Temporal and between-site variation in helminth communities of bank voles (*Myodes glareolus*) from N.E. Poland. 1. Regional fauna and component community levels

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SUMMARY

Helminth infections were studied in bank voles (*Myodes glareolus*) from 3 woodland sites in N.E. Poland in the late summers of 1999 and 2002, to assess the temporal stability of derived statistics describing the regional helminth fauna and component community structure, and spatial influence on the latter. Regional helminth fauna changed dramatically between the two years, primarily due to a fall in the abundance of *Syphacia petrusewiczi* but was partially compensated for by an increase in *Mesocestoides lineatus* and *Cladotaenia globifera*. It was dominated by nematodes overall, but more so in 1999 than in 2002 when larval cestodes were more frequent. Most derived parameters for component community structure varied considerably between sites and the two surveys, the hierarchical order for sites not being maintained between surveys. They were susceptible to the disproportionate influence of three relatively rare, unpredictable species with the greatest overall aggregated distribution among hosts. Jaccard's similarity index was less influenced by the rare species, showing greater stability between sites and across years. In conclusion, temporal variation confounded any site-specific characteristics of the summary measures quantified in this study and their usefulness is therefore restricted to the years in which the surveys were conducted.

Key words: helminths, bank vole, *Myodes glareolus*, *Clethrionomys*, regional helminth fauna, component communities, site-specific variation.

INTRODUCTION

The study of helminth parasite communities in small wild mammals has attracted a lot of attention over the years, and at the heart of the on-going debate is the uncertainty about the degree to which these communities are structured, interactive or isolationist, stable or ephemeral (and therefore the extent to which they are predictable) and the relative importance of the factors that contribute to variation in community structure (Montgomery and Montgomery, 1990; Poulin, 1997, 2007). Typically, hierarchical arrangements characterize helminth communities (Esch *et al.* 1990; Poulin, 2004) and to some extent structure, stability and predictability depend upon the level of organization that is considered. However, the extent to which the derived parameters reflecting the characteristics of each community at each level of organization can vary temporally or spatially has seldom been evaluated comprehensively through empirical studies (Hartvigsen and Kennedy, 1993; Timi and Poulin, 2003; Calvete *et al.* 2004). Despite the wealth of publications on helminths of rodents, there are few studies that tackle these issues satisfactorily (Kisielewska, 1970*a*, *b*; Haukisalmi *et al.* 1987; Montgomery and Montgomery, 1989, 1990; Tenora and Stanek, 1995).

At the highest level of organization is the total helminth fauna of a given species of host across its entire geographical range (Poulin, 1997). Most often, however, animals are sampled on a smaller geographical scale and, based on pooled data derived from different populations of hosts sampled from a range of sites within the defined region, the regional helminth fauna form the next level of organization. Helminths encountered in populations of hosts within any region constitute component communities, and these in turn are comprised of infracommunities represented by all the parasites within individual hosts. Each level of organization is subject to different evolutionary and ecological pressures,

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and the degree to which derived parameters used to describe communities vary/show temporal and/or spatial stability will depend on the particular organizational level (Poulin, 1997).

Since infracommunities are the shortest lived, corresponding to a fraction of the life-time of their host, we may expect these to be the most dynamic, showing the greatest spatial and temporal variation. In the case of bank voles, *Myodes glareolus*, infracommunities may last just a few months in the summer period, although autumn-born voles live longer and each year sufficient individuals survive through the long winter to repopulate the woodland habitats in the following spring (Pucek *et al*. 1969; Alibhai and Gipps, 1985). Component communities are presumed to be longer lived (between several and many host life-times, depending on the stability of the particular population), and therefore intuitively might be expected to be more predictable. Changes at this level depend primarily on colonization events introducing new species to the population of hosts, or extinction through loss of transmission potential. The regional parasite fauna should be even more stable, cushioned against excessive temporal variation by the large number of component communities, temporally and spatially linked to differing extents, which are included within it. Most stable of all should be the total helminth fauna of the host species across its entire geographical range, which can change only through evolutionary events such as the capture of new helminth species through host switching or the allopatric subdivision of parasite lineages through host isolation. These processes commence initially within infracommunities and, if they persist these can spread through component communities to eventually feed over time into regional helminth communities and the total helminth fauna of the host.

Helminth component communities are known to vary in composition, species richness, prevalence etc. between populations of hosts living in sites which may be quite proximal to one another, and in some cases these variations have been linked to differences in habitat quality (Montgomery and Montgomery, 1990; Abu-Madi *et al*. 2000; Calvete *et al*. 2004; Behnke *et al*. 2004; Eira *et al*. 2006). In other cases, however, marked variation in component communities has been found in rodents living in virtually indistinguishable habitats (Behnke *et al*. 2001). But, are such differences between sites maintained over years or are they ephemeral, and if so over what time scale do they vary? Is the rank order of measures of community structure stable over the short/medium/long-term or does it change unpredictably across component communities that are spatially distant? Are predictability or change properties of regional, component or infracommunities? There are very few long-term studies in this field that adequately address these issues (Montgomery and Montgomery, 1990).

In our earlier work we found that the helminth infracommunities of bank voles were characterized by medium-term stability in a woodland site in N.E. Poland (Bajer *et al*. 2005). Based on a study conducted in 1999, we also reported detectable and quantifiable differences in community structure of helminths in voles living in 3 semi-isolated woodland habitats in the same region (Behnke *et al*. 2001). We re-examined each of these populations in 2002, sampling at the same time of year as in the original study to avoid seasonal factors. Over evolutionary time these three individual subpopulations of voles constitute part of a continuum across the western Palaearctic region to which bank voles are indigenous (Corbett, 1978; Spitzenberger, 1999), and by pooling data on helminth infections from all three sites, the derived summary statistics reflect the local helminth fauna of the Mazury region in Poland. Although bank voles can colonize unoccupied territory at the rate of 2–4·5 km year^{-1} given suitable continuous habitat (Smal and Fairley, 1984), their dispersal distance is generally much shorter (Gliwicz and Ims, 2000) and even closely located populations differ genetically (Aars *et al*. 1998; Gerlach and Musolf, 2000) suggesting that mixing is neither frequent nor extensive in the short term. It is therefore unlikely that there had been any substantial or frequent exchange of individuals between the three woodlands in our study during ecological time because of lack of connectivity between the woods (Van Apeldoorn *et al*. 1992): they are too distant from one another and are separated by substantial barriers (lakes, canals and open pasture/cultivated land; see Behnke *et al*. 2001) that impede the movement of voles. In ecological time each of these essentially represents a semi-isolated population of hosts, and therefore, summary statistics for helminth infections of voles from each location at this intermediate level reflect helminth component communities of different host populations within the region.

Here we first assess how the regional parasite fauna has changed between the two surveys and then quantify the extent to which between-site differences in component community structure are confounded by temporal effects. Given the above discussion concerning our expectations of stability at the regional and component community levels, our null hypothesis is that the regional helminth fauna and helminth component communities in wild bank voles living in semi-isolated sites within the region, are generally predictable and relatively unchanging in the medium term (2–5 years or so), despite the evident within-year seasonal effects, and the expected age-effects on individual infracommunities. In the accompanying paper we consider effects on infracommunities (Behnke *et al*. 2008).

MATERIALS AND METHODS

Study sites

The study sites were located in Mazury in the north eastern corner of Poland, in the vicinity of Jezioro (Lake) Śniardwy and the towns of Mikołajki, Ryn and Pisz as described comprehensively by Behnke *et al*. (2001). Site 1 is referred to as Urwitałt (N 53°48·153, EO 21°39·784), Site 2 as Tałty (N 53°53·644, EO 21°33·049) and Site 3 as Pilchy (N 53°42·228, EO 21°48·499) after nearby settlements.

Voles

In this paper we refer to bank voles as *Myodes glareolus* following the recent recommendations that *Myodes* rather than *Clethrionomys* is the valid name for this genus of rodents (Wilson and Reeder, 2005; Carleton *et al*. 2003). The methods used for trapping rodents, for sampling and processing trapped animals and establishing age categories have all been fully described in Behnke *et al*. (2001).

Measures of community structure

Measures of component community structure were identical to those used by Behnke *et al*. (2001), following Kennedy and Hartvigsen (2000). The total number of helminth species, the Berger-Parker Dominance Index and the unbiased Simpson's Index of Diversity (ID) for each site in each year and on pooled data are given. In some analyses we have excluded *S. petrusewiczi*, and in others this species as well as the 2 larval cestodes, *M. lineatus* and *C. globifera*, are excluded because these three species can cause extremely high infections, numbering several hundred/thousand worms, despite an overall low prevalence in the population. We tested the idea that these species, in particular, exert a disproportionate influence on indicators of community structure, and we compared values with and without these species.

Similarity between sites and in different years was compared by Jaccard's and Sale's Similarity Indices for the latter following Montgomery and Montgomery (1990) using:

$$\mathrm{C_{ij}} = 1 - 0{\cdot}5 \sum_{k}^{s} |\mathrm{p_{ik}} - \mathrm{p_{jk}}|,$$

where $\mathrm{C_{ij}}$ is the proportional similarity between surveys *i* and *j*, and varies from 0 to 1. $\mathrm{p_{ik}} - \mathrm{p_{jk}}$ are the proportions of the total helminth fauna at each survey comprising the *k*th species and *s* is the number of species. The sign of $\mathrm{p_{ik}} - \mathrm{p_{jk}}$ is converted to positive before summing.

Statistical analysis

The statistical approach adopted has also been documented comprehensively in the earlier publications (Behnke *et al*. 2001; Bajer *et al*. 2005).

Prevalence data (percentage of animals infected with all helminths) are given with 95% confidence limits, calculated as described by Rohlf and Sokal (1995) employing bespoke software. The distribution of voles, among age and sex classes and in relation to different sites and the years of the surveys, and prevalence of infection with all helminths combined were analysed by maximum likelihood techniques based on log linear analysis of contingency tables using the software package SPSS (version 12.0.1). Full factorial models incorporated the intrinsic factors age (3 age classes) and sex (2 levels, males and females) and the extrinsic factors site (3 levels) and year of survey (2 levels, 1999 and 2002). Infection was considered as a binary factor (present/absent). Beginning with the most complex model, involving all possible main effects and interactions, those combinations that did not contribute significantly to explaining variation in the data were eliminated in a stepwise fashion beginning with the highest-level interaction. A minimum sufficient model was then obtained, for which the likelihood ratio of χ^2 was not significant, indicating that the model was sufficient in explaining the data. The importance of each term (i.e. interactions involving infection) in the final model was assessed by the probability that its exclusion would alter the model significantly and these values are given in the text.

We used Taylor's Power Law (Taylor, 1961) to identify species of helminths that showed most variation and hence less predictability. The logarithms of mean abundance and variance (of abundance) were calculated separately for each of the 3 sites and in the 2 years of the surveys for each of the 7 most prevalent species of helminths recorded, and when prevalence was zero, those cells were excluded. The line graphs were fitted in Microsoft Office Excel 2003 (by least squares methods) and the statistical analysis of the regression of log transformed variance on abundance was carried out in SPSS version 12.01 for Windows.

RESULTS

Myodes glareolus

In total, 358 bank voles were sampled from the 3 study sites: 139 in 1999 and 219 in 2002. The structure of the sampled host population by year, site and age is summarized in Table 1.

The numbers of voles examined from the 3 sites did not differ significantly in respect of the 2 sexes. However, the distribution of voles among the 3 age groups varied both between sites ($\chi^2_4 = 13{\cdot}0$, $P = 0{\cdot}011$), and between years ($\chi^2_2 = 6{\cdot}8$, $P = 0{\cdot}033$). As expected, voles in age class 2 formed the largest proportion of the sampled animals from all 3 sites (42·9, 46·5 and 40·2% for Urwitałt, Tałty and Pilchy respectively). The youngest age class was least

Table 1. Numbers of *Myodes glareolus* examined by year of survey, site and host age

(Statistical analysis: The minimum sufficient model was site $*$ age class + year $*$ age class $\chi^2_{24} = 28{\cdot}8$, $P = 0{\cdot}227$.)

Site	Year	Age class 1	2	3	Total by year	Total by site
Urwitałt	1999	3	23	14	40	
	2002	15	25	32	72	
	Combined	18	48	46		112
Tałty	1999	11	21	9	41	
	2002	23	32	18	73	
	Combined	34	53	27		114
Pilchy	1999	22	26	10	58	
	2002	19	27	28	74	
	Combined	41	53	38		132
Total by year						
	1999	36	70	33	139	
	2002	57	84	78	219	
Total by age		93	154	111		
TOTAL						358

represented at Urwitałt (16·1% of voles from this site), but formed a similar percentage at Tałty and Pilchy (29·8 and 31·1% respectively) and conversely the oldest voles were best represented at Urwitałt (41·1%), and approximately equally at Tałty (23·7%) and Pilchy (28·8%). Overall, with sites combined, the youngest age class was similarly represented in both years of the study (25·9% and 26·0% in 1999 and 2002 respectively), although there were differences between the sites. In 1999 age class 2 voles comprised a larger percentage of the catch compared to 2002 (50·4% and 38·4%, respectively) and accordingly age class 3 voles were more common in 2002 (23·7% and 35·6%, respectively).

Changes in the regional helminth community structure with time

Quantitative changes. In total, combining all 3 sites and both years, 13 501 helminths were recovered, but there was a substantial reduction (71·8%) in the total number of helminths recovered between 1999 (10 529) and 2002 (2972) even though more voles were sampled in 2002 (Table 1). When sample size was taken into consideration the reduction was even more marked (82·1%; mean in 1999 = 75·7 and in 2002 = 13·6). This change between years was predominantly due to *S. petrusewiczi* which accounted for 70·5% (9516) of all the worms recovered, but which declined in abundance substantially between the 2 surveys (Behnke *et al.* 2008). Without *S. petrusewiczi* and with sample size taken into consideration, helminth burdens declined moderately (by 13·5%; mean number of helminths in 1999 = 12·1 and in 2002 = 10·5).

Two other species had a marked effect on the total number of helminths recovered: *Mesocestoides* sp. and *C. globifera*, both of which are relatively infrequent but when present, often number in hundreds. Without these species, and without *S. petrusewiczis* and with sample size taken into consideration, the remaining total worm burdens changed more markedly (totals of worms recovered = 1547 in 1999, and 1388 in 2002 and means = 11·1 and 6·3 respectively). The change represented a reduction of 43·0%, mainly attributable to these species increasing abundance in 2002 (when 460 *M. lineatus* and 450 *C. globifera* were recovered, compared with 140 and zero, respectively in 1999).

Two hundred and ninety one voles (81·3%, [77·7–85·6]) carried at least 1 species of helminth (85·6% [79·3–90·9] in 1999 and 78·5% [73·1–84·0] in 2002). The difference between years was not significant (with site, age and sex taken into account, log-linear model, year $*$ presence/absence of helminths $\chi^2_1 = 2{\cdot}874$, $P = 0{\cdot}09$).

Taxa comprising the regional community. Fourteen species of helminths were recorded in total, 8 nematodes and 6 cestodes (Tables 2 and 3), 11 in 1999 and 13 in 2002. Of these 1 nematode species was recorded in 1999 (*Trichuris* sp.) but not in 2002, and 2 (*A. annulosa* and Nematoda sp.) in 2002 but not 1999. One species of larval cestode (*C. globifera*) was recorded in 2002 but not in 1999 (Table 2 and for further details see Behnke *et al.* 2008).

The regional helminth community, combining all the data, was clearly dominated by nematodes which accounted for 90·7% of all the helminths (68·6% when *S. petrusewiczi* was excluded). Larval

Table 2. Presence or absence of helminth species by site and year

			Site		
Taxon	Species	Year	Urwitałt	Tałty	Pilchy
Nematodes	*Heligmosomum mixtum*	1999	+	+	–
		2002	+	+	–
	Heligmosomoides glareoli	1999	+	+	+
		2002	+	+	+
	Syphacia petrusewiczi	1999	+	+	+
		2002	+	+	–
	Aspiculuris tetraptera	1999	+	+	+
		2002	+	+	+
	Mastophorus muris	1999	+	–	+
		2002	+	+	+
	Aonchotheca annulosa	1999	–	–	–
		2002	+	+	–
	Trichuris sp.	1999	–	–	+
		2002	–	–	–
Cestodes	*Catenotaenia henttoneni*	1999	+	+	+
		2002	+	+	+
	Paranoplocephala omphalodes	1999	+	–	–
		2002	+	+	–
	Mesocestoides lineatus	1999	+	+	+
		2002	+	+	+
	Taenia martis	1999	–	–	+
		2002	+	–	+
	Taenia mustelae	1999	+	–	+
		2002	+	+	+
	Cladotaenia globifera	1999	–	–	–
		2002	+	–	+

(+, present; –, absent.)

Table 3. Measures of component community structure by site and year of study

(The measures of component community structure listed here follow Kennedy and Hartvigsen (2000). The Berger-Parker dominance index is the proportion of all helminths sampled represented by the dominant species. The dominant species is that showing the highest proportion in each subset of data. The unbiased Simpson's index of diversity was calculated as $(1-\Sigma_i p_i^2)\times(n/(n-1))$ where n = total number of helminths in data subset and p is the proportion of the i^{th} species (Lande, 1996).)

		Site			
	Year	Urwitałt	Tałty	Pilchy	Combined
Total no. of helminth species identified	1999	9	6	9	11
	2002	12	11	8	13
	Combined	**12**	**11**	**10**	**14**
Berger-Parker dominance index	1999	0·934	0·909	0·685	0·840
	2002	0·469	0·521	0·399	0·232
	Combined	**0·820**	**0·794**	**0·554**	**0·705**
Dominant species	1999	*S. petrusewiczi*	*S. petrusewiczi*	*A. tetraptera*	*S. petrusewiczi*
	2002	*S. petrusewiczi*	*Mesocestoides*	*A. tetraptera*	*A. tetraptera*
	Combined	***S. petrusewiczi***	***S. petrusewiczi***	***A. tetraptera***	***S. petrusewiczi***
Simpson's index	1999	0·125	0·169	0·456	0·285
	2002	0·732	0·622	0·710	0·835
	Combined	**0·322**	**0·353**	**0·629**	**0·483**

cestodes accounted for 8·1%, and 1·2% were strobilate intestinal cestodes. However, the composition changed between the 2 sampling periods. In 1999, intestinal nematodes accounted for 98·5% of the helminths, whereas in 2002 this figure dropped to 63·3%, and these values fell only marginally when *S. petrusewiczi* was discounted (90·5 and 52·5%, respectively). Accordingly, cestode larvae were more numerous in 2002 compared with 1999 (31·9% versus 1·4% of total helminths, respectively)

Table 4. Percentage distribution of higher taxa by site

(Sp = *Syphacia petrusewiczi*; Ml = *Mesocestoides lineatus*; Cg = *Cladotaenia globifera*; U = Urwitałt; T = Tałty; P = Pilchy.)

		Percentage distribution by site*								
		All helminths			Excluding Sp			Excluding Sp, Ml and Cg		
	Year	U	T	P	U	T	P	U	T	P
All helminths	1999	43·5	50·2	6·3	20·9	33·1	46·0	19·7	29·5	50·8
	2002	48·8	25·3	25·9	33·6	32·8	33·6	37·4	26·0	36·6
	Combined	44·4	44·6	11·1	28·4	32·5	39·1	28·1	26·8	45·1
Intestinal nematodes	1999	43·6	50·0	6·4	19·0	29·7	51·3			
	2002	57·0	17·0	26·0	32·8	26·5	40·7			
	Combined	45·2	44·7	10·1	24·9	27·3	47·8			
Adult cestodes	1999	82·0	13·3	4·7						
	2002	75·3	21·3	3·4						
	Combined	76·2	20·6	3·2						
Larval cestodes	1999	31·2	64·4	4·4				26·6	0	73·4
	2002	28·3	42·6	29·2				38·3	27·0	34·6
	Combined	29·6	46·8	23·6				38·2	25·0	36·8

* Percentage distribution is based on data adjusted for sample size.

and even more so when *S. petrusewiczi* was excluded (47·5% versus 9·5% of total helminths).

Measures of component community structure

Higher taxa. Eighty nine percent of the helminths recovered were from Urwitałt and Tałty (Table 4), but whereas at Urwitałt the values were comparable in 1999 and 2002, at Tałty the percentage distribution fell by half, and in 2002 a greater percentage of the helminths was recovered from Pilchy (25·9% in 2002 versus 6·3% in 1999). Examining the higher taxa more closely, values for intestinal nematodes, adult and larval cestodes were more stable at Urwitałt compared with Tałty and Pilchy. In both years the highest percentages of adult cestodes were observed in voles from Urwitałt, and despite a fall of approximately one third, most of the larval cestodes were recovered in both years from voles from Tałty.

When *S. petrusewiczi* was excluded from the data, the percentage distribution of the remaining helminths was more similar across the 3 sites in the combined data set and in 2002. However, in 1999 the situation was reversed in comparison to the earlier analysis. This time, 46% of the remaining helminths were encountered at Pilchy (rather than just 6·3% as in the total database). Exclusion of *M. lineatus* and *C. globifera* changed the balance even more in favour of Pilchy in 1999 and in the combined database, although in 2002 there was little difference between Pilchy and Urwitałt. Much the same was evident for intestinal nematodes. Exclusion of *S. petrusewiczi* resulted in most remaining nematodes being attributable to voles from Pilchy.

Total species richness, dominant species and diversity indices by site. Between years, the number of helminth species recorded at Urwitałt and Tałty increased by 3 and 5, respectively and at Pilchy decreased by 1 (Table 3). Berger-Parker dominance indices were lower at all three sites in 2002 and the highest index was obtained for Tałty in 2002, compared with Urwitałt in 1999. In both years the index was lowest at Pilchy.

At both Urwitałt and Pilchy the dominant species remained the same (*S. petrusewiczi* and *A. tetraptera*, respectively) but at Tałty *Mesocestoides* sp. replaced *S. petrusewiczi* in 2002 (Table 3). Because the communities were less dominated by the oxyuroid nematodes in 2002 compared with 1999, and with the additional species recovered at 2 sites, Simpson's indices of diversity were higher in 2002, overall and at each site.

Similarity indices. Table 5 shows the values calculated for Sale's and Jaccard's similarity indices. Jaccard's index, which is based on presence/absence data, varied less (range = 0·44–0·81) than Sale's index, which takes relative abundance of species into consideration.

The greatest similarity in Jaccard's index was between Urwitałt in both years (1999 and 2002) and between Urwitałt 1999 and Tałty in both 1999, between Urwitałt and Tałty in 2002, and 2002 and also between these two sites with years combined. Values for Pilchy were generally lower irrespective of the comparison. When *S. petrusewiczi*, *M. lineatus* and *C. globifera* were excluded the index changed very little in most cases, a reflection of the fact that these species were relatively rare in the population.

Table 5. Sale's and Jaccard's similarity indices between sites and in each of the years, between sites with years combined, and between years with sites combined

(Data are given for all helminths, and separately after exclusion of *S. petrusewiczi* (Sp), *M. lineatus* (Ml) and *C. globifera* (Cg).)

	Sale's Similarity Index							Jaccard's Similarity Index						
	U02	T99	T02	P99	P02	**Tc**	**Pc**	U02	T99	T02	P99	P02	**Tc**	**Pc**
U99	**0·54**	0·93	0·07	0·01	0·01			**0·75**	0·67	0·82	0·64	0·6		
U99 (excluding Sp, Ml, Cg)	**(0·34)**	(0·15)	(0·27)	(0·05)	(0·05)			**(0·78)**	(0·57)	(0·78)	(0·56)	(0·71)		
U02		0·56	0·28	0·14	0·34				0·5	0·77	0·62	0·58		
U02 (excluding Sp, Ml, Cg)		(0·43)	(0·62)	(0·32)	(0·50)				(0·44)	(0·8)	(0·6)	(0·56)		
T99			**0·09**	0·07	0·08					**0·55**	0·5	0·44		
T99 (excluding Sp, Ml, Cg)			**(0·79)**	(0·70)	(0·61)					**(0·44)**	(0·38)	(0·5)		
T02				0·32	0·35						0·54	0·5		
T02 (excluding Sp, Ml, Cg)				(0·66)	(0·65)						(0·45)	(0·56)		
P99					**0·53**							**0·6**		
P99 (excluding Sp, Ml, Cg)					**(0·78)**							**(0·71)**		
Uc						0·87	0·10						0·77	0·69
Uc (excluding Sp, Ml, Cg)						(0·43)	(0·31)						(0·8)	(0·6)
Tc							0·11							0·5
Tc (excluding Sp, Ml, Cg)							(0·68)							(0·45)
99 vs 02		0·39								0·71				
99 vs 02 (excluding Sp, Ml, Cg)		(0·73)								(0·73)				

U = Urwitałt; T = Tałty; P = Pilchy; 99 = 1999; 02 = 2002; Uc = Urwitałt with years combined; Tc = Tałty with years combined; Pc = Pilchy with years combined. Comparisons of individual sites between 1999 and 2002 are highlighted in bold.

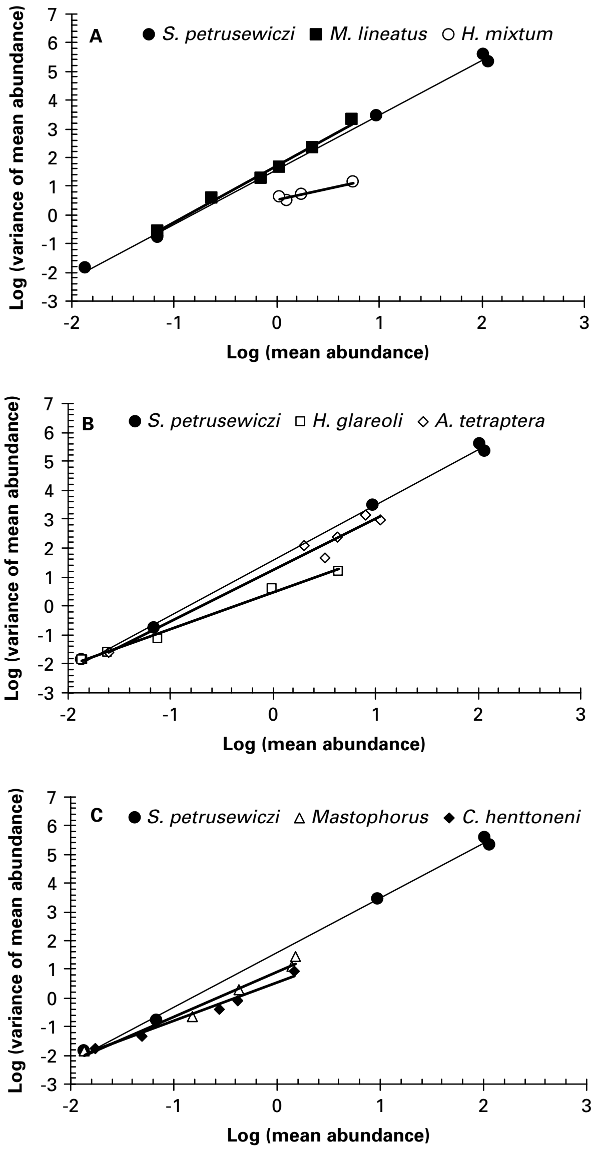

Fig. 1. Taylor's power relationship for the most prevalent species in the study. The figures show the relationships between the log-transformed variance of abundance and log transformed abundance for each of 7 species. The relationship for *Syphacia petrusewiczi* is shown for reference in each figure. The other species are as shown in the embedded legend. For statistical analysis see Table 4.

Sale's index showed markedly greater changes, ranging from 0·01 to 0·93. Between years, Sale's index was very similar and midrange at Urwitałt and Pilchy, but dropped markedly at Tałty. Urwitałt and Tałty were very similar in 1999, but following the change at Tałty between the years, far less so in 2002, Sale's index dropping from 0·93 to 0·28. Nevertheless, with years combined Urwitałt and Tałty were very similar but quite different from Pilchy. When *S. petrusewiczi*, *M. lineatus* and *C. globifera* were excluded the index changed quite dramatically in most cases, emphasizing that despite their low prevalence in the population, these helminths had an enormous influence on the index. The greatest similarity was between Tałty and Pilchy, both of which now generated a much higher index for the comparison between years.

Relationship between variance and mean abundance for the most prevalent taxa

The data suggest that *S. petrusewiczi* and the larval cestodes, *M. lineatus* and *C. globifera*, have the greatest influence on the indicators of community structure both at the local regional fauna level and the component community level. Therefore we examined the relationship between the logarithms of the means of abundance and logarithms of the variances of abundance (Taylor, 1961) with these species (*C. globifera* could not be tested because of insufficient degrees of freedom since it was encountered only in 2 sites in 2002, but not at all in 1999) and compared these to the slopes for this relationship generated for the other prevalent species. We expected *S. petrusewiczi* and *M. lineatus* to show the steepest relationships with the highest values for the slope (b). The results are summarized in Fig. 1 and the statistical analysis is given in Table 6, and these show that the slope of the regression of log variance of the mean abundance of *M. lineatus* on log mean abundance was steeper than that of any of the other species. *S. petrusewiczi* had a very similar slope, both just less than 2. The shallowest slopes were those of *H. mixtum* and *H. glareoli*, and only the former among these two generated a slope less than 1. It is worth noting that a slope of less than 1 for Taylor's Power Law indicates an under-dispersed, uniform distribution, unusual for a parasitic organism.

DISCUSSION

The data and the analysis presented in this paper show that the majority of the indicators of regional helminth fauna and component community structure were remarkably fluid, with substantial variation between the 2 years. Given the evidence that there is some stability of the more common species in the medium-term at the infracommunity level (Bajer *et al*. 2005; Behnke *et al*. 2008), and our expectations for stability at the higher levels of community organization (regional and component communities; see Introduction section), this was not what we had expected. The temporal variability of the derived values utilized in this and in other studies (Montgomery and Montgomery, 1990) to summarize regional and component community structure is therefore of fundamental interest, and raises the question of whether they serve any useful purpose. It is pertinent to assess next the species that were primarily responsible for temporal instability of the key measures.

Table 6. Taylor's power law relationships for the most prevalent species in the study

(For each species the log of the variance of the mean abundance was regressed on the log of the mean abundance, with data calculated separately for each of the three sites in each of 2 years, hence maximum $n=6$. However, because in some subsets of data specific parasites were not found (prevalence = 0%) these subsets were excluded, and for this reason the degrees of freedom fall below 4 in some cases.)

	Regression		ANOVA				t-test for slope*
Species	Slope (b) ±	S.E.M.	F	D.F.†	r^2	P	t
M. lineatus	1·972	0·094	437·8	1,4	0·989	<0·001	20·9
S. petrusewiczi	1·906	0·051	1415·9	1,3	0·997	<0·001	37·6
A. tetraptera	1·776	0·158	127·0	1,4	0·962	<0·001	11·3
M. muris	1·572	0·131	143·8	1,3	0·973	0·001	12·0
C. henttoneni	1·324	0·124	113·2	1,4	0·957	<0·001	10·6
H. glareoli	1·269	0·054	548·0	1,4	0·991	<0·001	23·4
H. mixtum	0·794	0·173	21·0	1,2	0·869	0·045	4·58

* Test of slope greater than zero.
† Degrees of freedom.

At the core of this between-year variation were 3 species, the oxyuroid *S. petrusewiczi* and two cestodes, *M. lineatus* and *C. globifera*, that exploit bank voles as their intermediate hosts. All 3 species show low to modest prevalence in the bank voles in the region (Behnke *et al*. 2001; Bajer *et al*. 2005) and elsewhere (Le Pesteur *et al*. 1992; Haukisalmi and Henttonen, 1993), but when they do occur their numbers can be extremely high. This was reflected in this study in the highest gradients for Taylor's Power Law relationship, and in the case of *S. petrusewiczi* the low values of *k*, the aggregation constant, and high indices of dispersion and discrepancy (see accompanying paper, Behnke *et al*. 2008).

The highest individual worm burden recorded for *S. petrusewiczi* in this study was 4026 worms (mature male vole from Urwitałt in 1999), this one vole accounting for 29·8% of all the helminths recovered from the 358 voles in the study. Although not common, in our experience such heavily infected animals are not rare either. In another study we reported a bank vole with 6130 worms of this species (Bajer *et al*. 2005). In fact, in the current study, only 25 voles were infected and of these 8 had worm burdens in the range 181 to 4026. Thus, although prevalence was low (Behnke *et al*. 2008) *S. petrusewiczi* nevertheless contributed substantially to total worm burdens and the Berger-Parker index, Sale's similarity index and, as can be seen from Table 3, figured prominently among the dominant species by this criterion. Bajer *et al*. (2005) discussed some of the underlying factors that are responsible for this aggregation of worms in specific hosts. *Syphacia* spp. females migrate through the intestine when fully gravid and emerge through the anal sphincter to lay their eggs in large batches on the peri-anal surface. Since the eggs are rapidly infective, transmission most probably relies on close contact between animals, for example when sleeping in family groups in their nests and allogrooming, and if one individual becomes infected through contact with voles from outside social groups, the worms spread rapidly through the remainder of the group, particularly among naïve juveniles (Lewis, 1987). There is also some evidence that prevalence and abundance of *Syphacia* spp. increase when the population density is high and fall when it is low (Lewis, 1968; Kisielewska, 1970*a*; Montgomery and Montgomery, 1988; Haukisalmi and Henttonen, 1990), and the substantial drop in the prevalence of *S. petrusewiczi* between 1999 (when vole densities were very high; 18·8/1000 trap hours at Urwitałt, see Bajer *et al*. 2001) and 2002 (when they were lower at 8·6, 8·1 and 15·7/1000 trap hours at Urwitałt, Tałty and Pilchy respectively; Behnke *et al*. unpublished data) is consistent with this view. Because *S. petrusewiczi* were aggregated in just a few hosts in large numbers, they had a major impact on indicators of regional fauna and component community structure. When prevalence and abundance were high, such as in 1999, the influence of *S. petrusewiczi* on diversity indices was so overwhelming that other species hardly contributed to the calculations, generating Berger-Parker dominance indices above 0·9 (i.e. dominant species accounting for more than 90% of all worms) and correspondingly low Simpson's indices of diversity. Thus the absence of any animals heavily infected with *S. petrusewiczi* in 2002 (the heaviest infection was 388) was mainly responsible for the substantial drop in mean helminth burdens between the two years of our study, fall in the Berger-Parker dominance index and increase in Simpson's ID, illustrating how derived summary statistics such as those commonly used as measures of component community structure can be easily biased to give an illusion of major change.

The two cestodes exploit bank voles as intermediate hosts, but as far as is known, neither replicates asexually in these hosts (Loos-Frank, 1980*b*) as some other cestodes, including *Mesocestoides corti*, are known to do (Specht and Voge, 1965; Chernin and McLaren, 1983). Although we have seen many infected animals, we have never encountered dividing forms and this is consistent with the findings of Loos-Frank (1980*b*). It is worth also drawing attention here to the controversy about the species of *Mesocestoides* in bank voles in the region. A second species, *M. leptodactylus* was described by Loos-Frank (1980*a*) and shown to be the species infecting voles in Germany (Loos-Frank, 1980*b*). However, it was considered *nomen dubium* by Premier (1983) and Tenora (2004) and we have chosen to refer to it by its original name *M. lineatus*. The definitive hosts for *M. lineatus* are wild carnivores and the most likely host is the fox (*Vulpes vulpes*), although raccoon dogs (*Nyctereutes procyonoides*) also inhabit the forests where we trapped. Rodents probably become infected with *M. lineatus* when they feed on oribatid mites that in turn must get infected by feeding on contaminated food or directly on the faeces of the definitive host, although the role of a first intermediate host in the life-cycle of this species is still not fully resolved (Loos-Frank, 1991). *M. lineatus* was rare in our voles, affecting just 8 out of the 358 voles, but the heavy infections, 4 of which were in the range 35–393 (and total number of worms recovered = 612), had a disproportionate influence on summary statistics for the subsets of voles to which they belonged. *C. globifera* matures in owls and raptors such as kestrels, hawks and buzzards (Ferrer *et al.* 2004), for which bank voles are a major dietary component. Heavy infections in voles (2 infected animals harbouring 200 and 250 larvae respectively) are probably attributable to the consumption of large batches of transmission stages on just one occasion, probably through feeding on bird faeces or vegetation heavily contaminated with eggs from freshly deposited faeces. Parasite burdens with these species were not as numerous as those with *S. petrusewiczi* (Behnke *et al.* 2008), and both were more common in 2002, partly compensating for the loss of *S. petrusewiczi* in that year.

Another species that had some effect on summary measures was *A. tetraptera*. This species is normally considered to be a parasite of *Mus domesticus* and *M. musculus* (Behnke, 1975, 1976), but it has also been recorded from bank voles elsewhere (Sharpe, 1964). Experimental data show that *M. glareolus* cannot be easily infected with eggs derived from *M. musculus* (Behnke, 1974), and so it is possible that the form in bank voles is a cryptic species not yet clearly differentiated from that infecting *Mus* spp. However, we are not aware of any molecular genetic studies characterizing *Aspiculuris* spp. and comparing isolates from *M. glareolus* and *Mus* spp. The prevalence of *A. tetraptera* also increased from 1999 to 2002, but curiously the abundance fell overall (Behnke *et al.* 2008), and we have data that suggest a long-term trend of rising prevalence of this species across several years (Bajer *et al.* unpublished). As the accompanying paper shows (Behnke *et al.* 2008) the prevalence of *A. tetraptera* remained stable at about 58% at Pilchy, but increased markedly at both Urwitałt and Tałty. Thus, in addition to the major fluctuations in summary statistics caused by *S. petrusewiczi* and the two cestodes, there is also a slower long-term trend reflected in the increasing importance of this species in the component community structure of bank voles in our study sites.

Underlying the dramatic changes associated with *S. petrusewiczi* and the slower long-term change with *A. tetraptera*, there are also changes in prevalence and abundance of the more stable core species, such as *H. mixtum* and *H. glareoli*, and for both of these site effects are more important than temporal ones (see Behnke *et al.* 2008).

Although most of the summary statistics reflecting regional and component community structure could not be tested statistically, it is evident that, to a large extent, the more marked changes between the years were driven by the disproportionate influence of *S. petrusewiczi*, *M. lineatus* and *C. globifera*. In contrast, the core species provided an element of underlying stability in the summary indices between years and the sporadic occurrence of the other rare species probably made little difference to these calculations other than by contributing to species richness at regional helminth fauna and component community levels. Whilst the range of rarer species in any given location can be eventually assessed comprehensively, it requires large sample sizes since species richness at the community level is dependent on sample size (Walther *et al.* 1995: Dove and Cribb, 2006). To a large extent these rare species are not specific to bank voles and their transmission is dependent on the presence of other hosts in the vicinity. *Taenia martis* and *T. mustelae* are both parasites of mustelids (Verster, 1969; Loos-Frank, 2000), and their population sizes and worm burdens determine the risk of infection for voles, which act as intermediate hosts. Both hosts are highly mobile mammals, and their populations probably show marked fluctuations in specific woodlands, but when they are present they contribute infective stages of the tapeworms they harbour, adding species richness at the component community level for that site.

We conclude that, with the exception of overall prevalence of helminths at the regional faunal level and Jaccard's similarity index at the component community level, other indicators of regional and component community structure in bank voles in our study sites varied considerably between years and the rank order of sites in relation to any specific measure changed unpredictably. Attention has been drawn previously to the variability in measures of helminth species richness between surveys of the same host (Poulin and Mouillot, 2004). To a large extent the variation in the derived measures reported in the current study was accounted for by those species of helminths that have the potential for extreme aggregation, developing exceptionally high worm burdens, or depend on the presence of vagile definitive hosts that seed the environment with transmission stages and have a greater potential than bank voles to move between sites, and hence to cross-contaminate bank vole populations. A further tier of complexity was derived from those helminth species whose prevalence in a specific component community was subject to long-term trends of increasing prevalence and abundance. Clearly the usefulness of the summary measures, reflecting regional helminth fauna and component community structure of helminths in bank voles, employed in this study was restricted to the years in which the surveys were conducted. These indices varied considerably between the two years of the surveys, and hence temporal changes confounded any site-specific characteristics at this level. On these grounds we can now reject our prediction that helminth communities in bank voles should not vary markedly between years at the regional and component community levels.

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