Long-term spatiotemporal stability and dynamic changes in helminth infracommunities of bank voles (*Myodes glareolus*) in NE Poland

MACIEJ GRZYBEK[1,2], ANNA BAJER[3], MAŁGORZATA BEDNARSKA[3], MOHAMMED AL-SARRAF[3], JOLANTA BEHNKE-BOROWCZYK[4], PHILIP D. HARRIS[5], STEPHEN J. PRICE[1], GABRIELLE S. BROWN[1], SARAH-JANE OSBORNE[1]†, EDWARD SIŃSKI[3] *and* JERZY M. BEHNKE[1]*

[1] *School of Life Sciences, University of Nottingham, University Park, Nottingham NG7 2RD, UK*
[2] *Department of Parasitology and Invasive Diseases, Faculty of Veterinary Medicine, University of Life Sciences in Lublin, 12 Akademicka Street, 20-950 Lublin, Poland*
[3] *Department of Parasitology, Faculty of Biology, Institute of Zoology, University of Warsaw, 1 Miecznikowa Street, 02-096 Warsaw, Poland*
[4] *Department of Forest Pathology, Faculty of Forestry, Poznań University of Life Sciences, 71C Wojska Polskiego Street, 60-625 Poznan, Poland*
[5] *National Centre for Biosystematics, Natural History Museum, University of Oslo, N-0562 Oslo 5, Norway*

(*Received 27 May 2015; revised 19 August 2015; accepted 19 August 2015; first published online 7 October 2015*)

SUMMARY

Parasites are considered to be an important selective force in host evolution but ecological studies of host-parasite systems are usually short-term providing only snap-shots of what may be dynamic systems. We have conducted four surveys of helminths of bank voles at three ecologically similar woodland sites in NE Poland, spaced over a period of 11 years, to assess the relative importance of temporal and spatial effects on helminth infracommunities. Some measures of infracommunity structure maintained relative stability: the rank order of prevalence and abundance of *Heligmosomum mixtum*, *Heligmosomoides glareoli* and *Mastophorus muris* changed little between the four surveys. Other measures changed markedly: dynamic changes were evident in *Syphacia petrusewiczi* which declined to local extinction, while the capillariid *Aonchotheca annulosa* first appeared in 2002 and then increased in prevalence and abundance over the remaining three surveys. Some species are therefore dynamic and both introductions and extinctions can be expected in ecological time. At higher taxonomic levels and for derived measures, year and host-age effects and their interactions with site are important. Our surveys emphasize that the site of capture is the major determinant of the species contributing to helminth community structure, providing some predictability in these systems.

Key words: helminth infracommunities, bank voles, *Myodes glareolus*, *Clethrionomys*, helminths, nematodes, cestodes, site-specific parasite variation.

INTRODUCTION

Our understanding of helminth communities in vertebrates such as rodents is mostly based on destructive, cross-sectional studies conducted over a relatively short period of time, typically 1–3 years (Lewis, 1968; Montgomery and Montgomery, 1988; Behnke *et al*. 2001; Bajer *et al*. 2005; Jackson *et al*. 2014). While several workers have addressed seasonal changes in helminth burdens in wild rodents (Tenora and Zejda, 1974; Langley and Fairley, 1982; Montgomery and Montgomery, 1988; Abu-Madi *et al*. 2000; Bajer *et al*. 2005), there are relatively few long-term quantitative studies, spanning a decade or even more, that have been comprehensively analysed (but for longer-term changes in helminths of rodents see also Elton *et al*. 1931; Kisielewska, 1970*a*; Haukisalmi *et al*. 1988; Tenora and Staněk, 1995; and in other mammals Keith *et al*. 1985; Boag *et al*. 2001; Cattadori *et al*. 2008; Cornell *et al*. 2008 in lagomorphs; the long-term study on parasites of sheep on Soay, Pemberton and Hayward, personal communication).

A key theoretical question concerns the role of parasite species and communities in the evolution of their hosts. Immunoparasitological perspectives (e.g. Jackson *et al*. 2014) focus on the role of parasites in shaping the immunological profile of the host; alternatively, studies focused on life history strategies test predictions that parasites can modify life history parameters (Barnard *et al*. 2002, 2003). However, it is important to establish whether the patterns that have been detected in particular hosts in specific locations are repeatable over longer ecologically relevant periods of time, if we are to infer that parasites

---

* Corresponding author. School of Life Sciences, University of Nottingham, University Park, Nottingham NG7 2RD, UK. E-mail: jerzy.behnke@nottingham.ac.uk
† Current address: Department of Plant Biology and Crop Science, Rothamsted Research, Harpenden, Herts AL5 2JQ, UK.

Parasitology (2015), **142**, 1722–1743.
doi:10.1017/S0031182015001225

can influence host speciation. Long-term studies allow the robustness and repeatability of detected trends to be assessed and provide an opportunity to relate species richness, as well as diversity, prevalence and abundance of individual parasites to climatic, environmental and host demographic changes over time (Tenora, Wiger and Barus, 1979; Haukisalmi *et al.* 1988; Haukisalmi and Henttonen, 1990, 2000; Hudson *et al.* 2006). The resulting models can then allow informed predictions about the consequences of climate change for human health and that of our livestock (Huntley *et al.* 2014).

Some short-term studies have reported relatively stable patterns of infection with helminths in European rodents, with common helminths maintaining their dominant status and rarer species fluctuating more unpredictably (Kisielewska, 1970*a*; Montgomery and Montgomery, 1990; Bajer *et al.* 2005; Knowles *et al.* 2013). In spite of this relative stability, it is the minor fluctuations in the common species that are primarily responsible for between-year variation in derived measures such as diversity indices and species richness (Behnke *et al.* 2008*b*). Others have reported more dynamic changes in particular helminths (Tenora, Wiger and Barus, 1979; Haukisalmi *et al.* 1988; Montgomery and Montgomery, 1990; Tenora and Staněk, 1995; Behnke *et al.* 1999) and especially in measures of component community structure (Behnke *et al.* 2008*a*).

Building on our earlier published studies in NE Poland (Behnke *et al.* 2001, 2008*a*, *b*), here we report on four cross-sectional studies of the helminth parasites of bank voles conducted over an 11-year period (1999, 2002, 2006 and 2010) in order to assess the longer-term stability of helminth communities in these hosts. As we reported recently when analysing haemoparasites of the same animals (Bajer *et al.* 2014), the work was conducted in the same three sites and in the same locations within each wood, at the same time of year. Our primary objective was to assess the relative importance of temporal *vs* spatial factors in affecting helminth infracommunities in bank voles in our study sites.

MATERIALS AND METHODS

Study sites

Our study sites have been described comprehensively in earlier papers by Behnke *et al.* (2001, 2008*a*, *b*). They are located in the Mazury lake district region in the NE corner of Poland, in the vicinity of Jezioro (Lake) Śniardwy and the towns of Mikołajki, Ryn and Pisz. Site 1 is referred to as Urwitałt (N 53° 48·153, EO 21°39·784), Site 2 as Tałty (N 53°53·644, EO 21°33·049) and Site 3 as Pilchy (N 53°42·228, EO 21°48·499) after nearby settlements. These sites are within 10 km of one another in a NE to SW transect but separated by lakes, rivers, canals and pastures and therefore are isolated from one another in ecological time, although the host species is panmictic and genetic studies have revealed some gene flow between the three populations (Kloch *et al.* 2010). The sites were sampled at the same time of year in each year of the study (last two weeks of August and the first two weeks of September).

Terminology and collection of bank voles

In this paper we refer to *Myodes glareolus* for bank voles following Carleton *et al.* (2003, 2014) and not *Clethrionomys glareolus* as in earlier studies and argued by Tesakov *et al.* (2010). The methods used for trapping rodents, and for sampling and processing trapped animals have all been fully described (Behnke *et al.* 2001, 2008*a*, *b*). Age categories were established as described earlier using principal components analysis in the software package IBM SPSS Statistics Version 21 (IBM Corporation) of a range of morphological measures including body weight and dried eye lens weight (Behnke *et al.* 2001) and three age classes were established. Age class 1 voles were immature juveniles, age class 2 voles were mostly young adults and age class 3 were breeding older animals.

Identification and quantification of endoparasites

The entire alimentary tracts were brought back to the University of Nottingham in either 70% ethanol (2010) or in 10% formalin (1999, 2002 and 2006) for dissection. The fixed intestines were opened carefully in water or Hanks' saline and examined under a dissecting microscope. All parasite specimens were identified, sexed and stored in tubes containing 70% ethanol. Tapeworms were stained using borax carmine, dehydrated in ethanol and mounted in Canada Balsam for microscopical examination. In this paper we refer to *Aspiculuris* as *Aspiculuris tianjinensis*, rather than *Aspiculuris tetraptera* as previously stated, because recent molecular genetic data and morphological observations have revealed that the *Aspiculuris* species parasitizing bank voles is not *A. tetraptera* but a close relative, *A. tianjinensis* (Liu et al. 2012; Behnke *et al.* 2016).

Statistical analysis

Prevalence values (percentage of animals infected) are given with 95% confidence limits (CL_{95}), calculated by bespoke software based on the tables of Rohlf and Sokal (1995). Abundance of infection (including both infected and non-infected animals) is summarized by arithmetic means and standard errors of the mean (S.E.M.).

The degree of aggregation in the data was calculated 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 as well as the residuals from general linear models (GLM) were also tested for goodness of fit to negative binomial, positive binomial and Poisson models by χ^2 as described by Elliott (1977).

The statistical approach adopted has been documented comprehensively in our earlier publications (Behnke *et al.* 2001, 2008*a*, *b*; Bajer *et al.* 2005). For analysis of prevalence we used maximum likelihood techniques based on log linear analysis of contingency tables in the software package IBM SPSS. This approach is based on categorical values of the factors of interest, which are used to fit hierarchical loglinear models to multidimensional cross-tabulations using an iterative proportional-fitting algorithm and detects associations between the factors, one of which may be presence/absence of infection. Initially, full factorial models were fitted, incorporating as factors SEX (2 levels, males and females), AGE (3 levels), YEAR of study (4 levels, 1999, 2002, 2006, 2010), and SITE (3 levels, Urwitałt, Tałty, Pilchy). The presence or absence of parasites (INFECTION) was considered as a binary factor. All these five factors were fitted initially to all models that were evaluated. For each level of analysis, beginning with the most complex model involving all possible main effects and interactions, those combinations that did not contribute significantly to explaining variation were eliminated stepwise beginning with the highest level interaction (backward selection procedure). A minimum sufficient model was then obtained, for which the likelihood ratio of χ^2 was not significant, indicating that the 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. The remaining terms in the final model that did not include INFECTION (for example, variation among sites in the number of animals of each sex sampled [SITE × SEX]) are not given but can be made available from the authors on request.

For analyses of quantitative data conforming to Gaussian distributions we used GLM with normal errors implemented in R version 2.2·1 (R Core Development Team) and the residuals were checked for approximate goodness of fit to the Gaussian distribution. When the residuals failed to meet the requirements of Gaussian models we used GLM with negative binomial or Poisson error structures. Full factorial models that converged satisfactorily were simplified using the STEP procedure and tested for significance using deletion of terms beginning with the highest order interaction by comparing models with or without that interaction. Changes in deviance (*DEV*) are given for models based on Poisson errors (interpreted by χ^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 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 percentage of deviance accounted for by each significant main effect or interaction was calculated as recommended by Xu (2003) and reported by Behnke *et al.* (2008*b*).

If the data did not meet the assumptions of parametric tests, we employed non-parametric tests (Kruskal–Wallis test for *k* levels in a specified factor and the Mann–Whitney *U*-test where factors only had two levels, e.g. SEX).

We used canonical discriminant function analysis (CDF) in IBM SPSS as an additional approach to evaluate the relative importance of the influence of site and year on parasite burdens. Quantitative parasite data for each of the species of helminths were first standardized by $\log_e(x+1)$ transformation of individual worm burdens for each species, then subtraction of mean $\log_e$ value for each species and division by the standard deviation (S.D.) before analysis.

RESULTS

Numbers of voles and trapping effort

Table 1 summarizes the numbers of voles sampled by age class, sex, year and site. Trapping effort varied between surveys and sites depending on local and year specific constraints. In 2002, 2006 and 2010, relative host population density was recorded as the number of animals caught per 10 000 trap hours, but these data were not collected in the first survey in 1999, although it is known from other studies that 1999 was a year when bank vole density was high at Urwitałt (Bajer *et al.* 2005, recorded 85 and 188·3 voles/10 000 trap hours in August and September 1999, respectively, in Urwitałt) and Pilchy (personal observation). In 2002, the total of trap hours recorded was 33 520 (9356, 12 284 and 11 880 for Urwitałt, Tałty and Pilchy, respectively) and the number of bank voles was 85·5, 81·4 and 156·6/10 000 trap hours, respectively. In 2006 total trap hours were 71 112 (26 085, 25 004 and 20 023 for Urwitałt, Tałty and Pilchy, respectively) and the number of bank voles was 110·4, 61·7 and 131·9/10 000 trap hours, respectively). In 2010 total trap hours were 67 639 (14 927, 18 349 and 34 363 for Urwitałt, Tałty and Pilchy, respectively) and the number of bank voles was 125·3, 76·8 and 38·1/10 000 trap hours, respectively.

Prevalence and abundance of helminths

The overall prevalence of helminths (all species combined) was 79·7% (76·12–82·92). Prevalence

Table 1. Number of voles sampled in successive surveys, by site, and host age and sex

			Age class			Totals	
Site	Year	Sex	1	2	3	Row	Site and year
Urwitałt	1999	Male	0	15	5	20	
		Female	3	8	9	20	40
	2002	Male	9	13	18	40	
		Female	6	12	14	32	72
	2006	Male	12	30	8	50	
		Female	15	14	21	50	100
	2010	Male	8	33	9	50	
		Female	9	13	20	42	92
	Total males		29	91	40	160	
	Total females		33	47	64	144	
	Total combined sexes		62	138	104	304	
Tałty	1999	Male	3	13	4	20	
		Female	8	8	5	21	41
	2002	Male	16	15	8	39	
		Female	7	17	10	34	73
	2006	Male	16	11	6	33	
		Female	18	4	19	41	74
	2010	Male	16	14	26	56	
		Female	13	10	23	46	102
	Total males		51	53	44	148	
	Total females		46	39	57	142	
	Total sexes combined		97	92	101	290	
Pilchy	1999	Males	13	13	5	31	
		Females	9	13	5	27	58
	2002	Males	11	14	11	36	
		Females	8	13	17	38	74
	2006	Males	22	12	15	49	
		Females	24	6	17	47	96
	2010	Males	21	15	11	47	
		Females	13	12	28	53	100
	Total males		67	54	42	163	
	Total females		54	44	67	165	
	Total sexes combined		121	98	109	328	
Total by year	1999	Males	16	41	14	71	
		Females	20	29	19	68	
		Both sexes	36	70	33	139	
	2002	Males	36	42	37	115	
		Females	21	42	41	104	
		Both sexes	57	84	78	219	
	2006	Males	50	53	29	132	
		Females	57	24	57	138	
		Both sexes	107	77	86	270	
	2010	Males	45	62	46	153	
		Females	35	35	71	141	
		Both sexes	80	97	117	294	
Total by sex		Males	147	198	126	471	
		Females	133	130	188	451	
		Both sexes	280	328	314	922	

values were generally high throughout (Table 2 and Fig. 1A), especially among voles from Urwitałt. Although there was no independent effect of either YEAR or SITE, the rank order of prevalence of helminths at the three sites changed significantly over time (YEAR × SITE × INFECTION, $\chi^2_6 = 35·3$, $P < 0·001$). Prevalence was highest in voles from Urwitałt in 1999 and lowest in those from Pilchy, maintaining the highest values in Urwitałt in 2002 and 2006, but not in 2010 when prevalence was highest in the voles from Pilchy (Fig. 1A). There was no significant difference between the sexes (Table 2) but there was a highly significant increase in prevalence with increasing age of voles (Table 2; AGE × INFECTION, $\chi^2_2 = 104·9$, $P < 0·001$), total prevalence in the oldest class was in excess of 90% in each of the four surveys (Fig. 2A).

The overall abundance of helminths (all species combined) was 26·6 ± 5·68 worms per vole. Full factorial models with negative binomial errors did not converge satisfactorily, but the best fit was a model with all main effects and one interaction. However,

Table 2. Prevalence of higher taxa – all helminths combined, all nematodes combined and all cestodes combined by year, site, host sex and age class

	Helminths (all combined)	Nematodes (all combined)	Cestodes (all combined)	Cestodes (intestinal adults)	Cestodes (larval stages)
Year					
1999	85·6 (78·96–90·53)	85·6 (78·96–90·53)	12·9 (8·26–19·35)	8·6 (4·97–14·45)	5·0 (2·44–9·91)
2002	78·5 (74·56–82·11)	73·1 (68·81–76·95)	30·6 (26·55–34·94)	26·5 (22·62–30·72)	10·5 (7·95–13·65)
2006	85·6 (81·67–88·77)	83·0 (78·83–86·48)	18·1 (14·55–22·37)	16·3 (12·88–20·33)	2·6 (1·39–4·73)
2010	72·4 (67·54–76·88)	70·4 (65·43–74·97)	19·0 (15·25–23·52)	12·2 (9·19–16·09)	9·2 (6·57–12·71)
Site					
Urwitałt	86·5 (82·46–89·77)	83·6 (79·24–87·18)	33·9 (29·03–39·10)	26·6 (22·19–31·61)	13·5 (10·23–17·54)
Tałty	77·9 (73·35–81·97)	74·8 (70·09–79·04)	18·6 (14·88–23·03)	15·9 (12·40–20·00)	4·5 (2·75–7·14)
Pilchy	75·0 (69·96–79·43)	72·9 (67·66–77·50)	10·1 (7·13–13·88)	7·0 (4·65–10·38)	3·0 (1·61–5·59)
Sex					
Males	78·6 (72·58–83·68)	74·9 (68·72–80·31)	22·3 (17·12–28·34)	18·7 (13·87–24·57)	7·2 (4·41–11·52)
Females	80·9 (75·14–85·70)	79·2 (73·35–84·12)	18·8 (14·12–24·60)	13·7 (9·73–18·85)	6·7 (4·03–10·70)
Age					
Class 1	62·5 (57·42–67·33)	59·3 (54·20–64·23)	10·0 (7·26–13·50)	8·9 (6·42–12·34)	1·1 (0·39–2·79)
Class 2	80·8 (76·03–84·81)	77·7 (72·84–82·03)	18·0 (14·09–22·64)	14·0 (10·56–18·28)	4·6 (2·74–7·46)
Class 3	93·9 (90·82–96·08)	92·0 (88·55–94·51)	32·8 (27·93–38·11)	25·2 (20·79–30·10)	14·6 (11·20–18·87)

See text for statistical analysis.

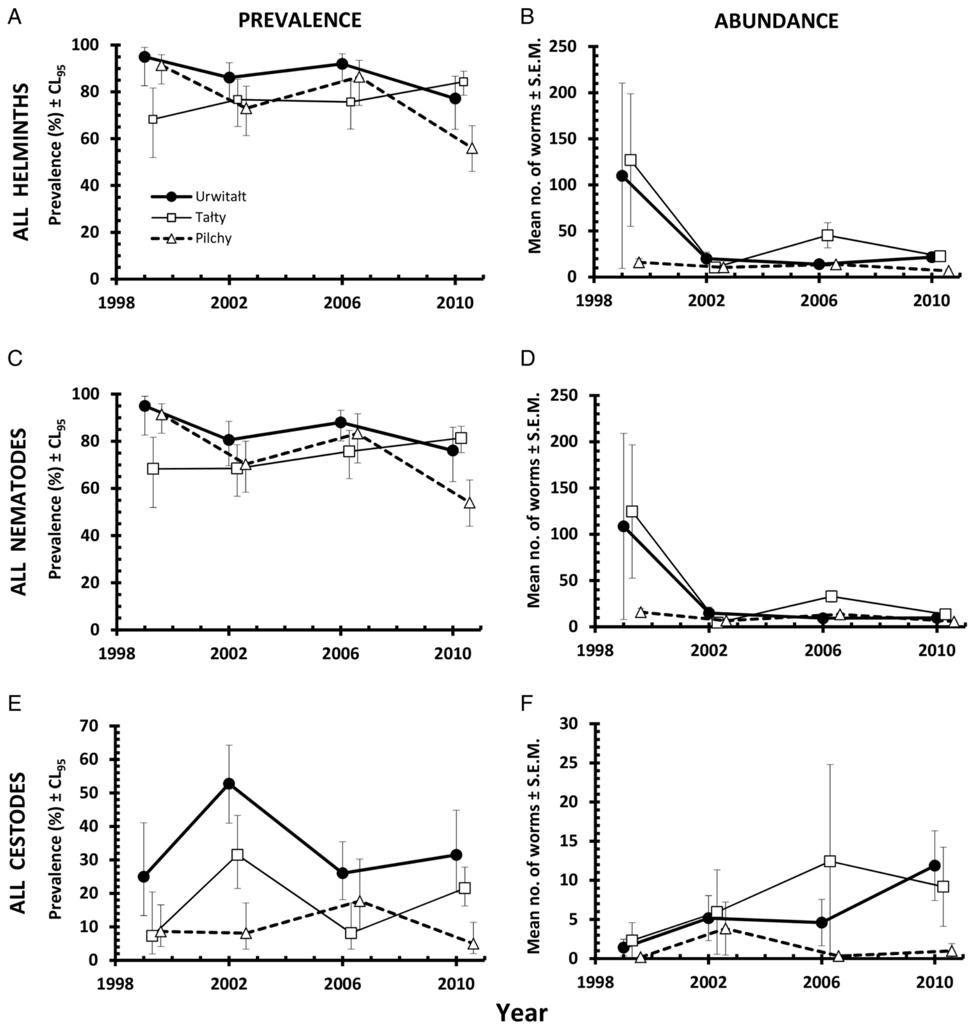

Fig. 1. Spatiotemporal dynamics at the three study sites in prevalence (A, C and E) and abundance (B, D and F) of all helminths (A and B), all nematodes (C and D), and of all cestodes (E and F). Key to symbols used in B, C, D, E and F, as in A.

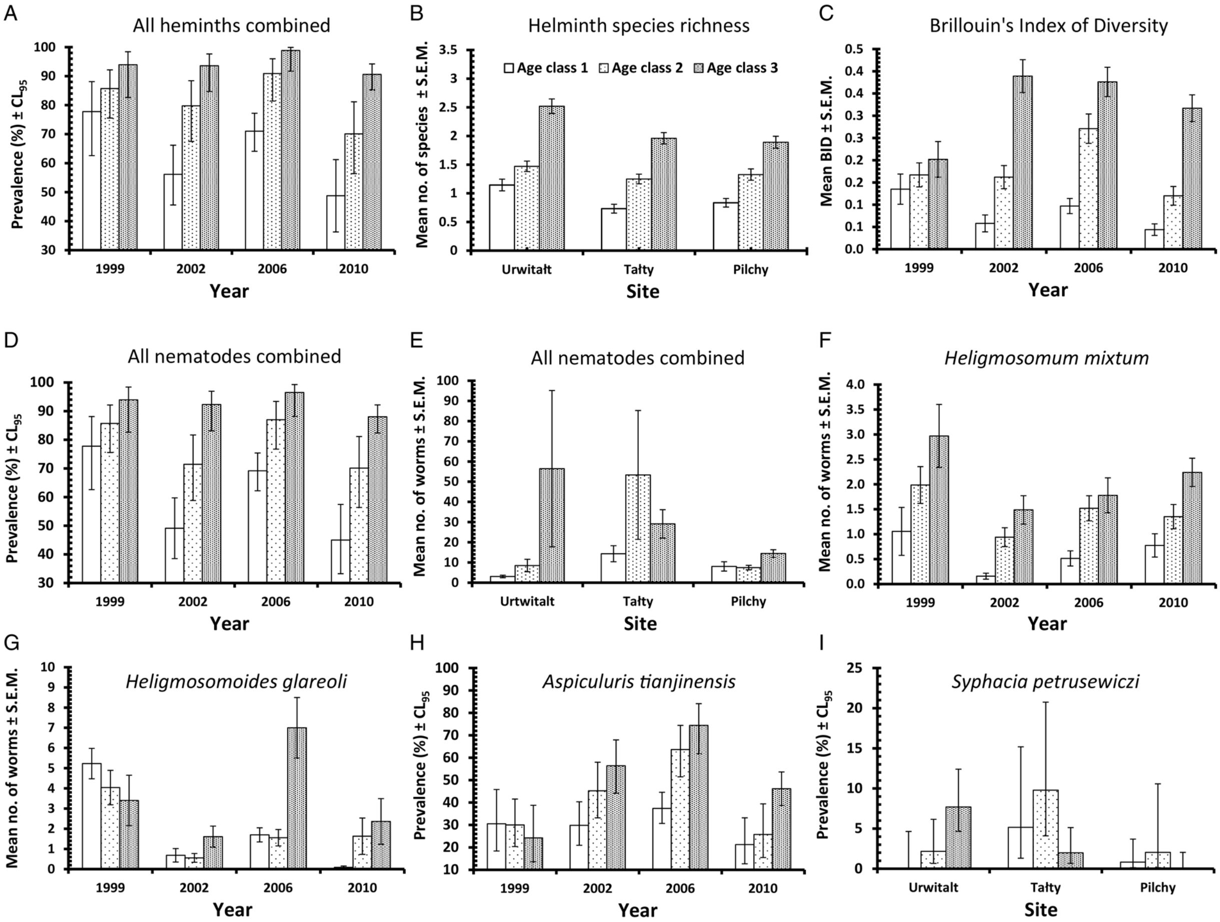

Fig. 2. Age-related changes in prevalence of all helminths (species combined) by year of survey (A), in helminth species richness by site of survey (B), in Brillouin's Index of Diversity by year of survey (C), in prevalence of nematodes (species combined) by year of survey (D), abundance of nematodes by site of survey (E), abundance of *H. mixtum* (F), abundance of *H. glareoli* (G), prevalence of *A. tianjinensis* by year of survey (H), prevalence of *S. petrusewiczi* by site (I). Key to symbols used as shown in panel B.

abundance did not differ significantly between the sexes and SEX was not a component in the interaction (Table 3; main effect of SEX on abundance of helminths, $LR_{1,913} = 0{\cdot}055$, $P = 0{\cdot}8$), and we therefore excluded SEX from the remaining analysis. Abundance varied significantly between the surveys (Table 3; main effect of YEAR, $LR_{3,914} = 116{\cdot}7$, $P < 0{\cdot}0001$) and between sites (main effect of SITE, $LR_{2,914} = 56{\cdot}4$, $P < 0{\cdot}0001$) but there was also a significant interaction between YEAR and SITE ($LR_{6,908} = 41{\cdot}7$, $P < 0{\cdot}0001$), which is illustrated in Fig. 1B. In 1999 helminth abundance was at its highest level (Table 3), but this was evident at two sites only, with those from Pilchy showing the lowest and most stable helminth abundance over the four surveys (Fig. 1B). Helminth abundance at Urwitałt and Tałty dropped markedly after 1999 and was only just higher than at Pilchy over the following surveys. Helminth abundance also increased markedly with host age (Table 3; main effect of AGE, $LR_{2,914} = 112{\cdot}3$, $P < 0{\cdot}0001$), being more than 4-fold higher among the oldest class compared with the youngest class.

Species richness

The overall mean species richness (MSR) was 1·47 ± 0·037. There was a weak main effect of YEAR (Table 3; $DEV_3 = -7{\cdot}8$, $P = 0{\cdot}05$) with MSR increasing over the first three surveys and then falling in 2010. There was more substantial variation between species richness of voles from the three sites, (Table 3; main effect of SITE, $DEV_2 = -24{\cdot}0$, $P < 0{\cdot}0001$) with relative rank order changing significantly over time (Fig. 3A; 2-way interaction YEAR × SITE, $DEV_6 = -42{\cdot}0$, $P < 0{\cdot}0001$). Thus, although MSR was highest at Urwitałt overall (notably in 2002, 2006 and 2010), in 1999 it was slightly higher for voles from Pilchy, and whilst at Urwitałt MSR declined from 2002 onwards, in Tałty MSR increased with time to peak in 2010.

MSR was significantly higher among female voles (Table 3, $DEV_1 = -4{\cdot}95$, $P = 0{\cdot}03$). MSR also increased significantly with vole age (Table 3; main effect of AGE, $DEV_2 = -7{\cdot}04$, $P = 0{\cdot}03$) at all sites, although in voles at Urwitałt, after a moderate increase between age classes 1 and 2 MSR increased

Table 3. Species richness, diversity and abundance of higher taxa – all helminths combined, all nematodes combined and all cestodes combined by year, site, host sex and age class

	Species richness	Brillouin's	Helminths	Nematodes	Cestodes (all combined)	Cestodes (intestinal adults)	Cestodes (larval stages)
Year							
1999	1·44 ± 0·076	0·17 ± 0·019	75·8 ± 35·86	74·6 ± 35·87	1·2 ± 0·74	0·11 ± 0·033	1·1 ± 0·74
2002	1·50 ± 0·081	0·22 ± 0·019	13·6 ± 3·25	8·6 ± 2·27	5·0 ± 2·32	0·66 ± 0·124	4·3 ± 2·31
2006	1·62 ± 0·066	0·24 ± 0·017	22·5 ± 4·15	17·2 ± 2·11	5·2 ± 3·56	0·32 ± 0·066	4·9 ± 3·56
2010	1·33 ± 0·069	0·18 ± 0·016	16·9 ± 2·65	9·7 ± 1·31	7·2 ± 2·27	0·22 ± 0·051	7·0 ± 2·27
Site							
Urwitałt	1·76 ± 0·071	0·25 ± 0·017	30·3 ± 13·46	23·8 ± 13·35	6·5 ± 1·81	0·63 ± 0·101	5·9 ± 1·81
Tałty	1·32 ± 0·059	0·16 ± 0·014	40·1 ± 11·14	31·8 ± 10·50	8·2 ± 3·87	0·26 ± 0·053	8·0 ± 3·86
Pilchy	1·33 ± 0·059	0·19 ± 0·015	11·3 ± 1·39	10·0 ± 1·12	1·3 ± 0·82	0·13 ± 0·032	1·2 ± 0·82
Sex							
Males	1·39 ± 0·049	0·19 ± 0·012	25·2 ± 9·07	20·5 ± 8·83	4·7 ± 2·10	0·39 ± 0·055	4·3 ± 2·10
Females	1·56 ± 0·056	0·22 ± 0·014	28·1 ± 6·75	22·4 ± 6·51	5·7 ± 1·80	0·28 ± 0·057	5·5 ± 1·80
Age							
Class 1	0·87 ± 0·049	0·08 ± 0·010	10·6 ± 1·97	9·1 ± 1·72	1·4 ± 0·98	0·16 ± 0·044	1·27 ± 0·977
Class 2	1·37 ± 0·054	0·18 ± 0·014	22·3 ± 9·10	20·8 ± 9·08	1·6 ± 0·57	0·22 ± 0·035	1·35 ± 0·570
Class 3	2·12 ± 0·066	0·34 ± 0·018	45·4 ± 13·56	33·1 ± 13·04	12·3 ± 3·91	0·61 ± 0·101	11·7 ± 3·90

See text for statistical analysis.

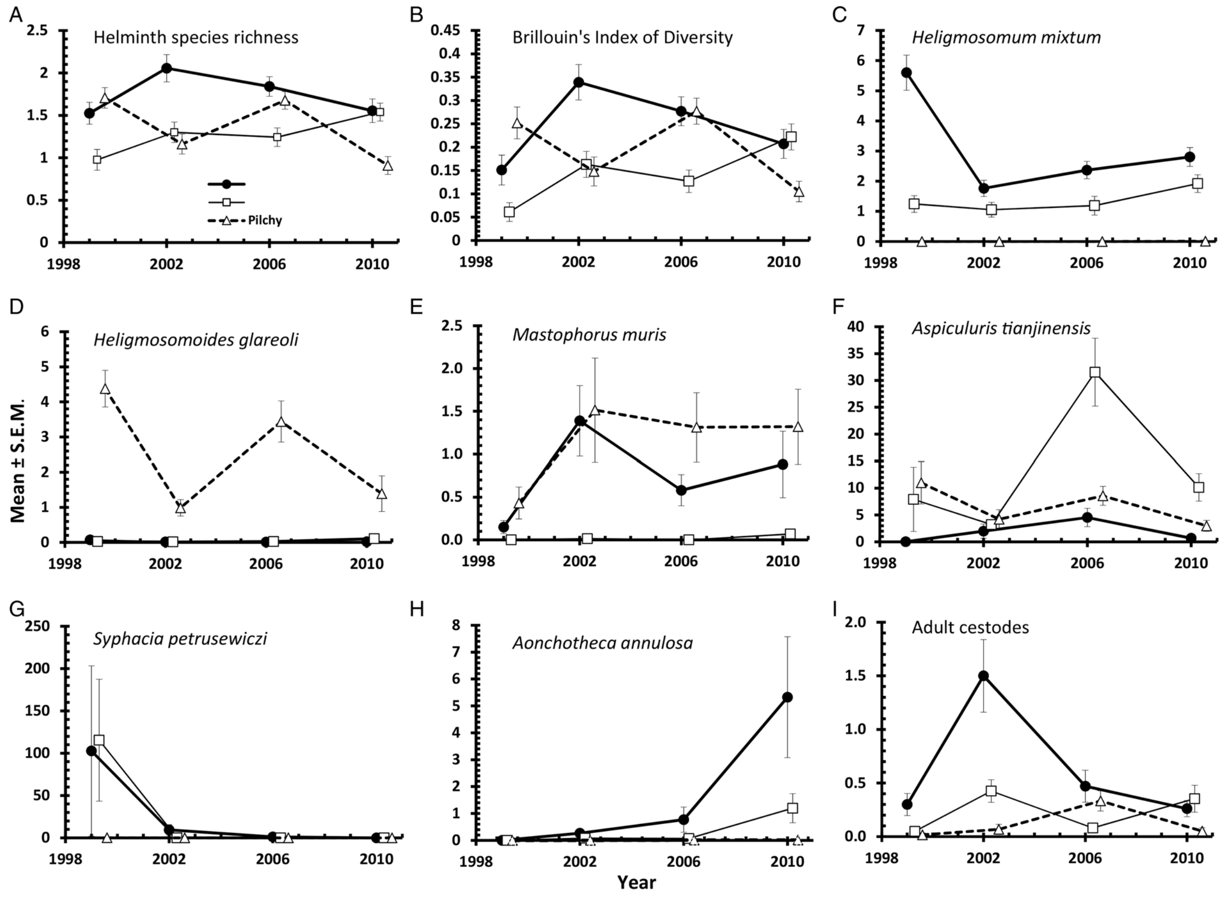

Fig. 3. Spatiotemporal dynamics in mean helminth species richness (A), Brillouin's Index of Diversity (B) and abundance of *H.mixtum* (C), *H. glareoli* (D), *M. muris* (E), *A. tianjinensis* (F), *S. petrusewiczi* (G), *A. annulosa* (H) and adult intestinal stages of cestodes (I). Key to symbols used as shown in panel A.

more markedly between age classes 2 and 3. In contrast accumulation of helminth species was more steady across all age classes at both Pilchy and Tałty (Fig. 2B; 2-way interaction SITE × AGE, $DEV_4 = -17{\cdot}8$, $P = 0{\cdot}0014$).

Species diversity

Brillouin's index of diversity (BID) increased significantly with host age (Table 3; main effect of AGE, $F_{2,915} = 82{\cdot}80$, $P < 0{\cdot}0001$), varied between years (Table 3; main effect of YEAR, $F_{3,916} = 4{\cdot}92$, $P = 0{\cdot}002$) and between study sites (Table 3; main effect of SITE, $F_{2,915} = 7{\cdot}08$, $P < 0{\cdot}001$) but there was no significant difference between the sexes.

However, these main effects were confounded by three significant 2–way interactions. The most significant was between YEAR and SITE ($F_{6,905} = 8{\cdot}57$, $P < 0{\cdot}0001$) accounting for 5·4% of explained deviance (Table 4). In the first three surveys (1999, 2002 and 2006) BID was higher in Urwitałt compared with Tałty, but in the last survey (2010) it was marginally higher at Tałty (Fig. 3B). Voles from Pilchy showed no consistent trends in BID over the four surveys with a higher value than at the other sites in 1999, equal with Urwitałt in 2006, but lower than at Urwitałt and Tałty in 2002 and 2010.

Although in each year of the study BID increased with increasing host age, the extent of these age related changes varied significantly between years (Fig. 2C; 2–way interaction YEAR × AGE, $F_{6,905} = 2{\cdot}66$, $P = 0{\cdot}014$). There was no overall effect of host sex on BID (Table 3), however, at Uwitałt, and to a lesser extent at Pilchy, mean BID was higher among female voles, while at Tałty mean BID was higher among male voles (Fig. 4A; 2-way interaction SITE × SEX, $F_{2,901} = 4{\cdot}03$, $P < 0{\cdot}0001$).

Frequency distributions and measures of aggregation

Frequency distributions were fitted to all species for which quantitative data were available, by site, by year and in relevant combinations. These were then tested for goodness of fit to the Poisson and to the positive and negative binomial distributions. For brevity we do not report these values, but as will be made clear below, all parasite burdens were over-dispersed and conformed best to the negative binomial distribution. Some were so aggregated that even GLM with negative binomial error structures failed to converge. All values are available from the authors on request.

Prevalence and abundance of nematodes

A total of 77% (73·3–80·36) of the bank voles were infected with nematodes, and as with the prevalence of all helminths combined the values for the

Table 4. Percentage of variation in data (deviance) explained by extrinsic and intrinsic factors affecting the measures of infracommunity structure and diversity, and the abundance of helminths

Source of variation	Percentage of deviance explained									
	MSR[a]	BID[b]	Total helminths	Total nematodes	*M. muris*	*H. mixtum*	*H. glareoli*	*A. tianjinensis*	*A. annulosa*	*C. henttoneni*
Site	2·60	1·53	0·87	0·74	**6·51**	**17·17**	**18·76**	**1·90**	6·76	2·54
Year	0·86	1·61	**1·78**	**2·82**	0·90	1·20	2·98	1·12	5·30	2·43
Age	0·78	**15·35**	1·62	1·22	3·49	2·46	2·13	0·15	**6·92/8·1**	2·68
Sex	0·55	<0·01	<0·01	<0·01	0·36	<0·01	<0·01	0·17	3·15	0·53
Site × age	2·08	–	–	0·42	1·51	–	–	–	–	–
Site × year	**4·78**	5·41	0·65	0·84	1·12	0·65	1·15	1·48	–	**3·33**
Site × sex	–	0·89	–	–	–	–	–	–	–	–
Year × age	–	1·75	–	–	–	0·81	1·57	–	–	–
Age × sex	–	–	–	–	1·20	–	–	0·58	–	–

In each case the output from the most parsimonious and appropriate minimum sufficient model is given. Thus, only the significant main effects and interactions, and non-significant main effects if a component of one of the interactions, have been included. Models for total helminth burden and individual species are models with negative binomial error structures unless stated otherwise below. For further details of the statistical models, see the text. Note that some 2–way and 3–way interactions and the 4–way interaction are not given because these were not significant.

Factors and interactions accounting for most deviance in each case are highlighted in bold.

[a] Mean species richness (model based on Poisson errors).

[b] Brillouin's index of diversity (model based on Gaussian errors).

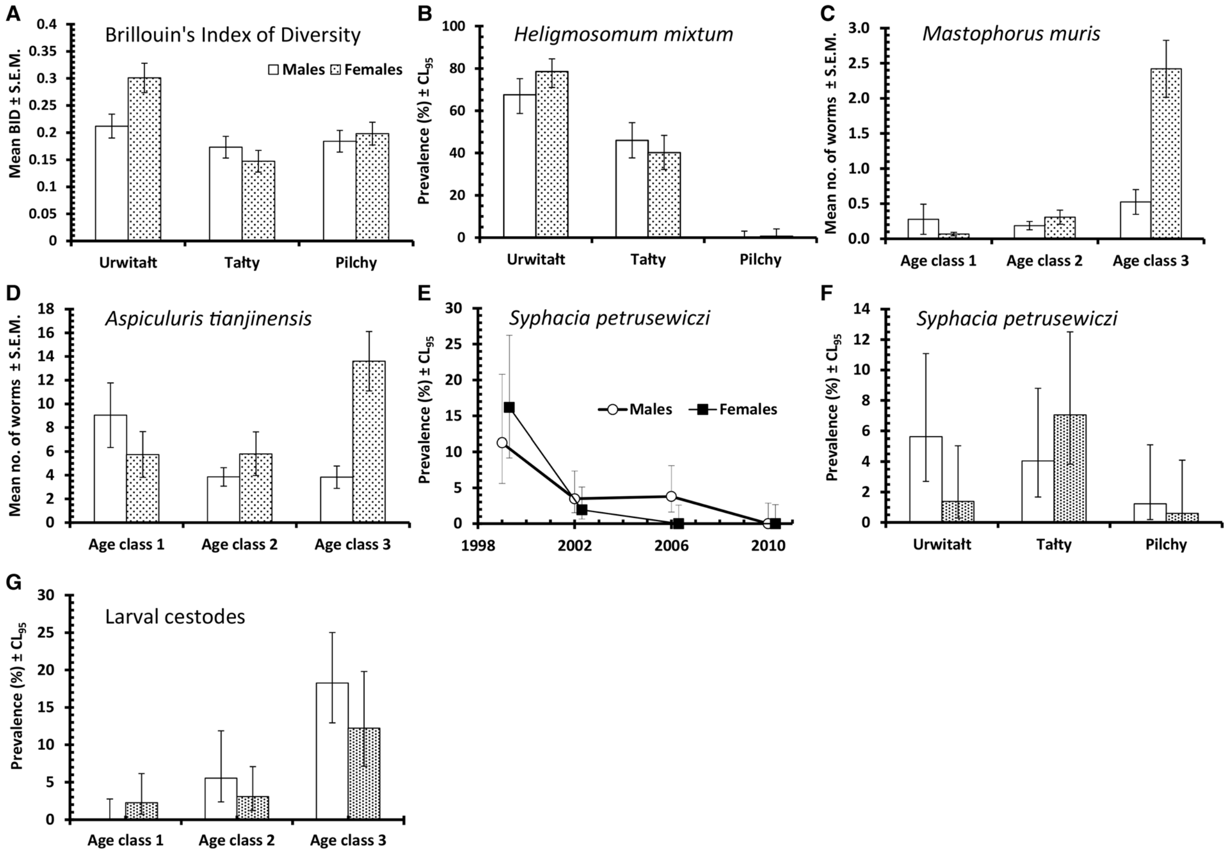

Fig. 4. Variation in host sex bias of Brillouin's Index of Diversity at the three study sites (A), in prevalence of *H. mixtum* at the three study sites (B), in abundance of *M. muris* by age class (C), in abundance of *A. tianjinensis* by age class (D), in prevalence of *S. petrusewiczi* by year of survey (E) and site (F), and in prevalence of larval cestodes (all species combined) (G). Key to symbols used in panels B, C, D, F and G, as in A.

prevalence of nematodes were consistently high throughout (exceeding 70% in all surveys, Table 2). The rank order of prevalence among voles at the three sites changed significantly over time (Fig. 1C; YEAR × SITE × INFECTION, $\chi^2_6 = 29{\cdot}6$, $P < 0{\cdot}001$) although there was no independent effect of either YEAR or SITE. Prevalence did not vary significantly between the sexes (Table 2) but there was a highly significant increase in prevalence with increasing age of voles (Table 2; AGE × INFECTION, $\chi^2_2 = 103{\cdot}2$, $P < 0{\cdot}001$) that was evident in each of the four surveys (Fig. 2D) with values ⩾88% in the oldest class throughout.

The abundance of nematodes (all species combined) was analysed as above for all helminths, with outcome much the same. In addition to the significant main effects of YEAR (Table 3; $LR_{3,914} = 175.1$, $P < 0.0001$) and SITE ($LR_{2,914} = 44.7$, $P < 0.0001$) and the interaction between these (Fig. 1D; $LR_{6,904} = 50.6$, $P < 0.0001$), and the main effect of AGE (Table 3; $LR_{2,914} = 78.0$, $P < 0.0001$), in this case there was also a significant interaction between SITE and AGE ($LR_{4,904} = 24.9$, $P < 0.0001$) which is illustrated in Fig. 2E. In Urwitałt and Pilchy mean nematode worm burden increased with age, but at Tałty the highest abundance was found in bank voles of age class 2, with a subsequent reduction among the oldest animals. Abundance did not vary significantly between the sexes.

Heligmosomum mixtum. This species was recovered from 347 bank voles (37·6% [33·62–41·81]), but was largely found in voles at two of the three sites (Urwitałt and Tałty; Table 5 and Fig. 5A). Although there was no independent effect of host sex, prevalence being almost identical in both sexes, there was a significant interaction with site of capture (SITE × SEX × INFECTION, $\chi^2_2 = 7{\cdot}1$, $P = 0{\cdot}029$). Prevalence was higher in female voles from Urwitałt and in males at Tałty (Fig. 4B). Since there was no overall effect of host sex and a weak interaction of SEX with SITE, we next fitted *post hoc* a model without SEX. This gave a highly significant effect of SITE (Table 5; $\chi^2_2 = 453{\cdot}7$, $P < 0{\cdot}001$). Prevalence of *H. mixtum* also varied significantly between years (Table 5; YEAR × INFECTION, $\chi^2_3 = 10{\cdot}76$, $P = 0{\cdot}013$) but the range of variation was narrow, just 8% (from 32·4% in 2002 to 40·5% in 2010). There was also a highly significant independent effect of host age (AGE × INFECTION, $\chi^2_2 = 57{\cdot}0$, $P < 0{\cdot}001$), prevalence increasing with host age (Table 5).

Table 5. Prevalence of individual species by year, site, host sex and age class

	H. mixtum	*H. glareoli.*	*M. muris*	*A. tianjinensis*	*S. petrusewiczi*	*A. annulosa*	*C. henttoneni*	*Mesocestoides* sp.	*T. martis*	*V. mustelae*
Year										
1999	40·3 (32·46–48·45)	36·0 (28·45–44·12)	10·1 (6·05–16·00)	28·8 (21·96–36·72)	13·7 (8·88–20·20)	0 (0–2·60)	7·9 (4·42–13·60)	2·2 (0·65–6·16)	0·7 (0·10–3·82)	2·2 (0·65–6·16)
2002	32·4 (28·27–36·88)	10·5 (7·95–13·65)	18·3 (14·94–22·09)	45·2 (40·65–49·76)	2·7 (1·56–4·65)	2·7 (1·56–4·65)	25·1 (21·37–29·26)	2·3 (1·24–4·10)	4·6 (2·98–6·85)	3·7 (2·25–5·75)
2006	37·4 (32·66–42·40)	24·1 (20·01–28·63)	14·4 (11·23–18·33)	56·7 (51·67–61·54)	1·9 (0·89–3·80)	8·1 (5·79–11·38)	14·8 (11·57–18·72)	2·2 (1·13–4·28)	0·4 (0·13–1·62)	0·4 (0·39–1·62)
2010	40·5 (35·42–45·68)	12·6 (9·49–16·48)	13·3 (10·09–17·23)	32·7 (27·93–37·78)	0 (0–1·10)	10·5 (7·68–14·21)	10·9 (7·97–14·60)	6·5 (4·30–9·54)	2·4 (1·21–4·59)	0·3 (0·11–1·66)
Site										
Urwitałt	72·7 (67·70–77·18)	2·3 (1·14–4·55)	19·4 (15·53–23·99)	25·0 (20·72–29·84)	3·6 (2·06–6·16)	12·2 (9·08–16·07)	24·3 (20·06–29·18)	7·2 (4·91–10·50)	5·26 (3·340–8·166)	1·3 (0·52–3·23)
Tałty	43·1 (38·06–48·28)	3·8 (2·21–6·30)	1·7 (0·78–3·73)	50·0 (44·82–55·18)	5·5 (3·57–8·40)	6·9 (4·66–10·01)	14·5 (11·17–18·51)	2·4 (1·24–4·61)	0·69 (0·230–2·225)	1·4 (0·57–3·26)
Pilchy	0·3 (0·09–1·74)	47·9 (42·35–53·38)	20·7 (16·55–25·55)	50·9 (45·40–56·43)	0·9 (0·28–2·76)	0·6 (0·19–2·25)	6·7 (4·41–10·02)	1·2 (0·44–3·21)	0·30 (0·093–1·738)	1·5 (0·62–3·63)
Sex										
Males	37·4 (31·06–44·11)	19·1 (14·22–25·07)	8·7 (5·56–13·36)	39·7 (33·24–46·44)	3·6 (1·72–7·03)	3·0 (1·35–6·23)	17·6 (12·97–23·35)	3·4 (1·60–6·76)	2·3 (0·94–5·42)	2·12 (0·805–5·153)
Females	37·9 (31·77–44·48)	18·8 (14·12–24·60)	20·2 (15·37–25·98)	44·6 (38·20–51·14)	2·9 (1·32–6·01)	10·0 (6·59–14·60)	12·2 (8·45–17·11)	3·8 (1·85–7·13)	1·8 (0·63–4·57)	0·67 (0·144–2·846)
Age										
Class 1	19·3 (15·56–23·66)	18·6 (14·89–22·89)	4·6 (2·91–7·28)	30·4 (25·88–35·22)	2·1 (1·07–4·23)	1·4 (0·61–3·28)	7·9 (5·51–11·11)	0·4 (0·12–1·64)	0 (0–1·05)	0·36 (0·122–1·636)
Class 2	42·4 (37·02–47·88)	16·8 (12·96–21·32)	10·7 (7·64–14·59)	40·5 (35·21–46·05)	4·3 (2·49–7·08)	3·0 (1·61–5·59)	13·1 (9·80–17·31)	2·4 (1·20–4·83)	1·8 (0·81–4·05)	0·61 (0·187–2·248)
Class 3	49·0 (43·65–54·43)	21·7 (17·49–26·40)	26·8 (22·23–31·81)	54·1 (48·75–59·52)	3·2 (1·73–5·68)	14·3 (10·91–18·52)	23·2 (18·96–28·12)	7·6 (5·22–11·06)	4·1 (2·42–6·85)	3·18 (1·730–5·682)

See text for statistical analysis.

The overall abundance of *H. mixtum* was 1·4 ± 0·084 worms/vole, but there was a marked difference between sites (Table 6; GLM with negative binomial errors, main effect of SITE, $LR_{2,914} = 455{\cdot}0$, $P < 0{\cdot}0001$), with just one worm recovered from a vole from Pilchy in the entire period and the majority of worms from Urwitałt. There was also a highly significant effect of YEAR (Table 6; $LR_{3,914} = 26{\cdot}8$, $P < 0{\cdot}0001$), and a 2-way interaction (YEAR × SITE, $LR_{6,902} = 14{\cdot}2$, $P = 0{\cdot}027$) which is shown in Fig. 3C. The rank order of abundance was maintained across all four surveys but the differences between sites were most marked in 1999. Abundance of this species also increased with vole age (Table 6; $LR_{2,914} = 55{\cdot}4$, $P < 0{\cdot}0001$), and while overall there was a similar age-related pattern in all four surveys, there were also significant discrepancies between age classes in successive surveys as shown in Fig. 2F (2–way interaction YEAR × AGE, $LR_{6,\ 902} = 17{\cdot}7$, $P = 0{\cdot}007$). There was no significant difference in abundance of *H. mixtum* between male and female voles.

Heligmosomoides glareoli. The prevalence of *H. glareoli* was 19·0% (15·90–22·48) overall, but there was a marked discrepancy between sites (Table 5). Prevalence was markedly higher in voles at Pilchy compared with the other two sites although the extent of the difference varied between the surveys (Fig. 5B; YEAR × SITE × INFECTION, $\chi^2_6 = 17{\cdot}8$, $P = 0{\cdot}007$). Confining the analysis *post hoc* to bank voles from Pilchy revealed a highly significant effect of YEAR ($\chi^2_2 = 39{\cdot}9$, $P < 0{\cdot}001$), but prevalence did not vary with host sex or age classes. There was also a weaker YEAR × SEX × AGE × INFECTION interaction ($\chi^2_6 = 12{\cdot}8$, $P = 0{\cdot}047$), which we did not explore further.

The overall mean abundance of *H. glareoli* was 0·9 ± 0·10 worms/vole, but very few worms were found among voles from Urwitałt and Tałty (Table 6). This parasite was mostly encountered in Pilchy (GLM with negative binomial errors, main effect of SITE $LR_{2,914} = 315{\cdot}2$, $P < 0{\cdot}0001$), where the mean abundance across all four surveys was 2·4 ± 0·26. There was also a significant main effect of YEAR ($LR_{3,914} = 42{\cdot}0$, $P < 0{\cdot}0001$) and a 2-way interaction between YEAR and SITE ($LR_{6,902} = 15{\cdot}4$, $P = 0{\cdot}018$) as illustrated in Fig. 3D; worm burdens were very low and changed little in Urwitałt and Tałty, but were much higher at Pilchy, with two high abundance years and two relatively low abundance years. There was no significant difference in abundance between the sexes in the entire dataset (Table 6), or when confined to Pilchy alone (main effect of SEX, $LR_{1,321} = 0{\cdot}5$, $P =$ NS; males = 2·1 ± 0·263, females = 2·7 ± 0·457). Abundance increased significantly with increasing age (Table 6; main effect of AGE, $LR_{2,914,} = 29{\cdot}7$, $P < 0{\cdot}0001$), and even more markedly when confined to the voles from Pilchy (1·7 ± 0·25,

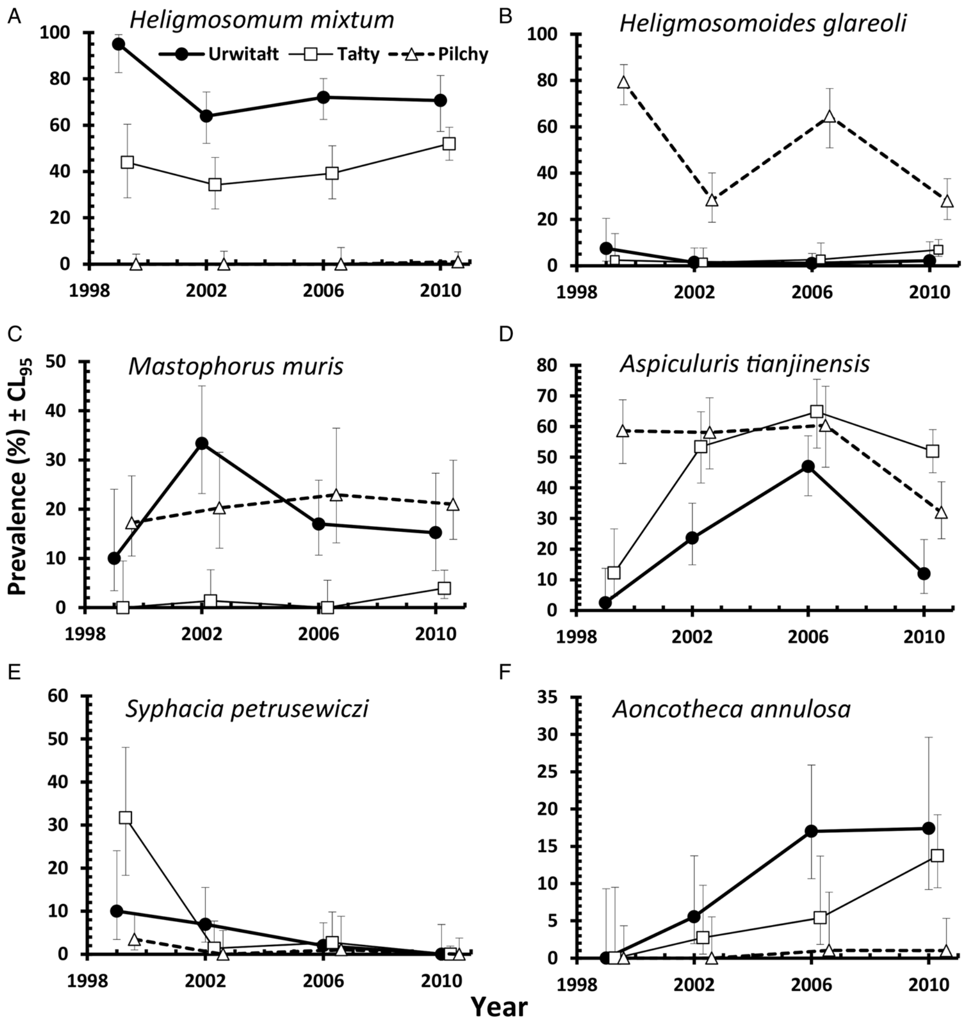

Fig. 5. Spatiotemporal dynamics in prevalence of individual species; *H. mixtum* (A), *H. glareoli* (B), *M. muris* (C), *A. tianjinensis* (D), *S. petrusewiczi* (E), *A. annulosa* (F). Key to symbols used as shown in panel A.

2·0 ± 0·37, 3·6 ± 0·65, for age classes 1–3, respectively; $LR_{2,322} = 28{\cdot}0$, $P < 0{\cdot}0001$). However, in the full dataset there was a significant interaction between YEAR and AGE ($LR_{6,902} = 21{\cdot}2$, $P = 0{\cdot}002$), indicating that the pattern of the age-related changes in abundance varied between years. This remained significant when just confined to voles from Pilchy ($LR_{6,316} = 26{\cdot}6$, $P < 0{\cdot}0001$; Fig. 2G). It can be seen that in 1999, abundance declined with increasing vole age at Pilchy, while in the remaining years it increased, as in the overall dataset (Table 6).

Mastophorus muris. The overall prevalence of *M. muris* was 14·3% (11·59–17·52). This species was more common in bank voles from Urwitałt and Pilchy than Tałty (Table 5), but over time prevalence varied differently between sites (Fig. 5C; YEAR × SITE × INFECTION, $\chi^2_6 = 12{\cdot}7$, $P = 0{\cdot}048$). Prevalence was most stable at Pilchy and somewhat more variable at Urwitałt. There was also a highly significant increase in prevalence with host age (Table 5; AGE × INFECTION, $\chi^2_2 = 59{\cdot}0$, $P < 0{\cdot}001$) and a discrepancy between the sexes, with prevalence in female bank voles being 2·3-fold higher than in males (Table 5; SEX × INFECTION, $\chi^2_1 = 17{\cdot}8$, $P < 0{\cdot}001$).

Mastophorus muris was less abundant than the species considered above (overall abundance = 0·70 ± 0·099), but there was a marked difference in abundance between sites (Table 6; GLM with negative binomial errors, main effect of SITE, $LR_{2,913} = 84{\cdot}9$, $P < 0{\cdot}0001$) with abundance much lower at Tałty. Moreover, the extent of this difference between sites varied significantly between surveys (Fig. 3E; 2-way interaction, SITE × YEAR, $LR_{6,901} = 13{\cdot}4$, $P = 0{\cdot}038$; main effect of YEAR, $LR_{3,913} = 11{\cdot}1$, $P = 0{\cdot}011$, Table 6). Overall, abundance increased with host age (Table 6; main effect of AGE, $LR_{2,913} = 44{\cdot}0$, $P < 0{\cdot}0001$) but this age related increase was most apparent among voles from Pilchy (Fig. 6; 2-way interaction, AGE × SITE, $LR_{4,901} = 18{\cdot}0$, $P = 0{\cdot}0012$), although in all three sites, despite the differences in overall abundance, age class 3 voles showed the highest abundance. Female bank voles showed a higher abundance than males (Table 6; main effect of

Table 6. Abundance of individual species by year, site, sex and age class

	H. mixtum	*H. glareoli*	*M. muris*	*A. tianjinensis*	*S. petrusewiczi*	*A. annulosa*	*C. henttoneni*	*Mesocestoides* sp.	*T. martis*	*V. mustelae*
Year										
1999	2·0 ± 0·27	1·9 ± 0·28	0·22 ± 0·082	6·9 ± 2·46	63·6 ± 35·90	0 ± 0	0·10 ± 0·033	1·0 ± 0·74	0·007 ± 0·007	0·029 ± 0·018
2002	0·9 ± 0·13	0·3 ± 0·09	0·97 ± 0·249	3·1 ± 0·79	3·1 ± 2·12	0·11 ± 0·056	0·64 ± 0·125	2·1 ± 1·80	0·050 ± 0·016	0·119 ± 0·063
2006	1·2 ± 0·015	1·2 ± 0·23	0·68 ± 0·161	13·4 ± 2·06	0·4 ± 0·33	0·31 ± 0·174	0·29 ± 0·065	4·9 ± 3·55	0·004 ± 0·004	0·011 ± 0·011
2010	1·5 ± 0·16	0·5 ± 0·18	0·75 ± 0·194	4·7 ± 0·99	0 ± 0	2·09 ± 0·738	0·20 ± 0·051	6·6 ± 2·24	0·048 ± 0·026	0·003 ± 0·003
Site										
Urwitałt	2·8 ± 0·18	0·02 ± 0·009	0·81 ± 0·165	2·2 ± 0·67	16·1 ± 13·33	1·93 ± 0·709	0·60 ± 0·101	5·2 ± 1·69	0·059 ± 0·015	0·016 ± 0·009
Tałty	1·4 ± 0·15	0·05 ± 0·017	0·03 ± 0·013	13·5 ± 2·13	16·3 ± 10·36	0·46 ± 0·193	0·24 ± 0·052	7·5 ± 0·4	0·028 ± 0·024	0·045 ± 0·030
Pilchy	0·003 ± 0·003	2·43 ± 0·264	1·20 ± 0·227	6·3 ± 1·02	0·02 ± 0·011	0·01 ± 0·004	0·13 ± 0·032	0·4 ± 0·29	0·003 ± 0·003	0·049 ± 0·034
Sex										
Males	1·3 ± 0·11	0·76 ± 0·102	0·31 ± 0·086	5·5 ± 0·95	12·6 ± 8·79	0·08 ± 0·032	0·38 ± 0·055	3·8 ± 2·05	0·025 ± 0·008	0·064 ± 0·030
Females	1·4 ± 0·13	1·02 ± 0·178	1·12 ± 0·179	9·0 ± 1·31	8·2 ± 6·39	1·51 ± 0·493	0·26 ± 0·057	4·6 ± 1·70	0·033 ± 0·017	0·009 ± 0·005
Age										
Class 1	0·6 ± 0·11	0·75 ± 0·121	0·18 ± 0·113	7·5 ± 1·69	0·1 ± 0·04	0·03 ± 0·020	0·15 ± 0·044	0·9 ± 0·91	0 ± 0	0·007 ± 0·007
Class 2	1·4 ± 0·13	0·61 ± 0·121	0·24 ± 0·053	4·6 ± 0·86	13·8 ± 9·07	0·04 ± 0·013	0·20 ± 0·035	1·3 ± 10·2	0·021 ± 0·009	0·027 ± 0·025
Class 3	2·0 ± 0·17	1·30 ± 0·246	1·66 ± 0·258	9·7 ± 1·57	16·2 ± 12·98	2·23 ± 0·706	0·59 ± 0·101	10·2 ± 3·77	0·064 ± 0·025	0·073 ± 0·038

See text for statistical analysis.

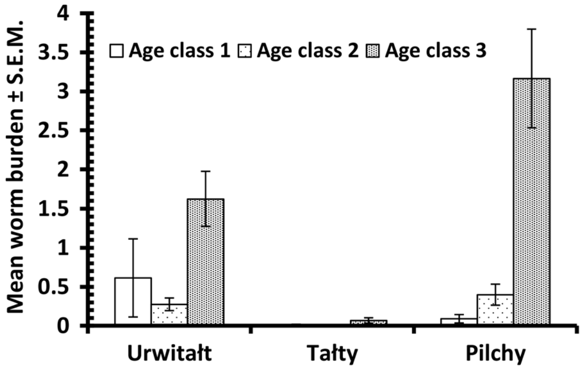

Fig. 6. Age-related changes in abundance of *M. muris* by site.

SEX, $LR_{1,913} = 4{\cdot}42$, $P = 0{\cdot}036$), especially in age class 3 voles, but not in the youngest animals (Fig. 4C; 2–way interaction, AGE × SEX, $LR_{2,9101} = 14{\cdot}2$, $P = 0{\cdot}0008$).

Aspiculuris tianjinensis. This was the most common nematode with an overall prevalence of 42·1% (37·98–46·27) and it was twice as common at Tałty and Pilchy compared with Urwitałt (Table 5). There were marked changes in prevalence between the surveys, but their magnitude varied between sites (Fig. 5D; YEAR × SITE × INFECTION, $\chi^2_6 = 49{\cdot}3$, $P < 0{\cdot}001$). Whilst at Pilchy prevalence varied very little in the first three surveys (58·1–60·4%) before falling by about 50% in 2010, at both Urwitałt and Tałty prevalence increased in the first three surveys before the dip at both sites in 2010. Prevalence also increased consistently with increasing host age (Table 5; AGE × INFECTION, $\chi^2_2 = 63{\cdot}6$, $P < 0{\cdot}001$) and this was consistent in three of the four surveys but not in 1999, when there was essentially no age–related effect on prevalence (Fig. 2H). There was no significant difference in prevalence between the sexes (Table 5).

Aspiculuris tianjinensis was also the most abundant intestinal nematode (mean worm burden = 7·2 ± 0·81). Overall abundance was highest in voles from Tałty (Table 6; GLM with negative binomial errors, main effect of SITE, $LR_{2,913} = 73{\cdot}0$, $P < 0{\cdot}0001$), but this was confounded by significant variation between years (Table 6; main effect of YEAR, $LR_{3,913} = 42{\cdot}7$, $P < 0{\cdot}0001$) and the interaction between these factors (Fig. 3F; YEAR × SITE, $LR_{6,905} = 55{\cdot}6$, $P < 0{\cdot}0001$). Abundance was consistently lower throughout among voles from Urwitałt, not exceeding 4·5 worms recovered in 2006, but among voles from Tałty there was a marked peak of abundance in 2006 with a mean of 31·5, even though in earlier years abundance had been moderate and similar to that at the other two sites (Fig. 3F). On average the abundance of *A. tianjinensis* was almost twice as high among female compared with male voles (Table 6; main effect of SEX,

$LR_{1,913} = 6{\cdot}5$, $P = 0{\cdot}01$), but this was confounded by a significant interaction with host age (SEX × AGE, $LR_{2,905} = 21{\cdot}6$, $P < 0{\cdot}0001$). Figure 4D shows that among male voles, abundance was highest in the youngest animals and then declined, but among female voles it rose with host age to peak among the oldest age class.

Syphacia petrusewiczi. This species had an overall prevalence of 3·3% (2·02–5·08), but showed a marked reduction in prevalence across the four surveys with no parasites at all recovered from 294 bank voles in 2010 (Table 5). Figure 5E shows that prevalence dropped in all three sites with time and despite the originally higher prevalence at Tałty in 1999, there was no significant YEAR × SITE × INFECTION interaction. However, the fall in prevalence with successive surveys differed between the sexes (Fig. 4E; YEAR × SEX × INFECTION, $\chi^2_3 = 7{\cdot}87$, $P = 0{\cdot}049$) with a lower prevalence initially in males but a slower fall over time. The directions of the sex- and age-effects on prevalence also differed significantly between sites with higher prevalence in females at Tałty but not at the other two sites (Fig. 4F; SITE × SEX × INFECTION, $\chi^2_2 = 7{\cdot}61$, $P = 0{\cdot}022$), and peaking in age class 2 voles in two sites but not at Urwitałt (Fig. 2I; SITE × AGE × INFECTION, $\chi^2_4 = 13{\cdot}4$, $P = 0{\cdot}01$).

With so few infected bank voles ($n = 30$) statistical analysis of the abundance of *S. petrusewiczi* could not be carried out reliably with any of the transformations attempted (negative binominal errors, log-transformed, Box-Cox transformed or models with only main effects, none converged). Therefore, non-parametric tests were used. Abundance dropped markedly in all sites as the study progressed (Table 6; Kruskal–Wallis test, effect of YEAR, $\chi^2_3 = 59{\cdot}83$, $P < 0{\cdot}0001$) with complete loss of this species by 2010. There were also significant differences in abundance between sites (Table 6). *Syphacia petrusewiczi* was found both in Urwitałt and Tałty but very rarely in Pilchy (Kruskal–Wallis test, $\chi^2_2 = 10{\cdot}58$, $P = 0{\cdot}005$), even in the early years when the species was still present in these study sites. Abundance did not differ significantly between sexes (Table 6) and age classes.

Aonchotheca annulosa. The overall prevalence of this species was 6·4% (4·58–8·78). There was a highly significant difference in prevalence among voles from the three sites (Table 5; SITE × INFECTION, $\chi^2_2 = 47{\cdot}1$, $P < 0{\cdot}0001$). The relative ranking of sites was consistent throughout (highest prevalence at Urwitałt, intermediate at Tałty and lowest at Pilchy in all years; Fig. 5F), despite the rise of prevalence at all three sites with successive surveys (Table 5; YEAR × INFECTION, $\chi^2_3 = 32{\cdot}8$, $P < 0{\cdot}0001$). Prevalence also increased significantly with host age (Table 5; AGE × INFECTION, $\chi^2_2 = 40{\cdot}9$, $P < 0{\cdot}0001$) and was female biased (Table 5; SEX × INFECTION, $\chi^2_1 = 12{\cdot}3$, $P < 0{\cdot}0001$).

Quantitative analysis of abundance of *A. annulosa* was problematic since only 59 voles were infected. No interactions proved significant and models with the four main effects only, failed to converge. Analysis was conducted therefore on two separate models with negative binomial errors (model 1, year + age + sex; model 2, site + sex + age). Abundance changed significantly with successive surveys (Table 6; model 1, main effect of YEAR, $LR_3 = 37{\cdot}3$, $P < 0{\cdot}0001$) and there was a significant difference in abundance among voles from the three different sites (Table 6; model 2, main effect of SITE, $LR_2 = 47{\cdot}6$, $P < 0{\cdot}0001$), with bank voles from Urwitałt showing higher abundance than those from Tałty and Pilchy. Abundance also increased with host age (Table 6; model 1 main effect of AGE, $LR_2 = 49{\cdot}5$, $P < 0{\cdot}0001$; model 2 $LR_2 = 57{\cdot}6$, $P < 0{\cdot}0001$) and differed between the sexes (Table 6; model 1 main effect of SEX, $LR_1 = 21{\cdot}7$, $P < 0{\cdot}0001$) with female voles carrying a mean worm burden 18·7 times heavier than that of males.

Trichuris arvicolae. *Trichuris arvicolae* was only recovered from four age class 3 female voles, all from Pilchy. One infected vole was from 1999 and three from 2010. Two of the animals with *T. arvicolae* in 2010 carried two worms each and the other two only had a single worm. These data were not analysed further.

Prevalence and abundance of cestodes

Prevalence of cestodes was 20·6% (17·37–24·21) overall (intestinal dwelling adults + larvae combined), highest among voles from Urwitałt in all four surveys and lower at the other two sites, with significant spatiotemporal variation as illustrated in Fig. 1E (YEAR × SITE × INFECTION, $\chi^2_6 = 25{\cdot}6$, $P < 0{\cdot}0001$). Prevalence was higher among male bank voles (Table 2; SEX × INFECTION, $\chi^2_1 = 4{\cdot}75$, $P = 0{\cdot}029$) and increased significantly with host age (Table 2; AGE × INFECTION, $\chi^2_2 = 50{\cdot}4$, $P < 0{\cdot}0001$).

Analysis of abundance was problematic and could only be carried out using non-parametric tests. Overall abundance was 5·2 ± 1·39 worms/vole but this varied between surveys (Table 3; Kruskal–Wallis test, $\chi^2_3 = 20{\cdot}11$, $P < 0{\cdot}0001$) increasing by 6·3-fold between 1999 and 2010. Cestodes were more abundant in bank voles from Tałty and Urwitałt than from Pilchy (Kruskal–Wallis test, $\chi^2_2 = 59{\cdot}06$, $P < 0{\cdot}0001$); abundance in Tałty being 6·3 times higher than in Pilchy (Table 3). Abundance increased significantly with host age (Kruskal–Wallis test, $\chi^2_2 = 53{\cdot}75$, $P < 0{\cdot}0001$) with much higher abundance among the oldest animals compared with both younger classes (Table 3), but did not differ significantly between the sexes.

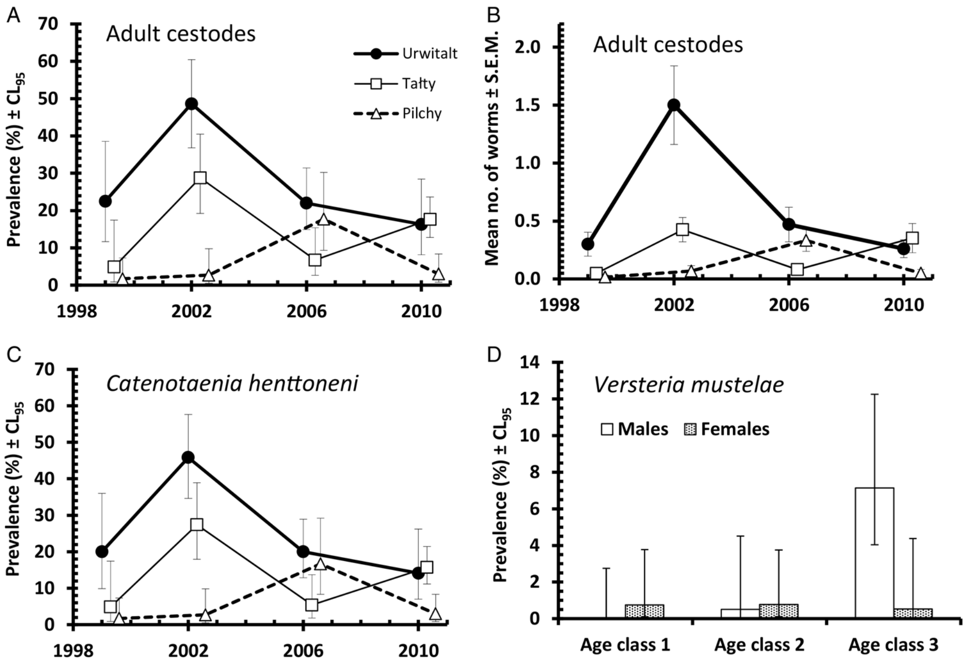

Fig. 7. Spatiotemporal dynamics in prevalence of adult intestinal cestodes (A); abundance of intestine dwelling adult cestodes (B); prevalence of *C. henttoneni* (C); sex bias among age classes in prevalence of *V. mustelae* (D). Key to symbols used in B and C, as in A.

Prevalence and abundance of adult cestodes

Prevalence of intestinal-dwelling adult stages of cestodes, whether mature or not fecund, was 16·3% (13·36–19·61). Summary data for prevalence by each of the four main effects is shown in Table 2. Prevalence was relatively high in 2002, when most of the infected voles were from Urwitałt. Prevalence increased with host age and there appeared to be bias in favour of higher prevalence among male voles. These effects could not be evaluated statistically in a full factorial model, because of complex interactions which could not be broken down further (YEAR × SITE × SEX × INFECTION, $\chi^2_6 = 15·3$, $P = 0·018$ and SITE × SEX × AGE × INFECTION, $\chi^2_4 = 11·9$, $P = 0·018$). However, analysis by 1-way χ^2-tests showed that there were highly significant effects of YEAR ($\chi^2_3 = 25·4$), SITE ($\chi^2_2 = 46·2$), and AGE ($\chi^2_2 = 30·2$, $P < 0.001$ in all cases) and a weaker effect of SEX ($\chi^2_1 = 4.14$, $P = 0.042$). Figure 7A illustrates the spatiotemporal dynamics: prevalence was highest at Urwitałt and lowest at Pilchy in three of the four surveys. Peak prevalence occurred among voles from Urwitałt in 2002.

Abundance was low with an overall mean of 0·34 ± 0·040. Mean abundances for all four main effects are shown in Table 3. Attempts at analyses by GLM failed to converge so we used non-parametric tests. Over time, changes in abundance showed a very similar pattern to those for prevalence (Fig. 7B; YEAR $\chi^2_3 = 28·0$, $P < 0·001$), which is not unexpected given that the mean worm burden was less than one, and that 95 out of the 150 voles infected with adult tapeworms carried just one adult worm. All the remaining main effects were significant (for SEX, $U = 100{,}810$, $P = 0·037$ [bias in favour of males]; SITE $\chi^2_2 = 45·5$, $P < 0·001$ [most abundant at Urwitałt and least at Pilchy]; AGE $\chi^2_2 = 32·1$, $P < 0·001$ [most abundant in age class 3 voles and least in age class 1]).

Prevalence and abundance of individual adult cestode species

Of the three species of adult cestodes identified in this study only one, *Catenotaenia henttoneni*, was present in sufficient numbers to merit statistical analysis. In total 138 bank voles harboured *C. henttoneni* with an overall prevalence of 15·0% (12·18–18·18). As with the analysis of all adult cestodes, backward selection of full factorial models gave two complex interactions (YEAR × SITE × SEX × INFECTION, $\chi^2_6 = 14·5$, $P = 0·024$ and SITE × SEX × AGE × INFECTION, $\chi^2_4 = 11·0$, $P = 0·026$) that could not be broken down further. Prevalence values for all four main effects are shown in Table 4. This species was most prevalent in Urwitałt and in Tałty (Table 5), showing the highest prevalence at Urwitałt in three of the four surveys (Fig. 7C). At Pilchy this species remained relatively rare. Although overall a higher percentage of male voles were infected compared with females, there was no consistency with sex bias changing between the sexes in particular years and sites. For example, in 2002, prevalence among male bank voles in Urwitałt was higher than among females (males = 55·0% [38·70–70·09], females = 34·4% [21·83–48·80]), whereas in Tałty it was in the opposite direction (males = 25·6% [13·99–41·51], females = 29·4% [17·70–44·24]). Similarly, although overall prevalence values increased with host age (Table 5), the age effect was not consistent in both sexes and at all three sites. Males at all three sites showed increasing prevalence with host age, but among female voles only those from Pilchy followed the same pattern. Females from Urwitałt showed the lowest prevalence in age class 2, whilst in Tałty this was the age class with the highest prevalence (data not shown).

The mean abundance of *C. henttoneni* was 0·32 ± 0·039 worms/vole. Mean values for each of the four main effects are shown in Table 6 and since this was the dominant cestode in the intestine, the values are very similar to those for all adult intestinal cestodes combined (Table 3). As above there was a significant SITE × YEAR interaction (not shown; GLM with negative binomial errors, $LR_{6,907} = 35{\cdot}7$, $P < 0{\cdot}0001$) and this followed a very similar pattern to that in Fig 7B for all intestinal adult cestodes combined. All main effects significantly affected abundance (YEAR, $LR_{3,913} = 26{\cdot}7$, $P < 0{\cdot}0001$; SITE, $LR_{2,913} = 28{\cdot}0$, $P < 0{\cdot}0001$; AGE, $LR_{2,913} = 29{\cdot}5$, $P < 0{\cdot}0001$ and SEX $LR_{1,913} = 5{\cdot}7$, $P = 0{\cdot}017$), but additional interactions could not be tested because more complex models failed to converge.

Other adult cestodes were rarer: *Paranoplocephala omphalodes* was present in the 1999, 2002 and 2010 surveys at Urwitałt and Pilchy only (prevalence, 1·3% (0·5–3·2) and 0·7% (0·2–2·2), respectively) and just one adult *Arostrilepis horrida* specimen was recovered during the whole study (from a female vole at Urwitałt in 2006). However infections with these adult cestodes were not analysed further because of their low prevalence and abundance.

Prevalence and abundance of larval stages of cestodes

Four species of larval cestodes were recovered from the bank voles, two from the peritoneal cavity (*Mesocestoides* sp. and *Taenia martis*) and two from the liver (*Versteria mustelae* and *Cladotaenia globifera*). The overall prevalence was 6·9% (5·03–9·38). Analysis of prevalence at this level showed that there was a highly significant difference between sites (Table 2; SITE × INFECTION, $\chi^2_2 = 29{\cdot}1$, $P < 0{\cdot}001$). Most infected voles came from Urwitałt, with prevalence being much lower among voles from the other two sites and little difference between the latter (Table 2). Prevalence also varied significantly between the successive surveys (Table 2; YEAR × INFECTION, $\chi^2_3 = 15{\cdot}5$, $P = 0{\cdot}001$) but there was no consistent trend with two peak years (2002 and 2010), and lower prevalence in the other years. Although prevalence increased with host age (Table 2), this was confounded by host sex (Fig. 4G; AGE × SEX × INFECTION, $\chi^2_2 = 6{\cdot}6$, $P = 0{\cdot}037$), because prevalence was higher in male compared with female voles among age classes 2 and 3, but not among the youngest animals in age class 1.

Analysis of abundance (Table 3) was not possible by GLM but non-parametric tests showed that the effects of SITE ($\chi^2_2 = 30{\cdot}2$, $P < 0{\cdot}001$ [most abundant in Tałty, least in Pilchy]), YEAR ($\chi^2_3 = 14{\cdot}9$, $P = 0{\cdot}002$ [most abundant in 2010, least in 1999]), and AGE ($\chi^2_2 = 46{\cdot}3$, $P < 0{\cdot}001$ [most abundant in age class 3 and least in age class 1]) were all significant. There was no significant difference in abundance between the sexes.

Prevalence and abundance of individual larval cestode species

Mesocestoides sp. was present in all surveys in all sites, except at Pilchy in 2006. The overall prevalence was 3·6% (2·29–5·47) and mean abundance was 4·2 ± 1·34. Prevalence was almost identical in the first three surveys, but much higher in 2010 (Table 5; YEAR × INFECTION, $\chi^2_2 = 9{\cdot}5$, $P = 0{\cdot}023$) and mean abundance (Table 6) likewise increased from 1999 to 2010. *Mesocestoides* sp. was most commonly encountered at Urwitałt (Table 5; SITE × INFECTION, $\chi^2_2 = 18{\cdot}0$, $P < 0{\cdot}001$), but abundance was numerically higher at Tałty (Table 6) and the parasite was largely confined to the oldest animals (Table 5; AGE × INFECTION, $\chi^2_2 = 24{\cdot}2$, $P < 0{\cdot}001$), which also showed the highest overall abundance of worms (Table 6). There was no significant difference in prevalence or abundance between the sexes.

Taenia martis was less common (2·1% [1·15–3·64]), with an overall mean abundance of 0·03 ± 0·009. It was found predominantly at Urwitałt (Table 5; SITE × INFECTION, $\chi^2_2 = 21{\cdot}1$, $P < 0{\cdot}001$ and for abundance see Table 6), and among the oldest voles (Table 5; AGE × INFECTION, $\chi^2_2 = 13{\cdot}1$, $P = 0{\cdot}001$ and for abundance see Table 6). Prevalence was highest in 2002 (Table 5; YEAR × INFECTION, $\chi^2_3 = 11{\cdot}8$, $P = 0{\cdot}008$).

Versteria mustelae (previously known as *Taenia mustelae*; Nakao *et al.* 2013) was rarer still (overall prevalence = 1·4% [0·70–2·80] and abundance = 0·037 ± 0·016). In contrast to *T. martis* prevalence did not vary between sites (Table 5) although mean abundance was lower among voles from Urwitałt. However, there was a reduction in prevalence and abundance in the last two surveys (Table 5; YEAR × INFECTION, $\chi^2_3 = 11{\cdot}8$, $P = 0{\cdot}008$), and although prevalence appeared to increase with host age, this was confounded by an interaction with host sex (AGE × SEX × INFECTION, $\chi^2_2 = 6{\cdot}3$, $P = 0{\cdot}043$). As can be seen in Fig. 7D prevalence was very similar (<1%) in females in all age classes, but increased with

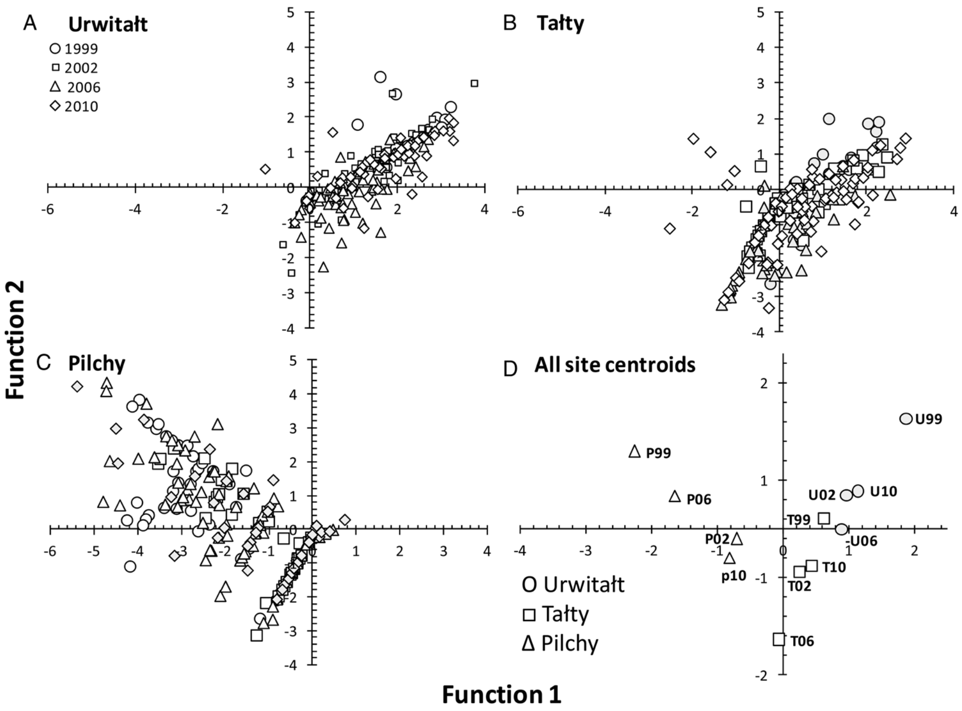

Fig. 8. Scatter plots and a plot of the centroids of functions 1 and 2 derived from Canonical Discriminant Function Analysis for 14 species of helminths in voles grouped by site and year. A, Urwitałt; B, Tałty; C, Pilchy. Key for symbols representing the four surveys in different years are the same for A, B and C and are given in the legend in A. D shows the centroids, each site represented by a different symbol as explained in the legend, and each point annotated with either U, T or P for Urwitałt, Tałty and Pilchy, respectively, and 99, 02, 06 and 10 representing the years 1999, 2002, 2006 and 2010, respectively.

age in males, exceeding 7% in age class 3 voles. Abundance also increased with host age (Table 6) but this was not tested because of the low prevalence, and as with prevalence the highest value for abundance was among age class 3 male voles (0·175 ± 0·093; in age class 3 females abundance = 0·005 ± 0·005).

Cladotaenia globifera was found in 2002 and 2010. It was present in one vole each from Urwitałt and Pilchy in 2002 and from Tałty in 2006, with an overall mean abundance of 0·60 ± 0·363, and the highest abundance value from a single vole from Pilchy (250 larvae).

Sources of variation in abundance data

The data in Table 4 show the percentage of deviance accounted for by each of the specific factors and their interactions, as fitted in minimal sufficient models in GLMs. For four of the six individual species in this analysis (*M. muris, H. mixtum, H. glareoli* and *A. tianjinensis*.) SITE was clearly the strongest source of deviance. For *A. annulosa* it was AGE, although SITE was of a similar magnitude and for *C. henttoneni* the interaction between SITE and YEAR accounted for the greatest percentage of deviance, but SITE, YEAR and AGE were all of a similar magnitude. For two measures, YEAR was the main source of deviance (total helminths and total nematodes) although in both cases AGE was second in importance. For BID, AGE clearly accounted for a substantial proportion of deviance but the interaction between SITE and YEAR was next in importance. For MSR the SITE × YEAR interaction was dominant and SITE was second in importance.

Canonical discriminant function (CDF) analysis

CDF analysis generated 11 axes that cumulatively accounted for 100% of the variance in the data. Axis 1 (Eigenvalue = 1·209) accounted for 57·8% of the variance and Axis 2 (Eigenvalue = 0·276) for a further 13·2%. Since together these two axes accounted for 71·0% of the variance the remaining axes were not examined further. Axis 1 (Fig. 8) essentially contrasts *H. mixtum* (0·64) with *H. glareoli* (−0·68), hence the scatter of data points from Urwitałt and Tałty towards the positive range of the Function 1 axis, and those from Pilchy in the negative range. There were additional positive but minor contributions to this axis from *A. annulosa* (0·15) and *C. henttoneni* (0·15) and negative from *A. tianjinensis*. (−0·22). Axis 2 contrasts *H. glareoli* (0·65) with *A. tianjinensis* (−0·53), with additional positive contributions from *H. mixtum* (0·36) and *M. muris* (0·22). *Heligmosomoides glareoli* was mostly found at Pilchy and *M. muris* at Pilchy and Urwitałt, while *A. tianjinensis* was most abundant in Tałty. Figure 8D shows that the centroids for Urwitałt are the four most positive on the Function 1 axis followed by those from Tałty in the centre and Pilchy the four most negative on this axis, so there was no overlap of centroids from the three sites along the Function 1 axis. This contrasts with extensive overlap on the vertical Function 2 axis for centroids from Urwitałt and Pilchy, and three of the lowest, most negative on this axis being those from Tałty.

DISCUSSION

The data presented in this paper are based on systematic surveys of helminth parasites of wild rodents exploiting exactly the same study sites over a period of more than a decade. As such the dataset represents one of the longest longitudinal studies on wild rodents in the literature. Perhaps the most interesting outcome is that despite the 11-year period between the first and the fourth survey, some indicators of helminth population structure have remained remarkably stable. At the highest taxonomic level the prevalence of all helminths and of all nematodes (all species combined in each case), in each of the three sites showed relatively little change over the study period, as was also the case for core species such as *H. mixtum, H. glareoli* and *M. muris*. Our data for *H. mixtum* (particularly at Tałty) have some similarity to those of Bugmyrin *et al.* (2005) who found that annual prevalence of this species over the period between 1996 and 2003 varied only between 20 and 40%. Although the worm burdens in that study were lower (generally less than an average of one worm/host) the annual mean burdens hardly varied between years, similarly to our observations at Tałty. *Heligmosomum mixtum* has been reported previously to have highly stable underdispersed or weakly aggregated population dynamics (Haukisalmi 1986; Haukisalmi et al 1996) and this stability has been linked to the predictable occurrence of this core nematode taxon across wide geographical areas and through relatively long periods of time. However, in our study, the best-fit distribution by far for *H. mixtum* was a negative binomial distribution, and this remained so even when the data from Pilchy (where it was extremely rare) were omitted from the analysis. Therefore, the long-term stability of this species in our sites must be attributable to other factors which are currently not understood, but likely hypotheses can be linked to the ecological characteristics of the two woodlands in which this species was most common and possibly intrinsic factors including genetic which are known to differ between these bank vole populations (Kloch *et al.* 2010).

Equally of interest was our finding that where differences in prevalence of *H. mixtum, H. glareoli* and *M. muris* existed between sites, they were largely maintained across the entire period. *Heligmosomum mixtum* always showed the highest prevalence in Urwitałt, followed by Tałty, and with the exception of a single worm collected in 2010, was otherwise absent from Pilchy. *Heligmosomoides glareoli* consistently showed the highest prevalence in Pilchy, and *M. muris* showed similar prevalence in Urwitałt and Pilchy but was rare in Tałty. So for these three species and also at the higher taxonomic level of combined helminths and combined nematodes, there was stability and a high degree of predictability in prevalence.

In marked contrast other measures of infracommunity structure showed dramatic, dynamic changes over the period of study and some species had a disproportionate influence on measures of abundance at the higher taxonomic level. In the cases of both combined helminths and combined nematodes, abundance dropped markedly after the 1999 survey and then stabilized at a considerably lower level. The explanation in this case was the disappearance of *S. petrusewiczi* from each of the three sites over the period, a species that is often found with very high worm burdens in some infected hosts. In 1999 the maximum recorded burden was 4026 worms in a single vole. Abundance was lower in 2002 and then, despite increased sampling effort in the following two surveys, the parasite disappeared completely (our unpublished observations in 2014 also showed no *Syphacia* in any of these populations). All *Syphacia* species have the potential to give rise to very intense infections with thousands of worms in a single individual, probably mostly as a result of autoinfection, but usually in only a few intensely infected individuals (Grear and Hudson, 2011). Why this parasite should die out in each of these three populations is not known since there has been virtually no noticeable ecological change over the period in the sites, other than the generally well perceived climatic trends associated with global warming throughout Europe (Michalska, 2011; Institute of Meteorology and Water Management, Poland, 2013; European Environment Agency, 2014) and infrequent harvesting of trees from the forests by the Polish Government’s Department of Forestry (Nadleśnictwo Pisz 2014; Zając̨zkowski *et al.* 2014). None of the three sites in which we sampled voles has been directly affected by felling, but adjoining areas have been felled and replanted, and in 2002 parts of the Pilchy site adjoining, but not directly at our sampling site, experienced significant wind damage.

In marked contrast to the disappearance of *S. petrusewiczi*, other species increased significantly in prevalence and abundance. *Aonchotheca annulosa* was notable among these species. It was not detected at all in any of the voles sampled in 1999. It then increased steadily in Urwitałt, to a lesser extent in Tałty but was still found only sporadically in Pilchy. This increase in both prevalence and abundance of *A. annulosa* across the 11 years of our study bears some similarity to the consistent increase in prevalence of *Aonchotheca murissylvatici* (previously *Capillaria murissylvatici* and a sister species of *A. annulosa;* Moravec, 1982, 2000) in bank voles over 5 years reported by Haukisalmi *et al.* (1988). In some respects the increase in *A. annulosa* in Urwitałt and Tałty was mirrored by the loss of *S. petrusewiczi*; whether these events were related causally, or just by coincidence in timing, is not known. Not surprisingly therefore, the values of helminth species richness and BID remained relatively steady without major change as loss of one species was compensated by gain of the other.

In relative terms SITE was a key factor in explaining prevalence and abundance of *M. muris, H. mixtum* and *H. glareoli* and to some extent also *A. tianjinensis* confirming that for these species the local environment, whether habitat or host-determined, was relatively stable across the decade of sampling, enabling uninterrupted transmission between hosts, and was therefore an important driver of the intensity of worm burdens. For other species such as *A. annulosa, C. henttoneni* and even MSR, SITE also explained a significant percentage of deviance in quantitative statistical models, but additionally other factors came into play, so changes over time, host age and different statistical interactions were more important. The CDF analysis (Fig. 8) was particularly instructive in showing that on the basis of the two major axes, largely influenced by the dominant species of helminths, the three sites each delineated their own space on the figure and the centroids for each site clustered closer to one another than to those from other sites with no overlap from the four surveys. This interpretation of the outcomes of the analysis therefore provides support for our hypothesis that the helminth communities in bank voles living in each of the three sites are characterized by certain combinations of species, which show little overall change over the course of a decade. Hence, the site of capture of animals plays a pivotal role in predicting likelihood that they will be infected by a particular species, or combination of helminth species.

The relatively greater influence of extrinsic factors, compared with intrinsic factors, on helminth communities has parallels in other host-helminth systems and site of capture in particular is known to play a major role since it largely determines the infective stages that hosts are likely to be exposed to (Mollhagan, 1978; Abu-Madi *et al.* 1998; Calvete *et al.* 2004; Booth, 2006). The spectrum of infective agents in any given locality is dependent primarily on the availability of the most abundant hosts in the vicinity and the parasites that they carry, and stochastic events (local introductions/ extinctions) can drastically alter the local range of available pathogens. However, the ecology of the environment provides a major source of variation for the risk of infection since both the survival of resident and introduced infective stages of parasites may be affected, and as expected helminth communities have been found to vary between rodents sampled in ecologically quite different habitats (Kinsella, 1974; Martin and Huffman, 1980; Haukisalmi *et al.* 1987; Montgomery and Montgomery, 1988, 1989; Abu-Madi *et al.* 1998, 2000; Simões *et al.* 2010; Ribas *et al.* 2011), although not universally (Haukisalmi *et al.* 1987; Milazzo *et al.* 2003). However, it is relevant that, as here, helminth communities in wild rodents have also been found to differ significantly among animals from sites which differ very little ecologically and are located in close proximity to one another (Montgomery and Montgomery, 1990; Behnke *et al.* 2001; Krasnov *et al.* 2010).

As expected many measures of infracommunity structure increased with host age (Tenora and Zejda, 1974; Montgomery and Montgomery, 1989). The worm burdens of individual species, helminth species richness and diversity all generally increased, whether examined in year specific cohorts or by site. There were few exceptions, as indicated earlier. This pattern of increasing prevalence and abundance of worm burdens with host age has been reported consistently in wild rodents (Montgomery and Montgomery, 1989; Janova *et al.* 2010), including bank voles (e.g. *Apostatandrya macrocephala* in Haukisalmi *et al.* 1988 and *H. mixtum* in Bugmyrin *et al.* 2005) and is almost certainly generated through the accumulation of these long-lived parasites throughout the life of the host (e.g. *M. muris* is believed to live for at least a year in wild rodents (Rausch and Tiner, 1949, citing Kirschenblatt, 1938)). Some studies show a decline in intestinal nematode burdens in older animals, perhaps indicating acquired resistance to infection (Haukisalmi *et al.* 1988; Gregory, Montgomery and Montgomery, 1992; Behnke *et al.* 1999), but there was little evidence of such a decline with age in our data, other than in the occasional data subset, as for example in *H. glareoli* in 1999. This lack of evidence for immunological resistance may be due to the high mortality experienced by *M. glareolus* at these sites; with 50% survival time for bank voles at Urwitałt varying between 1 and 3 months (Paziewska *et al.* 2012), in order to detect immunological elimination in the current dataset, the effect would have to be particularly strong. Overall, as Fig. 2 shows, the increase in worm burdens with host age was among the strongest intrinsic and most consistent effects on parasite prevalence and abundance observed in the current work and particularly marked in the case of helminth diversity.

In contrast to the age effect, there were few cases of sex-biased prevalence or abundance. We found no evidence for a sex bias in *H. mixtum*, as reported by Haukisalmi *et al.* (1988), and more recently by

Bugmyrin *et al.* (2005). In our case convincing and consistent disparities between the sexes were detected only in *M. muris* and *A. annulosa* and in both cases prevalence was higher in females and cumulatively this was sufficient to generate a significant female sex bias in MSR of helminths. The higher prevalence of *M. muris* in female bank voles compared with males, has been discussed in some detail in Grzybek *et al.* (2015), and has been reported previously in these populations (Behnke *et al.* 2008*b*). Haukisalmi *et al.* (1988), also found a higher prevalence and intensity of *M. muris* in older female bank voles that had overwintered and survived until the autumn, but reported a trend in the opposite direction among summer born mature bank voles. In our data, all other cases of significant sex effects arose only as interactions, with the balance changing between dominance in males and then females depending on year of survey or site. The few instances of sex bias in helminth infections in our data are consistent with the literature for wild rodents, where generally it has been found that differences between the sexes in the worm burdens they carry are minimal (Kisielewska 1970*b*; O'Sullivan, Smal and Fairley, 1984; Abu-Madi *et al.* 2000; Bordes *et al.* 2012) but we cannot exclude the possibility that sex-bias is season dependent. All of our sampling was conducted in late summer and early autumn period and it is possible that at other times of the year, host sex-differences in the abundance of some species are more evident and perhaps related to seasonally dependent sexual dichotomy in reproductive behaviour (Bajer *et al.* 2005).

Although our study was based on destructive cross-sectional surveys, our trap lines covered only a very small area of the extensive forests in each site. Cross-sectional studies based on destructive sampling will have consequences for host populations if conducted too frequently, depending on the number of animals culled and the frequency and extent of culling relative to the total population. Host population density is known to influence parasite burdens (Arneberg, 2001), so any marked reduction in host population as a result of intervention is likely to have an impact on helminth community structure. Moreover, migration of animals from neighbouring areas into a sample site where density has been reduced may alter the parasite community structure subtly. However, from other work in contiguous forest sites, and elsewhere, it is known that bank vole populations decline markedly in the winter and early spring each year but return to a peak in late summer or autumn (Alibhai and Gipps, 1985; Bujalska, 2000; Bajer *et al.* 2005). Sampling at 3 or 4-year intervals, at the peak of population density in early autumn, therefore constitutes a reasonable compromise in facilitating assessment of helminth populations in bank voles without imposing major losses on the host population and destabilizing the transmission of parasites. An alternative is to adopt mark-release-recapture methods to generate longitudinal data based on indirect measures of parasite burdens acquired by non-destructive methods such as by faecal egg counts (FEC; Knowles *et al.* 2013). There is a strong positive correlation between parasite numbers and FEC in some species (Keymer and Hiorns, 1986; Quinnell, 1992), and FEC are widely used to assess intestinal helminth infections in humans (Bundy, 1990; Levecke *et al.* 2011). However, although FEC can be useful in a prevalence context framework, it is not helpful for the estimation of some parasite burdens such as those of pinworms of the genus *Syphacia* spp. (among the most common genus of helminths of European wild rodents). *Syphacia* spp. release eggs onto the perianal surface of their hosts and not in feces (Lewis and D'Silva, 1986; Baker, 2007) and egg shedding by pinworms can be intermittent (Lewis and D'Silva, 1980; Hill, Randolph and Mandrell, 2009). Reliance on FEC also misses juvenile, as yet non-fecund worms, and males, in circumstances where sex ratio may not be unity (Anderson, 1982). Most importantly however, egg output by helminths is density dependent (Anderson, 1982), and FEC cannot be always extrapolated to estimate worm burden accurately (Ghazal and Avery, 1974). Density dependence is well understood at an intraspecific level, but is also known to occur between parasite species, and understanding inter-specific interactions is another goal of studies such as this one (data currently in preparation for publication); it is impossible using FEC to distinguish between inter-specific effects on egg outputs of individual worms, and inter-specific effects on worm density. It is pertinent also that some helminths, most notably *Syphacia* spp. show a highly aggregated distribution of worm burdens among hosts (Scott and Gibbs, 1986; Grear and Hudson, 2011) and some rodents may harbour thousands of individual worms, as found in the current study. This overdispersed distribution would be entirely missed by FEC (Baker, 2007), because as stated above relatively few *Syphacia* eggs actually end up in the feces. It is also relevant that FEC cannot quantify the larval stages of helminths that reside deep within the host in organs such as the liver (e.g. tapeworm cysts *Taenia taeniaeformis, V. mustellae, C. globifera*), and for which rodents act as intermediate hosts. Again, as we have found, the parasite burdens with some of these species may be immense; for example, several hundred *Mesocestoides* individuals may occur in a single host animal (Behnke *et al.* 2008*a*).

Finally, the work reported in this paper, has been built on our earlier publications (Behnke *et al.* 2001, 2008*b*), extending the period over which the helminth communities of bank voles in our three sites in NE Poland have been monitored by further 8 years (2006 and 2010). Our data emphasize that despite the fluctuations that characterize the prevalence and abundance of the rarer species, there is a large element of stability generated by the dominant species, which show little change over time. This contrasts with the patterns of change detected for haemoparasites, where each of the five species studied showed a different pattern of spatiotemporal change over the 11 years (Bajer *et al.* 2014). The picture with helminths is further complicated by clear trends leading to extinction of species (as in the case of *S. petrusewiczi*, at least in our sites, but presumably not elsewhere in the vicinity) and the influx of new species (as in the case of *A. annulosa*) which in time may eventually join the dominant species as established members of the community at particular sites. Our research has generated a long-term dataset, which provides fundamental information about the community ecology of a complex natural system and our findings caution against snap-shot, single cross-sectional surveys that may not provide all the relevant information for hypotheses about parasite-derived long-term selective pressures on hosts living in specific sites. The baseline data we have generated provide a foundation to explore the mechanisms that shape long-term trends in complex communities and continued monitoring of this system will strengthen inferences and focus hypotheses.

ACKNOWLEDGEMENTS

We thank Mgrs Grzegorz Górecki and Anna Zaborowska, the wardens of the field station at Urwitałt, for the use of the facilities. We wish to acknowledge the support of the forestry departments responsible for the woodland sites utilized in our study (Nadleśnictwa Giżycko, Mikołajki and Orzysz). Finally we thank all the undergraduate student helpers from both NU and WU who helped with field work during the four expeditions to our study sites.

FINANCIAL SUPPORT

We thank the Universities of Nottingham and Warsaw for enabling this study through financial support for travel and consumables. Our work was additionally supported by travel grants from the Royal Society (JMB), the British Ecological Society (JMB), the Grabowski Fund (JMB), the Polish State Committee for Scientific Research (KBN, AB), the Ogden Trust (GSB) and by the KBN and British Council's Young Scientist Programme (AB).

REFERENCES

Abu-Madi, M. A., Behnke, J. M., Lewis, J. W. and Gilbert, F. S. (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, M. A., Behnke, J. M., Lewis, J. W. and Gilbert, F. S. (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.

Alibhai, S. K. and Gipps, J. H. W. (1985). The population dynamics of bank voles. In *The Ecology of Woodland Rodents, Bank voles and Wood Mice* (ed. Flowerdew, J. R., Gurnell, J. and Gipps, J. H. W.), pp. 277–313. Clarendon Press, Oxford. *Symposia of the Zoological Society of London* Vol. **55**.

Anderson, R. M. (1982). The population dynamics and control of hookworm and roundworm infections. In *Population Dynamics of Infectious Diseases. Theory and Applications* (ed. Anderson, R. M.), pp. 67–108. Chapman and Hall, London.

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.

Bajer, A., Behnke, J. M., Pawelczyk, A., Kulis, K., Sereda, M. J. 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.

Bajer, A., Welc-Falęciak, R., Bednarska, M., Alsarraf, M., Behnke-Borowczyk, J., Siński, E. and Behnke, J. M. (2014). Long-term spatiotemporal stability and dynamic changes in the haemoparasite community of bank voles (*Myodes glareolus*) in NE Poland. *Microbial Ecology* **68**, 196–211.

Baker, D. G. (2007). Parasites of rats and mice. In *Flynn's Parasites of Laboratory Animals*, 2nd Edn (ed. Baker, D. G.), pp. 339–340. Blackwell Publishing, Ames, IA.

Barnard, C. J., Behnke, J. M., Bajer, A., Bray, D., Race, T., Frake, K., Osmond, J., Dinmore, J. and Siński, E. (2002). Local variation in endoparasite intensities of bank voles (*Clethrionomys glaroelus*) from ecologically similar sites: morphometric and endocrine correlates. *Journal of Helminthology* **76**, 103–112.

Barnard, C. J., Kuliś, K., Behnke, J. M., Bajer, A., Gromadzka-Ostrowska, J., Stachon, M. and Siński, E. (2003). Local variation in helminth burdens of bank voles (*Clethrionomys glareolus*) from ecologically similar sites: temporal stability and relationships with hormone concentrations and social behaviour. *Journal of Helminthology* **77**, 185–195.

Behnke, J. M., Lewis, J. W., Mohd Zain, S. N. and Gilbert, F. S. (1999). Helminth infections in *Apodemus sylvaticus* in southern England: interactive effects of host-age, sex and year on prevalence and abundance of infections. *Journal of Helminthology* **73**, 31–44.

Behnke, J. M., Barnard, C. J., Bajer, A., Bray, D., Dinmore, J., Frake, K., Osmond, J., Race, T. and Siński, 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, J. M., Bajer, A., Harris, P. D., Newington, L., Pidgeon, E., Rowlands, G., Sheriff, C., Kuliś-Malkowska, K., Siński, E., Gilbert, F. S. and Barnard, C. J. (2008*a*). 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, J. M., Bajer, A., Harris, P. D., Newington, L., Pidgeon, E., Rowlands, G., Sheriff, C., Kuliś-Malkowska, K., Siński, E., Gilbert, F. S. and Barnard, C. J. (2008*b*). Temporal and between-site variation in helminth communities of bank voles (*Myodes glareolus*) from NE Poland. 2. The infracommunity level. *Parasitology* **135**, 999–1018.

Behnke, J. M., Stewart, A., Bajer, A., Grzybek, M., Harris, P. D., Lowe, A., Ribas, A., Smales, L. and Vandegrift, K. J. (2016). Bank voles (*Myodes glareolus*) and house mice (*Mus musculus musculus/domesticus*) in Europe are each parasitized by their own distinct species of *Aspiculuris* (Nematoda, Oxyurida). *Parasitology* (Epub ahead of print) doi:10.1017/S0031182015000864.

Boag, B., Lello, J., Fenton, A., Tompkins, D. M. and Hudson, P. J. (2001). Patterns of parasite aggregation in the wild European rabbit (*Oryctolagus cuniculus*). *International Journal for Parasitology* **31**, 1421–1428.

Booth, M. (2006). The role of residential location in apparent helminth and malaria associations. *Trends in Parasitology* **22**, 359–362.

Bordes, F., Ponlet, N., de Bellocq, J. G., Ribas, A., Krasnov, B. R. 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.

Bugmyrin, S. V., Ieshko, E. P., Anikanova, V. A. and Bespyatova, L. A. (2005). Patterns of host-parasite interactions between the nematode *Heligmosomum mixtum* (Schulz, 1952) and the bank vole (*Clethrionomys glareolus* Schreber, 1780). *Parasitologia* **39**, 414–422.

Bujalska, G. (2000). The bank vole population in Crab-apple Island. *Polish Journal of Ecology* **48** (Suppl.), 97–106.

Bundy, D. A. P. (1990). Is the hookworm just another geohelminth? Chapter 10. In *Hookworm Disease. Current Status and New Directions* (ed. Schad, G. A. and Warren, K. S.), pp. 147–164. Taylor and Francis, London.

Calvete, C., Blanco-Aguiar, J. A., Virgós, E., Cabezas-Díaz, S. and Villafuerte, R. (2004). Spatial variation in helminth community structure in the red-legged partridge (*Alectoris rufa* L.): effects of definitive host density. *Parasitology* **129**, 101–113.

Carleton, M. D., Musser, G. G. and Pavlinov, I. A. (2003). *Myodes* Pallas, 1811, is the valid name for the genus of red-backed voles. In *Systematics, Phylogeny and Paleontology of Small Mammals. Proceedings of the International Conference Devoted to the 90th Anniversary of Prof. I.M. Gromov, Saint Petersburg, November 2003* (ed. Averianov, A. and Abramson, N.), p. 96.

Carleton, M. D., Gardner, A. L., Pavlinov, I. Y. and Musser, G. G. (2014). The valid generic name for red-backed voles (Muroidea: Cricetidae: Arvicolinae): restatement of the case for *Myodes* Pallas, 1811. *Journal of Mammology* **95**, 943–959.

Cattadori, I. M., Boag, B. and Hudson, P. J. (2008). Parasite co-infection and interaction as drivers of host heterogeneity. *International Journal for Parasitology* **38**, 371–380.

Cornell, S. J., Bjornstad, O. N., Cattadori, I. M., Boag, B. and Hudson, P. J. (2008). Seasonality, cohort-dependence and the development of immunity in a natural host-nematode system. *Proceedings of the Royal Society B* **275**, 511–518.

Elliott, J. M. (1977). *Some Methods for the Statistical Analysis of Samples of Benthic Invertebrates*. Freshwater Biological Association, Cumbria, UK.

Elton, C., Ford, E. B., Baker, J. R. and Gardner, A. D. (1931). The health and parasites of a wild mouse population. *Proceedings of the Royal Zoological Society, London* **101**, 657–721.

European Environment Agency (2014). http://www.eea.europa.eu/themes/climate.

Ghazal, A. M. and Avery, R. A. (1974). Population dynamics of *Hymenolepis nana* in mice: fecundity and the 'crowding effect'. *Parasitology* **69**, 403–415.

Grear, D. A. and Hudson, P. (2011). The dynamics of macroparasite host-self-infection: a study of the patterns and processes of pinworm (Oxyuridae) aggregation. *Parasitology* **138**, 619–627.

Gregory, R. D., Montgomery, S. S. J. and Montgomery, W. I. (1992). Population biology of *Heligmosomoides polygyrus* (Nematoda) in the wood mouse. *Journal of Animal Ecology* **61**, 749–757.

Grzybek, M., Bajer, A., Behnke-Borowczyk, J., Al-Sarraf, M. and Behnke, J. M. (2015). 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. (1986). Frequency distributions of helminths in microtine rodents in Finnish Lapland. *Annales Zoologici Fennici* **23**, 141–150.

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. (2000). The 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. (1987). Parasitism by helminths in the grey-sided vole (*Clethrionomys rufocanus*) in northern Finland: influence of density, habitat and sex of the host. *Journal of Wildlife Diseases* **23**, 233–241.

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.

Haukisalmi, V., Henttonen, H. and Vikman, P. (1996). Variability of sex ratio, mating probability and egg production in an intestinal nematode in its fluctuating host population. *International Journal for Parasitology* **26**, 755–764.

Hill, W. A., Randolph, M. M. and Mandrell, T. D. (2009). Sensitivity of perianal tape impressions to diagnose pinworm (*Syphacia* spp.) infections in rats (*Rattus norvegicus*) and mice (*Mus musculus*). *Journal of the American Association for Laboratory Animal Science* **48**, 378–380.

Hudson, P. J., Cattadori, I. M., Boag, B. and Dobson, A. P. (2006). Climatic disruption and parasite-host dynamics: patterns and processes associated with warming and frequency of extreme climatic events. *Journal of Helminthology* **80**, 175–182.

Huntley, J. W., Fürsich, F. T., Alberti, M., Hethke, M. and Liu, C. (2014). A complete Holocene record of trematode-bivalve infection and implications for the response of parasitism to climate change. *Proceedings of the National Academy of Sciences, USA* **111**, 18150–18155.

Institute of Meteorology and Water Management (Instytut Meteorologii i Gospodarki Wodnej) National Research Institute of Poland (Państwowy Instytut Badawczy) (2013). Climate change and climate variability in Poland. In *COP19/CMP9 United Nations Climate Change Conference, Warsaw, Poland, 11–22 November 2013*.

Jackson, J. A., Hal, A. J., Friber, I. M., Ralli, C., Lowe, A., Zawadzka, M., Turner, A. K., Stewart, A., Birtles, R. J., Paterson, S., Bradley, J. E. and Begon, M. (2014). An immunological marker of tolerance to infection in wild rodents. *PLoS Biology* **12**, e1001901.

Janova, E., Skoric, M., Heroldova, M., Tenora, F., Fictum, P. and Pavlik, I. (2010). Determinants of the prevalence of *Heligmosomum costellatum* (Heligmosomidae: Trichostrongyloidea) in a common vole population in southern Moravia, Czech Republic. *Journal of Helminthology* **84**, 410–414.

Keith, L. B., Cary, J. R., Yuill, T. M. and Keith, I. M. (1985). Prevalence of helminths in a cyclic snowshoe hare population. *Journal of Wildlife Diseases* **21**, 233–253.

Keymer, A. E. and Hiorns, R. W. (1986). Faecal egg counts and nematode fecundity: *Heligmosomoides polygyrus* and laboratory mice. *Parasitology* **93**, 189–203.

Kinsella, J. M. (1974). Comparison of helminth parasites of the cotton rat, *Sigmodon hispidus*, from several habitats in Florida. *American Museum Novitates* **2540**, 1–11.

Kirschenblatt, N. I. (1938). Die Gesetzmaessigkeiten der Dynamik der Parasitenfauna bei den maeuseaehnlichen Nagetieren (Muriden) in Transkaukasien. Dissertation. University of Leningrad, pp. 5–92 (In Russian, with a German Summary).

Kisielewska, K. (1970*a*). 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 *Bialowieża National Park*. *Acta Parasitologica Polonica* **18**, 121–147.

Kisielewska, K. (1970*b*). Ecological organization of intestinal helminth groupings in *Clethrionomys glareolus* (Schreb.) (Rodentia). III. Structure of the helminth groupings in *C. glareolus* populations of various forest biocoenoses in Poland. *Acta Parasitologica Polonica* **18**, 163–176.

Kloch, A., Babik, W., Bajer, A., Siński, E. and Radwan, J. (2010). Effects of an MHC-DRB genotype and allele number on the load of gut parasites in the bank vole *Myodes glareolus*. *Molecular Ecology* **19**, 255–265.

Knowles, S. C. L., Fenton, A., Petchey, O. L., Jones, T. R., Barber, R. and Pedersen, A. B. (2013). Stability of within-host-parasite communities in a wild mammal system. *Proceedings of the Royal Society B* **280**, 20130598.

Krasnov, B. R., Mouillot, D., Shenbrot, G. I., Khokhlova, I. S., Vinarski, M. V., Korallo-Vinarskaya, N. P. and Poulin, R. (2010). Similarity in ectoparasite faunas of Palaearctic rodents as a function of host phylogenetic, geographic or environmental distances: which matters the most? *International Journal for Parasitology* **40**, 807–817.

Langley, R. and Fairley, J. S. (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.

Levecke, B., Behnke, J. M., Ajjampur, S. S. R., Albonico, M., Ame, S. M., Charlier, J., Geiger, S. M., Hoa, N. T. V., Kamwa Ngassam, R. I., Kotze, A. C., McCarthy, J. S., Montresor, A., Periago, M. V., Roy, S., Tchuem Tchuente, L.-A., Thach, D. T. C. and Vercruysse, J. (2011). A comparison of the sensitivity and fecal egg counts of the McMaster egg counting and kato-katz thick smear methods for soil-transmitted helminths. *PLoS Neglected Tropical Diseases* **5**, e1201.

Lewis, J. W. (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, J. W. and D'Silva, J. (1980). Rhythmic egg deposition by the oxyurid nematode *Syphacia muris* in the rat. *Journal of Zoology, London* **191**, 429–433.

Lewis, J. W. and D'Silva, J. (1986). The life-cycle of *Syphacia muris* Yamaguti (Nematoda: Oxyuroidea) in the laboratory rat. *Journal of Helminthology* **60**, 39–46.

Liu, B., Bu, Y. and Zhang, L. (2012). A new species of *Aspiculuris* Schulz, 1924 (Nematoda, Heteroxynematidae) from the gray-sided vole, *Clethrionomys rufocanus* (Rodentia, Cricetidae), from Tianjin, China. *Acta Parasitologica* **57**, 311–315.

Martin, J. L. and Huffman, D. G. (1980). An analysis of the community and population dynamics of the helminths of *Sigmodon hispidus* (Rodentia: Cricetidae) from three central Texas vegetational regions. *Proceedings of the Helminthological Society of Washington* **47**, 247–255.

Michalska, B. (2011). Tendencies of air temperature changes in Poland. *Prace i Studia Geograficzne* **47**, 67–75.

Milazzo, C., Casanova, J. C., Aloise, G., Ribas, A. and Cagnin, M. (2003). Helminths of the bank vole *Clethrionomys glareolus* (Rodentia, Arvicolinae) in southern Italy. *Italian Journal of Zoology* **70**, 333–337.

Mollhagan, T. (1978). Habitat influence on helminth parasitism of the cotton rat in western Texas, with remarks on some of the parasites. *The Southwestern Naturalist* **23**, 401–407.

Montgomery, S. S. J. and Montgomery, W. I. (1988). Cyclic and non-cyclic dynamics in populations of the helminth parasites of wood mice *Apodemus sylvaticus*. *Journal of Helminthology* **62**, 78–90.

Montgomery, S. S. J. and Montgomery, W. I. (1989). Spatial and temporal variation in the infracommunity structure of helminths of *Apodemus sylvaticus* (Rodentia: Muridae). *Parasitology* **98**, 145–150.

Montgomery, S. S. J. and Montgomery, W. I. (1990). Structure, stability and species interactions in helminth communities of wood mice *Apodemus sylvaticus*. *International Journal for Parasitology* **20**, 225–242.

Moravec, F. (1982). Proposal of a new systematic arrangement of nematodes of the family Capillariidae. *Folia Parasitologica* **29**, 119–132.

Moravec, F. (2000). Review of capillariid and trichosomoidid nematodes from mammals in the Czech Republic and the Slovak Republic. *Acta Societatis Zoologicae Bohemicae* **64**, 271–304.

Nadleśnictwo Pisz (2014). *Monitoring Stanu Lasu*. Nadleśnictwo Pisz, Lasy Państwowe, Poland. http://www.pisz.bialystok.lasy.gov.pl/documents/62733/22275741/monitoring+stanu+lasu+24-03-2014.pdf.

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.

O'Sullivan, H. M., Smal, C. M. and Fairley, J. S. (1984). A study of parasitic infestations in populations of small rodents (*Apodemus sylvaticus* and *Clethrionomys glareolus*) on Ross Island, Killarney. *Journal of Life Sciences of the Royal Dublin Society* **5**, 29–42.

Paziewska, A., Harris, P. D., Zwolińska, L., Bajer, A. and Siński, E. (2012). Differences in the ecology of *Bartonella* infections of *Apodemus flavicollis* and *Myodes glareolus* in a boreal forest. *Parasitology* **139**, 881–893.

Poulin, R. (1993). The disparity between observed and uniform distributions: a new look at parasite aggregation. *International Journal for Parasitology* **23**, 937–944.

Quinnell, R. J. (1992). The population dynamics of *Heligmosomoides polygyrus* in an enclosure population of wood mice. *Journal of Animal Ecology* **61**, 669–679.

Rausch, R. and Tiner, J. D. (1949). Studies on the parasitic helminths of the North Central States. II. Helminths of voles (*Microtus* spp.). Preliminary report. *American Midland Naturalist* **41**, 665–694.

Ribas, S. A., Guivier, E., Xuéreb, A., Chaval, Y., Cadet, P., Poulle, M.-L., Sironen, T., Voutilainen, L., Henttonen, H., Cosson, J.-F. and Charbonnel, N. (2011). Concomitant influence of helminth infection and landscape on the distribution of Puumala hantavirus in its reservoir, *Myodes glareolus*. *BMC Microbiology* **11**, 30.

Rohlf, F. J. and Sokal, R. R. (1995). *Statistical Tables*. Freeman W.H. and Company, San Francisco.

Scott, M. E. and Gibbs, H. C. (1986). Long-term population dynamics of pinworms (*Syphacia obvelata* and *Aspiculuris tetraptera*) in mice. *Journal of Parasitology* **72**, 652–662.

Simões, R., Gentile, R., Rademaker, V., D'Andrea, P., Herrera, H., Freitas, T., Lanfredi, R. and Maldonado, A., Jr. (2010). Variation in the helminth community structure of *Thrichomys pachyurus* (Rodentia: Echimyidae) in two sub-regions of the Brazilian Pantanal: the effects of land use and seasonality. *Journal of Helminthology* **84**, 266–275.

Tenora, F. and Staněk, M. (1995). Changes of the helminthofauna in several muridae and Arvicolidae at Lednice in Moravia. II. Ecology. *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis* **43**, 57–65.

Tenora, F. and Zejda, J. (1974). The helminth synusy of *Clethrionomys glareolus* in a lowland forest and its changes. *Acta Scientiarum Naturalium – Academiae Scientiarum Bohemoslovacae, Brno* **6**, 1–48.

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.

Tesakov, A. S., Lebedev, V. S., Bannikova, A. A. and Abramson, N. I. (2010). *Clethrionomys* Tilesius, 1850 is the valid generic name for red-backed voles and *Myodes* Pallas, 1811 is a junior synonym of *Lemmus* Link, 1795. *Russian Journal of Theriology* **9**, 83–86.

Xu, R. (2003). Measuring explained variation in linear mixed effects models. *Statistics in Medicine* **22**, 3527–3541.

Zajączkowski, G., Jabłoński, M., Jabłoński, T., Małecka, M., Kowalska, A., Małachowska, J. and Piwnicki, J. (2014). *Raport o stanie lasów w Polsce 2013*. Centrum Informacyjne Lasów Państwowych, Warszawa, Poland.