

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

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26 SUMMARY

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

42

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

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48 INTRODUCTION

49 Our understanding of helminth communities in vertebrates such as rodents is mostly based on
50 destructive, cross sectional studies conducted over a relatively short period of time, typically one to
51 three years (Lewis, 1968; Montgomery and Montgomery, 1988; Behnke *et al.* 2001; Bajer *et al.*
52 2005; Jackson *et al.* 2014). While several workers have addressed seasonal changes in helminth
53 burdens in wild rodents (Tenora and Zejda, 1974; Langley and Fairley, 1982; Montgomery and
54 Montgomery, 1988; Abu-Madi *et al.* 2000; Bajer *et al.* 2005), there are relatively few longer term
55 quantitative studies, spanning a decade or even more, that have been comprehensively analysed (but
56 for longer-term changes in helminths of rodents see also Elton *et al.* 1931, Kisieleska, 1970a,
57 Haukisalmi, Henttonen and Tenora, 1988, Tenora and Staněk, 1995; and in other mammals Cornell
58 *et al.* 2008, Keith *et al.* 1985, Boag *et al.* 2001, Cattadori *et al.* 2008 in lagomorphs; the long-term
59 study on parasites of sheep on Soay, Pemberton and Hayward *pers. com.*).

60 A key theoretical question concerns the role of parasite species and communities in the
61 evolution of their hosts. Immunoparasitological perspectives (e.g. Jackson *et al.* 2014) focus on the
62 role of parasites in shaping the immunological profile of the host; alternatively, studies focused on
63 life history strategies test predictions that parasites can modify life history parameters (Barnard *et*
64 *al.* 2002, 2003). However, it is important to establish whether the patterns that have been detected
65 in particular hosts in specific locations are repeatable over longer ecologically relevant periods of
66 time, if we are to infer that parasites can influence host speciation. Long-term studies allow the
67 robustness and repeatability of detected trends to be assessed and provide an opportunity to relate
68 species richness, as well as diversity, prevalence and abundance of individual parasites to climatic,
69 environmental and host demographic changes over time (Tenora, Wiger and Barus, 1979;
70 Haukisalmi, Henttonen and Tenora, 1988; Haukisalmi and Henttonen, 1990, 2000; Hudson *et al.*

71 2006). The resulting models can then allow informed predictions about the consequences of climate
72 change for human health and that of our livestock (Huntley *et al.* 2014).

73 Some short-term studies have reported relatively stable patterns of infection with helminths
74 in European rodents, with common helminths maintaining their dominant status and rarer species
75 fluctuating more unpredictably (Montgomery and Montgomery, 1990; Bajer *et al.* 2005;
76 Kisielewska, 1970a; Knowles *et al.* 2013). In spite of this relative stability, it is the minor
77 fluctuations in the common species that are primarily responsible for between-year variation in
78 derived measures such as diversity indices and species richness (Behnke *et al.* 2008b). Others have
79 reported more dynamic changes in particular helminths (Tenora, Wiger and Barus, 1979; Tenora
80 and Staněk, 1995; Haukisalmi, Henttonen and Tenora, 1988; Montgomery and Montgomery, 1990;
81 Behnke *et al.* 1999) and especially in measures of component community structure (Behnke *et al.*
82 2008a).

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

91

92 MATERIALS AND METHODS

93 *Study sites*

94 Our study sites have been described comprehensively in earlier papers by Behnke *et al.* (2001,
95 2008a, b). They are located in Mazury in the north eastern corner of Poland, in the vicinity of
96 Jezioro (Lake) Śniardwy and the towns of Mikołajki, Ryn and Pisz. Site 1 is referred to as Urwiłtał
97 (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
98 (N 53° 42.228, EO 21° 48.499) after nearby settlements. These sites are within 10 km of one another
99 in a NE to SW transect but separated by lakes, rivers, canals and pastures and therefore are isolated
100 from one another in ecological time, although the host species is panmictic and genetic studies have
101 revealed some gene flow between the three populations (Kloch *et al.* 2010). The sites were sampled
102 at the same time of year in each year of the study (last two weeks of August and the first two weeks
103 of September).

104

105 *Terminology and collection of bank voles*

106 In this paper we refer to *Myodes glareolus* for bank voles following Carleton *et al.* (2003, 2014) and
107 not *Clethrionomys glareolus* as in earlier studies and argued by Tesakov *et al.* (2010). The methods
108 used for trapping rodents, and for sampling and processing trapped animals have all been fully
109 described (Behnke *et al.* 2001, 2008a,b). Age categories were established as described earlier
110 (Behnke *et al.* 2001).

111

112 *Identification and quantification of endoparasites*

113 The entire alimentary tracts were brought back to the University of Nottingham in either 70%
114 ethanol (2010) or in 10% formalin (1999, 2002 and 2006) for dissection. The fixed intestines were
115 opened carefully in water or Hanks' saline and examined under a dissecting microscope. All

116 parasite specimens were identified, sexed and stored in tubes containing 70% ethanol. Tapeworms
117 were stained using borax carmine, dehydrated in ethanol and mounted Canada Balsam for
118 microscopical examination. In this paper we refer to *Aspiculuris* as *Aspiculuris tianjinensis*, rather
119 than *A. tetraptera* as previously stated, because recent molecular genetic data and morphological
120 observations have revealed that the *Aspiculuris* species parasitizing bank voles is not *A. tetraptera*
121 but a close relative, *A. tianjinensis* (Liu, 2012; Behnke *et al.* 2016).

122

123 *Statistical analysis*

124 Prevalence values (percentage of animals infected) are given with 95% confidence limits
125 (CL₉₅), calculated by bespoke software based on the tables of Rohlf and Sokal (1995). Abundance
126 of infection (including both infected and non-infected animals) is summarised by arithmetic means
127 and standard errors of the mean (S.E.M.).

128 The degree of aggregation in the data was calculated by the index of discrepancy (*D*) as
129 described by Poulin (1993) and the index of dispersion (*I*, variance to mean ratio). Frequency
130 distributions of raw values from individual taxa as well as the residuals from general linear models
131 were also tested for goodness of fit to negative binomial, positive binomial and Poisson models by
132 χ^2 as described by Elliott (1977) and the negative binomial exponent *k* is given as appropriate.

133 The statistical approach adopted has been documented comprehensively in our earlier
134 publications (Behnke *et al.* 2001, 2008a,b; Bajer *et al.* 2005). For analysis of prevalence we used
135 maximum likelihood techniques based on log linear analysis of contingency tables in the software
136 package IBM SPSS Statistics Version 21 (IBM Corporation). Initially, full factorial models were
137 fitted, incorporating as factors SEX (2 levels, males and females), AGE (3 levels), YEAR of study
138 (4 levels, 1999, 2002, 2006, 2010), and SITE (3 levels, Urwitałt, Tałty, Pilchy). The presence or

139 absence of parasites (INFECTION) was considered as a binary factor. These explanatory factors
140 were fitted initially to all models that were evaluated. For each level of analysis in turn, beginning
141 with the most complex model, involving all possible main effects and interactions, those
142 combinations that did not contribute significantly to explaining variation in the data were eliminated
143 in a stepwise fashion beginning with the highest level interaction (backward selection procedure). A
144 minimum sufficient model was then obtained, for which the likelihood ratio of χ^2 was not
145 significant, indicating that the model was sufficient in explaining the data. The importance of each
146 term (i.e. interactions involving INFECTION) in the final model was assessed by the probability
147 that its exclusion would alter the model significantly and these values relating to interactions that
148 included INFECTION are given in the text. The remaining terms in the final model that did not
149 include INFECTION (for example, variation among sites in the number of animals of each sex
150 sampled [SITE xSEX]) are not given but can be made available from the authors on request.

151 For analyses of quantitative data conforming to Gaussian distributions we used general
152 linear models (GLM) with normal errors implemented in R version 2.2.1 (R Core Development
153 Team) and the residuals were checked for approximate goodness of fit to the Gaussian distribution.
154 When the residuals failed to meet the requirements of Gaussian models we used generalised linear
155 models with negative binomial or Poisson error structures. Full factorial models that converged
156 satisfactorily were simplified using the STEP procedure and tested for significance using deletion of
157 terms beginning with the highest order interaction by comparing models with or without that
158 interaction. Changes in deviance (*DEV*) are given for models based on Poisson errors (interpreted
159 by χ^2), for models based on Gaussian errors we give *F* and for those based on negative binomial
160 errors the likelihood ratio (*LR*). Minimum sufficient models were then fitted (all significant
161 interactions and main effects plus any main effects that featured in interactions) and the process was
162 repeated to obtain values for changes in deviance, test statistics and probabilities. The percentage of

163 deviance accounted for by each significant main effect or interaction was calculated as
164 recommended by Xu (2003) and reported by Behnke *et. al* (2008b).

165 If the data did not meet the assumptions of parametric tests, we employed non-parametric
166 tests (Kruskal Wallis test for k levels in a specified factor and the Mann Whitney U -test where
167 factors only had 2 levels, e.g. SEX).

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

173

174 **Results**

175 *Numbers of voles and trapping effort*

176 Table 1 summarizes the numbers of voles sampled by age class, sex, year and site. Trapping effort
177 varied between surveys and sites depending on local and year specific constraints. In 2002, 2006
178 and 2010, relative host population density was recorded as the number of animals caught per 10,000
179 trap hours, but these data were not collected in the first survey in 1999, although it is known from
180 other studies that 1999 was a year when bank vole density was high at Urwitałt (Bajer *et al.* (2005)
181 recorded 85 and 188.3 voles/10,000 trap hours in August and September 1999 respectively in
182 Urwitałt) and Pilchy (pers. obs.). In 2002, the total of trap hours recorded was 33520 (9356, 12284
183 and 11880 for Urwitałt, Tałty and Pilchy respectively) and the number of bank voles was 85.5, 81.4
184 and 156.6/10,000 trap hours respectively. In 2006 total trap hours were 71112 (26085, 25004 and

185 20023 for Urwitałt, Tałty and Pilchy respectively) and the number of bank voles was 110.4, 61.7
186 and 131.9/10,000 trap hours respectively). In 2010 total trap hours were 67639 (14927, 18349 and
187 34363 for Urwitałt, Tałty and Pilchy respectively) and the number of bank voles was 125.3, 76.8
188 and 38.1/10,000 trap hours respectively.

189

190 *Prevalence and abundance of helminths*

191 The overall prevalence of helminths (all species combined) was 79.7% (76.12 - 82.92). Prevalence
192 values were generally high throughout (Table 2 and Fig. 1A), especially among voles from
193 Urwitałt. Although there was no independent effect of either YEAR or SITE, the rank order of
194 prevalence of helminths at the three sites changed significantly over time (YEAR x SITE x
195 INFECTION, $\chi^2_6=35.3$, $P<0.001$). Prevalence was highest in voles from Urwitałt in 1999 and
196 lowest in those from Pilchy, maintaining the highest values in Urwitałt in 2002 and 2006, but not in
197 2010 when prevalence was highest in the voles from Pilchy (Fig. 1A). There was no significant
198 difference between the sexes (Table 2) but there was a highly significant increase in prevalence
199 with increasing age of voles (Table 2; AGE x INFECTION, $\chi^2_2=104.9$, $P<0.001$), total prevalence
200 in the oldest class was in excess of 90% in each of the four surveys (Fig. 2A).

201 The overall abundance of helminths (all species combined) was 26.6 ± 5.68 worms per vole.
202 Full factorial models with negative binomial errors did not converge satisfactorily, but the best fit
203 was a model with all main effects and one interaction. However, abundance did not differ
204 significantly between the sexes and SEX was not a component in the interaction (Table 3; main
205 effect of SEX on abundance of helminths, $LR_{1,913}=0.055$, $P=0.8$), and we therefore excluded SEX
206 from the remaining analysis. Abundance varied significantly between the surveys (Table 3; main
207 effect of YEAR, $LR_{3,914}=116.7$, $P<0.0001$) and between sites (main effect of SITE, $LR_{2,914}=56.4$,

208 $P < 0.0001$) but there was also a significant interaction between YEAR and SITE ($LR_{6,908} = 41.7$,
209 $P < 0.0001$), which is illustrated in Fig. 1B. In 1999 helminth abundance was at its highest level
210 (Table 3), but this was evident at two sites only, with those from Pilchy showing the lowest and
211 most stable helminth abundance over the four surveys (Fig. 1B). Helminth abundance at Urwitałt
212 and Tały dropped markedly after 1999 and was only just higher than at Pilchy over the following
213 surveys. Helminth abundance also increased markedly with host age (Table 3; main effect of AGE,
214 $LR_{2,914} = 112.3$, $P < 0.0001$), being more than four-fold higher among the oldest class compared with
215 the youngest class.

216

217 *Species Richness*

218 The overall mean species richness (MSR) was 1.47 ± 0.037 . There was a weak main effect of
219 YEAR (Table 3; $DEV_3 = -7.8$, $P = 0.05$) with MSR increasing over the first three surveys and then
220 falling in 2010. There was more substantial variation between species richness of voles from the
221 three sites, (Table 3; main effect of SITE, $DEV_2 = -24.0$, $P < 0.0001$) with relative rank order
222 changing significantly over time (Fig. 3A; 2-way interaction YEAR x SITE, $DEV_6 = -42.0$,
223 $P < 0.0001$). Thus, although MSR was highest at Urwitałt overall (notably in 2002, 2006 and 2010),
224 in 1999 it was slightly higher for voles from Pilchy, and whilst at Urwitałt MSR declined from 2002
225 onwards, in Tały MSR increased with time to peak in 2010.

226 MSR was significantly higher among female voles (Table 3, $DEV_1 = -4.95$, $P = 0.03$). MSR
227 also increased significantly with vole age (Table 3; main effect of AGE, $DEV_2 = -7.04$, $P = 0.03$) at
228 all sites, although in voles at Urwitałt, after a moderate increase between age classes 1 and 2 MSR
229 increased considerably between age classes 2 and 3. In contrast accumulation was more steady

230 across all age classes at both Pilchy and Tałty (Fig. 2B; 2-way interaction SITE x AGE, $DEV_4 =$ -
231 17.8, $P=0.0014$).

232

233 *Species Diversity*

234 Brillouin's index of diversity (BID) increased significantly with host age (Table 3; main effect of
235 AGE, $F_{2,915}=82.80$, $P<0.0001$), varied between years (Table 3; main effect of YEAR, $F_{3,916}=4.92$,
236 $P=0.002$) and between study sites (Table 3; main effect of SITE, $F_{2,915}=7.08$, $P<0.001$) but there
237 was no significant difference between the sexes.

238 However, these main effects were confounded by 3 significant 2-way interactions. The most
239 significant was between YEAR and SITE ($F_{6,905}=8.57$, $P<0.0001$) accounting for 5.4% of explained
240 deviance (Table 4). In the first three surveys (1999, 2002 and 2006) BID was higher in Urwitałt
241 compared to Tałty, but in the last survey (2010) it was marginally higher at Tałty (Fig. 3B). Voles
242 from Pilchy showed no consistent trends in BID over the four surveys with a higher value than at
243 the other sites in 1999, equal with Urwitałt in 2006, but lower than at Urwitałt and Tałty in 2002
244 and 2010.

245 Although in each year of the study BID increased with increasing host age, the extent of
246 these age related changes varied significantly between years (Fig. 2C; 2-way interaction YEAR x
247 AGE, $F_{6,905}=2.66$, $P=0.014$). There was no overall effect of host sex on BID (Table 3), however, at
248 Uwitałt, and to a lesser extent at Pilchy, mean BID was higher among female voles, while at Tałty
249 mean BID was higher among male voles (Fig. 4A; 2-way interaction SITE x SEX, $F_{2,901}=4.03$,
250 $P<0.0001$).

251

252 *Frequency distributions and measures of aggregation.*

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

259

260 *Prevalence and abundance of nematodes*

261 Seventy seven percent (73.3 - 80.36) of the bank voles were infected with nematodes, and as with
262 the prevalence of all helminths combined the values for the prevalence of nematodes were
263 consistently high throughout (exceeding 70% in all surveys, Table 2). The rank order of prevalence
264 among voles at the three sites changed significantly over time (Fig. 1C; YEAR x SITE x
265 INFECTION, $\chi^2_6=29.6$, $P<0.001$) although there was no independent effect of either YEAR or
266 SITE. Prevalence did not vary significantly between the sexes (Table 2) but there was a highly
267 significant increase in prevalence with increasing age of voles (Table 2; AGE x INFECTION,
268 $\chi^2_2=103.2$, $P<0.001$) that was evident in each of the four surveys (Fig. 2D) with values $\geq 88\%$ in the
269 oldest class throughout.

270 The abundance of nematodes (all species combined) was analysed as above for all
271 helminths, with much the same outcome. In addition to the significant main effects of YEAR (Table
272 3; $LR_{3,914}=175.1$, $P<0.0001$) and SITE ($LR_{2,914}=44.7$, $P<0.0001$) and the interaction between these
273 (Fig. 1D; $LR_{6,904}=50.6$, $P<0.0001$), and the main effect of AGE (Table 3; $LR_{2,914}=78.0$, $P<0.0001$),
274 in this case there was also a significant interaction between SITE and AGE ($LR_{4,904}=24.9$,

275 $P<0.0001$) which is illustrated in Fig. 2E. In Urwitałt and Pilchy mean nematode worm burden
276 increased with age, but at Tały the highest abundance was found in bank voles of age class 2, with
277 a subsequent reduction among the oldest animals. Abundance did not vary significantly between the
278 sexes.

279

280 *Heligmosomum mixtum*

281 This species was recovered from 347 bank voles (37.6% [33.62 - 41.81]), but was largely found in
282 voles at two of the three sites (Urwitałt and Tały; Table 5 and Fig. 5A). Although there was no
283 independent effect of host sex, prevalence being almost identical in both sexes, there was a
284 significant interaction with site of capture (SITE x SEX x INFECTION, $\chi^2_2=7.1$, $P=0.029$).
285 Prevalence was higher in female voles from Urwitałt and in males at Tały (Fig. 4B). Since there
286 was no overall effect of host sex and a weak interaction of SEX with SITE, we next fitted *post hoc* a
287 model without SEX. This gave a highly significant effect of SITE (Table 5; $\chi^2_2=453.7$, $P<0.001$).
288 Prevalence of *H. mixtum* also varied significantly between years (Table 5; YEAR x INFECTION,
289 $\chi^2_3=10.76$, $P=0.013$) but the range of variation was narrow, just 8% (from 32.4% in 2002 to 40.5%
290 in 2010). There was also a highly significant independent effect of host age (AGE x INFECTION,
291 $\chi^2_2=57.0$, $P<0.001$), prevalence increasing with host age (Table 5).

292 The overall abundance of *H. mixtum* was 1.4 ± 0.084 worms/vole, but there was a marked
293 difference between sites (Table 6; GLM with negative binomial errors, main effect of SITE,
294 $LR_{2,914}=455.0$, $P<0.0001$), with just one worm recovered from a vole from Pilchy in the entire
295 period and the majority of worms from Urwitałt. There was also a highly significant effect of
296 YEAR (Table 6; $LR_{3,914}=26.8$, $P<0.0001$), and a 2-way interaction (YEAR x SITE, $LR_{6,902}=14.2$,
297 $P=0.027$) which is shown in Fig. 3C. The rank order of abundance was maintained across all four

298 surveys but the differences between sites were most marked in 1999. Abundance of this species also
299 increased with vole age (Table 6; $LR_{2,914}=55.4$, $P<0.0001$), and while overall there was a similar
300 age-related pattern in all four surveys, there were also significant discrepancies between age classes
301 in successive surveys as shown in Fig. 2F (2-way interaction YEAR x AGE, $LR_{6,902}=17.7$,
302 $P=0.007$). There was no significant difference in abundance of *H. mixtum* between male and female
303 voles.

304

305 *Heligmosomoides glareoli*

306 The prevalence of *H. glareoli* was 19.0% (15.90 - 22.48) overall, but there was a marked
307 discrepancy between sites (Table 5). Prevalence was markedly higher in voles at Pilchy compared
308 to the other two sites although the extent of the difference varied between the surveys (Fig. 5B;
309 YEAR x SITE x INFECTION, $\chi^2_6=17.8$, $P=0.007$). Confining the analysis *post hoc* to bank voles
310 from Pilchy revealed a highly significant effect of YEAR ($\chi^2_2=39.9$, $P<0.001$), but prevalence did
311 not vary with host sex or age classes. There was also a weaker YEAR x SEX x AGE x INFECTION
312 interaction ($\chi^2_6=12.8$, $P=0.047$), which we did not explore further.

313 The overall mean abundance of *H. glareoli* was 0.9 ± 0.10 worms/vole, but very few worms
314 were found among voles from Urwitałt and Tały (Table 6). This parasite was mostly encountered
315 in Pilchy (GLM with negative binomial errors, main effect of SITE $LR_{2,914}=315.2$, $P<0.0001$),
316 where the mean abundance across all four surveys was 2.4 ± 0.26 . There was also a significant main
317 effect of YEAR ($LR_{3,914}=42.0$, $P<0.0001$) and a 2-way interaction between YEAR and SITE
318 ($LR_{6,902}=15.4$, $P=0.018$) as illustrated in Fig. 3D; worm burdens were very low and changed little in
319 Urwitałt and Tały, but were much higher at Pilchy, with two high abundance years and two
320 relatively low abundance years. There was no significant difference in abundance between the sexes

321 in the entire dataset (Table 6), or when confined to Pilchy alone (main effect of SEX , $LR_{1,321}=0.5$,
322 $P=NS$; males $=2.1 \pm 0.263$, females $= 2.7 \pm 0.457$). Abundance increased significantly with
323 increasing age (Table 6; main effect of AGE, $LR_{2,914}= 29.7$, $P<0.0001$), and even more markedly
324 when confined to the voles from Pilchy (1.7 ± 0.25 , 2.0 ± 0.37 , 3.6 ± 0.65 , for age classes 1-3,
325 respectively; $LR_{2,322}=28.0$, $P<0.0001$). However, in the full dataset there was a significant
326 interaction between YEAR and AGE ($LR_{6,902}=21.2$, $P=0.002$), indicating that the pattern of the age-
327 related changes in abundance varied between years. This remained significant when just confined to
328 voles from Pilchy ($LR_{6,316}=26.6$, $P<0.0001$; Fig. 2G). It can be seen that in 1999, abundance
329 declined with increasing vole age at Pilchy, while in the remaining years it increased, as in the
330 overall dataset (Table 6).

331

332 *Mastophorus muris*

333 The overall prevalence of *M. muris* was 14.3% (11.59 - 17.52). This species was more common in
334 bank voles from Urwitait and Pilchy than Tałty (Table 5), but over time prevalence varied
335 differently between sites (Fig. 5C; YEAR x SITE x INFECTION, $\chi^2_6=12.7$, $P=0.048$). Prevalence
336 was most stable at Pilchy and somewhat more variable at Urwitait. There was also a highly
337 significant increase in prevalence with host age (Table 5; AGE x INFECTION, $\chi^2_2=59.0$, $P<0.001$)
338 and a discrepancy between the sexes, with prevalence in female bank voles being 2.3 fold higher
339 than in males (Table 5; SEX x INFECTION, $\chi^2_1=17.8$, $P<0.001$).

340 *Mastophorus muris* was less abundant than the species considered above (overall abundance
341 $= 0.70 \pm 0.099$), but there was a marked difference in abundance between sites (Table 6; GLM with
342 negative binomial errors, main effect of SITE, $LR_{2,913}=84.9$, $P<0.0001$) with abundance much lower
343 at Tałty. Moreover, the extent of this difference between sites varied significantly between surveys

344 (Fig. 3E; 2-way interaction, SITE x YEAR, $LR_{6,901}=13.4$, $P=0.038$; main effect of YEAR,
345 $LR_{3,913}=11.1$, $P=0.011$, Table 6). Overall, abundance increased with host age (Table 6; main effect
346 of AGE, $LR_{2,913}=44.0$, $P<0.0001$) but this age related increase was most apparent among voles from
347 Pilchy (Fig. 6; 2-way interaction, AGE x SITE, $LR_{4,901}=18.0$, $P=0.0012$), although in all three sites,
348 despite the differences in overall abundance, age class 3 voles showed the highest abundance.
349 Female bank voles showed a higher abundance than males (Table 6; main effect of SEX,
350 $LR_{1,913}=4.42$, $P=0.036$), especially in age class 3 voles, but not in the youngest animals (Fig. 4C; 2-
351 way interaction, AGE x SEX, $LR_{2,9101}=14.2$, $P=0.0008$).

352

353 *Aspicularis tianjinensis*

354 This was the most common nematode with an overall prevalence of 42.1% (37.98 - 46.27) and it
355 was twice as common at Tały and Pilchy compared with Urwitá (Table 5). There were marked
356 changes in prevalence between the surveys, but their magnitude varied between sites (Fig.5D;
357 YEAR x SITE x INFECTION, $\chi^2_6=49.3$, $P<0.001$). Whilst at Pilchy prevalence varied very little in
358 the first three surveys (58.1- 60.4%) before falling by about 50% in 2010, at both Urwitá and Tały
359 prevalence increased in the first three surveys before the dip at both sites in 2010. Prevalence also
360 increased consistently with increasing host age (Table 5; AGE x INFECTION, $\chi^2_2=63.6$, $P<0.001$)
361 and this was consistent in three of the four surveys but not in 1999, when there was essentially no
362 age-related effect on prevalence (Fig. 2H). There was no difference in prevalence between the
363 sexes (Table 5).

364 *A. tianjinensis* was also the most abundant intestinal nematode (mean worm burden = $7.2 \pm$
365 0.81). Overall abundance was highest in voles from Tały (Table 6; GLM with negative binomial
366 errors, main effect of SITE, $LR_{2,913}=73.0$, $P<0.0001$), but this was confounded by significant

367 variation between years (Table 6; main effect of YEAR, $LR_{3,913}=42.7$, $P<0.0001$) and the interaction
368 between these factors (Fig. 3F; YEAR x SITE, $LR_{6,905}=55.6$, $P<0.0001$). Abundance was
369 consistently lower throughout among voles from Urwitalt, not exceeding 4.5 worms recovered in
370 2006, but among voles from Tałty there was a marked peak of abundance in 2006 with a mean of
371 31.5, even though in earlier years abundance had been moderate and similar to that at the other two
372 sites (Fig. 3F). On average the abundance of *A. tianjinensis* was almost twice as high among female
373 compared with male voles (Table 6; main effect of SEX, $LR_{1,913}=6.5$, $P=0.01$), but this was
374 confounded by a significant interaction with host age (SEX x AGE, $LR_{2,905}=21.6$, $P<0.0001$). Fig.
375 4D shows that among male voles, abundance was highest in the youngest animals and then
376 declined, but among female voles it rose with host age to peak among the oldest age class.

377

378 *Syphacia petruszewiczi*

379 This species had an overall prevalence of 3.3% (2.02 - 5.08), but showed a marked reduction in
380 prevalence across the 4 surveys with no parasites at all recovered from 294 bank voles in 2010
381 (Table 5). Fig. 5E shows that prevalence dropped in all 3 sites with time and despite the originally
382 higher prevalence at Tałty in 1999, there was no significant YEAR x SITE x INFECTION
383 interaction. However, the fall in prevalence with successive surveys differed between the sexes
384 (Fig. 4E; YEAR x SEX x INFECTION, $\chi^2_3=7.87$, $P=0.049$) with a lower prevalence initially in
385 males but a slower fall over time. The directions of the sex- and age-effects on prevalence also
386 differed significantly between sites with higher prevalence in females at Tałty but not at the other
387 two sites (Fig. 4F; SITE x SEX x INFECTION, $\chi^2_2=7.61$, $P=0.022$), and peaking in age class 2
388 voles in two sites but not at Urwitalt (Fig. 2I; SITE x AGE x INFECTION, $\chi^2_4=13.4$, $P=0.01$).

389 With so few infected bank voles ($n=30$) statistical analysis of the abundance of *S.*
390 *petrusewiczii* could not be carried out reliably with any of the transformations attempted (negative
391 binominal errors, log-transformed, Box-Cox transformed or models with only main effects, none
392 converged). Therefore, non-parametric tests were used. Abundance dropped markedly in all sites as
393 the study progressed (Table 6; Kruskal-Wallis test, effect of YEAR, $\chi^2_3=59.83$, $P<0.0001$) with
394 complete loss of this species by 2010. There were also significant differences in abundance between
395 sites (Table 6). *S. petrusewiczii* was found both in Urwitałt and Tały but very rarely in Pilchy
396 (Kruskal Wallis test, $\chi^2_2=10.58$, $P=0.005$), even in the early years when the species was still present
397 in these study sites. Abundance did not differ significantly between sexes (Table 6) nor age classes
398 (despite the arithmetic increase in mean worm burdens with host age).

399

400 *Aonchotheca annulosa*

401 The overall prevalence of this species was 6.4% (4.58 - 8.78). There was a highly significant
402 difference in prevalence among voles from the three sites (Table 5; SITE x INFECTION, $\chi^2_2=47.1$,
403 $P<0.0001$). The relative ranking of sites was consistent throughout (highest prevalence at Urwitałt,
404 intermediate at Tały and lowest at Pilchy in all years; Fig. 5F), despite the rise of prevalence at all
405 three sites with successive surveys (Table 5; YEAR x INFECTION, $\chi^2_3=32.8$, $P<0.0001$).
406 Prevalence also increased significantly with host age (Table 5; AGE x INFECTION, $\chi^2_2=40.9$,
407 $P<0.0001$) and was female biased (Table 5; SEX x INFECTION, $\chi^2_1=12.3$, $P<0.0001$).

408 Quantitative analysis of abundance of *A. annulosa* was problematic since only 59 voles were
409 infected. No interactions proved significant and models with the four main effects only, failed to
410 converge. Analysis was conducted therefore on 2 separate models with negative binomial errors
411 (model 1, year +age+ sex; model 2, site +sex+ age). Abundance changed significantly with

412 successive surveys (Table 6; model 1, main effect of YEAR, $LR_3=37.3$, $P<0.0001$) and there was a
413 significant difference in abundance among voles from the three different sites (Table 6; model 2,
414 main effect of SITE, $LR_2=47.6$, $P<0.0001$), with bank voles from Urwitałt showing higher
415 abundance than those from Tałty and Pilchy. Abundance also increased with host age (Table 6;
416 model 1 main effect of AGE, $LR_2=49.5$, $P<0.0001$; model 2 $LR_2=57.6$, $P<0.0001$) and differed
417 between the sexes (Table 6; model 1 main effect of SEX, $LR_1=21.7$, $P<0.0001$) with female voles
418 carrying a mean worm burden 18.7 times heavier than that of males.

419

420 *Trichuris arvicolae*

421 *Trichuris arvicolae* was only recovered from four age class 3 female voles, all from Pilchy. One
422 infected vole was from 1999 and three from 2010. Two of the animals with *T. arvicolae* in 2010
423 carried 2 worms each and the other two only had a single worm. These data were not analysed
424 further.

425

426 *Prevalence and abundance of cestodes*

427 Prevalence of cestodes was 20.6% (17.37 - 24.21) overall (intestinal dwelling adults + larvae
428 combined), highest among voles from Urwitałt in all four surveys and lower at the other 2 sites,
429 with significant spatiotemporal variation as illustrated in Fig. 1E (YEAR x SITE x
430 INFECTION, $\chi^2_6=25.6$, $P<0.0001$). Prevalence was higher among male bank voles (Table 2; SEX x
431 INFECTION, $\chi^2_1=4.75$, $P=0.029$) and increased significantly with host age (Table 2; AGE x
432 INFECTION, $\chi^2_2=50.4$, $P<0.0001$).

433 Analysis of abundance was problematic and could only be carried out using non-parametric
434 tests. Overall abundance was 5.2 ± 1.39 worms/vole but this varied between surveys (Table 3;
435 Kruskal-Wallis test, $\chi^2_3 = 20.11$, $P < 0.0001$) increasing by 6.3 fold between 1999 and 2010. Cestodes
436 were more abundant in bank voles from Tałty and Urwitałt than from Pilchy (Kruskal-Wallis test,
437 $\chi^2_2 = 59.06$, $P < 0.0001$); abundance in Tałty being 6.3 times higher than in Pilchy (Table 3).
438 Abundance increased significantly with host age (Kruskal-Wallis test, $\chi^2_2 = 53.75$, $P < 0.0001$) with
439 much higher abundance among the oldest animals compared with both younger classes (Table 3),
440 but did not differ significantly between the sexes.

441

442 *Prevalence and abundance of adult cestodes*

443 Prevalence of intestinal-dwelling adult stages of cestodes, whether mature or not fecund, was 16.3%
444 (13.36 - 19.61). Summary data for prevalence by each of the four main effects is shown in Table 2.
445 Prevalence was relatively high in 2002, when most of the infected voles were from Urwitałt.
446 Prevalence increased with host age and there appeared to be bias in favour of higher prevalence
447 among male voles. These effects could not be evaluated statistically in a full factorial model,
448 because of complex interactions which could not be broken down further (YEAR x SITE x SEX x
449 INFECTION, $\chi^2_6 = 15.3$, $P = 0.018$ and SITE x SEX x AGE x INFECTION, $\chi^2_4 = 11.9$, $P = 0.018$).
450 However, non-parametric tests showed that there were highly significant effects of YEAR, SITE,
451 and AGE (Kruskal-Wallis test, $P < 0.001$ in all cases) and a weaker effect of SEX (Mann-Whitney *U*
452 test, $P = 0.037$). Fig. 7A illustrates the spatiotemporal dynamics : prevalence was highest at Urwitałt
453 and lowest at Pilchy in three of the four surveys. Peak prevalence occurred among voles from
454 Urwitałt in 2002.

455 Abundance was low with an overall mean of 0.34 ± 0.040 . Mean abundances for all four
456 main effects are shown in Table 3. Attempts at analyses by GLM failed to converge so we used
457 non-parametric tests. Over time, changes in abundance showed a very similar pattern to those for
458 prevalence (Fig. 7B; YEAR $\chi^2_3=28.0$, $P<0.001$), which is not unexpected given that the mean worm
459 burden was less than one, and that 95 out of the 150 voles infected with adult tapeworms carried
460 just one adult worm. All the remaining main effects were significant (for SEX, $U=100,810$,
461 $P=0.037$ [bias in favour of males]; SITE $\chi^2_2=45.5$, $P<0.001$ [most abundant at Urwitait and least at
462 Pilchy]; AGE $\chi^2_2=32.1$, $P<0.001$ [most abundant in age class 3 voles and least in age class 1]).

463

464 *Prevalence and abundance of individual adult cestode species*

465 Of the three species of adult cestodes identified in this study only one, *Catenotaenia henttoneni*,
466 was present in sufficient numbers to merit statistical analysis. In total 138 bank voles harboured *C.*
467 *henttoneni* with an overall prevalence of 15.0% (12.18 - 18.18). As with the analysis of all adult
468 cestodes, backward selection of full factorial models gave two complex interactions (YEAR x SITE
469 x SEX x INFECTION, $\chi^2_6=14.5$, $P=0.024$ and SITE x SEX x AGE x INFECTION, $\chi^2_4=11.0$,
470 $P=0.026$) that could not be broken down further. Prevalence values for all four main effects are
471 shown in Table 4. This species was most prevalent in Urwitait and in Taity (Table 5), showing the
472 highest prevalence at Urwitait in three of the four surveys (Fig. 7C). At Pilchy this species remained
473 relatively rare. Although overall a higher percentage of male voles were infected compared to
474 females, there was no consistency with sex bias changing between the sexes in particular years and
475 sites. For example, in 2002, prevalence among male bank voles in Urwitait was higher than among
476 females (males = 55.0% [38.70 - 70.09], females = 34.4% [21.83 - 48.80]), whereas in Taity it was
477 in the opposite direction (males = 25.6% [13.99 - 41.51], females = 29.4% [17.70 - 44.24]).

478 Similarly, although overall prevalence values increased with host age (Table 5), the age effect was
479 not consistent in both sexes and at all three sites. Males at all three sites showed increasing
480 prevalence with host age, but among female voles only those from Pilchy followed the same
481 pattern. Females from Urwitałt showed the lowest prevalence in age class 2, whilst in Tały this was
482 the age class with the highest prevalence (data not shown).

483 The mean abundance of *C. henttoneni* was 0.32 ± 0.039 worms/vole. Mean values for each
484 of the four main effects are shown in Table 6 and since this was the dominant cestode in the
485 intestine, the values are very similar to those for all adult intestinal cestodes combined (Table 3). As
486 above there was a significant SITE x YEAR interaction (not shown; GLM with negative binomial
487 errors, $LR_{6,907}=35.7$, $P<0.0001$) and this followed a very similar pattern to that in Fig 7B for all
488 intestinal adult cestodes combined. All main effects significantly affected abundance (YEAR,
489 $LR_{3,913}=26.7$, $P<0.0001$; SITE, $LR_{2,913}=28.0$, $P<0.0001$; AGE, $LR_{2,913}=29.5$, $P<0.0001$ and SEX
490 $LR_{1,913}=5.7$, $P=0.017$), but additional interactions could not be tested because more complex models
491 failed to converge.

492 Other adult cestodes were rarer: *Paranoplocephala omphalodes* was present in the 1999,
493 2002 and 2010 surveys at Urwitałt and Pilchy only (prevalence, 1.3% (0.5 - 3.2) and 0.7% (0.2 -
494 2.2), respectively) and just one adult *Arostrilepis horrida* specimen was recovered during the whole
495 study (from a female vole at Urwitałt in 2006). However infections with these adult cestodes were
496 not analysed further because of their low prevalence and abundance.

497

498 *Prevalence and abundance of larval stages of cestodes*

499 Four species of larval cestodes were recovered from the bank voles, two from the peritoneal cavity
500 (*Mesocestoides* sp. and *Taenia martis*) and two from the liver (*Versteria mustelae* and *Cladotaenia*

501 *globifera*). The overall prevalence was 6.9% (5.03 - 9.38). Analysis of prevalence at this level
502 showed that there was a highly significant difference between sites (Table 2; SITE x INFECTION,
503 $\chi^2=29.1$, $P<0.001$). Most infected voles came from Urwitait, with prevalence being much lower
504 among voles from the other two sites and little difference between the latter (Table 2). Prevalence
505 also varied significantly between the successive surveys (Table 2; YEAR x INFECTION, $\chi^2_3=15.5$,
506 $P=0.001$) but there was no consistent trend with two peak years (2002 and 2010), and lower
507 prevalence in the other years. Although prevalence increased with host age (Table 2), this was
508 confounded by host sex (Fig. 4G; AGE x SEX x INFECTION, $\chi^2_2=6.6$, $P=0.037$), because
509 prevalence was higher in male compared with female voles among age classes 2 and 3, but not
510 among the youngest animals in age class 1.

511 Analysis of abundance (Table 3) was not possible by GLM but non-parametric tests showed
512 that the effects of SITE ($\chi^2_2=30.2$, $P<0.001$ [most abundant in Tałty, least in Pilchy]), YEAR
513 ($\chi^2_3=14.9$, $P=0.002$ [most abundant in 2010, least in 1999]), and AGE ($\chi^2_2=46.3$, $P<0.001$ [most
514 abundant in age class 3 and least in age class 1]) were all significant. There was no significant
515 difference in abundance between the sexes.

516

517 *Prevalence and abundance of individual larval cestode species*

518 *Mesocestoides* sp. was present in all surveys in all sites, except at Pilchy in 2006. The
519 overall prevalence was 3.6% (2.29 - 5.47) and mean abundance was 4.2 ± 1.34 . Prevalence was
520 almost identical in the first three surveys, but much higher in 2010 (Table 5; YEAR x INFECTION,
521 $\chi^2_2=9.5$, $P=0.023$) and mean abundance (Table 6) likewise increased from 1999 to 2010.

522 *Mesocestoides* sp. was most commonly encountered at Urwitait (Table 5; SITE x INFECTION, χ^2_2
523 $=18.0$, $P<0.001$), but abundance was numerically higher at Tałty (Table 6) and the parasite was

524 largely confined to the oldest animals (Table 5; AGE x INFECTION, $\chi^2_2=24.2$, $P<0.001$), which
525 also showed the highest overall abundance of worms (Table 6). There was no significant difference
526 in prevalence or abundance between the sexes.

527 *Taenia martis* was less common (2.1% [1.15 - 3.64]), with an overall mean abundance of
528 0.03 ± 0.009 . It was found predominantly at Urwitakt (Table 5; SITE x INFECTION, $\chi^2_2=21.1$,
529 $P<0.001$ and for abundance see Table 6), and among the oldest voles (Table 5; AGE x
530 INFECTION, $\chi^2_2=13.1$, $P=0.001$ and for abundance see Table 6). Prevalence was highest in 2002
531 (Table 5; YEAR x INFECTION, $\chi^2_3=11.8$, $P=0.008$).

532 *Versteria mustelae* (previously known as *Taenia mustelae*; Nakao *et al.* 2013) was rarer still
533 (overall prevalence =1.4% [0.70 - 2.80] and abundance = 0.037 ± 0.016). In contrast to *T. martis*
534 prevalence did not vary between sites (Table 5) although mean abundance was lower among voles
535 from Urwitakt. However, there was a reduction in prevalence and abundance in the last two surveys
536 (Table 5; YEAR x INFECTION, $\chi^2_3=11.8$, $P=0.008$), and although prevalence appeared to increase
537 with host age, this was confounded by an interaction with host sex (AGE x SEX x INFECTION,
538 $\chi^2_2=6.3$, $P=0.043$). As can be seen in Fig. 7D prevalence was very similar (<1%) in females in all
539 age classes, but increased with age in males, exceeding 7% in age class 3 voles. Abundance also
540 increased with host age (Table 6) but this was not tested because of the low prevalence, and as with
541 prevalence the highest value for abundance was among age class 3 male voles (0.175 ± 0.093 ; in
542 age class 3 females abundance = 0.005 ± 0.005).

543 *Cladotaenia globifera* was found in 2002 and 2010. It was present in one vole each from
544 Urwitakt and Pilchy in 2002 and from Tały in 2006, with an overall mean abundance of $0.60 \pm$
545 0.363 , and the highest abundance value from a single vole from Pilchy (250 larvae).

546

547 *Sources of variation in abundance data*

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

558

559 *Canonical Discriminant Function Analysis*

560 Canonical discriminant function (CDF) analysis generated 11 axes that cumulatively accounted for
561 100% of the variance in the data. Axis 1 (Eigenvalue =1.213) accounted for 57.5% of the variance
562 and Axis 2 (Eigenvalue =0.277) for a further 13.1%. Since together these two axes accounted for
563 70.7% of the variance the remaining axes were not examined further. Axis 1 (Fig. 8) essentially
564 contrasts *H. mixtum* (0.64) with *H. glareoli* (-0.68), hence the scatter of data points from Urwitałt
565 and Tały towards the positive range of the Function 1 axis, and those from Pilchy in the negative
566 range. There were additional positive but minor contributions to this axis from *A. annulosa* (0.15)
567 and *C. henttoneni* (0.15) and negative from *A. tianjinensis.* (-0.22). Axis 2 contrasts *H. glareoli*
568 (0.64) with *A. tianjinensis* (-0.53), with additional positive contributions from *H. mixtum* (0.36) and
569 *M. muris* (0.22). *H. glareoli* was mostly found at Pilchy and *M. muris* at Pilchy and Urwitałt, while

570 *A. tianjinensis* was most abundant in Tałty. Fig. 8D shows that the centroids for Urwitałt are the
571 four most positive on the Function 1 axis, followed by those from Tałty in the centre and Pilchy the
572 four most negative on this axis, so there was no overlap of centroids from the 3 sites along the
573 Function 1 axis. This contrasts with extensive overlap on the vertical Function 2 axis for centroids
574 from Urwitałt and Pilchy, and three of the lowest, most negative on this axis being those from Tałty.

575

576 DISCUSSION

577 The data presented in this paper are based on systematic surveys of helminth parasites of wild
578 rodents exploiting exactly the same study sites over a period of more than a decade. As such the
579 dataset represents one of the longest longitudinal studies on wild rodents in the literature. Perhaps
580 the most interesting outcome is that despite the 11 year period between the first and the fourth
581 survey, some indicators of helminth population structure have remained remarkably stable. At the
582 highest taxonomic level the prevalence of all helminths and of all nematodes (all species combined
583 in each case), in each of the three sites showed relatively little change over the study period, as was
584 also the case for core species such as *H. mixtum*, *H. glareoli* and *M. muris*. Our data for *H. mixtum*
585 (particularly at Tałty) have some similarity to those of Bugmyrin *et al.* (2005) who found that
586 annual prevalence of this species over the period between 1996 and 2003 varied only between 20
587 and 40%. Although the worm burdens in that study were lower (generally less than an average of
588 one worm/host) the annual mean burdens hardly varied between year, similarly to our observations
589 at Tałty. *H. mixtum* has been reported previously to have highly stable under-dispersed or weakly
590 aggregated population dynamics (Haukisalmi *et al.* 1986, 1996) and this stability has been linked to
591 the predictable occurrence of this core nematode taxon across wide geographical areas and through
592 relatively long periods of time. However, in our study, the best-fit distribution by far for *H. mixtum*

593 was a negative binomial distribution, and this remained so even when the data from Pilchy (where it
594 was extremely rare) were omitted from the analysis. Therefore, the long-term stability of this
595 species in our sites must be attributable to other factors which are currently not understood, but we
596 hypothesise are likely to be linked to the ecological characteristics of the two woodlands in which
597 this species was most common and possibly intrinsic factors including genetic which are known to
598 differ between these bank vole populations (Kloch *et al.* 2010).

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

607 In marked contrast other measures of infracommunity structure showed dramatic, dynamic
608 changes over the period of study and some species had a disproportionate influence on measures of
609 abundance at the higher taxonomic level. In the cases of both combined helminths and combined
610 nematodes, abundance dropped markedly after the 1999 survey and then stabilized at a considerably
611 lower level. The explanation in this case was the disappearance of *S. petruszewiczi* from each of the
612 three sites over the period, a species that is often found with very high worm burdens in some
613 infected hosts. In 1999 the maximum recorded burden was 4,026 worms in a single vole.
614 Abundance was lower in 2002 and then, despite increased sampling effort in the following two
615 surveys, the parasite disappeared completely (our unpublished observations in 2014 also showed no
616 *Syphacia* in any of these populations). *Syphacia* species all have the potential to give rise to very

617 intense infections with thousands of worms in a single individual, probably mostly as a result of
618 autoinfection, but usually in only a few intensely infected individuals (Grear and Hudson, 2011).
619 Why this parasite should die out in each of these three populations is not known since there has
620 been virtually no noticeable ecological change over the period in the sites, other than the generally
621 well perceived climatic trends associated with global warming throughout Europe (European
622 Environment Agency, 2014; Michalska, 2011; Institute of Meteorology and Water Management,
623 Poland, 2013) and infrequent harvesting of trees from the forests by the Polish Government's
624 Department of Forestry (Zajączkowski *et al.* 2014; Nadleśnictwo Pisz 2014). None of the three sites
625 in which we sampled voles has been directly affected by felling, but adjoining areas have been
626 felled and replanted, and in 2002 parts of the Pilchy site adjoining, but not directly at, our sampling
627 site, experienced significant wind damage.

628 In marked contrast to the disappearance of *S. petrusewiczii*, other species increased
629 significantly in prevalence and abundance. *A. annulosa* was notable among these species. It was not
630 detected at all in any of the voles sampled in 1999. It then increased steadily in Urwitałt, to a lesser
631 extent in Tałty but was still found only sporadically in Pilchy. This increase in both prevalence and
632 abundance of *A. annulosa* across the 11 years of our study bears some similarity to the consistent
633 increase in prevalence of *Aoncotheca murissylvatici* (previously *Capillaria murissylvatici* and a
634 sister species of *A. annulosa*; Moravec, 1982; 2000) in bank voles over five years reported by
635 Haukisalmi, Henttonen and Tenora (1988). In some respects the increase in *A. annulosa* in Urwitałt
636 and Tałty was mirrored by the loss of *S. petrusewiczii* although whether these events were related
637 causally, or just by coincidence in timing, is not known. Not surprisingly therefore, the values of
638 helminth species richness and Brillouin's index of diversity remained relatively steady without
639 major change as loss of one species was compensated by gain of the other.

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

657 The relatively greater influence of extrinsic factors, compared with intrinsic factors, on
658 helminth communities has parallels in other host-helminth systems and site of capture in particular
659 is known to play a major role since it largely determines the infective stages that hosts are likely to
660 be exposed to (Mollhagan, 1978; Abu-Madi *et al.* 1998; Calvete *et al.* 2004; Booth, 2006). The
661 spectrum of infective agents in any given locality is dependent primarily on the availability of the
662 most abundant hosts in the vicinity and the parasites that they carry, and stochastic events (local
663 introductions/ extinctions) can drastically alter the local range of available pathogens. However, the

664 ecology of the environment provides a major source of variation for the risk of infection since both
665 the survival of resident and introduced infective stages of parasites may be affected, and as expected
666 helminth communities have been found to vary between rodents sampled in ecologically quite
667 different habitats (Kinsella, 1974; Martin and Huffman, 1980; Haukisalmi, Henttonen and Tenora,
668 1987; Montgomery and Montgomery, 1988, 1989; Abu-Madi *et al.* 1998, 2000; Simões *et al.* 2010;
669 Ribas *et al.* 2011), although not universally (Haukisalmi, Henttonen and Tenora, 1987; Milazzo *et*
670 *al.* 2003). However, it is relevant that, as here, helminth communities in wild rodents have also been
671 found to differ significantly among animals from sites which differ very little ecologically and are
672 located in close proximity to one another (Behnke *et al.* 2001; Montgomery and Montgomery,
673 1990; Krasnov *et al.* 2010).

674 As expected many measures of infracommunity structure increased with host age (Tenora
675 and Zejda, 1974; Montgomery and Montgomery, 1989). The worm burdens of individual species,
676 helminth species richness and diversity all generally increased, whether examined in year specific
677 cohorts or by site. There were few exceptions, as indicated earlier. This pattern of increasing
678 prevalence and abundance of worm burdens with host age has been reported consistently in wild
679 rodents (Montgomery and Montgomery, 1989; Janova *et al.* 2010), including bank voles (e.g.
680 *Apostatandrya macrocephala* in Haukisalmi, Henttonen and Tenora, 1988 and *H. mixtum* in
681 Bugmyrin *et al.* 2005) and is almost certainly generated through the accumulation of these long-
682 lived parasites throughout the life of the host (e.g. *M. muris* is believed to live for at least a year in
683 wild rodents (Rausch and Tiner, 1949, citing Kirschenblatt, 1938)). Some studies show a decline in
684 intestinal nematode burdens in older animals, perhaps indicating acquired resistance to infection
685 (Haukisalmi, Henttonen and Tenora, 1988; Gregory, Montgomery and Montgomery, 1992; Behnke
686 *et al.* 1999), but there was little evidence of such a decline with age in our data, other than in the
687 occasional data subset, as for example in *H. glareoli* in 1999. This lack of evidence for

688 immunological resistance may be due to the high mortality experienced by *C. glareolus* at these
689 sites; with 50% survival time for bank voles at Urwitałt varying between one and three months
690 (Paziewska *et al.* 2012), in order to detect immunological elimination in the current data set, the
691 effect would have to be particularly strong. Overall, as Fig. 2 shows, the increase in worm burdens
692 with host age was among the strongest intrinsic and most consistent effects on parasite prevalence
693 and abundance observed in the current work and particularly marked in the case of helminth
694 diversity.

695 In contrast to the age effect, there were few cases of sex-biased prevalence or abundance.
696 We found no evidence for a sex bias in *H. mixtum*, as reported by Haukisalmi, Henttonen and
697 Tenora (1988), and more recently Bugmyrin *et al.* (2005). In our case convincing and consistent
698 disparities between the sexes were detected only in *M. muris* and *A. annulosa* and in both cases
699 prevalence was higher in females and cumulatively this was sufficient to generate a significant
700 female sex bias in MSR of helminths. The higher prevalence of *M. muris* in female bank voles
701 compared with males, has been discussed in some detail in Grzybek *et al.* (2015), and has been
702 reported previously in these populations (Behnke *et al.* 2008b). Haukisalmi, Henttonen and Tenora
703 (1988), also found a higher prevalence and intensity of *M. muris* in older female bank voles that had
704 overwintered and survived until the autumn, but reported also a trend in the opposite direction
705 among summer born mature bank voles. In our data, all other cases of significant sex effects arose
706 only as interactions, with the balance changing between dominance in males and then females
707 depending on year of survey or site. The few instances of sex bias in helminth infections in our data
708 are consistent with the literature for wild rodents, where generally it has been found that differences
709 between the sexes in the worm burdens they carry are minimal (Kisielewska 1970b; Abu-Madi *et*
710 *al.* 2000; O’Sullivan, Smal and Fairley, 1984; Bordes *et al.* 2012) but we cannot exclude the
711 possibility that sex-bias is season dependent. All of our sampling was conducted in late summer and

712 early autumn period and it is possible that at other times of the year, host sex-differences in the
713 abundance of some species are more evident and perhaps related to seasonally dependent sexual
714 dichotomy in reproductive behaviour.(Bajer et al., 2005).

715 Although our study was based on destructive cross-sectional surveys, our trap lines covered
716 only a very small area of the extensive forests in each site. Cross-sectional studies based on
717 destructive sampling will have consequences for host populations if conducted too frequently,
718 depending on the number of animals culled and the frequency and extent of culling relative to the
719 total population. Host population density is known to influence parasite burdens (Arneberg, 2001),
720 so any marked reduction in host population as a result of intervention is likely to have an impact on
721 helminth community structure. Moreover, migration of animals from neighbouring areas into a
722 sample site where density has been reduced may alter the parasite community structure subtly.
723 However, from other work in contiguous forest sites, and elsewhere, it is known that bank vole
724 populations decline markedly in the winter and early spring each year but return to a peak in late
725 summer or autumn (Alibhai and Gipps, 1985; Bujalska, 2000; Bajer *et al.* 2005). Sampling at three
726 or four-year intervals, at the peak of population density in early autumn, therefore, constitutes a
727 reasonable compromise in facilitating assessment of helminth populations in bank voles without
728 imposing major losses on the host population and destabilizing the transmission of parasites. An
729 alternative is to adopt mark-release-recapture methods (MRR) to generate longitudinal data based
730 on indirect measures of parasite burdens acquired by non-destructive methods such as by faecal egg
731 counts (FEC; Knowles *et al.* 2013). There is a strong positive correlation between parasite numbers
732 and FEC in some species (Keymer and Hiorns, 1986; Quinnell, 1992), and FEC are widely used to
733 assess intestinal helminth infections in humans (Bundy, 1990; Levecke *et al.* 2011). However,
734 although FEC can be useful in a prevalence context framework, it is not helpful for the estimation
735 of some parasite burdens such as those of pinworms of the genus *Syphacia* spp. (among the most

736 common genus of helminths of European wild rodents). *Syphacia* spp. release eggs onto the
737 perianal surface of their hosts and not in faeces (Lewis and D'Silva, 1986; Baker, 2007) and egg
738 shedding by pinworms can be intermittent (Lewis and D'Silva, 1980; Hill, Randolph and Mandrell,
739 2009). Reliance on FEC also misses juvenile, as yet non-fecund worms, and males, in
740 circumstances where sex ratio may not be unity (Anderson, 1982). Most importantly however, egg
741 output by helminths is density dependent (Anderson, 1982), and FEC cannot be always extrapolated
742 to estimate worm burden accurately (Ghazal and Avery, 1974). Density dependence is well
743 understood at an intra-specific level, but is also known to occur between parasite species, and
744 understanding inter-specific interactions is another goal of studies such as this one (data currently in
745 preparation for publication); it is impossible using FEC to distinguish between inter-specific effects
746 on egg outputs of individual worms, and interspecific effects on worm density. Finally, some
747 helminths, most notably *Syphacia* spp. show a highly aggregated distribution of worm burdens
748 among hosts (Scott and Gibbs, 1986; Grear and Hudson, 2011) and some rodents may harbour
749 thousands of individual worms, as found in the current study. This overdispersed distribution would
750 be entirely missed by faecal egg counts (Baker, 2007), because as stated above relatively few
751 *Syphacia* eggs actually end up in the faeces. It is also relevant that FEC cannot quantify the larval
752 stages of helminths that reside deep within the host in organs such as the liver (e.g. such as
753 tapeworm cysts *Taenia taeniaeformis*, *V. mustellae*, *C. globifera*), and for which rodents act as
754 intermediate hosts. Again, as we have found, the parasite burdens with some of these species may
755 be immense; for example, several hundred *Mesocestoides* individuals may occur in a single host
756 animal (Behnke *et al.* 2008a).

757 Finally, the work reported in this paper, has built on our earlier publications (Behnke *et al.*
758 2001, 2008b), extending the period over which the helminth communities of bank voles in our three
759 sites in NE Poland have been monitored by a further 8 years (2006 and 2010). Our data emphasize

760 that despite the fluctuations that characterise the prevalence and abundance of the rarer species,
761 there is a large element of stability generated by the dominant species which show little change over
762 time. This contrasts with the patterns of change detected for haemoparasites, where each of the five
763 species studied showed a different pattern of spatiotemporal change over the eleven years (Bajer *et*
764 *al.* 2014). The picture with helminths is further complicated by clear trends leading to extinction of
765 species (as in the case of *S. petruszewiczi*, at least in our sites, but presumably not elsewhere in the
766 vicinity) and the influx of new species (as in the case of *A. annulosa*) which in time may eventually
767 join the dominant species as established members of the community at particular sites. Our research
768 has generated a long-term dataset, which provides fundamental information about the community
769 ecology of a complex natural system and our findings caution against snap-shot, single cross-
770 sectional surveys that may not provide all the relevant information for hypotheses about parasite-
771 derived long-term selective pressures on hosts living in specific sites. The baseline data we have
772 generated provide a foundation to explore the mechanisms that shape long-term trends in complex
773 communities and continued monitoring of this system will strengthen inferences and focus
774 hypotheses.

775

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787

788 REFERENCES

- 789 **Abu-Madi, M. A., Behnke, J. M., Lewis, J. W. and Gilbert, F. S.** (1998). Descriptive
790 epidemiology of *Heligmosomoides polygyrus* in *Apodemus sylvaticus* from three contrasting
791 habitats in south-east England. *Journal of Helminthology* **72**, 93-100.
- 792 **Abu-Madi, M. A., Behnke, J. M., Lewis, J. W. and Gilbert, F. S.** (2000). Seasonal and site
793 specific variation in the component community structure of intestinal helminths in *Apodemus*
794 *sylvaticus* from three contrasting habitats in south-east England. *Journal of Helminthology* **74**,
795 7-16.
- 796 **Alibhai, S. K. and Gipps, J. H. W.** (1985). The population dynamics of bank voles. In *The Ecology*
797 *of Woodland Rodents, Bank voles and Wood Mice* (Eds J.R. Flowerdew, J. Gurnell and
798 J.H.W. Gipps). Clarendon Press, Oxford. *Symposia of the Zoological Society of London* **55**,
799 277-313.
- 800 **Anderson, R. M.** (1982). The population dynamics and control of hookworm and roundworm
801 infections In *Population Dynamics of Infectious Diseases. Theory and Applications* (ed.
802 R.M.Anderson) Chapman and Hall, London Pp 67-108.
- 803 **Arneberg, P.** (2001). An ecological law and its macroecological consequences as revealed by studies
804 of relationships between host densities and parasite prevalence. *Ecography* **24**, 352-358.
- 805 **Bajer, A., Behnke, J. M., Pawelczyk, A., Kulis, K., Sereida, M. J. and Siński, E.** (2005). Medium-
806 term temporal stability of the helminth component community structure in bank voles
807 (*Clethrionomys glareolus*) from the Mazury Lake District region of Poland. *Parasitology* **130**,
808 213-228.

- 809 **Bajer, A., Welc-Faleciak, R., Bednarska, M., Alsarraf, M., Behnke-Borowczyk, J., Siński, E.**
810 **and Behnke, J. M.** (2014). Long-term spatiotemporal stability and dynamic changes in the
811 haemoparasite community of bank voles (*Myodes glareolus*) in NE Poland. *Microbial*
812 *Ecology* **68**, 196-211.
- 813 **Baker, D. G.** (2007). Parasites of rats and mice. In: Baker DG, editor. *Flynn's Parasites of*
814 *Laboratory Animals*, 2nd ed. Ames (IA): Blackwell Publishing. Pp 339–340.
- 815 **Barnard, C. J., Behnke, J. M., Bajer, A., Bray, D., Race, T., Frake, K., Osmond, J., Dinmore, J.**
816 **and Siński E.** (2002). Local variation in endoparasite intensities of bank voles
817 (*Clethrionomys glareolus*) from ecologically similar sites: morphometric and endocrine
818 correlates. *Journal of Helminthology* **76**, 103-112
- 819 **Barnard, C. J., Kuliś, K., Behnke, J. M., Bajer, A., Gromadzka-Ostrowska, J, Stachon, M. and**
820 **Siński, E.** (2003). Local variation in helminth burdens of bank voles (*Clethrionomys*
821 *glareolus*) from ecologically similar sites: temporal stability and relationships with hormone
822 concentrations and social behaviour. *Journal of Helminthology* **77**, 185-195.**Behnke, J. M.,**
823 **Bajer, A., Harris, P. D., Newington, L., Pidgeon, E., Rowlands, G., Sheriff, C., Kuliś-**
824 **Malkowska, K., Siński, E., Gilbert, F. S. and Barnard, C. J.** (2008a). Temporal and
825 between-site variation in helminth communities of bank voles (*Myodes glareolus*) from N.E.
826 Poland. 1. Regional fauna and component community levels. *Parasitology* **135**, 985-997.
- 827 **Behnke, J. M., Bajer, A, Harris, P. D., Newington, L., Pidgeon, E., Rowlands, G., Sheriff, C.,**
828 **Kuliś-Malkowska, K., Siński, E., Gilbert, F. S., and Barnard, C. J.** (2008b) Temporal and
829 between-site variation in helminth communities of bank voles (*Myodes glareolus*) from NE
830 Poland. 2. The infracommunity level. *Parasitology* **135**, 999 -1018.
- 831 **Behnke, J. M., Barnard, C. J., Bajer, A., Bray, D., Dinmore, J., Frake, K., Osmond, J., Race, T.**
832 **and Siński E.** (2001). Variation in the helminth community structure in bank voles
833 (*Clethrionomys glareolus*) from three comparable localities in the Mazury Lake District
834 region of Poland. *Parasitology* **123**, 401-414.
- 835 **Behnke, J. M., Lewis, J. W., Mohd Zain, S. N. and Gilbert, F. S.** (1999). Helminth infections in
836 *Apodemus sylvaticus* in southern England: interactive effects of host-age, sex and year on
837 prevalence and abundance of infections. *Journal of Helminthology* **73**, 31 - 44.

- 838 **Behnke, J. M., Stewart, A., Bajer, A., Grzybek, M., Harris, P. D, Lowe, A. , Ribas, A., Smales,**
839 **L. and Vandegrift, K. J.** (2016). Bank voles (*Clethrionomys glareolus*) and house mice (*Mus*
840 *musculus musculus/domesticus*) in Europe are each parasitized by their own distinct species of
841 *Aspiculuris* (Nematoda, Oxyurida). *Parasitology* Under review.
- 842 **Boag, B., Lello, J., Fenton, A., Tompkins, D.M. and Hudson, P.J.** (2001). Patterns of parasite
843 aggregation in the wild European rabbit (*Oryctolagus cuniculus*). *International Journal for*
844 *Parasitology* **31**, 1421–1428.
- 845 **Booth, M.** (2006). The role of residential location in apparent helminth and malaria associations.
846 *Trends in Parasitology* **22**, 359-362.
- 847 **Bordes, F., Ponlet, N., de Bellocq, J. G., Ribas, A., Krasnov, B. R. and Morand, S.** (2012). Is
848 there sex-biased resistance and tolerance in Mediterranean wood mouse (*Apodemus*
849 *sylvaticus*) populations facing multiple helminth infections ? *Oecologia* **170**, 123-135.
- 850 **Bugmyrin, S. V., Ieshko, E. P., Anikanova, V. A. and Bespyatova, L. A.** (2005). Patterns of host-
851 parasite interactions between the nematode *Heligmosomum mixtum* (Schulz, 1952) and the
852 bank vole (*Clethrionomys glareolus* Schreber, 1780). *Parasitologia* **39**, 414-422.
- 853 **Bujalska, G.** (2000). The bank vole population in Crab-apple Island. *Polish Journal of Ecology* **48**
854 (Suppl.), 97-106.
- 855 **Bundy, D. A. P.** (1990). Is the hookworm just another geohelminth? Chapter 10 In *Hookworm*
856 *Disease. Current Status and New Directions*. Eds G.A.Schad and K.S.Warren. , Pp 147-164;
857 London: Taylor and Francis.
- 858 **Calvete, C., Blanco-Aguilar, J. A., Virgós, E., Cabezas-Díaz, S. and Villafuerte, R.** (2004). Spatial
859 variation in helminth community structure in the red-legged partridge (*Alectoris rufa* L.):
860 effects of definitive host density. *Parasitology* **129**, 101-113.
- 861 **Carleton, M. D., Gardner, A. L., Pavlinov, I. Y. and Musser, G. G.** (2014). The valid generic
862 name for red-backed voles (Muroidea: Cricetidae: Arvicolinae): restatement of the case for
863 *Myodes* Pallas, 1811. *Journal of Mammology* **95**, 943-959.
- 864 **Carleton, M. D., Musser, G. G. and Pavlinov, I. A.** (2003). *Myodes* Pallas, 1811, is the valid name
865 for the genus of red-backed voles. In *Systematics, Phylogeny and Paleontology of Small*
866 *Mammals. Proceedings of the International Conference devoted to the 90th anniversary of*

867 Prof. I.M. Gromov, November 2003, Saint Petersburg (ed. Averianov, A. and Abramson, N.),
868 P. 96.

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

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

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

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

878 **European Environment Agency** (2014). <http://www.eea.europa.eu/themes/climate>. Accessed 16th
879 September 2014.

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

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

884 **Gregory, R. D., Montgomery, S. S. J. and Montgomery, W. I.** (1992). Population biology of
885 *Heligmosomoides polygyrus* (Nematoda) in the wood mouse. *Journal of Animal Ecology* **61**,
886 749-757.

887 **Grzybek, M., Bajer, A., Behnke-Borowczyk, J., Alsarraf, M. and Behnke, J.M.** (2015) Female
888 host sex-biased parasitism with the rodent stomach nematode *Mastophorus muris* in wild
889 bank voles (*Myodes glareolus*). *Parasitology Research* **114**, 523-533.

890 **Haukisalmi, V.** 1986. Frequency distributions of helminths in microtine rodents in Finnish Lapland.
891 *Annales Zoologici Fennici* **23**, 141-150.

- 892 **Haukisalmi, V. and Henttonen, H.** (1990). The impact of climatic factors and host density on the
893 long-term population dynamics of vole helminths. *Oecologia* **83**, 309-315.
- 894 **Haukisalmi, V. and Henttonen, H.** (2000). The variability of helminth assemblages and populations
895 in the bank vole *Clethrionomys glareolus*. *Polish Journal of Ecology* **48** (Suppl.), 219 – 231.
- 896 **Haukisalmi, V., Henttonen, H. and Tenora, F.** (1987). Parasitism by helminths in the grey-sided
897 vole (*Clethrionomys rufocanus*) in northern Finland: influence of density, habitat and sex of
898 the host. *Journal of Wildlife Diseases* **23**, 233-241.
- 899 **Haukisalmi, V., Henttonen, H. and Tenora, F.** (1988). Population dynamics of common and rare
900 helminths in cyclic vole populations. *Journal of Animal Ecology* **57**, 807-825.
- 901 **Haukisalmi V., Henttonen H. and Vikman P.** 1996. Variability of sex ratio, mating probability
902 and egg production in an intestinal nematode in its fluctuating host population. *International*
903 *Journal for Parasitology* **26**, 755-764.
- 904 **Hill, W. A., Randolph, M. M. and Mandrell, T. D.** (2009) Sensitivity of perianal tape impressions
905 to diagnose pinworm (*Syphacia* spp.) infections in rats (*Rattus norvegicus*) and mice (*Mus*
906 *musculus*). *Journal of the American Association for Laboratory Animal Science* **48**, 378-380.
- 907 **Hudson, P. J., Cattadori, I. M., Boag, B., and Dobson, A. P.** (2006). Climatic disruption and
908 parasite-host dynamics: patterns and processes associated with warming and frequency of
909 extreme climatic events. *Journal of Helminthology* **80**, 175-182.
- 910 **Huntley, J. W., Fürsich, F. T., Alberti, M., Hethke, M. and Liu, C.** (2014). A complete Holocene
911 record of trematode-bivalve infection and implications for the response of parasitism to
912 climate change. *Proceedings of the National Academy of Sciences, USA* **111**, 18150-18155.
- 913 **Institute of Meteorology and Water Management (Instytut Meteorologii i Gospodarki Wodnej)**
914 **National Research Institute of Poland (Państwowy Instytut Badawczy)** (2013). Climate
915 change and climate variability in Poland. COP19/CMP9 United Nations Climate Change
916 Conference, 11-22 November 2013, Warsaw, Poland.
- 917 **Jackson, J. A., Hal, A. J., Friber, I. M., Ralli, C., Lowe, A., Zawadzka, M., Turner, A. K.,**
918 **Stewart, A., Birtles, R. J., Paterson, S., Bradley, J. E. and Begon, M.** (2014). An
919 immunological marker of tolerance to infection in wild rodents. *PLoS Biology* **12**, e1001901.

- 920 **Janova, E., Skoric, M., Heroldova, M., Tenora, F., Fictum, P. and Pavlik, I.** (2010).
921 Determinants of the prevalence of *Heligmosomum costellatum* (Heligmosomidae:
922 Trichostrongyloidea) in a common vole population in southern Moravia, Czech Republic.
923 *Journal of Helminthology* **84**, 410-414.
- 924 **Keith, L. B., Cary, J. R., Yuill, T. M. and Keith, I. M.** (1985). Prevalence of helminths in a cyclic
925 snowshoe hare population. *Journal of Wildlife Diseases* **21**, 233-253.
- 926 **Keymer, A. E. and Hiorns, R. W.** (1986). Faecal egg counts and nematode fecundity:
927 *Heligmosomoides polygyrus* and laboratory mice. *Parasitology* **93**, 189-203.
- 928 **Kinsella, J. M.** (1974). Comparison of helminth parasites of the cotton rat, *Sigmodon hispidus*, from
929 several habitats in Florida. *American Museum Novitates* 2540, 1-11.
- 930 **Kirschenblatt, N. I.** (1938). Die Gesetzmaessigkeiten der Dynamik der Parasitenfauna bei den
931 mauseaehnlichen Nagetieren (Muriden) in Transkaukasien . Dissertation of the University of
932 Leningrad pp.5-92 (In Russian, with a German Summary).
- 933 **Kisielewska, K.** (1970a). Ecological organization of intestinal helminth groupings in *Clethrionomys*
934 *glareolus* (Schreb.) (Rodentia). 1. Structure and seasonal dynamics of helminth groupings in a
935 host population in the *Bialowieza National Park*. *Acta Parasitologica Polonica* **18**, 121-147.
- 936 **Kisielewska, K.** (1970b). Ecological organization of intestinal helminth groupings in *Clethrionomys*
937 *glareolus* (Schreb.) (Rodentia). III. Structure of the helminth groupings in *C. glareolus*
938 populations of various forest biocoenoses in Poland. *Acta Parasitologica Polonica* **18**, 163-
939 176.
- 940 **Kloch, A., Babik, W., Bajer, A., Siński, E. and Radwan, J.** (2010). Effects of an MHC-DRB
941 genotype and allele number on the load of gut parasites in the bank vole *Myodes glareolus*.
942 *Molecular Ecology* **19**, 255-265.
- 943 **Knowles, S. C. L., Fenton, A., Petchey, O. L., Jones, T. R., Barber, R., Pedersen, A. B.** (2013).
944 Stability of within-host-parasite communities in a wild mammal system. *Proceedings of the*
945 *Royal Society B* **280**: 20130598.
- 946 **Krasnov, B. R., Mouillot, D., Shenbrot, G. I., Khokhlova, I. S., Vinarski, M. V., Korrallo-**
947 **Vinarskaya, N. P. and Poulin, R.** (2010). Similarity in ectoparasite faunas of Palaearctic

- 948 rodents as a function of host phylogenetic, geographic or environmental distances: Which
949 matters the most? *International Journal for Parasitology* **40**, 807-817.
- 950 **Langley, R. and Fairley, J. S.** (1982). Seasonal variations in infestations of parasites in a wood
951 mouse *Apodemus sylvaticus* population in the west of Ireland. *Journal of Zoology, London*
952 **198**, 249-261.
- 953 **Levecke, B., Behnke, J. M., Ajjampur, S. S. R., Albonico, M., Ame, S. M., Charlier, J., Geiger,**
954 **S. M., Hoa, N. T. V., Kamwa Ngassam, R. I., Kotze, A. C., McCarthy, J. S., Montresor,**
955 **A., Periago, M. V., Roy, S., Tchuem Tchuente, L.-A., Thach, D. T. C. and Vercruyssen, J.**
956 (2011). A Comparison of the Sensitivity and Fecal Egg Counts of the McMaster Egg
957 Counting and Kato-Katz Thick Smear Methods for Soil-Transmitted Helminths. *PLoS*
958 *Neglected Tropical Diseases* **5**, e1201.
- 959 **Lewis, J. W.** (1968). Studies on the helminth parasites of the long-tailed field mouse, *Apodemus*
960 *sylvaticus sylvaticus* from Wales. *Journal of Zoology, London* **154**, 287-312.
- 961 **Lewis, J. W. and D'Silva, J.** (1980) Rhythmic egg deposition by the oxyurid nematode *Syphacia*
962 *muris* in the rat. *Journal of Zoology, London* **191**, 429-433.
- 963 **Lewis, J. W. and D'Silva, J.** (1986) The life-cycle of *Syphacia muris* Yamaguti (Nematoda:
964 Oxyuroidea) in the laboratory rat. *Journal of Helminthology* **60**, 39-46.
- 965 **Liu, B., Bu, Y. and Zhang, L.** (2012). A new species of *Aspiculuris* Schulz, 1924 (Nematoda,
966 Heteroxynematidae) from the gray-sided vole, *Clethrionomys rufocanus* (Rodentia,
967 Cricetidae), from Tianjin, China. *Acta Parasitologica* **57**, 311-315.
- 968 **Martin, J. L. and Huffman, D. G.** (1980). An analysis of the community and population dynamics
969 of the helminths of *Sigmodon hispidus* (Rodentia: Cricetidae) from three central Texas
970 vegetational regions. *Proceedings of the Helminthological Society of Washington* **47**, 247-
971 255.
- 972 **Michalska, B.** (2011). Tendencies of air temperature changes in Poland. *Prace i Studia Geograficzne*
973 **47**, 67-75.

- 974 **Milazzo, C., Casanova, J. C., Aloise, G., Ribas, A. and Cagnin, M.** (2003). Helminths of the bank
975 vole *Clethrionomys glareolus* (Rodentia, Arvicolinae) in southern Italy. *Italian Journal of*
976 *Zoology* **70**, 333-337.
- 977 **Mollhagan, T.** (1978). Habitat influence on helminth parasitism of the cotton rat in western Texas,
978 with remarks on some of the parasites. *The Southwestern Naturalist* **23**, 401-407.
- 979 **Montgomery, S. S. J. and Montgomery, W. I.** (1988). Cyclic and non-cyclic dynamics in
980 populations of the helminth parasites of wood mice *Apodemus sylvaticus*. *Journal of*
981 *Helminthology* **62**, 78-90.
- 982 **Montgomery, S. S. J. and Montgomery, W. I.** (1989). Spatial and temporal variation in the
983 infracommunity structure of helminths of *Apodemus sylvaticus* (Rodentia: Muridae).
984 *Parasitology* **98**, 145-150.
- 985 **Montgomery, S. S. J. and Montgomery, W. I.** (1990). Structure, stability and species interactions
986 in helminth communities of wood mice *Apodemus sylvaticus*. *International Journal for*
987 *Parasitology* **20**, 225-242.
- 988 **Moravec, F.** (1982). Proposal of a new systematic arrangement of nematodes of the family
989 Capillariidae. *Folia Parasitologica* **29**, 119-132.
- 990 **Moravec, F.** (2000). Review of capillariid and trichosomoidid nematodes from mammals in the
991 Czech Republic and the Slovak Republic. *Acta Societatis Zoologicae Bohemicae* **64**, 271-304.
- 992 **Nadleśnictwo Pisz** (2014). *Monitoring Stanu Lasu*. Nadleśnictwo Pisz, Lasy Państwowe, Poland.
993 [http://www.pisz.bialystok.lasy.gov.pl/documents/62733/22275741/monitoring+stanu+lasu+24](http://www.pisz.bialystok.lasy.gov.pl/documents/62733/22275741/monitoring+stanu+lasu+24-03-2014.pdf)
994 [-03-2014.pdf](http://www.pisz.bialystok.lasy.gov.pl/documents/62733/22275741/monitoring+stanu+lasu+24-03-2014.pdf). Accessed 19th September 2014.
- 995 **Nakao, M., Lavikainen, A., Iwaki, T, Haukisalmi, V., Konyaev, S., Oku, Y., Okamoto, M. and**
996 **Ito, A.** (2013). Molecular phylogeny of the genus *Taenia* (Cestoda: Taeniidae): Proposals for
997 the resurrection of *Hydatigera* Lamarck, 1816 and the creation of a new genus *Versteria*.
998 *International Journal for Parasitology* **43**, 427-437.
- 999 **O'Sullivan, H. M., Smal, C. M. and Fairley, J. S.** (1984). A study of parasitic infestations in
1000 populations of small rodents (*Apodemus sylvaticus* and *Clethrionomys glareolus*) on Ross
1001 Island, Killarney. *Journal of Life Sciences of the Royal Dublin Society* **5**, 29-42.

- 1002 **Paziewska, A., Harris, P. D., Zwolińska, L., Bajer, A. and Siński, E.** (2012). Differences in the
1003 ecology of *Bartonella* infections of *Apodemus flavicollis* and *Myodes glareolus* in a boreal
1004 forest. *Parasitology* **139**, 881-893.
- 1005 **Poulin, R.** (1993). The disparity between observed and uniform distributions: a new look at parasite
1006 aggregation. *International Journal for Parasitology* **23**, 937-944.
- 1007 **Quinnell R. J.** (1992). The population dynamics of *Heligmosomoides polygyrus* in an enclosure
1008 population of wood mice. *Journal of Animal Ecology* **61**, 669-679.
- 1009 **Rausch, R. and Tiner, J. D.** (1949). Studies on the parasitic helminths of the North Central States.
1010 II. Helminths of voles (*Microtus* spp.). Preliminary report. *American Midland Naturalist* **41**,
1011 665-694.
- 1012 **Ribas, S. A., Guivier, E., Xuéreb, A., Chaval, Y., Cadet, P., Poulle, M.-L., Sironen, T.,**
1013 **Voutilainen, L., Henttonen, H., Cosson, J.-F., Charbonnel, N.** (2011). Concomitant
1014 influence of helminth infection and landscape on the distribution of Puumala hantavirus in its
1015 reservoir, *Myodes glareolus*. *BMC Microbiology* **11**, 30.
- 1016 **Rohlf, F. J. and Sokal, R. R.** (1995). *Statistical Tables*. Freeman W.H. and Company, San
1017 Francisco.
- 1018 **Scott, M. E. and Gibbs, H. C.** (1986). Long-term population dynamics of pinworms (*Syphacia*
1019 *obvelata* and *Aspicularis tetraptera*) in mice. *Journal of Parasitology* **72**, 652-662.
- 1020 **Simões, R., Gentile, R., Rademaker, V., D'Andrea, P., Herrera, H., Freitas, T., Lanfredi, R. and**
1021 **Maldonado, A. Jr.** (2010). Variation in the helminth community structure of *Thrichomys*
1022 *pachyurus* (Rodentia: Echimyidae) in two sub-regions of the Brazilian Pantanal: the effects of
1023 land use and seasonality. *Journal of Helminthology* **84**, 266-275.
- 1024 **Tenora, F and Staněk, M.** (1995). Changes of the helminthofauna in several muridae and
1025 Arvicolidae at Lednice in Moravia. II. Ecology. *Acta Universitatis Agriculturae et*
1026 *Silviculturae Mendelianae Brunensis* **43** 57-65.
- 1027 **Tenora, F. and Zejda, J.** (1974). The helminth synusy of *Clethrionomys glareolus* in a lowland
1028 forest and its changes. *Acta Scientiarum Naturalium - Academiae Scientiarum*
1029 *Bohemoslovacae*, Brno **6**, 1-48.

- 1030 **Tenora, F., Wiger, R. and Barus, V.** (1979). Seasonal and annual variations in the prevalence of
1031 helminths in a cyclic population of *Clethrionomys glareolus*. *Holarctic Ecology* **2**, 176-
1032 181. **Tesakov, A. S., Lebedev, V. S., Bannikova, A. A. and Abramson, N. I.** (2010).
1033 *Clethrionomys* Tilesius, 1850 is the valid generic name for red-backed voles and *Myodes*
1034 Pallas, 1811 is a junior synonym of *Lemmus* Link, 1795. *Russian Journal of Theriology* **9**, 83-
1035 86.
- 1036 **Xu, R.** (2003). Measuring explained variation in linear mixed effects models. *Statistics in Medicine*
1037 **22**, 3527-3541.
- 1038 **Zajączkowski, G., Jabłoński, M., Jabłoński, T., Malecka, M., Kowalska, A., Małachowska, J.**
1039 **and Piwnicki, J.** (2014). *Raport o stanie lasów w Polsce 2013*. Centrum Informacyjne Lasów
1040 Państwowych, Warszawa, Poland.
- 1041
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1043 Table 1. Number of voles sampled in successive surveys, by site, and host age and sex
 1044

			Age class			Totals		
Site	Year	Sex	1	2	3	Row	Site & year	
Urwitaft	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		
Tafty	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			

1097						
1098	Total by sex	Males	147	198	126	471
1099		Females	133	130	188	451
1100		Both sexes	280	328	314	922
1101	<hr/>					

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					
Urwitalt	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)
Talty	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

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)
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
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
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
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
Site						
Urwitalt	1.76 ± 0.071	0.25 ± 0.017	30.3 ± 13.46	23.8 ± 13.35	6.5 ± 1.81	0.63 ± 0.101
Talty	1.32 ± 0.059	0.16 ± 0.014	40.1 ± 11.14	31.8 ± 10.50	8.2 ± 3.87	0.26 ± 0.053
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
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
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
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
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
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

See text for statistical analysis

Table 3 (cont'd). 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

		Cestodes larval stages)
Year		
	1999	1.1 ±0.74
	2002	4.3 ±2.31
	2006	4.9 ±3.56
	2010	7.0 ±2.27
Site		
	Urwitalt	5.9 ±1.81
	Talty	8.0 ±3.86
	Pilchy	1.2 ±0.82
Sex		
	Males	4.3 ±2.10
	Females	5.5 ±1.80
Age		
	Class 1	1.27 ±0.977
	Class 2	1.35 ±0.570
	Class 3	11.7 ±3.90

See text for statistical analysis

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 ¹	BID ²	Total Helminths	Total nematodes	<i>M. muris</i>	<i>H. mixtum</i>	<i>H. glareoli</i>	<i>A. tianjinensis</i>	<i>A. annulosa</i>	<i>C. henttoneni</i>
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.)

1. Mean species richness (model based on Poisson errors); 2. Brillouin's index of diversity (model based on Gaussian errors).

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

	<i>H. mixtum</i>	<i>H. glareoli.</i>	<i>M. muris</i>	<i>A. tianjinensis</i>	<i>S. petruszewiczi</i>	<i>A. annulosa</i>
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)
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)
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)
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)
Site						
Urwitalt	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)
Talty	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)
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)
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)
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)
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)
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)
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)

See text for statistical analysis.

Table 5. Continued

	<i>C. henttoneni</i>	<i>Mesocestoides</i> sp.	<i>T. martis</i>	<i>V. mustelae</i>
Year				
1999	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	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	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	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				
Urwitalt	24.3(20.06-29.18)	7.2 (4.91-10.50)	5.26 (3.340-8.166)	1.3(0.52-3.23)
Talty	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	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	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	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	7.9(5.51-11.11)	0.4 (0.12-1.64)	0 (0-1.05)	0.36 (0.122-1.636)
Class 2	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	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.

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

	<i>H. mixtum</i>	<i>H. glareoli</i>	<i>M. muris</i>	<i>A. tianjinensis</i>	<i>S. petruszewiczi</i>	<i>A. annulosa</i>
Year						
1999	2.0 ± 0.27	1.9 ± 0.28	0.22 ± 0.082	6.9 ± 2.46	63.6 ± 35.90	0 ± 0
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
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
2010	1.5 ± 0.16	0.5 ± 0.18	0.75 ± 0.194	4.7 ± 0.99	0 ± 0	2.09 ± 0.738
Site						
Urwitalt	2.8 ± 0.18	0.02 ± 0.009	0.81 ± 0.165	2.2 ± 0.67	16.1 ± 13.33	1.93 ± 0.709
Talty	1.4 ± 0.15	0.05 ± 0.017	0.03 ± 0.013	13.5 ± 2.13	16.3 ± 10.36	0.46 ± 0.193
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
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
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
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
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
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

See text for statistical analysis

Table 6 cont'd

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

	<i>C. henttoneni</i>	<i>M. lineatus</i>	<i>T. martis</i>	<i>V. mustelae</i>
Year				
1999	0.10 ± 0.033	1.0 ± 0.74	0.007 ± 0.007	0.029 ± 0.018
2002	0.64 ± 0.125	2.1 ± 1.80	0.050 ± 0.016	0.119 ± 0.063
2006	0.29 ± 0.065	4.9 ± 3.55	0.004 ± 0.004	0.011 ± 0.011
2010	0.20 ± 0.051	6.6 ± 2.24	0.048 ± 0.026	0.003 ± 0.003
Site				
Urwitalt	0.60 ± 0.101	5.2 ± 1.69	0.059 ± 0.015	0.016 ± 0.009
Talty	0.24 ± 0.052	7.5 ± 0.4	0.028 ± 0.024	0.045 ± 0.030
Pilchy	0.13 ± 0.032	0.4 ± 0.29	0.003 ± 0.003	0.049 ± 0.034
Sex				
Males	0.38 ± 0.055	3.8 ± 2.05	0.025 ± 0.008	0.064 ± 0.030
Females	0.26 ± 0.057	4.6 ± 1.70	0.033 ± 0.017	0.009 ± 0.005
Age				
Class 1	0.15 ± 0.044	0.9 ± 0.91	0 ± 0	0.007 ± 0.007
Class 2	0.20 ± 0.035	1.3 ± 10.2	0.021 ± 0.009	0.027 ± 0.025
Class 3	0.59 ± 0.101	10.2 ± 3.77	0.064 ± 0.025	0.073 ± 0.038

See text for statistical analysis

Legends to Figs

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. petruszewicz* by site (I). Key to symbols used as shown in panel B.

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. petruszewicz* (G), *A. annulosa* (H) and adult intestinal stages of cestodes (I). Key to symbols used as shown in panel A.

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. petruszewicz* by year of survey (E) and site (F), and prevalence of larval cestodes (all species combined) (G). Key to symbols used in panels B, C, D, F and G, as in A.

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

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

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.

Fig. 8. Scatter plots and a plot of the centroids of functions 1 and 2 derived from Canonical Discriminant Function Analysis for 16 species of helminths in voles grouped by site and year. A, Urwitalt; B, Tałty, C, Pilchy. Key for symbols representing the 4 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 Urwitalt, Tałty and Pilchy, respectively and 99, 02, 06 and 10 representing the years 1999, 2002, 2006 and 2010 respectively.

Fig.1

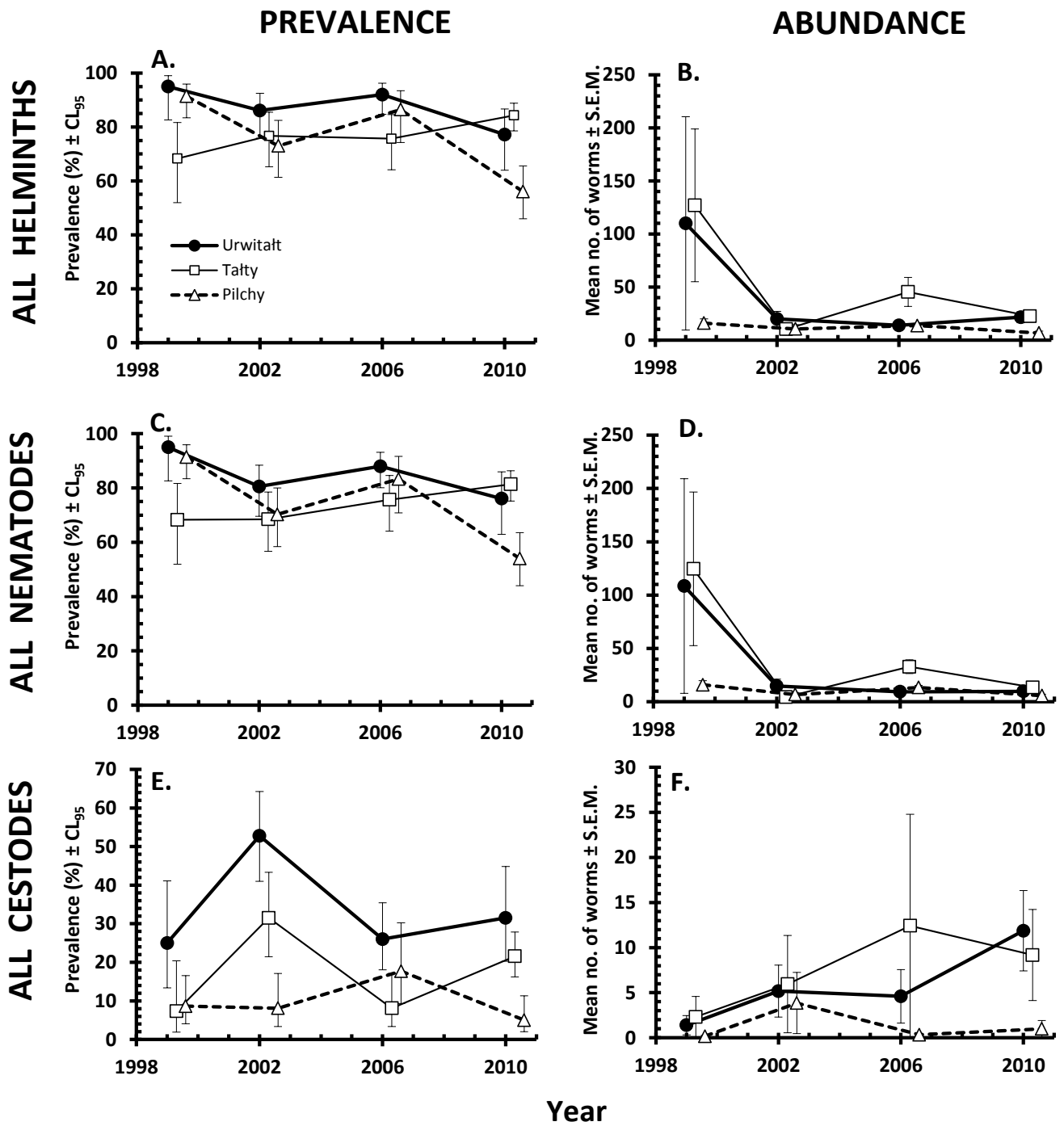


Fig. 2

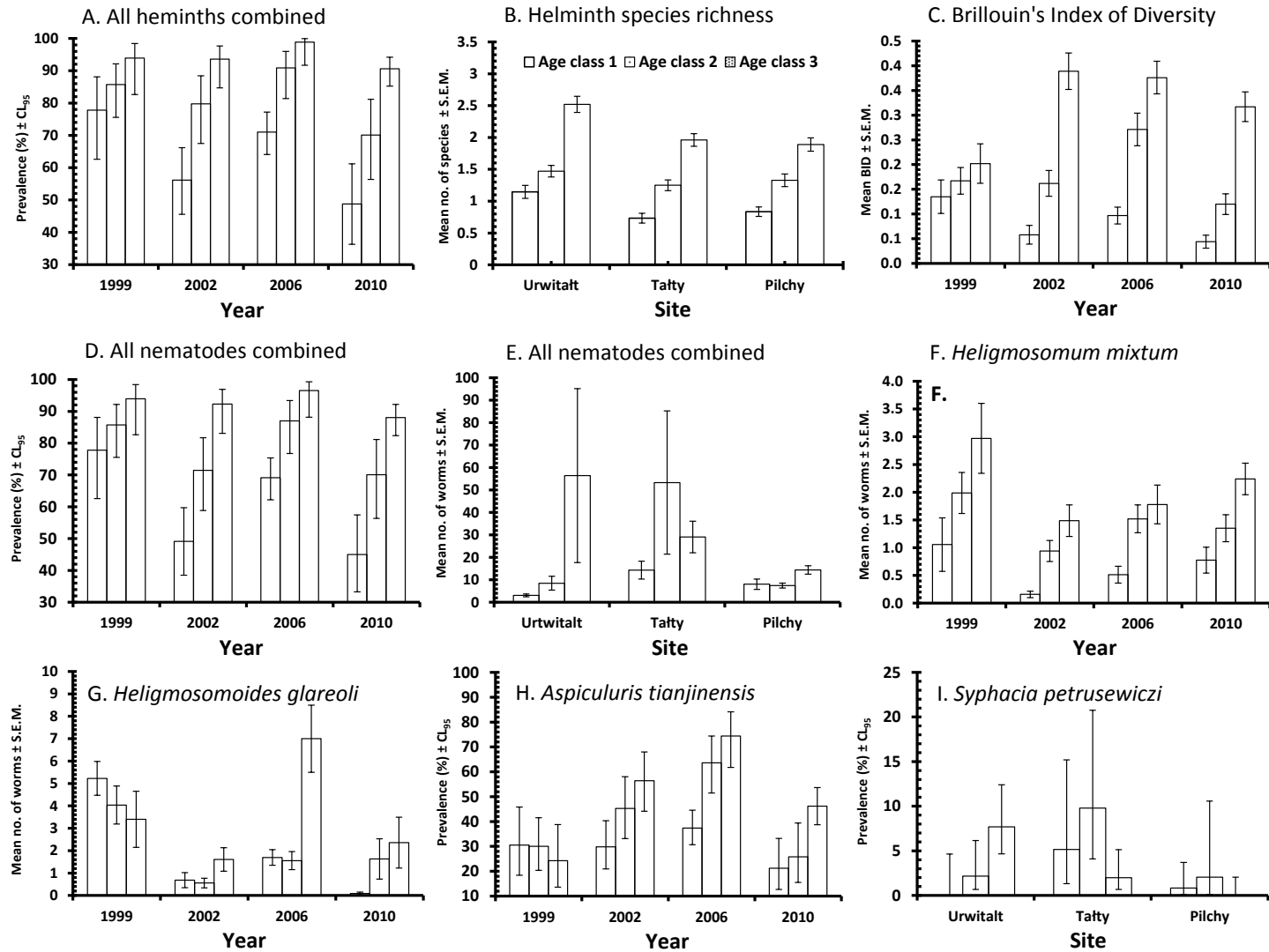


Fig. 3

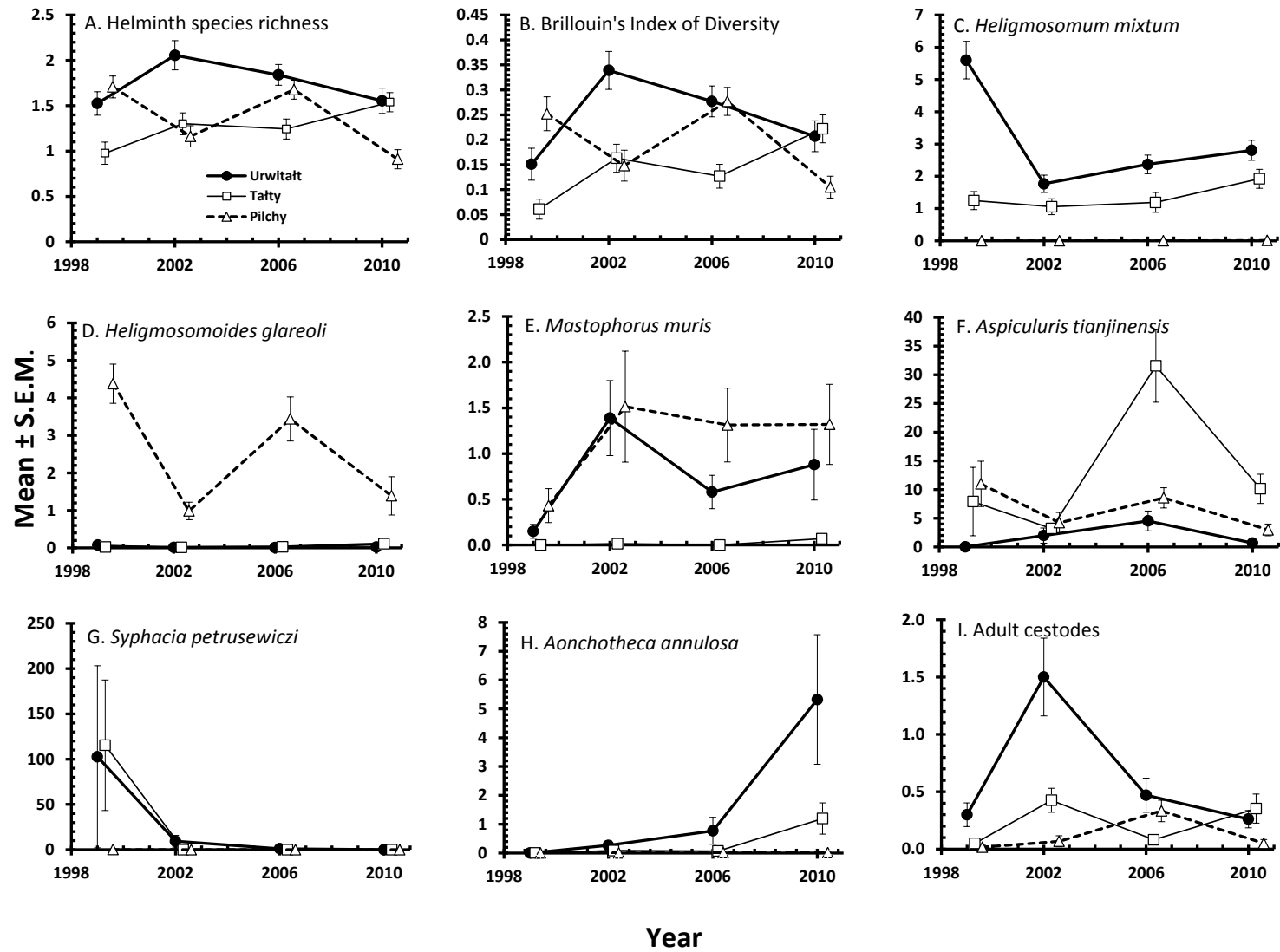


Fig. 4

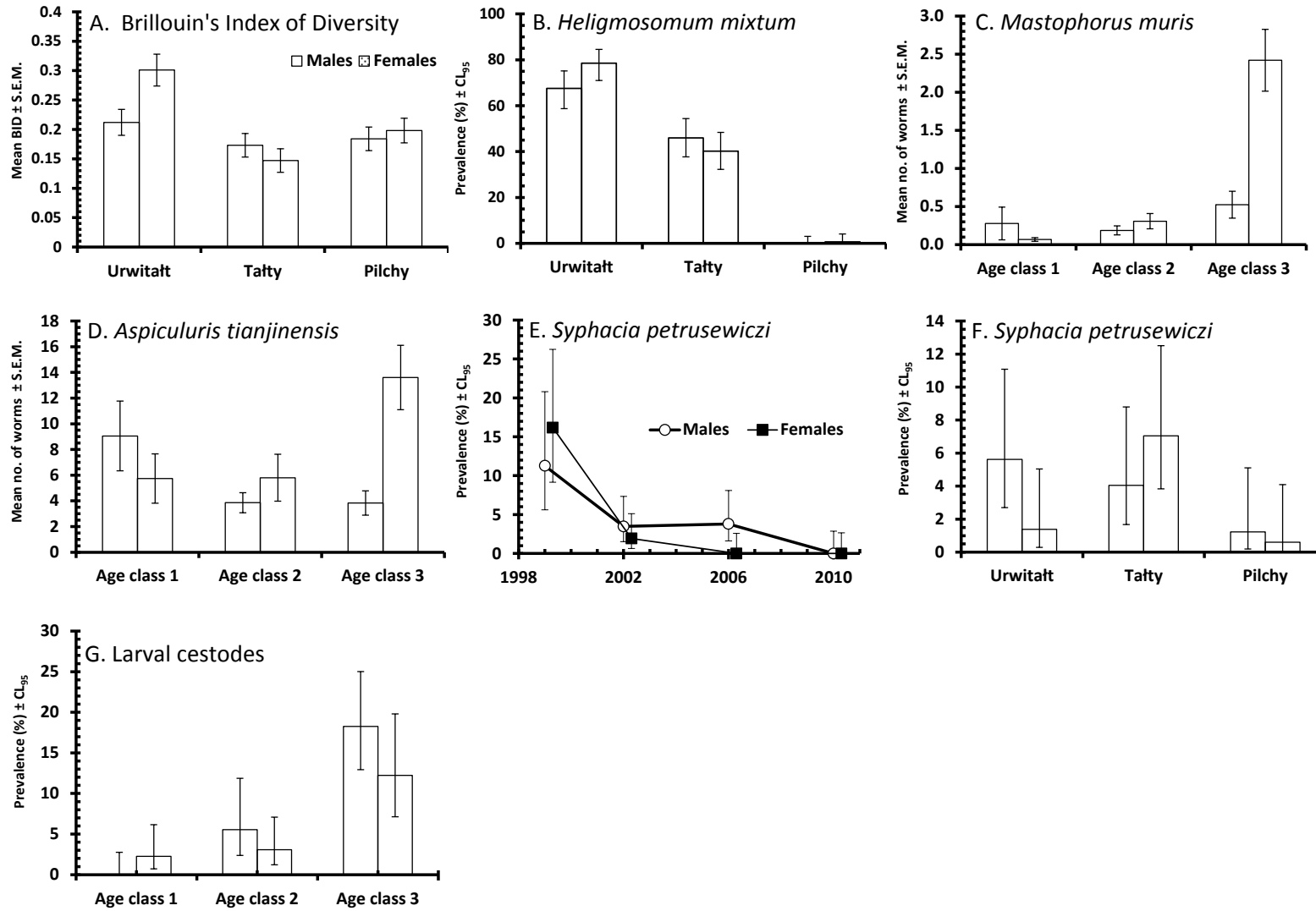


Fig. 5

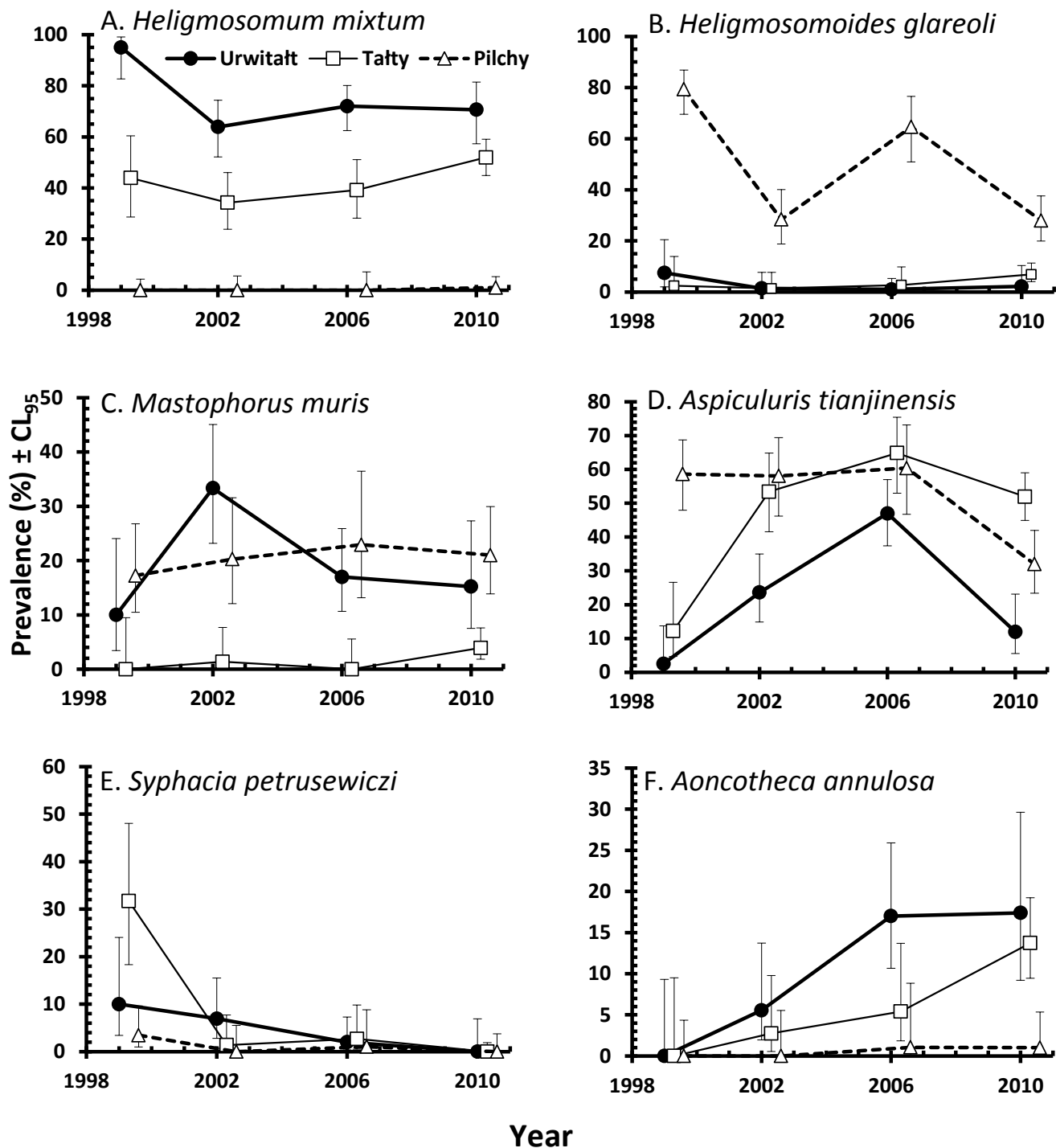


Fig. 6



Fig. 7

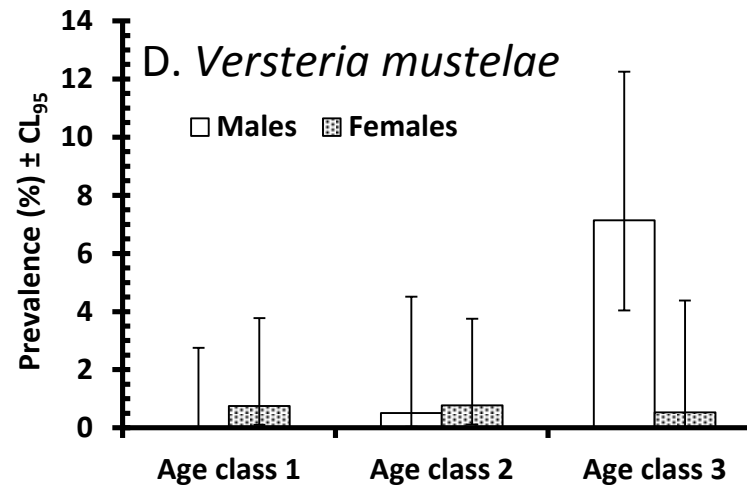
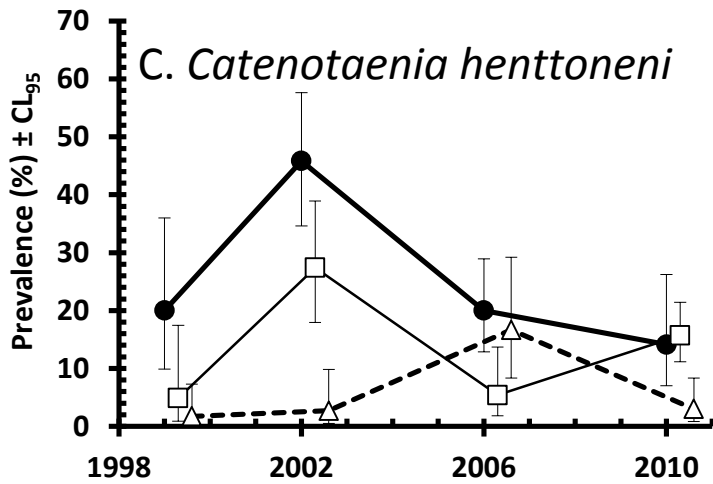
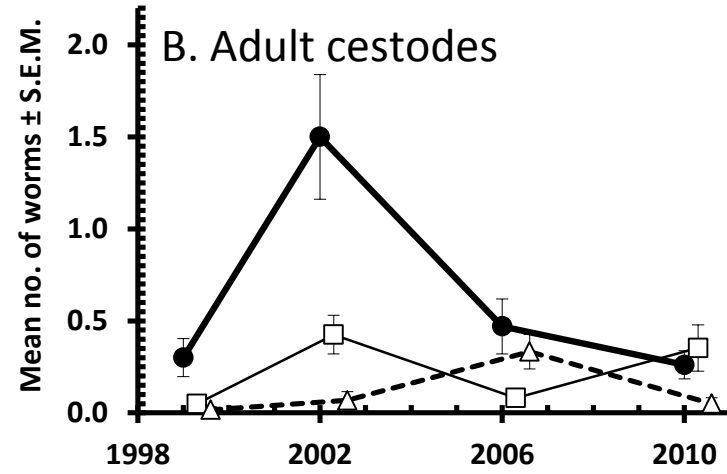
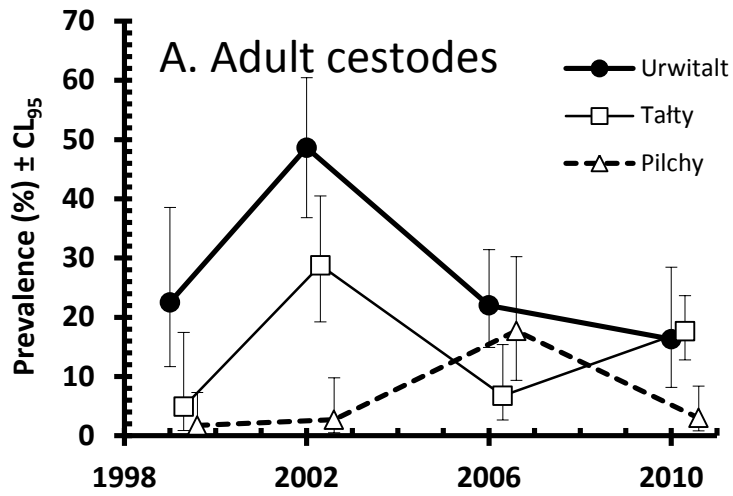


Fig. 8

