.082$).

Correlation between helminth species in mice using raw data and after correction for subset groupings

Correlations in worm numbers between two helminth species, in each case confining analyses to mice that carried both helminths, proved to be significant for *H. polygyrus* and *C. pusilla* ($r_s = 0.362$, $n = 31$, $P = 0.046$) and *C. vitta* and *C. pusilla* ($r_s = 0.607$, $n = 13$, $P = 0.028$), but neither indicated a robust relationship between the species involved, accounting for relatively little of the variation in each model ($R^2 = 0.146$ and 0.067, respectively). Correlations exploiting the whole dataset, revealed only one to be significant (*C. vitta* and *C. pusilla*, $r_s = 0.157$, $n = 440$, $P < 0.001$). Correlations between worm numbers were also undertaken after correcting these for subset groupings using residuals from the best fit GLMs described above. Again, we tested correlations between sets of two species in the entire dataset and in datasets confined to mice carrying at least one worm of each species. Of 12 possible permutations (six on complete datasets and six on datasets limited to species carrying the two species), only one proved to be significant (*H. polygyrus* × *C. pusilla*, $r_s = 0.360$, $n = 31$, $P = 0.047$).

Prevalence of other helminth species in the presence/absence of *H. polygyrus*

In an earlier paper by Behnke *et al.* (2009) the prevalence of other helminths and their species richness were reported to have increased with a rise in the worm burdens of *H. polygyrus*. Consistent with this finding, Sweeny *et al.* (2021a) also found that the presence of hymenolepid infections was occasionally associated with higher numbers of *H. polygyrus*. The data summarized in table 5 show that as the worm burden of *H. polygyrus* increased, the likelihood of additional helminth species becoming established also increased ($\chi^2_5 = 18.0$, $P = 0.003$). An upward trend in prevalences of other helminth species was also apparent when data were linked by either host sex ($\chi^2_5 = 18.0$, $P = 0.003$) or age ($\chi^2_5 = 14.2$, $P = 0.015$). However, an independent trend was less clear in the case of locality because of the much smaller numbers of mice in each data subset with resulting greater confidence intervals and some inconsistencies that generated a significant interaction (locality × *H. polygyrus* burden class × presence/absence of other helminth species, $\chi^2_{20} = 36.5$, $P = 0.014$). However, when *H. polygyrus* worm burdens were corrected for host sex, age and locality by fitting residuals from the MSM, the relationship with additional species of helminths was lost

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Table 5. Prevalence of other helminth species in mice without *Heligmosomoides polygyrus* and in mice with increasing worm burdens of *H. polygyrus* in the combined dataset relative to host sex, age and by geographical locality.

	Prevalence (%) of other species									
H. polygyyrus range	All mice	*n*	Males	*n*	Females	*n*	Juveniles	*n*	Mature	*n*
0	64.1	92	65.5	55	62.2	37	58.3	36	67.9	56
1–5	54.6	119	64.2	67	42.3	52	50.0	56	58.7	63
6–10	71.2	73	69.8	43	73.3	30	62.1	29	77.3	44
11–20	65.3	72	69.6	46	57.7	26	37.5	16	73.2	56
21–50	75.8	62	83.3	48	50.0	14	42.9	7	80.0	55
>50	90.9	22	85.7	14	100.0	8	83.3	6	93.8	16
H. polygyyrus range	Great Wood	*n*	Alderhurst	*n*	Rogate	*n*	Silwood	*n*	Ulverscroft	*n*
0	87.5	40	51.9	27	28.6	14	60.0	10	0	1
1–5	58.8	68	48.0	25	75.0	8	35.7	14	50.0	4
6–10	71.1	38	75.0	24	50.0	2	75.0	8	0	1
11–20	66.7	54	75.0	12	50.0	2	33.3	3	0	1
21–50	71.7	38	69.2	13	100.0	4	100.0	5	100.0	2
>50	88.9	18		0	100.0	3	100.0	1		0

(*H. polygyrus* residuals class × presence/absence of other helminth species, $\chi^2_5 = 7.58$, $P = 0.181$).

Number of other helminth species

The data in table 6 show that in the entire dataset, and with the exception of uninfected mice, as worm burdens of *H. polygyrus* increased, so too did the species richness of other helminths (Kruskal–Wallis, $H_5 = 14.52$, $P = 0.013$). However, when *H. polygyrus* worm burdens were corrected for host sex, age and locality by fitting residuals from the MSM, the relationship with other helminth species was lost ($H_5 = 9.94$, $P = 0.077$). Adjusting species richness of other helminths for the only significant factor, host age (GLM with Poison errors, for main effect of age $Dev_{1,\ 438} = 9.371$, $P = 0.0022$), and repeating both approaches above, made little difference to these results ($H_5 = 8.72$, $P = 0.121$ and $H_5 = 9.84$, $P = 0.080$, respectively).

As an alternative test, a GLM with Poisson errors was undertaken with helminth species richness of other helminths as the dependent variable and host sex, age and locality as explanatory factors, together with the number of *H. polygyrus* worms (Hpburden) as a covariate. Model selection in R identified a model with just host age and Hpburden as the preferred model (model 1, AICcWt = 0.49), although the stepwise deletion approach only found host age as a significant factor (for age $Dev_{1,437} = 7.78$, $P = 0.0053$; for Hpburden $Dev_{1,437} = 2.486$, $P = 0.115$). The next best model was very similar (AICcDelta in relation to model 1 = 0.46, ER = 1.26) with just host age (model 2, AICcWt = 0.39). Fitting the residuals of MSM for *H. polygyrus*, instead of the *H. polygyrus* worm burdens, resulted in host age as the only significant explanatory factor ($Dev_{1,438} = 9.37$ $P = 0.0022$). Finally, regression of residuals of MSM for species richness of other helminths on the residuals of MSM for *H. polygyrus* showed that the slope was not significant ($ß = 0.0484 \pm 0.04325$, $t = 1.12$, $P = 0.264$)

Discussion

Much as expected based on previous studies of the helminth parasites in wood mice from the British Isles (Sharpe, 1964; Lewis, 1968; Abu-Madi *et al.*, 1998), and other regions of Europe (Eira *et al.*, 2006; Miljević *et al.*, 2022), *H. polygyrus* and *S. stroma* were the two dominant helminths in this dataset. *Heligmosomoides polygyrus* showed the highest prevalence, while *S. stroma*, although less prevalent, accounted for more than three times as many helminths recovered, primarily due to extremely high worm burdens in some of the mice. As expected, the present data showed some evident locality-dependent effects in both prevalence (*H. polygyrus H. taeniaeformis* and *M. crenata*), and abundance (*H. polygyrus, S. stroma* and *C. vitta*) of helminth species. Mean worm burdens for *H. polygyrus* and *C. vitta* were higher in mice from Great Wood, compared with the other four sites. While there was no site effect for prevalence of *S. stroma*, varying only from 44.4% (Ulverscroft) to 57.0% (Great Wood), abundance of this species did vary significantly between localities, with the highest worm burdens in mice from Rogate, and only marginally lower in those from Great Wood. Ecological differences between habitats have been proposed as contributing factors explaining differences in prevalence and/or abundance of *H. polygyrus* (Lewis, 1968; Montgomery & Montgomery, 1989; Abu-Madi *et al.*, 1998) and *S. stroma* (Abu-Madi *et al.*, 2000) between geographical localities. For heteroxenous species, such as *C. vitta*, *H. taeniaeformis* and *M. crenata*, locality-dependent variation in worm burdens (Abu-Madi *et al.*, 2000) may be primarily linked with varying densities of intermediate hosts in woodland compared with grassland sites. In the present study the relatively high degrees of infection of *C. vitta* in mice from Great Wood are likely to be related to an increase in consumption of invertebrate intermediate hosts present in the ground fauna of Great Wood and to a lesser extent in Alderhurst, also a woodland site, but not at Ulverscroft

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Table 6. Species richness of other helminth species (excepting *Heligmosomoides polygyrus*) in relation to increasing worm burden classes *of H. polygyrus* and based on residuals from minimum sufficient generalized linear models.

H. polygyrus worm burden					Species richness	
Class	*n*	Range	Mean	SEM	Mean	SEM
1	92	0	0	0	0.84	0.079
2	119	1–5	2.9	0.13	0.70	0.071
3	73	6–10	7.9	0.17	0.95	0.089
4	72	11–20	14.6	0.32	0.83	0.086
5	62	21–50	31.5	1.17	0.94	0.094
6	22	>50	86.8	8.85	1.23	0.16
H. polygyrus residuals					Species richness	
Class	*n*	Range	Mean[a]	SEM	Mean	SEM
1	124	<−1.0	0.4	0.06	0.68	0.042
2	73	−0.50 to −1.00	4.4	0.29	0.56	0.058
3	108	−0.01 to 0.49	9.7	0.53	0.65	0.046
4	69	0 to 0.49	17.7	1.25	0.65	0.058
5	33	0.50 to 0.99	35.4	4.17	0.70	0.081
6	33	>0.99	61.7	7.59	0.82	0.068

[a]mean worm burden in class.

where none of the sampled mice were infected with this species, although the sample size in the latter was very low. The remaining two sites are mainly grassland and likely to harbour lower densities of invertebrates.

We had also expected to detect some host age effects on the prevalence and abundance of species, because helminths are mostly long-lived parasites, and accumulate in hosts with increasing age (Pascala & Dobson, 1988). Consistent with this concept, helminth species richness, prevalence of *S. stroma*, *C. vitta* and *M. crenata* and abundances of *H. polygyrus*, *S. stroma* and *C. pusilla* were all significantly higher in mature relative to juvenile mice. Prevalences of *H. polygyrus*, *C. pusilla* and abundance of *C. vitta* were also numerically higher in mature mice, but differences between age classes in these cases were insufficient to achieve statistical significance. Of the species identified in the present study, *C. vitta* has the longest generation time, and a known host age effect (Lewis, 1968; Behnke *et al.*, 1999; Loxton *et al.*, 2017). In addition, older wood mice have been found also to be more heavily infected with *H. polygyrus* (Sharpe, 1964; Lewis, 1968, 1992; Gregory *et al.*, 1992; Abu-Madi *et al.*, 1998; Loxton *et al.*, 2017), *S. stroma* (Lewis, 1968; Loxton *et al.*, 2017; Stuart *et al.*, 2020), *M. crenata* (Behnke *et al.*, 1999) and deer mice with *H. taeniaeformis* (Theis & Schwab, 1992).

Differences in the prevalence and abundance of helminths between the sexes were rare in this dataset, there being only one case, the prevalence of *S. stroma*. Consistent with our previously published finding (Behnke *et al.*, 1999), the prevalence of *S. stroma* was higher in male mice, although a sex difference in abundance of this species was not found in the current study. While some researchers have reported a difference between the sexes in prevalence and/or abundance of *S. stroma* (male bias in Lewis & Twigg, 1972; Behnke *et al.*, 1999; Stuart *et al.*, 2020), others have failed to detect an overall difference between the sexes (Lewis, 1968) and have noted that sex differences in this species are highly context dependent (Behnke *et al.*, 1999; Abu-Madi *et al.*, 2000). Although there was no sex-difference in either prevalence or abundance of *H. polygyrus*, interactions with age (prevalence) and locality (abundance) indicate inconsistent sex-bias that was context dependent in this species also. Male biased infections with *H. polygyrus* have been reported previously (Lewis, 1968; Lewis & Twigg, 1972), although not in all studies (Gregory, 1992; Gregory *et al.*, 1992; Behnke *et al.*, 1999; Babayan *et al.*, 2018), and when detected, sex-bias has been found to be context dependent (Abu-Madi *et al.*, 1998; Sweeney *et al.*, 2021a). No host sex-difference in infections with *C. vitta* was seen in wood mice by Lewis (1968), Behnke *et al.* (1999) and Abu-Madi *et al.* (2000), but Loxton *et al.* (2017) found evidence of female sex-bias, the extent of which varied between years of the study. The lack of host sex-dependent bias in infections with *H. taeniaefomis* concurs with the findings of Theis & Schwab (1992) in *Peromyscus maniculatus* in California, although Lewis & Twigg (1972) found male bias in abundance of this cestode in wood mice.

Associations between parasites, and especially those indicating competitive interactions are difficult to detect in field data acquired through destructive sampling or typically in cross-sectional surveys such as those conducted in the present work (Fenton *et al.*, 2014). Nevertheless, with over 400 records we felt justified in examining our data for evidence of associations in prevalence data and quantitative interactions based on abundance levels. One species of particular interest was *H. polygyrus*. This species is known to generate long-lasting chronic infections in its hosts (Robinson *et al.*, 1989; Gregory *et al.*, 1990), for which there is some evidence of interactions with other species, and

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whose laboratory maintained congener is known to secrete immunomodulatory factors that interfere with local mucosal immune responses (Hewitson *et al.*, 2011), making the host more susceptible to other infections in laboratory experimental studies (Behnke *et al.*, 1978). Indeed, consistent with this idea, prevalence of *S. stroma* was higher in mice with concurrent infections with *H. polygyrus* in Rogate, but this was not a consistent trend as in mice from Great Wood the prevalence of *S. stroma* was lower in mice infected with *H. polygyrus*. Interestingly, the abundance of *S. stroma* was higher in mice with *H. polygyrus* when possible confounding factors were not considered, but lost significance when subset grouping was taken into account in covariance distributions tests.

Although prevalences of both *C. vitta* and *C. pusilla* were numerically higher in mice with *H. polygyrus*, in neither case did this prove to be statistically significant. However, there was a significant correlation between *H. polygyrus* and *C. pusilla* worm burdens when analysis was restricted to the 31 mice that carried both species, and although this retained significance when host sex, age and locality were considered, this was a weak relationship. Nevertheless, this result supports the findings of Behnke *et al.* (2005), who also reported a significant quantitative association between these two species, even after controlling for quantified extrinsic and intrinsic factors. In an earlier study, it was shown that the species richness of other helminths increased in the presence of *H. polygyrus* and did so in a dose-dependent manner (Behnke *et al.*, 2009). While in the raw data of the current study both prevalence and species richness of other species were consistent with Behnke *et al.* (2009), in both cases when host sex, age and locality were controlled for, the effect was lost. Perhaps the strongest evidence for a positive association between species was seen in concurrent infections with the trematode *C. vitta* and the cestode *C. pusilla*. In the entire dataset, based on prevalence, a significant association indicating co-occurrence was evident in both sexes and age classes, and in each locality. The abundance of *C. pusilla* was higher in mice infected with *C. vitta* and vice versa. Covariance of these two species in the entire dataset was just significant but lost significance when other factors were taken into consideration. Nevertheless, the heteroxenous life cycles of both of these parasites, exploiting invertebrate intermediate hosts (molluscs and ants, and mites, respectively), which are likely to co-occur in the woodland litter, may partially explain their association in wood mice in the localities where they occurred.

Taken together the results of our analyses are not consistent with the existence of a highly interactive helminth community in the wood mice from the five subpopulations sampled. In several cases, promisingly significant effects in raw datasets were lost when controlled for intrinsic and extrinsic factors, and this is consistent with the conclusions of Haukisalmi & Henttonen (1998). Therefore, while the data support the existence of significant differences in helminth communities between different localities (i.e. different populations of hosts), and are consistent with marked host age effects (in all significant cases prevalence and worm burdens increasing with host age), differences in both parameters between the sexes, and associations and interactions between species appear to be highly context dependent, and at best moderate in their magnitude. While there is evidence that in the presence of *H. polygyrus*, *S. stroma* aggregate more posteriorly in the small intestine, indicating some interaction between these species at this level (Lewis *et al.*, 2021), analysis of our prevalence and abundance data by a variety of different approaches failed to find strong support for associations or interaction between these species. Since animal communities are defined by associations, correlations, interactions and interdependence between species (Margolis *et al.*, 1982; Morin, 2011; Leaper *et al.*, 2014), this inevitably leads to the conclusions that the helminths of wood mice are largely non-interactive and hence, perhaps better referred to as assemblages, rather than communities (Poulin, 1996b).

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