

# Long-term trends in helminth infections of wood mice (*Apodemus sylvaticus*) from the vicinity of Malham Tarn in North Yorkshire, England

## Research Article

**Cite this article:** Behnke JM, Rogan MT, Craig PS, Jackson JA, Hide G (2021). Long-term trends in helminth infections of wood mice (*Apodemus sylvaticus*) from the vicinity of Malham Tarn in North Yorkshire, England. *Parasitology* **148**, 451–463. <https://doi.org/10.1017/S0031182020002243>



Received: 3 September 2020  
Revised: 3 November 2020  
Accepted: 24 November 2020  
First published online: 1 December 2020

### Key words:

Abundance; age; cestodes; Digenea; *Heligmosomoides polygyrus*; helminths; nematodes; *Plagiorchis muris*; prevalence; sex; *Syphacia stroma*

### Author for correspondence:

Jerzy M. Behnke,  
E-mail: [jerzy.behnke@nottingham.ac.uk](mailto:jerzy.behnke@nottingham.ac.uk)

Jerzy M. Behnke<sup>1</sup> , Michael T. Rogan<sup>2</sup>, Philip S. Craig<sup>2</sup>, Joseph A. Jackson<sup>2</sup> and Geoff Hide<sup>2</sup> 

<sup>1</sup>School of Life Sciences, University of Nottingham, University Park, Nottingham NG7 2RD, UK and <sup>2</sup>Biomedical Research Centre, School of Science, Engineering and Environment, University of Salford, Salford M5 4WT, UK

### Abstract

Helminth infections in wood mice ( $n = 483$ ), trapped over a period of 26 years in the woods surrounding Malham Tarn in North Yorkshire, were analysed. Although 10 species of helminths were identified, the overall mean species richness was 1.01 species/mouse indicating that the helminth community was relatively depauperate in this wood mouse population. The dominant species was *Heligmosomoides polygyrus*, the prevalence (64.6%) and abundance (10.4 worms/mouse) of which declined significantly over the study period. Because of the dominance of this species, analyses of higher taxa (combined helminths and combined nematodes) also revealed significantly declining values for prevalence, although not abundance. Helminth species richness (HSR) and Brillouin's index of diversity (BID) did not show covariance with year, neither did those remaining species whose overall prevalence exceeded 5% (*Syphacia stroma*, *Aonchotheca murissylvatici* and *Plagiorchis muris*). Significant age effects were detected for the prevalence and abundance of all higher taxa, *H. polygyrus* and *P. muris*, and for HSR and BID, reflecting the accumulation of helminths with increasing host age. Only two cases of sex bias were found; male bias in abundance of *P. muris* and combined Digenea. We discuss the significance of these results and hypothesize about the underlying causes.

### Introduction

Several recent studies have emphasized the medium-term stability of helminth communities in wild rodents living in undisturbed natural ecosystems (Montgomery and Montgomery, 1990; Haukisalmi and Henttonen, 2000; Bajer *et al.*, 2005; Grzybek *et al.*, 2015a; Knowles *et al.*, 2015; Behnke *et al.*, 2019), supporting much earlier research conducted in the British Isles, Poland and in Finland (Elton *et al.*, 1931; Kisieleska, 1970; Haukisalmi *et al.*, 1988, respectively). In this context, stability relates to the qualitative and quantitative composition of helminth species in component communities (parasites found in a host population; see Poulin, 1997), and lack of significant long-term temporal changes in the prevalence and abundance of the dominant species in infracommunities. Historically, the first such studies were carried out by Elton *et al.* (1931) in Oxfordshire, England, working predominantly on *Apodemus sylvaticus*, but also on sympatric voles, followed by Kisieleska (1970) in Poland who reported on helminth communities of bank voles over periods spanning 9 years (1953–1961, inclusive). Over a decade later, Haukisalmi *et al.* (1988) working in Finland initially conducted studies over a slightly longer time span, 1977–1987, also in bank voles, and then extended for a further 10 years until 1997 (Haukisalmi and Henttonen, 2000).

Helminths infecting rodents are known to show marked seasonal variation in prevalence and abundance (Langley and Fairley, 1982; Gregory, 1992; Gregory *et al.*, 1992), both parameters usually experiencing some reduction in summer when there is a large influx of young uninfected animals following the breeding season (Kisieleska, 1970; Tenora *et al.*, 1979; Abu-Madi *et al.*, 1998; Haukisalmi *et al.*, 1988). However, despite this within-year variation, dominant helminth species are continuously present in rodent populations throughout the year and in every year. Although showing some between-year perturbation, when prevalence and abundance are measured in the late summer/autumn, relatively little change is generally recorded from year to year, reflecting the temporal stability of these host–parasite systems. Rarer species are less predictable, often showing sporadic occurrence with absence from sampled individuals in some years (Haukisalmi *et al.*, 1988; Behnke *et al.*, 2008a, 2008b). In the Finnish studies conducted initially on cyclic and later non-cyclic bank vole populations, one colonization event was recorded, when *Taenia polyacantha* was first recovered from sampled bank voles in the mid-1980s (Haukisalmi and Henttonen, 1993) but no species were lost over the period. In contrast, both such events, loss of species and gain of new species, were evident in recent studies in Poland, in which non-cyclic bank voles were assessed for parasite burdens in late summer in three ecologically similar but disparate sites (Behnke *et al.*, 2001). After the surveys of 1999 and 2002, the dominant species, *Syphacia*

*petruszewiczi* (dominance based on the Berger-Parker dominance index and evident in all three sites; Behnke *et al.*, 2008a), disappeared from the sampled populations, being totally absent also in subsequent surveys in 2006 and 2010 (Grzybek *et al.*, 2015a), and even more recently in 2014 and 2018 (unpublished data). In contrast, another species, *Aonchotheca annulosa*, was initially absent in 1999, but became more common and more abundant in each successive survey, in two of the three study sites that were monitored. Meanwhile, common species such as *Heligmosomum mixtum* and *Heligmosomoides glareoli*, remained stable in the population, showing only relatively minor changes in parameter values over successive surveys. A similar sequence of four, 4-yearly surveys of helminths in spiny mice (*Acomys dimidiatus*) in Egypt, also concluded that the prevalence and abundance of the dominant species (*Protospirura muricola*) was highly predictable and minor perturbations aside, relatively stable over time (Behnke *et al.*, 2019).

Although the helminth communities of wood mice (*A. sylvaticus*) in the British Isles have been studied and well described over the years, there are no long-term studies in the literature, in which populations have been monitored from year to year over periods exceeding 5 or so years (Elton *et al.*, 1931; Lewis, 1968; Abu-Madi *et al.*, 1988; Behnke *et al.*, 1999). Here, exploiting records of helminths identified during the University of Salford's annual field course at Malham Tarn Field Studies Centre in the Yorkshire Dales National Park, we report on the helminth community of wood mice from woodlands in the vicinity of the tarn. These data span a period of two and a half decades, and were always acquired at the same time of year in early autumn. In this first paper, we describe the depauperate nature of the helminth communities in these animals and significant temporal changes in parameter values, focusing particularly on unidirectional trends over the period that overlaid the between-year oscillations. In a subsequent paper, we will explore the relationship of significant trends in the dominant species to changes in host demography and locally recorded meteorological data.

## Materials and methods

### Study sites

Malham Tarn, Yorkshire, UK (grid reference SD 895673) lies at an altitude of 376 m and is the only upland marl lake in Britain. The wooded area around the tarn and estate buildings is relatively small (approximately 20 ha including some of the scrubland around the peripheries of the mature woodland, the latter currently covering about 15 ha), having been established in the late-18th century (about 1786), and is surrounded by moorland dominated by hill sheep farming. Mice were trapped overnight using baited Longworth traps which were set out for 2 days in September/October each year from 1993 to 2018. Trapping was conducted in an area of deciduous woodland approximately 50–200 m from the shore of the tarn. The sampling effort in each year was approximately equal, with 80 traps set over two nights (i.e. 160 trap nights). Previous studies, taken over 2 years at this same site (Boyce, 2013), have demonstrated that sampling at this time of the year produced the greatest trapping efficiency. Using identical trapping regimes, 70% of the annual catch of *A. sylvaticus* was recovered during the October sampling period (autumn) compared to 30% in the winter, spring and summer sampling periods combined. Although not entirely ideal, given the limited but not insubstantial trapping effort, we use the number of mice caught in each year as a proxy for the population density of wood mice in that year. These data were used to test the hypothesis that host population density is a key factor in

explaining abundance and prevalence of one of the helminths in our study.

### Laboratory procedures

Trapped mice were brought back to the study centre and were euthanized by over-exposure to chloroform, followed by exsanguination. The age of mice was estimated by nose to anus length for all mice. Three age classes were adopted corresponding to nose to anus lengths as follows: age class 1  $\leq 7.5$  cm; age class 2 = 7.5 to 8.4 cm; age class 3  $\geq 8.4$  cm. These broadly correspond to those used in our previous study (Rogan *et al.*, 2007), but were adjusted slightly by reducing the cut-off for age class 3 from 9.5 to 8.5, in order to ensure that sample sizes in each class were adequate for statistical analysis. Mice were sexed on dissection before removal of the alimentary canal for further investigation. The intestine was opened under physiological saline, the presence/absence of helminth species was noted and worm burdens were quantified. Parasites were removed from the intestine and sampled specimens were photographed. In cases where identity was obvious or infection intensities were high, not all individual parasites were photographed. With the exception of one larval nematode, all the remaining specimens were identified, and fixed in 10% neutral buffered formalin or 70% ethanol.

### Nomenclature of endoparasites

The facultative parasitic/phoretic nematode *Pelodera strongyloides* was detected and quantified in some years of the project, but not searched for systematically until 1998 onwards. *Pelodera* is not an intestinal species in rodents, living mostly in the lachrymal ducts and associated with the eyes and skin (Hominick and Aston, 1981), and has been excluded from all the derived variables in this study (i.e. helminth species richness (HSR), Brillouin's index of diversity (BID), prevalence and abundance of nematodes and helminths). Data on this species for the years 1998–2018 inclusive are available in a separate file in Supplementary material (S1). We refer to *Hydatigera taeniaeformis* (Batsch, 1786) (= *Taenia taeniaeformis*) following Nakao *et al.* (2013) and *Aonchotheca murissylvatici* (Diesing, 1851) López-Neyra, 1947 (= *Capillaria muris sylvatici*) following Moravec (2000).

### Statistical analysis

Throughout the analyses, our primary focus was on the temporal effect on parasite communities, hence overall change with time. For this reason, we also present values for some non-significant outcomes of model parameters as these underscore the robustness of stability in some parameters. We fitted YEAR as a covariate in linear statistical models (see below) to test the robustness and overall direction of change in parameter values over time. We also tested whether YEAR there were significant differences between years by fitting YEAR as a factor at 26 levels, corresponding to the years from 1993 to 2018, inclusive.

The degree of aggregation in the data was assessed by the index of discrepancy (*D*) as described by Poulin (1993) and the index of dispersion (*I*, variance to mean ratio). Frequency distributions of raw values from individual taxa were tested for goodness of fit to Gaussian, negative binomial, positive binomial and Poisson models by  $\chi^2$  as described by Elliott (1977) and the negative binomial exponent *k* is given as appropriate (for brevity we do not report the values here but see Supplementary material, Table S2).

Abundance of infection (including both infected and non-infected animals as recommended by Margolis *et al.*, 1982) is summarized by arithmetic means and standard errors of the mean (S.E.M.). For analyses of quantitative data conforming to

Gaussian distributions we used generalized linear models (GLMs) with normal errors implemented in R version 2.2.1 (R Core Development Team). We fitted models with number of parasites as the dependent variable and YEAR (as a covariate), SEX (fixed factor at two levels, males and females) and AGE (fixed factor at three levels, immature, young adults and mature older animals) as explanatory factors. In some models, YEAR (26 levels, 1993–2018, inclusive) was fitted instead as a fixed factor, and we also explored models with YEAR as a polynomial covariate and then compared these to models in which YEAR was fitted as a linear covariate. The residuals of all models were checked for approximate goodness of fit to the Gaussian distribution. When the residuals failed to meet the requirements of Gaussian models we used GLMs with negative binomial or Poisson error structures. Full factorial models that converged satisfactorily were simplified using the backward selection procedure and tested for significance at each step using the deletion of terms beginning with the highest order interaction by comparing models with or without that interaction (three-way interaction). This was followed by models based on main effects plus two-way interactions, and deletion of two-way interactions in turn, and so on until each main effect was evaluated in a model that only comprised of all main effects. Changes in deviance (DEV) are given for models based on Poisson errors (interpreted by  $\chi^2$ ), for models based on Gaussian errors we give  $F$  and for those based on negative binomial errors the likelihood ratio (LR). Minimum sufficient models (MSM) were then fitted (all significant interactions and main effects, plus any main effects that featured in interactions) and the process was repeated to obtain values for changes in deviance, test statistics and probabilities.

The acceptability of parametric models was evaluated through the goodness of fit of residuals from minimum sufficient GLMs to the distributions listed above, through Q–Q plots and through the estimation of the total deviance accounted for by the model. The percentage of deviance accounted for by each significant main effect or interaction was calculated as recommended by Xu (2003), and reported earlier by Behnke *et al.* (2008b) and more recently by Grzybek *et al.* (2015a). If the data did not meet the assumptions of parametric tests, we employed non-parametric tests in IBM-SPSS vs 24 [Kruskal–Wallis test for  $k$  levels in a specified factor (YEAR and AGE) and the Mann–Whitney  $U$ -test where factors only had two levels (e.g. SEX)] and in these cases interactions could not be tested.

Prevalence values (percentage of animals infected, based on the presence/absence of parasites and hence binomially distributed data) are given with 95% confidence limits [CL<sub>95</sub>, in square brackets in the text], calculated by bespoke software based on the tables of Rohlf and Sokal (1995). The prevalence of infection was analysed by GLMs with binomial errors, using the steps listed above.

## Results

### Wood mice

In total, 483 mice were autopsied, 293 (60.7%) males and 190 (39.3%) females. Age class 1 comprised of 86 (17.8%) mice, age class 2, 217 (44.9%) and age class 3, 180 (37.3%). The average number caught per annum was 19, but varied with a range from seven mice in each of years 2012 and 2015, to 45 mice in 2011 (Supplementary material, Table S3).

### Composition of the helminth fauna at the phylum and class taxonomic levels

The helminth community was dominated by nematodes, which accounted for 86.9% of the 7521 helminths that were recovered

and identified. Digenean trematodes accounted for most of the remainder (13.0%) and cestodes only 0.15%.

### Prevalence and abundance of combined helminth infections

The overall prevalence of helminths (all species combined) across the whole period was 72.9% (Table 1). Prevalence covaried significantly with YEAR (Fig. 1A; GLM with binomial errors,  $DEV_1 = 10.93$ ,  $P < 0.001$ ) and declined significantly over the period ( $\beta = -1.034$ ,  $R^2 = 0.226$ ,  $dof = 25$ ,  $t = -2.65$ ,  $P = 0.014$ ). Prevalence also differed significantly between the age classes (Table 2,  $DEV_2 = 18.65$ ,  $P < 0.0001$ ), increasing from the youngest to the oldest age class, but not between the sexes (Table 2;  $DEV_1 = 1.8$ ,  $P = 0.18$ ).

The overall abundance of helminths (all species combined) was  $15.6 \pm 1.40$ . We tested two GLMs. The first (with negative binomial errors) with YEAR as a covariate and SEX, AGE and SEX  $\times$  AGE as additional explanatory factors. Only AGE was significant ( $LR_{2,479} = 34.21$ ,  $P < 0.0001$ ). The lack of a significant effect of YEAR ( $LR_{1,478} = 2.00$ ,  $P = 0.16$ ) indicates that there was no consistent unidirectional long-term trend of change in the abundance of helminths over the period. In the second model, we fitted YEAR as a factor. AGE was again significant ( $LR_{2,454} = 29.0$ ,  $P < 0.0001$ ), but this time YEAR was also a significant explanatory factor ( $LR_{25,454} = 62.3$ ,  $P < 0.0001$ ), reflecting some of the between-year fluctuations in the abundance of helminths (Fig. 1B).

### Helminth species richness (HSR)

Most of the wood mice were infected with just one species of helminth (47.0% of all mice, and 64.5% of infected mice). Two species infections were less common (23.6%) and infections with three species were rare (2.3%). Mean HSR was  $1.01 \pm 0.035$ . Despite an apparent downward trend with year of study, especially in the latter years of the period (Fig. 1C), HSR did not covary significantly with year of study whether YEAR was fitted as linear (GLM with Poisson errors, YEAR as a covariate,  $DEV_1 = 1.77$ ,  $P = 0.18$ ) or second-order polynomial covariate (GLM with Poisson errors, YEAR as a second-order polynomial covariate,  $DEV_2 = 3.289$ ,  $P = 0.20$ ). Regression of mean annual values on year of study confirmed that the slope of HSR on YEAR was not significant ( $\beta = -0.14$ ,  $R^2 = 0.14$ ,  $dof = 25$ ,  $t = -1.98$ ,  $P = 0.06$ ), although close to the cut-off. An analysis of the second-order polynomial curve gave a marginally higher  $R^2$  (0.19), but also lacking significance ( $F_{2,23} = 2.77$ ,  $P = 0.083$ ). HSR did not differ significantly between the sexes (Table 3;  $DEV_1 = 1.84$ ,  $P = 0.17$ ) but there was a highly significant difference between age classes (Table 3;  $DEV_2 = 22.06$ ,  $P = 0.0001$ ), HSR increasing with host age. There were no significant interactions between these latter explanatory factors.

### Species diversity

The overall value for BID was  $0.099 \pm 0.009$ . BID did not covary significantly with YEAR (Fig. 1D; GLM with Gaussian errors, main effect of YEAR,  $F_{1,478} = 0.086$ ,  $P = 0.77$ ) but there was a significant difference between age classes (Table 3;  $F_{2,480} = 8.94$ ,  $P = 0.0002$ ), although not between the sexes ( $F_{1,478} = 3.04$ ,  $P = 0.082$ ). There were no significant interactions between these explanatory factors. However, BID varied between years (GLM with Gaussian errors, YEAR as a fixed factor, main effect of YEAR  $F_{25,455} = 1.79$ ,  $P = 0.011$ ), reflecting the fluctuations in value between the years illustrated in Fig. 1D.

**Table 1.** Overall prevalence and abundance of helminths (all years combined)

	Prevalence		Abundance	
	Mean	95% CL	Mean	±s.e.m.
<b>Nematoda</b>				
<i>Heligmosomoides polygyrus</i>	64.6	57.77–70.94	10.4	1.05
<i>Syphacia stroma</i>	9.3	5.98–14.13	2.73	0.697
<i>Aonchotheca murissylvatici</i>	6.4	3.76–10.60	0.34	0.122
<i>Aspiculuris tetraptera</i>	0.62	0.12–2.90	0.02	0.011
<i>Trichuris muris</i>	0.21	0.04–2.17	0.03	0.033
Nematoda sp.	0.21	0.04–2.17	0.002	0.002
All nematodes combined	<b>68.1</b>	<b>61.40–74.25</b>	<b>13.5</b>	<b>1.26</b>
<b>Digenea</b>				
<i>Plagiorchis muris</i>	17.0	12.26–22.79	1.95	0.525
<i>Brachylaemus recurvum</i>	0.83	0.16–3.26	0.08	0.07
All Digenea combined	<b>17.6</b>	<b>12.88–23.42</b>	<b>2.02</b>	<b>0.529</b>
<b>Cestoda</b>				
<i>Hydatigera taeniaeformis</i> <sup>a</sup>	0.62	0.120–2.900	0.006	0.004
<i>Hymenolepis</i> sp. <sup>b</sup>	0.62	0.120–2.900	0.010	0.007
<i>Cladotaenia globifera</i> <sup>a</sup>	0.62	0.120–2.900	0.006	0.004
All cestodes combined	<b>1.9</b>	<b>0.64–4.85</b>	<b>0.02</b>	<b>0.008</b>
All helminths combined	<b>72.9</b>	<b>66.31–78.56</b>	<b>15.57</b>	<b>1.402</b>

<sup>a</sup>These species were larval forms located in the livers of infected mice.

<sup>b</sup>These were mature worms in the small intestine.

### Prevalence and abundance of nematodes

#### All nematode species combined

Nematodes were the dominant taxon in this mouse population with 68.1% of the mice infected with one or more of the species listed in Table 1. The prevalence of nematodes (all species combined) showed significant covariation with YEAR (Fig. 2A; GLM with binomial errors, YEAR as covariate  $DEV_1 = 12.211$ ,  $P = 0.0005$ ) and declined significantly over the period ( $\beta = -1.181$  based on annual mean values,  $R^2 = 0.228$ ,  $dof_{25}$ ,  $t = -2.66$ ,  $P = 0.014$ ). Prevalence differed significantly between the age classes, rising from 44.2% in the youngest age class to 78.9% in the oldest mice (Table 2,  $DEV_2 = 25.7$ ,  $P < 0.0001$ ). There was no significant difference in prevalence between the sexes (Table 3;  $DEV_1 = 3.38$ ,  $P = 0.066$ ), although  $P$  was close to the borderline.

The overall mean value for nematode burdens was 13.5 worms/mouse (Table 1). Despite the apparent fall in the abundance of nematodes over the period (Fig. 2B), covariation of abundance with year of study was not significant ( $LR_{1,478} = 1.14$ ,  $P = 0.29$ ), but there was a significant difference between years reflecting fluctuations between the years illustrated in Fig. 2B (GLM with negative binomial errors, YEAR as a fixed factor,  $LR_{25,454} = 74.03$ ,  $P < 0.0001$ ). There was a highly significant increase in abundance with host age (Table 3;  $LR_{2,480} = 36.442$ ,  $P < 0.0001$ ) but no difference between the sexes ( $LR_{1,478} = 1.65$ ,  $P = 0.20$ ).

#### *Heligmosomoides polygyrus*

*Heligmosomoides polygyrus* was the most common nematode in this wood mouse population with an overall prevalence of 64.6% (Table 1) and accounted for 76.9% of all the nematodes identified and 66.8% of all helminths. Prevalence covaried significantly with YEAR (Fig. 3A; GLM with binomial errors,

$DEV_1 = 21.11$ ,  $P < 0.0001$ ) and declined significantly over the period ( $\beta = -1.447$  based on annual values,  $R^2 = 0.314$ ,  $dof_{25}$ ,  $t = -3.316$ ,  $P = 0.003$ ). Prevalence also increased significantly with host age (Table 4,  $DEV_2 = 27.81$ ,  $P < 0.001$ ) but despite the 10% higher value in male mice, it did not differ significantly between the sexes (Table 4,  $DEV_1 = 2.341$ ,  $P = 0.126$ ). However, when YEAR was fitted as a factor (instead of covariate) a significant interaction was detected between YEAR and SEX ( $DEV_{25} = 43.90$ ,  $P = 0.011$ ). Thus, the difference in prevalence between the sexes was not consistent from year to year and varied significantly between the years of the study. Prevalence was higher in male mice in 15 (58%) years, similar between the sexes in 2 (8%) years and higher in female mice in 9 (35%) years.

The overall abundance of *H. polygyrus* was  $10.4 \pm 1.05$ , but declined significantly over time (Fig. 3B; GLM with negative binomial errors, for main effect of YEAR as a covariate,  $LR_{1,479} = 21.526$ ,  $P < 0.0001$ ; regression of mean abundance on YEAR,  $\beta = -0.607$  based on annual mean values,  $R^2 = 0.260$ ,  $dof_{25}$ ,  $t = -2.907$ ,  $P = 0.008$ ). There was a highly significant effect of host age ( $LR_{2,479} = 48.9$ ,  $P < 0.0001$ ), with worm burdens increasing with host age (Table 4), but not between the sexes ( $LR_{1,478} = 0.18$ ,  $P = 0.7$ ) despite the arithmetically higher value for male mice compared with females.

#### *Syphacia stroma*

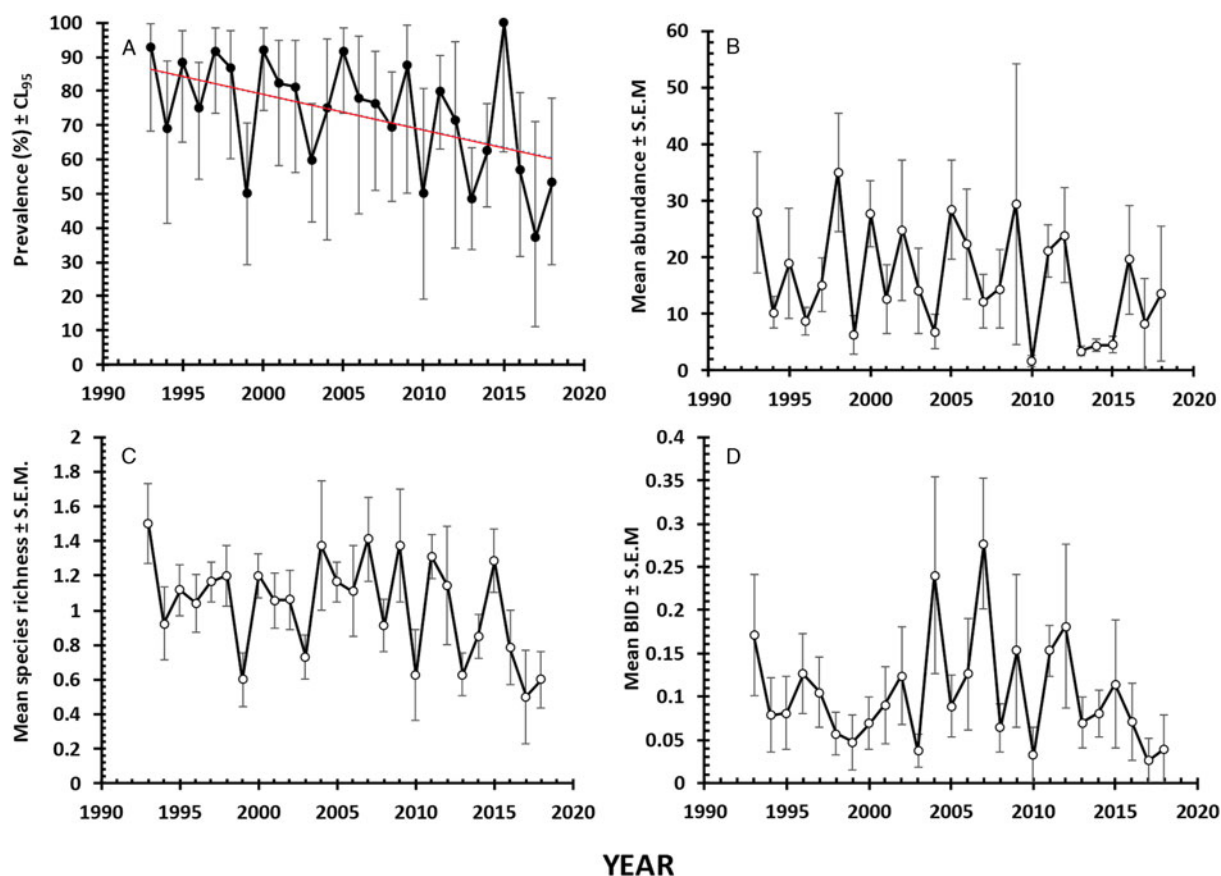
*Syphacia stroma* was the second most frequently encountered nematode (20.2% of all nematodes) but with only 45 of the mice harbouring this species, prevalence was low (Table 1). A borderline significant covariation of prevalence with YEAR ( $DEV_1 = 3.740$ ,  $P = 0.053$ ) was identified, but a highly significant difference between years was evident when YEAR was fitted as a factor ( $DEV_{25} = 53.373$ ,  $P < 0.001$ ). The latter was attributable to the sporadic occurrence of *Syphacia*, ranging from a high of 31.1% in 2011, to zero in 8 years of the study. As Fig. 3C shows, peaks of prevalence occurred irregularly at 1 to 4 year intervals, and were interspersed with years when prevalence was very low or zero. Although overall prevalence was 2.3% higher in male mice (Table 4) the difference between the sexes was not significant ( $DEV_1 = 0.093$ ,  $P = 0.76$ ), and despite the apparent age-related increase in values (Table 4), the age effect was also not significant ( $DEV_2 = 2.47$ ,  $P = 0.29$ ).

With so few mice carrying *S. stroma* and the sporadic occurrence of this species, the overall abundance at  $2.7 \pm 0.70$ , was low. In addition to its absence in 8 years, in 12 years mean abundance among the infected mice was less than one worm/host and exceeded 10 worms/mouse in only 3 years with a high of  $16.6 \pm 9.15$  in 2016. Although the best-fit distribution was negative binomial (Supplementary Table S2), GLMs with negative binomial errors failed to converge. Analysis by non-parametric tests showed that there was a highly significant difference in abundance between years (Table 4; Kruskal–Wallis test,  $H_{25} = 52.22$ ,  $P = 0.001$ ), but no difference between age classes ( $H_2 = 1.22$ ,  $P = 0.54$ ) or between the sexes (Mann–Whitney  $U$  test,  $z = 0.87$ ,  $P = 0.39$ ).

Since in the past, prevalence and abundance of *Syphacia* spp. have been linked to host population density, we also examined the correlation between host population density (as reflected in the number of mice caught in each year, given constant trapping effort each year) and both prevalence and abundance. However, neither was significant (Spearman's correlation test, for prevalence  $r_s = 0.121$ ,  $n = 26$ ,  $P = 0.56$ ; for abundance  $r_s = 0.111$ ,  $P = 0.59$ ).

#### *Aonchotheca murissylvatici*

As with *S. stroma*, *A. murissylvatici* occurred sporadically and unpredictably in this population of wood mice (Fig. 3D). It was detected in only 31 wood mice and in only 12 years of the study, and consequently overall prevalence was low (Table 1).



**Fig. 1.** Long-term trends and fluctuations in (A) prevalence of combined helminth infections, (B) abundance of combined helminths, (C) HSR and (D) BID. The trend line is provided to guide the eye (see text for statistical parameters).

**Table 2.** Prevalence of higher taxa (percentage infected of all species combined  $\pm$  95% CLs) by host sex and age

	Helminths	Nematodes	Digenea	Cestoda
Sex				
Males	75.8 [71.02–79.98]	72.0 [67.12–76.46]	19.1 [15.32–23.58]	1.7 [0.77–3.72]
Females	68.4 [58.77–76.77]	62.1 [52.42–70.91]	15.3 [9.32–23.40]	2.1 [0.44–7.17]
Age <sup>a</sup>				
Class 1	53.5 [40.55–65.92]	44.2 [32.05–57.11]	9.3 [3.94–19.59]	3.5 [0.72–11.84]
Class 2	72.8 [68.58–76.70]	68.7 [64.30–72.73]	14.3 [11.35–17.78]	2.3 [1.26–4.11]
Class 3	82.2 [73.91–88.45]	78.9 [70.45–85.65]	25.6 [18.20–34.41]	0.6 [0.05–4.27]

<sup>a</sup>Age class 1 were juvenile immature mice, age class 2 young adults and age class 3 older mature mice.

Prevalence did not covary with YEAR ( $DEV_1 = 1.255$ ,  $P = 0.263$ ), but differed significantly between years (YEAR as a factor,  $DEV_{25} = 51.9$ ,  $P = 0.0012$ ), ranging from zero to a maximum of 35.3% [16.64–59.37] in 2007. As can be seen in Table 4, prevalence only differed by 1% between the sexes and peaked in age class 2 mice at 8.3%, but neither the effects of age nor sex on prevalence were significant.

Abundance could only be analysed by non-parametric tests, and these revealed that abundance differed between years (Table 4; Kruskal–Wallis test,  $H_{25} = 52.0$ ,  $P = 0.001$ ) but not between age classes ( $H_2 = 3.81$ ,  $P = 0.149$ ) or sexes (Mann–Whitney  $U$  test,  $z = 0.441$ ,  $P = 0.66$ ) of the wood mice.

#### Other nematode species

Two other species of nematodes were recorded in the study. *Trichuris muris* was recovered in 1995 from a single mouse, an age class 3 female that carried 16 worms. *Aspiculuris tetraptera*

was recorded from three male mice (two, three and four worms each respectively), one in 2004, and two in 2013. A single unidentified nematode larva was recovered from an age class 3 male mouse in 2011.

#### Prevalence and abundance of digenean trematodes

##### Combined Digenea

The prevalence of Digenea was 17.6% [12.88–23.42], and the only significant effect was that from host age (GLM with binomial errors, for AGE  $DEV_1 = 13.60$ ,  $P = 0.0011$ ), prevalence increasing from 9.3% in the juvenile animals to 25.6% in the oldest age class (Table 2). Although the value for prevalence was just under 4% higher in male mice relative to females, there was no significant difference between the sexes ( $DEV_1 = 0.384$ ,  $P = 0.54$ ). Figure 2C illustrates how prevalence changed over the 26 years of the study. No Digenea were recorded in just 1 year (2015), but across

**Table 3.** HSR, diversity and abundance of higher taxa (mean  $\pm$  standard error) – all helminths combined, all nematodes combined, all digeneans combined, all cestodes combined, by host sex and age

	HSR	BID	Helminths	Nematoda	Digenea	Cestoda
Sex						
Males	1.08 $\pm$ 0.046	0.114 $\pm$ 0.012	17.7 $\pm$ 1.94	15.1 $\pm$ 1.68	2.6 $\pm$ 0.84	0.02 $\pm$ 0.008
Females	0.91 $\pm$ 0.054	0.076 $\pm$ 0.012	12.2 $\pm$ 1.92	11.0 $\pm$ 1.89	1.2 $\pm$ 0.34	0.03 $\pm$ 0.018
Age						
Class 1	0.640 $\pm$ 0.072	0.036 $\pm$ 0.012	6.5 $\pm$ 1.6	5.6 $\pm$ 1.50	0.9 $\pm$ 0.62	0.04 $\pm$ 0.020
Class 2	0.972 $\pm$ 0.051	0.092 $\pm$ 0.013	11.7 $\pm$ 1.77	9.7 $\pm$ 1.51	2.0 $\pm$ 0.98	0.03 $\pm$ 0.017
Class 3	1.233 $\pm$ 0.058	0.138 $\pm$ 0.015	24.6 $\pm$ 2.88	22.0 $\pm$ 2.66	2.6 $\pm$ 0.74	0.01 $\pm$ 0.006

the remaining years prevalence varied from a low of 4.3% in 2008 to a high of 44.4% in 2006. The minimum sufficient model did not include YEAR as a linear covariate ( $DEV_1 = 0.22$ ,  $P = 0.64$ ), and although a fifth-order polynomial curve (Fig. 2C; based on annual means,  $R^2 = 0.326$ ), with a peak in 2004–2005 was a better fit than a negative linear relationship ( $\beta = -0.222$ ,  $R^2 = 0.018$ ), this was also not significant in the GLM ( $DEV_5 = 8.0$ ,  $P = 0.16$ ).

Abundance of Digenea across the whole period was 2.02 worms/mouse (Table 1) and worm burdens conformed well to a negative binomial distribution (Table S2). Only host sex affected abundance significantly ( $LR_{1,479} = 4.10$ ,  $P = 0.043$ ), the mean worm burdens in males being just over twice that in female mice (Table 3). Abundance increased in value from the youngest to the oldest mice (Table 3), but with the other factors taken into account the difference between age classes was not significant ( $LR_{2,479} = 3.920$ ,  $P = 0.141$ ). Changes in abundance across the period are illustrated in Fig. 2D, where it can be seen that abundance did not covary linearly with YEAR (YEAR as a covariate,  $LR_{1,478} = 2.25$ ,  $P = 0.133$ ), but differed significantly between years (YEAR as a fixed factor,  $LR_{25,455} = 51.065$ ,  $P = 0.0016$ ). The marked peak in 2009, when only eight mice were assessed, is largely attributable to one mouse that carried 203 worms. Two other mice in that year had just a single worm and the rest were not infected.

#### *Plagiorchis muris*

The prevalence of *P. muris* did not show covariance with YEAR ( $DEV_1 = 0.197$ ,  $P = 0.66$ ), there being no obvious pattern or trend over the period (Fig. 3E), but differed significantly between years (YEAR as a factor,  $DEV_{25} = 40.91$ ,  $P = 0.023$ ). Prevalence was also significantly dependent on host age (Table 4,  $DEV_2 = 10.890$ ,  $P = 0.004$ ), but not on host sex ( $DEV_1 = 1.359$ ,  $P = 0.244$ ). In the model with YEAR fitted as a factor, a significant two-way interaction was also identified (YEAR  $\times$  SEX,  $DEV_{25} = 41.525$ ,  $P = 0.020$ ). This arose because although overall prevalence was male biased (Table 4), it was not consistent over the years. In 17 years, prevalence was male biased but in three there was no difference between the sexes and in six it was higher in female mice.

Changes in abundance over the years of the study are illustrated in Fig. 3F, where it can be seen that abundance was generally low (fewer than seven worms/mouse in 25 of the 26 years). Nevertheless, there was a marked exception in 2009, when one mouse carried 203 worms, and despite this spike, overall abundance did not covary significantly with years ( $LR_{1,478} = 2.028$ ,  $P = 0.15$ ), but there was a significant difference in abundance between years ( $LR_{25,457} = 46.12$ ,  $P = 0.0062$ ) when YEAR was fitted as a factor. The difference between age classes was not significant (GLM with negative binomial errors;  $LR_{2,478} = 4.65$ ,  $P = 0.098$ ) when other factors had been taken into account.

However, when tested independently by a non-parametric test, a significant difference was found (Kruskal–Wallis test,  $H_2 = 10.82$ ,  $P = 0.004$ ) and the upward trend with host age is evident in the data presented in Table 4. The abundance of *P. muris* varied significantly between the sexes ( $LR_{1,481} = 4.635$ ,  $P = 0.031$ ), with abundance in male mice more than twice that of female mice (Table 4).

#### *Other Digenea*

Only one other digenean species, *Brachylaemus recurvum*, was recorded in four mice, three of which had just a single worm, but one was more heavily infected with 34 worms.

#### *Prevalence and abundance of cestodes*

Only nine mice carried tapeworm infections (1.9%, Table 1), one each in 7 years and three in 1 year, so further analysis of the temporal effect was not undertaken. Prevalence by host sex and age is shown in Table 2 and abundance in Table 3, where the trends of falling prevalence and abundance with increasing host age are apparent, although neither was significant (for prevalence,  $DEV_2 = 4.23$ ,  $P = 0.12$ ; for abundance  $H_2 = 3.15$ ,  $P = 0.21$ ).

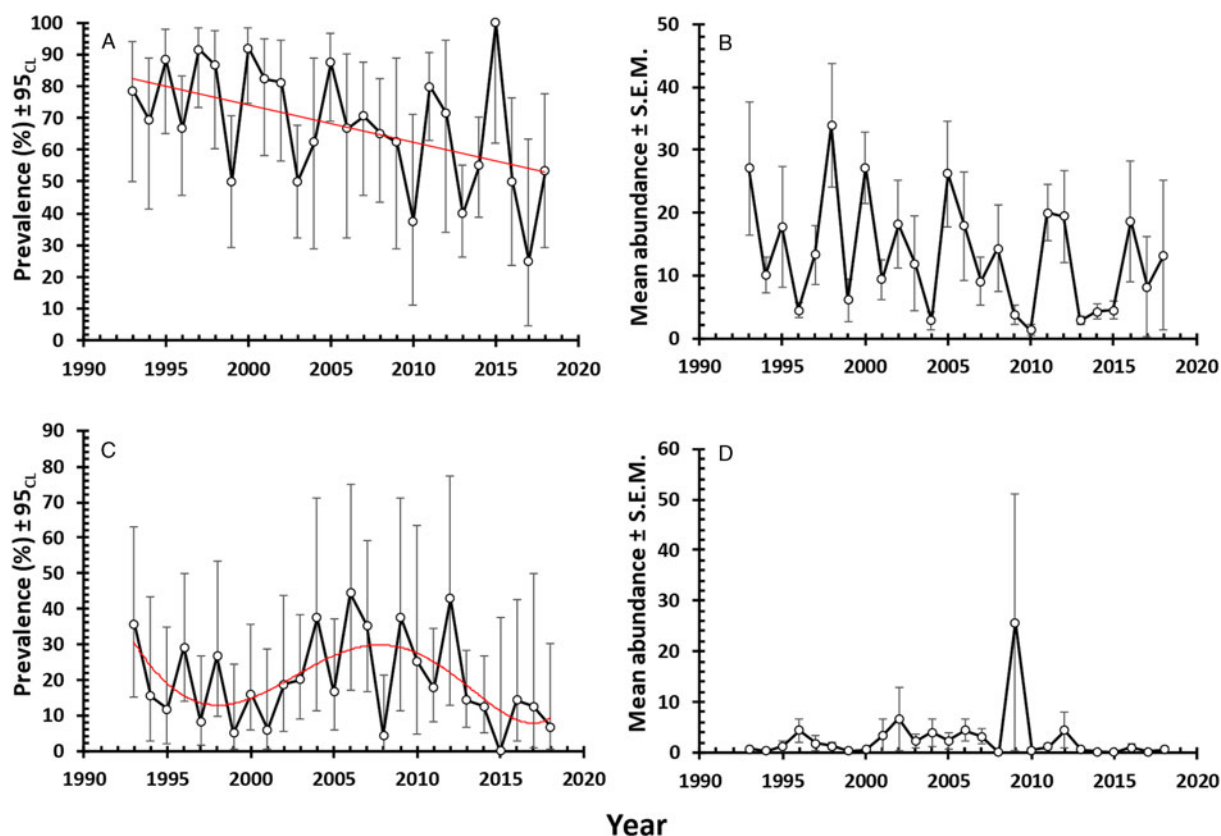
Each of the three taxa that were identified (*H. taeniaeformis* [larvae] *Cladotaenia globifera* [larvae] and *Hymenolepis* sp. [adults]) was recovered from three different individual mice.

#### *Sources of variation in abundance data*

Table 5 shows the percentage of deviance accounted for by each of the main effects in the MSMs of relevant GLMs. Where significant, covariance of YEAR accounted for up to 3.56% of deviance, and the greatest effect was in the prevalence of *H. polygyrus*. When YEAR was fitted as a factor, and therefore testing whether there was any significant difference between years, rather than covariance with YEAR, the percentage deviance was higher in most cases, and up to 22.54% in the case of prevalence with *A. murissylvatici*. Most GLMs identified AGE as playing a significant role, accounting for up to 6% of deviance (HSR) and in almost all cases reflecting a positive relationship with increasing host age. Host sex was only significant in the case of abundance of Digenea and the most abundant digenean species, *P. muris*, but the percentage deviance accounted for by host sex was very small, less than 1%.

#### Discussion

The helminth community of wood mice in our study sites, in the woods surrounding Malham Tarn, is known from earlier study to be relatively depauperate (Behnke et al., 2009), compared to wood mouse communities studied in other regions of the British Isles



**Fig. 2.** Long-term trends and fluctuations in (A) prevalence of nematodes (trend line as in legend for Fig. 1), (B) abundance of nematodes, (C) prevalence of Digenea (the fitted fifth order polynomial curve is illustrated in red and has the following equation:  $\text{Prevalence} = 8 \times 10^{-05}\text{YEAR}^5 - 0.7955\text{YEAR}^4 + 3183.9\text{YEAR}^3 - 6 \times 10^{+06}\text{YEAR}^2 + 6 \times 10^{+09}\text{YEAR} - 3 \times 10^{+12}$  and (D) abundance of Digenea.

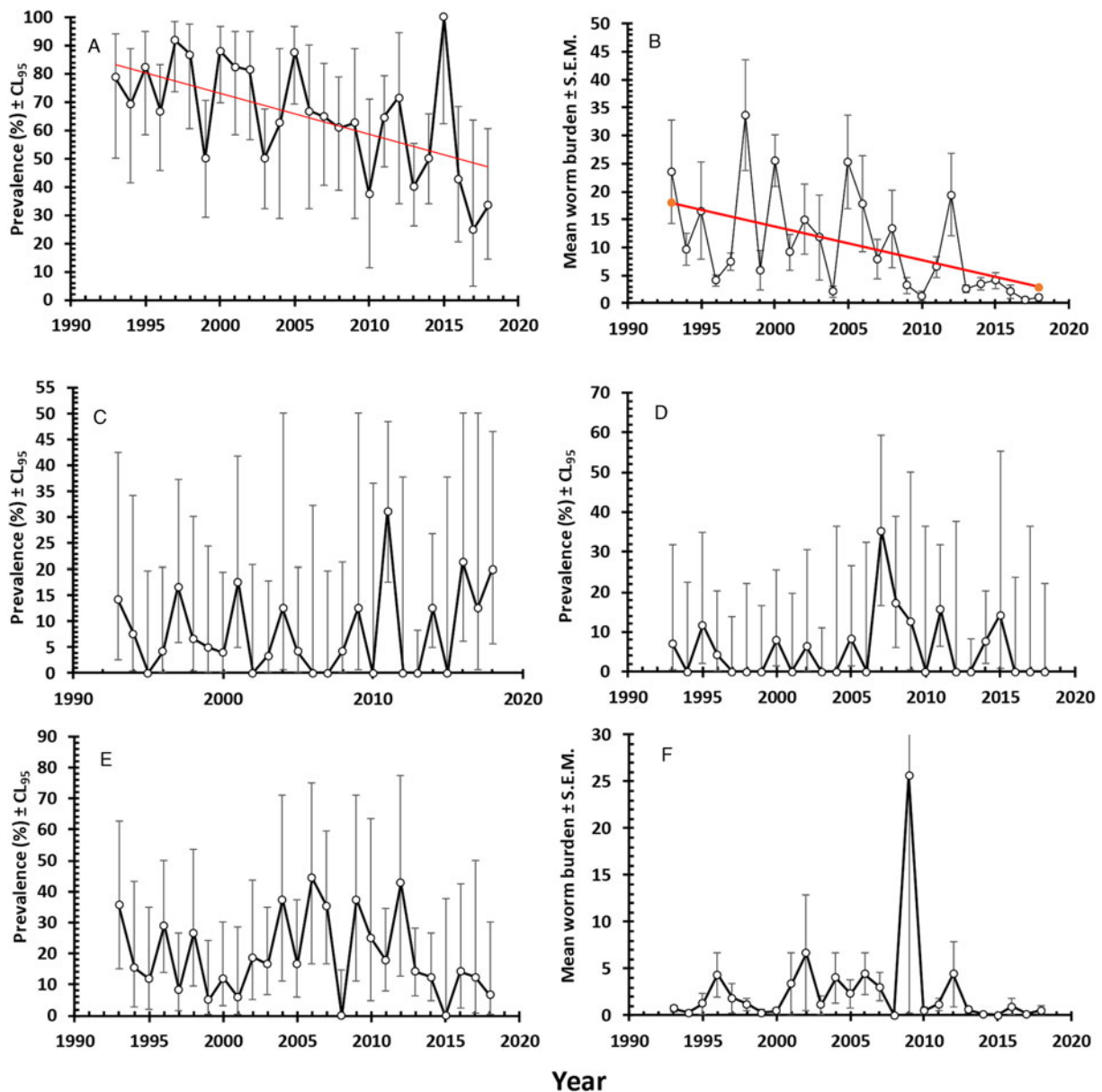
(Lewis, 1968; Montgomery and Montgomery, 1988, 1990; Abu-Madi *et al.*, 2000; Loxton *et al.*, 2017), in Europe (Feliu *et al.*, 1997; Mas-Coma *et al.*, 1998; Tenora, 2004; Milazzo *et al.*, 2005; Eira *et al.*, 2006; Bordes *et al.*, 2012) and further afield in northern Africa and parts of Asia (Asakawa and Tenora, 1996). It has some similarity to that described for bank voles in Norway where the prevalence of helminths was just 29.4% and only 12% harboured more than one helminth species (Tenora *et al.*, 1979). Essentially, the helminth community of wood mice from the Malham Tarn woodlands was dominated by just one helminth species, the nematode *H. polygyrus*. This species has been reported frequently to be the dominant helminth in wood mouse populations, often present in excess of 70% of the animals examined (O'Sullivan *et al.*, 1984; Abu-Madi *et al.*, 1998; Behnke *et al.*, 1999; Loxton *et al.*, 2017). All other species were much rarer, *P. muris* with a prevalence of 17% being the next most common species. This overall depauperate diversity of helminths and dominance by a single nematode species may be the result of a founder effect given the isolated nature of the wood in which *A. sylvaticus* were trapped in this project Mayr 1959; Orr, 2005). The relatively small size of the habitat may also increase the chance of stochastic extinctions of helminth species, while recolonization is less likely due to poor habitat connectivity (Diamond, 1975).

Given recent studies emphasizing the medium-term temporal stability of helminth infections in wild rodents (Knowles *et al.*, 2015; Grzybek *et al.*, 2015a; Behnke *et al.*, 2019), it was surprising to find that both prevalence and abundance of *H. polygyrus* declined significantly over the 26 years of this study. Moreover, since *H. polygyrus* was so dominant in this wood mouse population, the gradual temporal reduction of prevalence and abundance of this species had a marked knock-on effect on two other

parameters that we calculated: the prevalence of all helminths combined and that of combined nematodes. Although HSR did not decline significantly over the period, the covariance between HSR and YEAR (both linear and second-order polynomial) was close to significance and negative, and this again was driven primarily by the temporal changes in the abundance of *H. polygyrus*.

The relatively low values of BID and HSR (contrast e.g. with Montgomery and Montgomery, 1989 and Stuart *et al.*, 2020) both highlight the depauperate nature of the helminth community in the Malham Tarn wood mouse population. Eight of the 10 species identified were recovered from fewer than 5% of the mice, while 47% of all the mice, and 64.5% of infected mice, harboured just one species. None of the other taxa covaried significantly with time, although some were more prevalent in some years and even over several years, than during the rest of the period. Both *A. murissylvatici* and *P. muris* were more commonly encountered in particular periods (for *A. murissylvatici* 2007–2009; *P. muris* 2004–2012) and this was reflected in a higher BID in the period spanning those years.

*Plagiorchis muris* was the second most common helminth and while neither prevalence nor abundance showed any consistent long-term trend across the 26 years, both parameters varied significantly between years. In 24 of the 26 years prevalence of this species was 5% or higher, but abundance was generally low and less than one worm/mouse in 10 of the 24 years in which this species was detected. Similar low abundance of this species has been reported also in wood mice from Ireland (Langley and Fairley, 1982). Peaks of higher abundance occurred regularly over the period, but are not all clearly apparent in Fig. 3F because of the huge peak in 2009, when one mouse carried an unusually high burden. These peaks of prevalence and abundance have been associated previously with high spring and summer rainfall, when



**Fig. 3.** Prevalence and abundance of individual species over the years of the study. (A) Prevalence of *Heligmosomoides polygyrus*; (B) abundance of *H. polygyrus* which conformed well to a negative linear trend with year of study ( $\beta = -0.603 \pm 0.143$ ,  $R^2 = 0.034$ ,  $\text{dof}=481$ ,  $t = -4.23$ ,  $P < 0.0001$ ); (C) prevalence of *Syphacia stroma*; (D) prevalence of *Aonchotheca murissylvatici*; (E) prevalence of *Plagiorchis muris*; (F) abundance of *P. muris* (abundance in 2009 was  $25.6 \pm 25.3$ , as a consequence of one very heavily infected mouse that carried 203 worms). Trend lines are provided to guide the eye (see text for statistical parameters).

temporary pools of water are likely to enhance the occurrence of aquatic larval insects that act as second intermediate hosts of this species (Rogan *et al.*, 2007).

The third most common species was *S. stroma*, which showed atypical occurrence in this wood mouse population. Overall, prevalence was only 9.3% and abundance just 2.73 worms/mouse. The highest worm burden recorded was 180, and only five mice had worm burdens in excess of 100. The epidemiology of this species in the Malham Tarn woodlands clearly differs from that in other studied populations in the British Isles. Worm burdens of several hundred worms, even exceeding 1000 worms, have been recorded previously in British studies, with prevalence mostly higher than in the current study, generally over 50% and even close to 100% in some studies (Lewis, 1968; Sharpe, 1964; Lewis and Twigg, 1972; Behnke *et al.*, 1999; Abu-Madi *et al.*, 2000; Jackson *et al.*, 2009). *Syphacia* spp. are often also the dominant or co-dominant species in other rodents, e.g. voles (Ryan and Holland, 1996; Bajer *et al.*, 2005; Behnke *et al.*, 2008a,

2008b; Loxton *et al.*, 2017; Stuart *et al.*, 2020). These worms are transmitted directly between hosts through contact between individuals during reciprocal allogrooming and when gathering in burrows and nests. Their prevalence has been linked to host population density, since contact-transmitted parasites spread more easily between hosts when host density is high (for Oxyurida see Arneberg, 2001; for *Syphacia* see Lewis, 1968; Haukisalmi and Henttonen, 1990). However, not all workers have found evidence to support this concept (Pisanu *et al.*, 2002) and, despite the limitation in our estimate of population size (based on just 2 days of trapping and averaging 160 trap nights in each year of the study), there was no evidence in our data that either prevalence or abundance correlated positively with the numbers of mice caught/annum. The absence of this parasite in 8 years of the study indicates that the transmission of *S. stroma* in this wood mouse population is sporadic and relatively infrequent, but probably unrelated to host population density, and climatic variation, as the infective stages are



**Table 4.** Abundance (mean  $\pm$  standard error) and prevalence (%  $\pm$  [CL<sub>95</sub>]) of individual species by host sex and age

	<i>H. polygyrus</i>		<i>S. stroma</i>		<i>P. muris</i>		<i>A. murissylvatici</i>	
	Mean $\pm$ S.E.M.	% $\pm$ [CL <sub>95</sub> ]	Mean $\pm$ S.E.M.	% $\pm$ [CL <sub>95</sub> ]	Mean $\pm$ S.E.M.	% $\pm$ [CL <sub>95</sub> ]	Mean $\pm$ S.E.M.	% $\pm$ [CL <sub>95</sub> ]
Sex								
Males	11.5 $\pm$ 1.35	68.3 [63.20–72.94]	3.4 $\pm$ 1.06	10.2 [7.42–13.85]	2.6 $\pm$ 0.84	19.1 [15.32–23.58]	0.27 $\pm$ 0.087	6.8 [4.60–9.95]
Females	8.8 $\pm$ 1.68	58.9 [49.25–68.24]	1.7 $\pm$ 0.68	7.9 [3.83–14.92]	1.0 $\pm$ 0.29	13.7 [8.17–21.64]	0.46 $\pm$ 0.280	5.8 [2.59–11.94]
Age								
Class 1	3.8 $\pm$ 0.91	40.7 [28.54–53.60]	1.7 $\pm$ 1.23	7.0 [2.52–16.63]	0.8 $\pm$ 0.62	9.3 [3.94–19.59]	0.023 $\pm$ 0.016	2.3 [0.30–10.16]
Class 2	5.7 $\pm$ 0.77	63.1 [58.61–67.46]	3.6 $\pm$ 1.29	8.8 [6.49–11.72]	2.0 $\pm$ 0.98	14.3 [11.35–17.78]	0.332 $\pm$ 0.113	8.3 [6.09–11.20]
Class 3	19.2 $\pm$ 2.50	77.8 [68.99–84.62]	2.2 $\pm$ 0.86	11.1 [6.24–18.45]	2.4 $\pm$ 0.72	23.9 [16.68–32.73]	0.511 $\pm$ 0.298	6.1 [2.88–12.10]

contact-transmitted and therefore not subject to external weather conditions. The low prevalence of this species in the Malham Tarn wood mouse population is therefore intriguing, especially as *S. stroma* is a directly transmitted species, with no intermediate hosts (Lewis, 1968) and highly specific to *Apodemus* spp. (Stewart *et al.*, 2018b). In the absence of *A. flavicollis* in the study sites, even in the years when it was not represented in the mice we sampled, it must have persisted in other *A. sylvaticus* individuals in the woods, as it is unlikely to have been frequently re-introduced into the wood mouse population through immigrant hosts because of the extreme isolation of the Malham Tarn wood.

The capillariid nematode, *A. murissylvatici* likewise was characterized by low prevalence and abundance and showed an unpredictable, sporadic occurrence, present in some years, occasionally for more than a year, and then absent in the following year. However, in the case of *A. murissylvatici*, this pattern of occurrence was not unexpected, and in fact is typical for capillariid nematodes infecting *Apodemus* spp. as other studies have shown (Tenora and Zavadil, 1967; Lewis, 1968; Langley and Fairley, 1982; Montgomery and Montgomery, 1988; Tenora and Staněk, 1994; Loxton *et al.*, 2017; Abu-Madi *et al.*, 2000). Voles may be more susceptible, much higher prevalence having been recorded in these hosts (Thomas, 1953; Lewis and Twigg, 1972; Murúa, 1978; Loxton *et al.*, 2016; Stuart *et al.*, 2020), and are probably the main reservoirs of this species. Infections in *A. sylvaticus* most likely originate from inadvertent exposure to intermediate hosts or the environment contaminated by sympatric bank vole populations (*note*: the full life cycle has still not been elucidated, but as in other members of this genus is likely to include intermediate hosts such as earthworms; Moravec *et al.*, 1987). The remaining species were all relatively rare and all showed only sporadic, infrequent occurrence.

Our analysis showed that an age effect was a prominent feature of our data. As in numerous other studies of helminths in wild rodents (Elton *et al.*, 1931; Kisieleska, 1971; Montgomery and Montgomery, 1989; Gregory, 1992; Gregory *et al.*, 1992; Behnke *et al.*, 1999; Eira *et al.*, 2006; Jackson *et al.*, 2009, 2014; Friberg *et al.*, 2013), prevalence and intensity increased with host age in most cases, as did also both HSR and BID. This was expected, because it is now well established that in relation to the life span of wild rodents, most helminths are long-lived, avoiding host immunity through various strategies, and therefore in wild freely living animals, worms accumulate during the lifetime of the host, resulting in heavier worm burdens as animals become older (Behnke *et al.*, 1992; Maizels *et al.*, 2004). Accordingly, we found that the oldest animals in our population carried the most intense worm burdens and the greatest range and diversity of species. Nevertheless, there are studies showing convexity in age prevalence/intensity relationships, suggesting that in some cases resistance to further infection may develop in the oldest cohorts of mice (Gregory *et al.*, 1992; Behnke *et al.*, 1999; Luong *et al.*, 2010).

In contrast, and given the numerous studies that have reported sex-bias in helminth infections (Poulin, 1996; Zuk and McKean, 1996; Moore and Wilson, 2002; Sanchez *et al.*, 2011; Grzybek *et al.*, 2015b), it was perhaps surprising that we found a significant sex-effect in only the Digenea and essentially attributable just to *P. muris*. However, our finding of a male sex bias in both prevalence and abundance of *P. muris* contrasts with Rogan *et al.* (2007), who analysed *P. muris* burdens in the same animals from the period 1993–2005 and found that prevalence was only marginally higher in male (17.8%) compared with female (15.6%) mice and not significantly different between the sexes. Our data failed to support sex-bias in the case of *S. stroma* in agreement with Abu-Madi *et al.* (2000) but in contrast to

**Table 5.** Summary of factors (main statistical effects) affecting helminth taxa and derived parameters in the study and proportion of deviance explained in minimum sufficient models

Taxon/parameter	Model with year as covariate			Model with year as factor		
	Year	Age	Sex	Year	Age	Sex
Prevalence combined helminths	2.02, -ve <sup>a</sup>	3.40, +ve <sup>b</sup>	ns	10.44	3.43, +ve <sup>b</sup>	ns
Abundance combined helminths	ns	1.04	ns	1.92	0.90, +ve <sup>b</sup>	ns
HSR	ns	5.83, +ve	ns	ns	5.83, +ve <sup>b</sup>	ns
BID	ns	3.59, +ve	ns	8.97	4.27, +ve <sup>b</sup>	ns
Prevalence of combined nematodes	2.13, -ve	4.38, +ve	ns	12.09	4.86, +ve <sup>b</sup>	ns
Abundance of combined nematodes	ns	1.18, +ve	ns	2.42	1.10, +ve <sup>b</sup>	ns
Prevalence <i>H. polygyrus</i>	3.56, -ve	4.64, +ve	ns	11.62 <sup>c</sup>	4.95, +ve <sup>b</sup>	ns
Abundance of <i>H. polygyrus</i>	0.77, -ve	1.73, +ve	ns	3.32	1.56, +ve <sup>b</sup>	ns
Prevalence of <i>S. stroma</i>	1.25, +ve	ns	ns	17.50	ns	ns
Abundance of <i>S. stroma</i>	- <sup>d</sup>	-	-	- <sup>d</sup>	-	-
Prevalence of <i>A. murissylvatici</i>	ns	ns	ns	22.54	ns	ns
Abundance of <i>A. murissylvatici</i>	ns	1.90	ns	- <sup>d</sup>	-	-
Prevalence of combined Digenea	ns	3.03, +ve	ns	ns	3.03, +ve	ns
Abundance of combined Digenea	ns	ns	0.43, male <sup>e</sup>	5.30	1.15, +ve	ns
Prevalence of <i>P. muris</i>	ns	2.48, +ve	ns	9.56 <sup>c</sup>	2.22, +ve	ns
Abundance of <i>P. muris</i>	ns	ns	0.49, male <sup>e</sup>	4.91	ns	ns

<sup>a</sup>-ve = negative covariance, +ve = positive covariance.

<sup>b</sup>+ve = significant increase with age.

<sup>c</sup>Significant year × sex interaction, % deviance = 7.96%.

<sup>d</sup>Could not be assessed in GLM.

<sup>e</sup>Male = male biased sex difference.

Behnke et al. (1999), Muller-Graf et al. (1999), Eira et al. (2006), Jackson et al. (2009) and Stuart et al. (2020), all of who found that prevalence and/or abundance of worm burdens was significantly higher in male compared with female mice. Behnke et al. (1999) also found that worm burdens rose faster with increasing host age in males than in females. Curiously, in the case of *A. murissylvatici* the values suggested female biased infections (see also Grzybek et al., 2015b) although again the difference between the sexes was not sufficiently large enough to achieve statistical significance. Although some earlier studies have reported male-bias in infections with *H. polygyrus* (Lewis, 1968; Lewis and Twigg, 1972), others have failed to find a significant difference between the sexes (Sharpe, 1964; Gregory, 1992; Gregory et al., 1992; Abu-Madi et al., 1998; Behnke et al., 1999; Eira et al., 2006; Jackson et al., 2009; Babayan et al., 2018). Nevertheless, even in some of the latter studies the prevalence of *H. polygyrus* and worm burdens were reported to be arithmetically higher in male hosts (e.g. Gregory et al., 1992), as indeed we found for the arithmetic values of both prevalence and abundance. However, this apparent male bias was insufficient to merit statistical significance when other factors had been taken into account in GLMs. In this context, it is perhaps noteworthy that based on fecal egg counts rather than worm burdens, Ferrari et al. (2004) found no difference between the sexes in the prevalence of *H. polygyrus* but significant male bias in abundance. Following experimental intervention Ferrari et al. (2004) concluded that male *A. flavicollis* were more important than females in maintaining and spreading *H. polygyrus* in the host population. Nevertheless, taken in total, the lack of strong evidence for sex bias in our data (despite most parameters showing marginally higher arithmetic values in male mice compared with females) concurs with other studies that have also failed to find statistically

significant sex bias in helminth infections in wild rodents and have questioned the universality of this phenomenon (Schalk and Forbes, 1997; Čabrilo et al., 2018; Bordes et al., 2012).

In this study, we have examined an unusually long annual time series ( $n = 26$ ), for an endohelminth community that covers a period claimed to encompass large shifts in global climate (World Meteorological Organization, 2019). The sporadic occurrence of the rare helminth species recorded in this study was perhaps not surprising, in light of previous studies of temporal stability of helminth communities. In contrast, the significant downward trend in the prevalence of *H. polygyrus* and the associated higher taxa over more than two decades was unexpected, given the dominance of *H. polygyrus* in the helminth community and previous observations that such core community members tend towards temporal stability. The pattern of consistently falling prevalence and abundance over the 26 years of this study, overriding the between year oscillations in both parameters, differs from the more abrupt disappearance of *S. petrusewiczii* from bank voles in study sites in NE Poland, which occurred over a period of just 7 years (dominant species in 1999, and undetected in 2006).

Malham Tarn itself is situated at 377 m above sea level, and located on limestone is an alkaline lake, one of only eight such lakes in Europe. The surrounding woodlands in which we trapped animals are either located at the same altitude or even higher on the slopes rising to the escarpment in the north. These sites may experience harsh winters in comparison with other regions in the British Isles, as for example those in southern England where studies by Abu-Madi et al. (2000) and Behnke et al. (1999) were conducted. As far as we are aware, there have been no major changes in the structure/composition of the woodlands in which the wood mice were trapped over the period from 1993. Malham Tarn itself and the surrounding wet lands are designated

as a site of Special Scientific Interest (SSSI), with associated legal protection, and much of the area is a nature reserve. If very dominant species, such as *H. polygyrus* in the current study, can decline in prevalence and abundance so markedly as reported herein, moreover in a relatively undisturbed environment subject to conservation measures, then this suggests that major long-term functional re-adjustments in parasite communities may be more common than previously thought. Although we can be confident that the study sites utilized in the current research were not subject to any major intrusions from human activity, the concept of global warming is currently topical (Hudson *et al.*, 2006; Brooks and Hoberg, 2007; Houghton, 2009). In this context, a recent review has predicted extinction of parasite species, with up to 30% of parasitic worms, resulting from climate driven habitat loss alone (Carlson *et al.*, 2017). Moreover, the effects of within-habitat climate-driven environmental change on host-parasite systems are also likely to be important (Hudson *et al.*, 2006; Altizer *et al.*, 2013; Gethings *et al.*, 2015; Gehman *et al.*, 2018; Stewart *et al.*, 2018a; Jackson *et al.*, 2020) but this is an area where more empirical evidence is required. Fortunately, the Malham Tarn Study Centre does have a local meteorological station. This will provide an opportunity to assess whether the decline in the prevalence and abundance of *H. polygyrus* and the oscillations in parameter values for *P. muris* were related to specific weather conditions, or climatic changes, over the same period that affected parasite transmission directly or indirectly through effects on host demography. Such an analysis is complex and will be reported in a subsequent paper.

**Supplementary material.** The supplementary material for this article can be found at <https://doi.org/10.1017/S0031182020002243>.

**Acknowledgements.** We thank the Field Studies Council at Malham Tarn for use of their facilities, Dr R.A. Bray at The Natural History Museum, London, for confirmation of the identification of *Plagiorchis muris*. This project would not have been possible without the assistance of David Storey, Stephen Heath, Helen Bradshaw and Paul Titchmarsh, and especially the diligent work of students in the Level 6 Bioscience programmes at the University of Salford, between 1993 and 2018, and we are grateful to them for their contributions. We thank also Professors C. Holland and A. Bajer for their helpful advice on earlier drafts of the manuscript and Professor F. Gilbert for advice on aspects of the statistical analysis that we employed.

**Conflict of interest.** None.

**Ethical standards.** Permissions to sample from this site were given by the Field Studies Council (Rogan *et al.*, 2007; Boyce *et al.*, 2012, 2014) and the National Trust (Boyce *et al.*, 2012). Rodents were killed according to the 'Code of Practice for the Humane Killing of Animals under Schedule 1 of the Animals (Scientific Procedures) Act 1986'. Ethical approval was granted by the University of Salford Research Ethics and Governance Committee (most recently, REGC CST12/36, REGC STR1718-32 and REGC STR1819-12).

## References

- Abu-Madi MA, Behnke JM, Lewis JW and Gilbert FS (1998) Descriptive epidemiology of *Heligmosomoides polygyrus* in *Apodemus sylvaticus* from three contrasting habitats in south-east England. *Journal of Helminthology* **72**, 93–100.
- Abu-Madi MA, Behnke JM, Lewis JW and Gilbert FS (2000) Seasonal and site specific variation in the component community structure of intestinal helminths in *Apodemus sylvaticus* from three contrasting habitats in south-east England. *Journal of Helminthology* **74**, 7–16.
- Altizer S, Ostfeld RS, Johnson PTJ, Kutz S and Harvell CD (2013) Climate change and infectious diseases: from evidence to a predictive framework. *Science (New York, N.Y.)* **341**, 514–519.
- Arneberg P (2001) An ecological law and its macroecological consequences as revealed by studies of relationships between host densities and parasite prevalence. *Ecography* **24**, 352–358.
- Asakawa M and Tenora F (1996) A checklist of epidemiology of nematode parasites of the genus *Apodemus* (Murinae: Rodentia) throughout the world excluding Japan. *Journal of the Rakuno Gakuen University* **20**, 181–213.
- Babayan SA, Liu W, Hamilton G, Kilbride E, Rynkiewicz EC, Clerc M and Pedersen AB (2018) The immune and non-immune pathways that drive chronic gastrointestinal helminth burdens in the wild. *Frontiers in Immunology* **9**, 56.
- Bajer A, Behnke JM, Pawelczyk A, Kulis K, Sereda MJ and Siński E (2005) Medium-term temporal stability of the helminth component community structure in bank voles (*Clethrionomys glareolus*) from the Mazury Lake District region of Poland. *Parasitology* **130**, 213–228.
- Behnke JM, Barnard CJ and Wakelin D (1992) Understanding chronic nematode infections: evolutionary considerations, current hypotheses and the way forward. *International Journal for Parasitology* **22**, 861–907.
- Behnke JM, Lewis JW, Mohd Zain SN and Gilbert FS (1999) Helminth infections in *Apodemus sylvaticus* in southern England: interactive effects of host age, sex and year on the prevalence and abundance of infections. *Journal of Helminthology* **73**, 31–44.
- Behnke JM, Barnard CJ, Bajer A, Bray D, Dinmore J, Frake K, Osmond J, Race T and Sinski E (2001) Variation in the helminth community structure in bank voles (*Clethrionomys glareolus*) from three comparable localities in the Mazury Lake District region of Poland. *Parasitology* **123**, 401–414.
- Behnke JM, Bajer A, Harris PD, Newington L, Pidgeon E, Rowlands G, Sheriff C, Kuliś-Malkowska K, Siński E, Gilbert FS and Barnard C (2008a) Temporal and between-site variation in helminth communities of bank voles (*Myodes glareolus*) from N.E. Poland. 1. Regional fauna and component community levels. *Parasitology* **135**, 985–997.
- Behnke JM, Bajer A, Harris PD, Newington L, Pidgeon E, Rowlands G, Sheriff C, Kuliś-Malkowska K, Siński E, Gilbert FS and Barnard CJ (2008b) Temporal and between-site variation in helminth communities of bank voles (*Myodes glareolus*) from N.E. Poland. 2. The infracommunity level. *Parasitology* **135**, 999–1018.
- Behnke JM, Eira C, Rogan M, Gilbert FS, Torres J, Miquel J and Lewis JW (2009) Helminth species richness in wild wood mice, *Apodemus sylvaticus*, is enhanced by the presence of the intestinal nematode *Heligmosomoides polygyrus*. *Parasitology* **136**, 793–804.
- Behnke JM, Bajer A, Behnke-Borowczyk J, Clisham N, Gilbert FS, Glover A, Jeffery L, Kirk J, Mierzejewska EJ, Mills SC, Mohallal EME, Padgett O, Wainer R and Zalat S (2019) Long-term spatiotemporal stability and dynamic changes in helminth infracommunities of spiny mice (*Acomys dimidiatus*) in St. Katherine's Protectorate, Sinai, Egypt. *Parasitology* **146**, 50–73.
- Bordes F, Ponlet N, de Bellocq JG, Ribas A, Krasnov BR and Morand S (2012) Is there sex-biased resistance and tolerance in Mediterranean wood mouse (*Apodemus sylvaticus*) populations facing multiple helminth infections? *Oecologia* **170**, 123–135.
- Boyce K (2013) *Transmission Ecology of Gastrointestinal Trematodes of Small Mammals, Malham Tarn* (PhD thesis). University of Salford, UK.
- Boyce K, Hide G, Craig PS, Harris PD, Reynolds C, Pickles A and Rogan MT (2012) Identification of a new species of digenean *Notocotylus malhamensis* n. sp. (Digena: Notocotylidae) from the bank vole (*Myodes glareolus*) and the field vole (*Microtus agrestis*). *Parasitology* **139**, 1630–1639.
- Boyce K, Hide G, Craig PS, Reynolds C, Hussain M, Bodell AJ, Bradshaw H, Pickles A and Rogan MT (2014) A molecular and ecological analysis of the trematode *Plagiorchis elegans* in the wood mouse *Apodemus sylvaticus* from a periaquatic ecosystem in the UK. *Journal of Helminthology* **88**, 310–320.
- Brooks DR and Hoberg EP (2007) How will global climate change affect parasite-host assemblages? *Trends in Parasitology* **23**, 571–574.
- Čabrilo B, Jovanović VM, Bjelić Čabrilo O, Budinski I, Blagojević J and Vujošević M (2018) Is there a host sex bias in intestinal nematode parasitism of the yellow-necked mouse (*Apodemus Fl avicollis*) at Obedska Bara pond, Serbia? *Helminthologia* **55**, 247–250.
- Carlson CJ, Burgio KR, Dougherty ER, Phillips AJ, Bueno VM, Clements CF, Castaldo G, Dallas TA, Cizauskas CA, Cumming GS, Doña J, Harris NC, Jovani R, Mironov S, Muellerklein OC, Proctor H and Getz WM (2017) Parasite biodiversity faces extinction and redistribution in a changing climate. *Science Advances* **3**, e1602422.
- Diamond JM (1975) The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* **7**, 129–146.
- Eira C, Torres J, Vingada J and Miquel J (2006) Ecological aspects influencing the helminth community of the wood mouse *Apodemus sylvaticus* in Dunas de Mira, Portugal. *Acta Parasitologica* **51**, 300–308.

- Elliott JM (1977) *Some Methods for the Statistical Analysis of Samples of Benthic Invertebrates*. Cumbria, UK: Freshwater Biological Association.
- Elton C, Ford EB, Baker JR and Gardiner AD (1931) The health and parasites of a wild mouse population. *Proceedings of the Zoological Society of London* **1931**, 657–721.
- Feliu C, Renaud F, Catzeffis F, Hugot J-P, Durand P and Morand S (1997) A comparative analysis of parasite species richness of Iberian rodents. *Parasitology* **115**, 453–466.
- Ferrari N, Cattadori IM, Nespereira J, Rizzoli A and Hudson PJ (2004) The role of host sex in parasite dynamics: field experiments on the yellow-necked mouse *Apodemus flavicollis*. *Ecology Letters* **7**, 88–94.
- Friberg IM, Little S, Ralli C, Lowe A, Hall A, Jackson JA and Bradley JE (2013) Macroparasites at peripheral sites of infection are major and dynamic modifiers of systemic antimicrobial pattern recognition responses. *Molecular Ecology* **22**, 2810–2826.
- Gehman A-LM, Hall RJ and Byers JE (2018) Host and parasite thermal ecology jointly determine the effect of climate warming on epidemic dynamics. *Proceedings of the National Academy of Sciences of the United States of America* **115**, 744–749.
- Gethings OJ, Rose H, Mitchell S, Van Dijk J and Morgan ER (2015) Asynchrony in host and parasite phenology may decrease disease risk in livestock under climate warming: *Nematodirus battus* in lambs as a case study. *Parasitology* **142**, 1306–1317.
- Gregory RD (1992) On the interpretation of host-parasite ecology: *Heligmosomoides polygyrus* (Nematoda) in wild wood mouse (*Apodemus sylvaticus*) populations. *Journal of Zoology, London* **226**, 109–121.
- Gregory RD, Montgomery SSJ and Montgomery WI (1992) Population biology of *Heligmosomoides polygyrus* (Nematoda) in the wood mouse. *Journal of Animal Ecology* **61**, 749–757.
- Grzybek M, Bajer A, Bednarska M, Alsarraf M, Behnke-Borowczyk J, Harris PD, Price S, Brown GS, Osborne S-J, Siński E and Behnke JM (2015a) Long-term spatiotemporal stability and dynamic changes in helminth infracommunities of bank voles (*Myodes glareolus*) in NE Poland. *Parasitology* **142**, 1722–1743.
- Grzybek M, Bajer A, Behnke-Borowczyk J, Alsarraf M and Behnke JM (2015b) Female host sex-biased parasitism with the rodent stomach nematode *Mastophorus muris* in wild bank voles (*Myodes glareolus*). *Parasitology Research* **114**, 523–533.
- Haukisalmi V and Henttonen H (1990) The impact of climatic factors and host density on the long-term population dynamics of vole helminths. *Oecologia* **83**, 309–315.
- Haukisalmi V and Henttonen H (1993) Population dynamics of *Taenia polyacantha* metacestodes in the bank vole *Clethrionomys glareolus*. *Annales Zoologici Fennici* **30**, 81–84.
- Haukisalmi V and Henttonen H (2000) Variability of helminth assemblages and populations in the bank vole *Clethrionomys glareolus*. *Polish Journal of Ecology* **48**(Suppl.), 219–231.
- Haukisalmi V, Henttonen H and Tenora F (1988) Population dynamics of common and rare helminths in cyclic vole populations. *Journal of Animal Ecology* **57**, 807–825.
- Hominick WM and Aston AJ (1981) Association between *Pelodera strongyloides* (Nematoda: Rhabditidae) and wood mice, *Apodemus sylvaticus*. *Parasitology* **83**, 67–75.
- Houghton J (2009) *Global Warming: The Complete Briefing*, 4th Edn. Cambridge: Cambridge University Press.
- Hudson PJ, Cattadori IM, Boag B and Doson AP (2006) Climate disruption and parasite-host dynamics: patterns and processes associated with warming and the frequency of extreme climatic events. *Journal of Helminthology* **80**, 175–182.
- Jackson JA, Friberg IM, Bolch L, Lowe A, Ralli C, Harris PD, Behnke JM and Bradley JE (2009) Immunomodulatory parasites and toll-like receptor-mediated tumour necrosis factor alpha responsiveness in wild mammals. *BMC Biology* **7**, 16.
- Jackson JA, Hall AJ, Friberg IM, Ralli C, Lowe A, Zawadzka M, Turner AK, Stewart A, Birtles RJ, Paterson S, Bradley JE and Begon M (2014) An immunological marker of tolerance to infection in wild rodents. *PLoS Biology* **12**, e1001901.
- Jackson JA, Friberg IM, Hablützel PI, Masud N, Stewart A, Synnott R and Cable J (2020) Partitioning the environmental drivers of immunocompetence. *Science of the Total Environment* **747**, 141152.
- Kisielewska K (1970) Ecological organization of intestinal helminth groupings in *Clethrionomys glareolus* (Schreb.) (Rodentia). 1. Structure and seasonal dynamics of helminth groupings in a host population in the Białowieża National Park. *Acta Parasitologica Polonica* **18**, 121–147.
- Kisielewska K (1971) Intestinal helminths as indicators of the age structure of *Microtus arvalis* Pallas, 1778 population. *Bulletin de L'Academie Polonaise des Sciences. Serie des Sciences Biologiques Cl.II* **19**, 275–282.
- Knowles SCL, Fenton A, Petchey OL, Jones TR, Barber R and Pedersen AB (2015) Stability of within-host-parasite communities in a wild mammal system. *Proceedings of the Royal Society B* **280**, 20130598.
- Langley R and Fairley JS (1982) Seasonal variations in infestations of parasites in a wood mouse *Apodemus sylvaticus* population in the west of Ireland. *Journal of Zoology, London* **198**, 249–261.
- Lewis JW (1968) Studies on the helminth parasites of the long-tailed field mouse, *Apodemus sylvaticus sylvaticus* from Wales. *Journal of Zoology, London* **154**, 287–312.
- Lewis JW and Twigg GI (1972) A study of the internal parasites of small rodents from woodland areas in Surrey. *Journal of Zoology (London)* **166**, 61–77.
- Loxton KC, Lawton C, Stafford P and Holland CV (2016) Reduced helminth parasitism in the introduced bank vole (*Myodes glareolus*); more parasites lost than gained. *International Journal for Parasitology: Parasites and Wildlife* **5**, 175–183.
- Loxton KC, Lawton C, Stafford P and Holland CV (2017) Parasite dynamics in an invaded ecosystem: helminth communities of native wood mice are impacted by the invasive bank vole. *Parasitology* **144**, 1476–1489.
- Luong LT, Perkins SE, Grear DA, Rizzoli A and Hudson PJ (2010) The relative importance of host characteristics and co-infection in generating variation in *Heligmosomoides polygyrus* fecundity. *Parasitology* **137**, 1003–1012.
- Maizels RM, Balic A, Gomez-Escobar N, Nair M, Taylor MD and Allen JE (2004) Helminth parasites—masters of regulation. *Immunological Reviews* **201**, 89–116.
- Margolis L, Esch GW, Holmes JC, Kuris AM and Schad GA (1982) The use of ecological terms in parasitology (report of an ad hoc committee of The American Society of Parasitologists). *Journal of Parasitology* **68**, 131–133.
- Mas-Coma S, Esteban JG, Fuentes MV, Bargues MD, Valero M and Galan-Puchades MT (1998) Helminth parasites of small mammals (insectivores and rodents) on the Pityusic Island of Formentera (Balearic Archipelago). *Research and Reviews in Parasitology* **58**, 125–133.
- Mayr E (1959) Isolation as an evolutionary factor. *Proceedings of the American Philosophical Society* **103**, 221–230.
- Milazzo C, Aloise G, Cagnin M, Di Bella C, Geraci F, Feliu C and Casanova JC (2005) Helminths of *Apodemus sylvaticus* (Muridae) distributed on the Southern European border (Italian Peninsula). *Vie et Milieu* **55**, 45–51.
- Montgomery SSJ and Montgomery WI (1988) Cyclic and non-cyclic dynamics in populations of the helminth parasites of wood mice *Apodemus sylvaticus*. *Journal of Helminthology* **62**, 78–90.
- Montgomery SSJ and Montgomery WI (1989) Spatial and temporal variation in the infracommunity structure of helminths of *Apodemus sylvaticus* (Rodentia: Muridae). *Parasitology* **98**, 145–150.
- Montgomery SSJ and Montgomery WI (1990) Structure, stability and species interactions in helminth communities of wood mice *Apodemus sylvaticus*. *International Journal for Parasitology* **20**, 225–242.
- Moore SL and Wilson K (2002) Parasites as a viability cost of sexual selection in natural populations of mammals. *Science (New York, N.Y.)* **297**, 2015–2018.
- Moravec F (2000) Review of capillariid & trichosomoidid nematodes from mammals in the Czech Republic and the Slovak Republic. *Acta Societatis Zoologicae Bohemicae* **64**, 271–304.
- Moravec F, Prokopic P and Shilkas AV (1987) The biology of nematodes of the family Capillariidae Neveu-Lemaire, 1936. *Folia Parasitologica* **34**, 39–56.
- Muller-Graf CDM, Durand P, Feliu C, Hugot J-P, O'Callaghan CJO, Renaud F, Santalla F and Morand S (1999) Epidemiological and genetic variability of two species of nematodes (*Heligmosomoides polygyrus* and *Syphacia stroma*) of *Apodemus* spp. *Parasitology* **118**, 425–432.
- Murúa RE (1978) Studies on the ecology of parasites of *Apodemus sylvaticus* (L.) and *Clethrionomys glareolus* (Schreb.) (Rodentia): analysis of the parasite populations and their seasonal variation in the Bristol area. *Acta Parasitologica Polonica* **25**, 149–161.
- Nakao M, Lavikainen A, Iwaki T, Haukisalmi V, Konyaev S, Oku Y, Okamoto M and Ito A (2013) Molecular phylogeny of the genus *Taenia* (Cestoda: Taeniidae): Proposals for the resurrection of *Hydatigera Lamarck, 1816* and the creation of a new genus *Versteria*. *International Journal for Parasitology* **43**, 427–437.

- Orr HA (2005) The genetic basis of reproductive isolation: insights from *Drosophila*. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 6522–6526.
- O'Sullivan HM, Smal CM and Fairley JS (1984) A study of parasitic infestations in populations of small rodents (*Apodemus sylvaticus* and *Clethrionomys glareolus*) on Ross Island, Killarney. *Journal Life Sciences Royal Dublin Society* **5**, 29–42.
- Pisanu B, Chapuis J-L, Durette-Desset M-C and Morand S (2002) Epizootiology of *Syphacia obvelata* from a domestic mouse population on sub-Antarctic Kerguelen Archipelago. *Journal of Parasitology* **88**, 645–649.
- Poulin R (1993) The disparity between observed and uniform distributions: a new look at parasite aggregation. *International Journal for Parasitology* **23**, 937–944.
- Poulin R (1996) Sexual inequalities in helminth infections: a cost of being a male? *The American Naturalist* **147**, 287–295.
- Poulin R (1997) Species richness of parasite assemblages: evolution and patterns. *Annual Reviews of Ecology and Systematics* **28**, 341–358.
- Rogan MT, Craig PS, Hide G, Heath S, Pickles A and Storey DM (2007) The occurrence of the trematode *Plagiorchis muris* in the wood mouse *Apodemus sylvaticus* in North Yorkshire, UK. *Journal of Helminthology* **81**, 57–62.
- Rohlf FJ and Sokal RR (1995) *Statistical Tables*. San Francisco: Freeman W.H. and Company.
- Ryan S and Holland C (1996) The intestinal helminth community of wild woodmice *Apodemus sylvaticus* in County Wicklow. *Proceedings of the Royal Irish Academy* **96B**, 45–48.
- Sanchez A, Devevey G and Bize P (2011) Female-biased infection and transmission of the gastrointestinal nematode *Trichuris arvicolae* infecting the common vole, *Microtus arvalis*. *International Journal for Parasitology* **41**, 1397–1402.
- Schalk G and Forbes MR (1997) Male biases in parasitism of mammals: effects of study type, host age and parasite taxa. *Oikos* **78**, 67–74.
- Sharpe GI (1964) The helminth parasites of some small mammal communities. I. The parasites and their hosts. *Parasitology* **54**, 145–154.
- Stewart A, Hablützel PI, Brown M, Watson HV, Parker-Norman S, Tober AV, Thomason AG, Friberg IM, Cable J and Jackson JA (2018a) Half the story: thermal effects on within-host infectious disease progression in a warming climate. *Global Change Biology* **24**, 371–386.
- Stewart A, Lowe A, Smales L, Bajer A, Bradley J, Dwuznik D, Franssen F, Griffith J, Stuart P, Turner C, Zalesny G and Behnke JM (2018b) Parasitic nematodes of the genus *Syphacia* Seurat, 1916 infecting Muridae in the British Isles, and the peculiar case of *Syphacia frederici*. *Parasitology* **145**, 269–280.
- Stuart P, Paredis L, Henttonen H, Lawton C, Ochoa Torres CA and Holland CV (2020) The hidden faces of a biological invasion: parasite dynamics of invaders and natives. *International Journal for Parasitology* **50**, 111–123.
- Tenora F (2004) Corrections in the taxonomic position of the helminth-fauna of *Apodemus* spp. (Rodentia) in the Czech Republic. *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis* **52**, 7–14.
- Tenora F and Staněk M (1994) Changes of the helminthofauna in several Muridae and Arvicolidae at Lednice in Moravia. I. Systematics and taxonomy. *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis* **42**, 237–247.
- Tenora F and Zavadil R (1967) A contribution to the evaluation of capillariid nematodes found in rodents in Czechoslovakia. *Acta Universitatis Agriculturae* **15**, 357–368.
- Tenora F, Wiger R and Barus V (1979) Seasonal and annual variations in the prevalence of helminths in a cyclic population of *Clethrionomys glareolus*. *Holarctic Ecology* **2**, 176–181.
- Thomas RJ (1953) On the nematodes and trematode parasites of some small mammals from the Inner Hebrides. *Journal of Helminthology* **28**, 143–168.
- World Meteorological Organization (2019) WMO Statement on the State of the Global Climate in 2018. WMO-No. 1233. Geneva. ISBN 978-92-63-11233-0.
- Xu R (2003) Measuring explained variation in linear mixed effects models. *Statistics in Medicine* **22**, 3527–3541.
- Zuk M and McKean KA (1996) Sex differences in parasitic infections: patterns and processes. *International Journal for Parasitology* **26**, 1009–1024.