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Do the helminth parasites of wood mice interact?

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Summary

1. Two published data sets of helminths of the wood mouse *Apodemus sylvaticus* (L.) were analysed to test the hypothesis that the structure of these component communities is influenced by interactions between species. A range of tests, with differing null models, was applied to tease out the importance of controlling for subgroupings (e.g. sex, age, site, year, season) within the data when searching for significant associations based on prevalence (co-occurrence, presence/absence) or abundance (quantitative associations) data.
2. Significant differences from null models were detected for associations based on prevalence, but when subgroup constraints were taken into consideration, most lost significance. Among three and 15 pair-wise associations possible in data sets 1 and 2, respectively, only that between *Trichuris muris* and *Heligmosomoides polygyrus* was not dependent on context, and that between *H. polygyrus* and *Catenotaenia pusilla*, while always positive, varied in magnitude among sites of capture.
3. Pair-wise comparisons of abundance revealed three significant associations, only one of which (*H. polygyrus* with *C. pusilla*) still remained significant after controlling for quantified extrinsic and intrinsic factors. With increasing burdens of *H. polygyrus*, mice carried more of other helminth species and this relationship remained significant after controlling for confounding factors.
4. Overall, positive co-occurrences of pairs of helminths of *A. sylvaticus* were highly context dependent and quantitative associations were weak and not convincing. Therefore, interactions between parasites are unlikely to play a dominant role among the processes that structure the component community of helminths in wood mice, in selected study sites in the south of England.

Key-words: *Apodemus sylvaticus*, associations, cestodes, co-occurrence, *Heligmosomoides polygyrus*, helminths, interactions, nematodes.

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Introduction

The prevalence (percentage of animals infected) and abundance (mean worm burden, including all uninfected animals in a specific group) of parasitic helminths in wild rodents are known to be dependent on both extrinsic (temporal, seasonal and site effects) and intrinsic (age, sex) factors, which interact in various combinations to shape the component community structure in a given habitat at a specific time. The dominant influence on prevalence and abundance of specific helminths and on infracommunity species richness appears to stem from season (Kisielewska 1970a; Langley & Fairley 1982; Montgomery & Montgomery 1989; Abu-Madi *et al*. 2000), indirectly through the host's reproductive cycles and directly through variation in climatic conditions (i.e. seasonal effects on survival of transmission stages). Pronounced differences in helminth richness have been described from habitats differing in quality (Kisielewska 1970b; Montgomery & Montgomery 1990; Abu-Madi *et al*. 1998), as well as from sites that did not appear to differ ecologically (Behnke *et al*. 2001b) and when season and site were constant, marked differences were detected in the prevalence and abundance of some species between successive years (Montgomery & Montgomery 1990; Behnke *et al*. 1999). These short-term fluctuations and local spatial heterogeneity (Behnke *et al*. 2001b) contrast with the relative stability of helminth communities over a longer time frame and across a wider geographical

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region (Kisielewska 1970b; Keymer & Dobson 1987; Montgomery & Montgomery 1990; Bajer *et al*. 2005), when total and mean species richness may be considerably more stable.

Host age is perhaps the more important of the intrinsic factors, with younger animals generally harbouring fewer species of helminths and lower worm burdens (Kisielewska *et al*. 1973; Montgomery & Montgomery 1989; Abu-Madi *et al*. 1998). In comparison host sex has a weaker influence and has only occasionally been shown to affect prevalence and abundance of helminths in wild rodents (Behnke *et al*. 1999; Ferrari *et al*. 2004).

The prevalence and abundance of helminths may also be influenced by associations between species of parasites, which can be both synergistic (positive) and antagonistic (negative) (reviewed Behnke *et al*. 2001a). Such associations can be passive, arising for ecological/behavioural reasons because particular hosts are exposed to combinations of the infective stages of some helminths more so than others (e.g. aggregated in intermediate hosts: Lotz, Bush & Font 1995) and therefore become focused in some subsets of the population. Alternatively, they can arise through active interactions between species of parasites that alter the environment within the host (e.g. by immunomodulation or cross-immunity), with the consequence that the host becomes more or less susceptible to other species, or through direct interactions between pairs of parasites via competition for resources or sites within the host (Patrick 1991; Petney & Andrews 1998). While both antagonistic and synergistic interactions have been clearly demonstrated in laboratory-based experiments in rodents (Christensen *et al*. 1987; Behnke *et al*. 2001a) and recently Lello *et al*. (2004) have shown that such interactions exist among intestinal helminths in wild rabbits, data for the existence of interactions in wild rodents in Europe are scarce (Montgomery & Montgomery 1990). In part, this may be because few authors have analysed relevant data sets by appropriate statistical methods. However, even when such methods have been applied, with safeguards against inappropriate conclusions through careful standardization of data and use of appropriate null models, few if any associations have been detected (Haukisalmi & Henttonen 1998; Nilssen, Haugerud & Folstad 1998).

In this paper we re-analyse two data sets from our recent studies, in which the influence of both extrinsic and intrinsic factors on the component community structure of helminths in the wood mouse *Apodemus sylvaticus* (L.) was quantified and evaluated (Abu-Madi *et al*. 1998, 2000; Behnke *et al*. 1999). In Abu-Madi *et al*. (1998, 2000) helminth communities were studied across four seasons in a single year, in wood mice inhabiting three sites selected for contrasting habitat quality. In Behnke *et al*. (1999) helminth communities were studied at one of the earlier sites, in the autumn season across 4 years. With precise knowledge on the extent of the influence of such factors on each of the parasite species in our two studies, and the use of appropriate null models (Haukisalmi & Henttonen 1998), it was possible to seek evidence for co-occurrence and quantitative associations between helminths, with relevant factors taken into account (analysis of categorical data) or controlled for (analysis of quantitative data). This paper therefore addressed the hypothesis that helminth parasites of *A. sylvaticus* associate to varying degrees (antagonistically and synergistically, depending on combination) in host communities where total species richness is greater than one. In particular we predicted that *Heligmosomoides polygyrus* (Dujardin, 1845) would predispose mice to infection with other intestinal helminths, as there is good evidence that the related subspecies *H. p. bakeri* (Durette-Desset, Kinsella & Forrester 1972) is immunomodulatory in laboratory mice (Behnke 1987; Behnke, Barnard & Wakelin 1992; Monroy & Enriquez 1992). To test the hypothesis we present a framework for stepwise analysis, commencing with broad questions and then focusing on specific combinations of parasites. Such an approach may have wider relevance, especially in community ecology where it could be applied to replicate samples of any sampled community.

Materials and methods

The data utilized in this paper are derived from two earlier studies reported by Abu-Madi *et al*. (1998, 2000) and Behnke *et al*. (1999), and these should be consulted for information on the biology of the species involved. Table 1 summarizes the number of mice caught, the factors recorded in each study and the overall prevalence of each species of helminth. Details of the study sites, the methods used to catch and age mice, the numbers of animals sampled in specific sites at particular times of the year and between years and the parasites recorded are all comprehensively detailed in Abu-Madi *et al*. (1998, 2000) and Behnke *et al*. (1999). For brevity we report the analysis of data set 1 in detail, and only refer to data set 2 when relevant.

Associations of species were first examined by the variance ratio method described by Schluter (1984), re-evaluated by Lotz & Font (1994), which tests for net negative or positive associations among co-occurring species based on either presence/absence or quantitative data. Species-richness distributions were compared with the positive and negative binomial, and to Poisson distributions, and were tested for significance by χ^2. They were then compared with null models based on prevalence figures as described by Janovy *et al*. (1995) and to randomized subsampling of the data without and with subgroup constraints (see below) as reported by Haukisalmi & Henttonen (1998).

Matrices of pair-wise associations were constructed using overall prevalence data in order to identify pairs of species co-occurring more frequently than expected, and were tested by χ^2. Then, the role of each species in the context of quantified intrinsic and extrinsic factors known to affect the prevalence of each species (i.e. presence/absence data) was analysed by maximum likelihood techniques based on log-linear analysis of contingency

Table 1. Summary information on the two data sets used for analysis, including the prevalence of each species of helminth, the number of factors and levels of each factor employed in analysis and the number of each host sex examined

Species of helminths	Data set 1* prevalence	Data set 2† prevalence
Nematodes		
Heligmosomoides polygyrus	75·7	80·6
Syphacia stroma	40·1	56·7
Aonchotheca murissylvatici‡	2·5	8·2
Trichuris muris	0	19·4
Pelodera strongyloides	0	26·1
Cestoda		
Catenotaenia pusilla	18·3	0
Microsomacanthus crenata	0	24·6
Taenia taeniaeformis§	0	3·0
Digenea		
Corrigia vitta	5·3	17·9
Brachylaemus recurvum	0	3
Factors measured	No. of levels	No. of levels
Extrinsic		
site	3	1
year	1	4
season	4	1
Intrinsic		
sex	2	2
age	2	3
Hosts	No.	No.
males	210	91
females	189	43
combined	399	134

*Abu-Madi *et al*. (1998, 2000).
†Behnke *et al*. (1999).
‡Previously known as *Capillaria murissylvatici*, but see Moravec (1982, 2000).
§Strobilocercus stage.

tables implemented by the software package, Statgraphics Version 7. In addition to presence/absence data on each species, all intrinsic (sex and age of hosts) and extrinsic factors (site, year and season) known to influence the prevalence of parasites were also included so that their contributions to interactions between parasites could be assessed. 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 stepwise commencing 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.

Haukisalmi & Henttonen (1998) proposed testing the null hypothesis of no associations using a randomization test, an approach with a long history in ecological studies of competition (see Gotelli 2000), and furthermore suggested that randomization with and without subgroup constraints would be informative. These subgroupings of the data involve factors known to affect parasite prevalence (e.g. host age, site of capture, etc.). Although Haukisalmi & Henttonen (1998) only used presence–absence data in their tests, here we generalized to include abundance data.

Thus our approach was to randomize the observed occurrences (presence–absence) or abundances among hosts, while keeping total prevalence or abundance constant in a host × parasite species matrix (i.e. the column totals were fixed but the row totals were not), recently shown to be the best randomization method (Gotelli 2000). We randomized either across the entire data set, or within subgroups (e.g. host age, site of capture, etc.). Abundance data were log-transformed ($\ln(x + 1)$) before analysis. With bespoke software, we recorded the number of times out of 5000 randomizations that the observed covariance exceeded (or was lower in the case of negative covariance) the randomized covariance and used this proportion as a significance test. Note that with the presence–absence data there can only be four combinations of association between two parasites and hence for many randomizations the observed and randomized covariances were identical.

Except when using the randomization test, analyses of quantitative associations were conducted only on animals carrying at least one individual of each pair of species. Matrices of the outcome of Spearman's Rank Order Correlational analyses of the raw worm burdens were constructed as a guide to possible relationships (to avoid Type 1 errors). Pairs of species that showed a significant correlation or were close to significance were further analysed to test whether this may have been due to associations with other factors, rather than direct interactions between species. Two approaches were used: the first was the randomization test on the covariances as described above; the second was to remove the effects of these other factors on each parasite via ANOVAs (using GLIM 4: Royal Statistical Society 1993) with the inclusion

of the factors listed in Table 1. For these ANOVAS, models with negative binomial errors were used, but where the analysis would not converge satisfactorily, we employed models with normal errors, after normalization of the data by LOG10 ($x + 1$) transformation (Crawley 1993; Wilson & Grenfell 1997). These analyses are reported in full by Abu-Madi *et al*. (1998, 2000) and Behnke *et al*. (1999). The residuals were then re-examined for any correlation between them. If the correlation disappeared, then the association between the parasites might be attributable to covariation with these factors rather than direct interaction between the species concerned. The randomization test (on covariances) and the correlation test (i.e. on standardized covariances) are clearly related, but randomization makes no assumptions about the distribution of the data, unlike correlation.

To determine whether *H. polygyrus* in particular was associated with predisposition of hosts to infection with other helminths, three additional variables were calculated for each mouse: (1) the total number of other species harboured by each mouse (i.e. = infracommunity species richness, minus one if *H. polygyrus* present) was calculated; (2) the total additional worm burden (i.e. total worm burden, all species except *H. polygyrus*); (3) worm burden of other species as a percentage of total. For this last variable (3) the parasite burdens for each species for each mouse were expressed first as a percentage of the total worm burden of that species in all the mice in the relevant data set. This was done to control for the large difference in ranges of parasite burdens of the various species involved (see Abu-Madi *et al*. 1998, 2000; Behnke *et al*. 1999). The percentage values for all species harboured by individual mice, with the exception of *H. polygyrus*, were then summed. All three calculations were then repeated for *S. stroma*, which was included as a control because this species is not generally associated with immunodepression of the host (albeit there are some data to suggest that this may be the case for *S. muris*, Pearson & Taylor 1975). For each of these three variables, and for both *H. polygyrus* and for *S. stroma* separately, a GLIM analysis was carried out including all relevant factors. The residuals from minimum sufficient ANOVAS were saved and then used as variables in the correlational analyses described. To avoid the risk of Type I errors (72 tests) the Dunn–Sidak correction for multiple tests was implemented for the correlations and this required the cut-off value of P to be lowered to 0·0007 (Sokal & Rohlf 1981).

Results

CO-OCCURRENCES OF HELMINTHS BASED ON PREVALENCE DATA

Are there excesses of positive/negative co-occurrences regardless of species?

We first tested the independence of the occurrence of species comprising the component community by the community-wide variance ratio test of Schluter (1984). This gave $V = 1{\cdot}482$ and $\chi^2_{399} = 591{\cdot}1$ ($P < 0{\cdot}0001$), indicating that, based on prevalence data, there was an excess of positive associations among the species infecting the mice. This was also the case for data set 2 ($V = 1{\cdot}067$, $\chi^2_{134} = 142{\cdot}9$, $P < 0{\cdot}0001$).

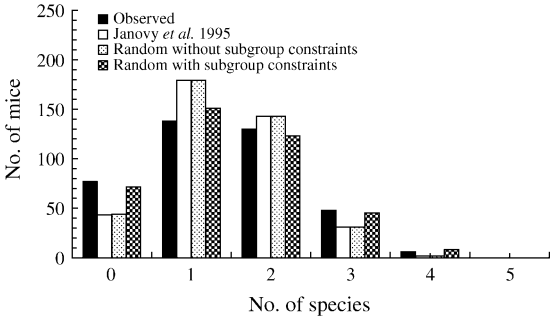

Fig. 1. Frequency distributions of infracommunity helminth species richness (data set 1) contrasting the observed frequency distribution with that predicted by the null models of Janovy *et al*. (1995) and Haukisalmi & Henttonen (1998) without and with subgroup constraints. For statistical analysis see text.

Do frequency distributions of infracommunity species richness (species density distributions) reveal evidence for co-occurrences?

The observed frequency distribution of species helminth richness (Fig. 1; goodness of fit to positive binomial $\chi^2_4 = 25{\cdot}2$, $P < 0{\cdot}001$; Poisson $\chi^2_4 = 25{\cdot}8$, $P < 0{\cdot}001$; negative binomial $\chi^2_4 = 2{\cdot}4$, $P = 0{\cdot}7$), was compared with the distribution predicted by the null model for interactions of parasite species in an assemblage (Janovy *et al*. 1995) and a highly significant difference was found ($\chi^2_4 = 52{\cdot}8$, $P < 0{\cdot}0001$). More mice than expected were without infections (Fig. 1), fewer than expected carried one and two species of helminths, but more than expected carried three and four species (for data set 2, there were fewer than expected carrying one, two or four helminth species, and more than expected carrying three or five species). When observed frequency distributions were compared with the distribution predicted by the randomization test without subgroup constraints, the result was almost identical (Fig. 1, $\chi^2_4 = 51{\cdot}9$ $P < 0{\cdot}0001$). However, when data were sampled within the subsets represented by the four quantified factors (randomization test with subgroup constraints; See Table 1 for subsets for data set 1), there was no difference between observed and predicted values (Fig. 1, $\chi^2_4 = 2{\cdot}7$, $P = 0{\cdot}6$). Analysis of data set 2 produced a similar result (before subgroup constraints, $\chi^2_4 = 24{\cdot}7$, $P = 0{\cdot}0002$ and after subgroup constraints, $\chi^2_4 = 9{\cdot}4$, $P = 0{\cdot}09$).

Which species of parasites co-occur (covary based on presence/absence data)?

For these analyses we only considered species with a prevalence exceeding 10%. A matrix of pairs of species

Table 2. Minimum sufficient maximum likelihood statistical model derived from all quantified factors and three helminth species (where prevalence > 10%) detected in data set 1 (Abu-Madi *et al*. 1998, 2000). Each line in the upper compartment represents a significant interaction that therefore forms part of the final model

Principal interactions in explaining variation in data*			Test of individual effects		
Extrinsic factors	Intrinsic factors	Parasites	χ^2	d.o.f.	P†
–		Hp, Ss, Cp	22·280	1	< 0·0001
Site		Hp, Ss	15·290	2	0·0005
Site		Hp, Cp	10·348	2	0·0057
Season	Age	Cp	8·368	3	0·0390
	Sex, age	Ss	7·785	1	0·0053
Site, season		Cp	26·441	6	0·0002
Site, season		Hp	28·186	6	0·0001
Site, season		Ss	21·206	6	0·0017
	Age	Hp	21·095	1	< 0·001
Site, season	Age		18·459	6	0·0052
Season	Sex		8·825	3	0·0317
Goodness-of-fit of the minimum sufficient model specified by the interactions listed above			135	303	1·0‡

*Site – three levels (Dungeness, Egham and Isle of Wight); season – four levels (spring, summer, autumn and winter); age – two levels (juvenile and adult); sex – two levels (male and female); infection – two levels for each of five species (infected or uninfected).
†Probability that excluding the effect will make a significant change to the model.
‡Probability that the data does not differ significantly from the minimum sufficient model described by the interactions listed.
Hp = *H. polygyrus*; Ss = *Syphacia stroma*; Cp = *C. pusilla*; d.o.f., degrees of freedom.

was prepared and the numbers of mice harbouring each pair of worms were compared with those expected from prevalence data. In the majority of cases more mice carried specific pairs of parasites than predicted from overall prevalence data alone. This difference was significant ($\chi^2_2 = 13{\cdot}8$, $P < 0{\cdot}001$), with the greatest contribution to the overall χ^2 being [in decreasing order (observed/expected)] *H. polygyrus* + *S. stroma* (143/121), *S. stroma* + *C. pusilla* (68/55), and *H. polygyrus* + *C. pusilla* (43/29); there were no negative associations. Analysis of data set 2, revealed no overall difference between observed and expected numbers.

The randomization test without subgroup constraints revealed the same order of relative importance for the positive associations: *H. polygyrus* + *S. stroma* (covariance = 0·055, $P < 0{\cdot}001$), *S. stroma* + *C. pusilla* (covariance = 0·034, $P < 0{\cdot}001$) and *H. polygyrus* + *C. pusilla* (covariance = 0·032, $P < 0{\cdot}001$), and no negative associations.

For data set 2, perhaps surprisingly in view of the earlier result, there was a significant overall difference between the observed distribution of covariance and that generated by random sampling of the data set (randomization test without subgroup constraints, $\chi^2_2 = 18{\cdot}6$, $P < 0{\cdot}001$). In decreasing order of importance were *H. polygyrus* + *T. muris* (covariance = 0·038, $P < 0{\cdot}001$), *S. stroma* + *H. polygyrus* (covariance = 0·036, $P = 0{\cdot}013$), *T. muris* + *M. crenata* (covariance = 0·035, $P = 0{\cdot}005$) and *M. crenata* + *H. polygyrys* (covariance = 0·033, $P = 0{\cdot}003$). No significant negative associations were found.

Are co-occurrences among species attributable to the influence of extrinsic and intrinsic factors rather than to parasite–parasite interactions?

We first applied the randomization test with subgroup constraints. Only the positive co-occurrence of *C. pusilla* with *H. polygyrus* retained significance ($P = 0{\cdot}012$). No negative relationships were revealed. In data set 2, three of the original positive co-occurrences retained significance: *H. polygyrus* + *T. muris* ($P < 0{\cdot}001$); *H. polygyrus* + *S. stroma* ($P = 0{\cdot}05$); and *T. muris* + *M. crenata* ($P = 0{\cdot}014$). However, the co-occurrence of two additional pairs of species now gained significance [the positive co-occurrence of *S. stroma* + *P. strongyloides* ($P = 0{\cdot}024$) and a negative co-occurrence of *P. strongyloides* with *H. polygyrus* ($P = 0{\cdot}05$)].

Table 2 summarizes the log-linear minimum sufficient model, based on prevalence. There were significant associations between species as three of the terms in the model incorporated more than one helminth species (Figs 2 and 3). However, all associations had additional terms that ranged from various combinations of factors to additional species of helminths. Thus, there were no independent interactions between pairs of species, unaffected by other variables. The most complex interaction involved *H. polygyrus*, *S. stroma* and *C. pusilla*. The prevalence of *C. pusilla* was highest in mice carrying both *H. polygyrus* and *S. stroma* and lowest in those without these parasites (Fig. 2).

H. polygyrus also showed two additional interactions, one with *S. stroma* and the other with *C. pusilla*, which

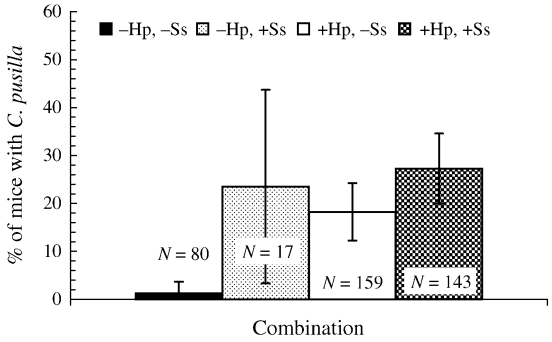

Fig. 2. The prevalence (± 95% confidence limits) of *C. pusilla* in mice without either *H. polygyrus* or *S. stroma*, without *H. polygyrus* but with *S. stroma*, with *H. polygyrus* but without *S. stroma* and with both species (data set 1). For statistical analysis see text and Table 2. The sample size is given above or in relevant columns.

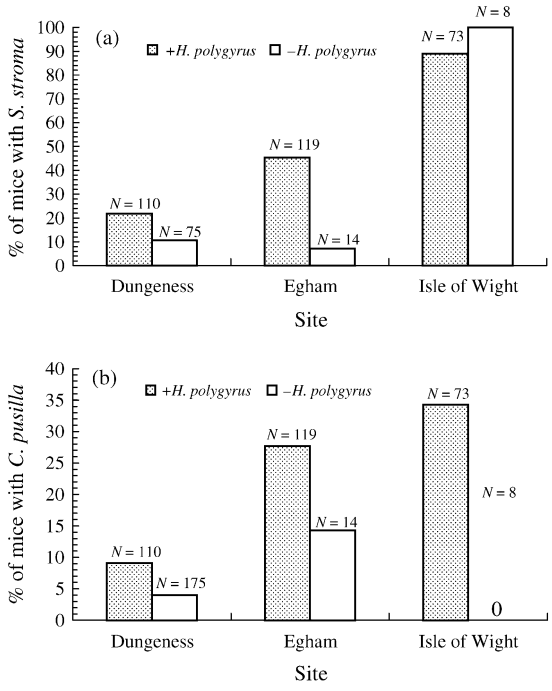

Fig. 3. Site-dependent co-occurrence of *H. polygyrus* with *S. stroma* (A) and with *C. pusilla* (B) in data set 1. For statistical analysis see text and Table 2. Figures close to the abscissa indicate zero values, those above the columns give the sample size.

were independent of each other but each dependent on site. *S. stroma* occurred more often in mice infected with *H. polygyrus*, than those without, in two sites (Dungeness and Egham), although there was little difference in prevalence in the Isle of Wight (Fig. 3A). However, at all three sites mice with *H. polygyrus* also showed a higher prevalence of *C. pusilla*, but prevalence among mice carrying *H. polygyrus* differed, being highest at the Isle of Wight, where *C. pusilla* was only found in mice with *H. polygyrus* (Fig. 3B).

For data set 2, the only two-way combination not complicated by interactions with other factors was between *H. polygyrus* and *T. muris*, the latter only occurring among mice with *H. polygyrus* (prevalence = 24·1%). All other helminth interactions lacked consistency across sites and/or years. However, it is noteworthy that *H. polygyrus* and *M. crenata* appeared in all three 3-way interactions in which the only significant terms were parasites. Omitting the third species in each case, the prevalence of *M. crenata* among mice carrying *H. polygyrus* was 28·7% compared with just 7·7% among mice without the latter species.

ASSOCIATIONS BETWEEN HELMINTHS BASED ON QUANTITATIVE DATA

Are increasing burdens of one species correlated with increasing or decreasing burdens of the second species?

The independence of parasite burdens of the species was tested by the community-wide variance ratio test of Schluter (1984). This gave $V = 1{\cdot}0884$ and $\chi^2_{399} = 434{\cdot}3$ (P = NS), lending little support to the existence of strong associations between the species involved.

Next we applied the randomization test without subgroup constraints (Table 3) and all three possible covariances between the three species (*H. polygyrus*, *S. stroma* and *C. pusilla*) were significant, but only one of these, i.e. that between *H. polygyrus* and *C. pusilla* retained significance when the randomization test was applied with subgroup constraints. The relationship between *H. polygyrus* and *C. vitta* also retained borderline significance.

Multiple correlational analyses were carried out on raw parasite burden values for each pair of species using only mice that harboured at least one individual of both species. The results are summarized in Table 3 and were used to select pairs of species for further analysis. Three of the correlations were significant or approached significance. The relationship between *H. polygyrus* and *S. stroma* and that between *H. polygyrus* and *C. pusilla* were both characterized by shallow gradients for the best fit line and accounting, respectively, for 5·2 and 5·5% of the variation. In each case the correlation between pairs of species may have arisen because of the confounding influence of some of the factors (site, season, sex, age) in the study. To control for these, correlational analyses were carried out on the residuals from minimum sufficient ANOVAs in GLIM, for each of these three pairs of species. Only the positive association between *H. polygyrus* and *C. pusilla* (Table 3 and Fig. 4A), accounting for just 10% of the variation in that data set, still retained significance.

Analysis of data set 2 gave similar results, except that of the five significant positive covariances (*H. polygyrus* + *S. stroma*, *H. polygyrus* + *M. crenata*, *H. polygyrus* + *T. muris*, *S. stroma* + *T. muris*, *M. crenata* + *T. muris*) identified from randomizations without constraints, just two retained significance when the test was applied with subgroup constraints: *H. polygyrus* + *S. stroma* (covariance = 0·428, $P = 0{\cdot}029$), and *H. polygyrus* + *T. muris* (covariance = 0·294, $P < 0{\cdot}001$). The matrix of correlational analyses between pairs of species (no. of

Table 3. Quantitative covariance of species (data set 1). Matrices of outcome from Spearman's correlation tests for pairs of helminth species and abundance covariance calculated by the randomization test. Each pair of values gives the result without and with subgroup constraints

	Hp	Ss	Cp
Ss	0·23 & –0·11* (*n* = 143, *P* = **0·006** & NS)† 1·175 (*P* < **0·001** & NS)‡		
Cp	0·24 & 0·32 (*n* = 68, *P* = 0·054 & **0·008**) 0·338 (*P* < **0·001** & **< 0·001**)	–0·38 & –0·04 (*n* = 43, *P* = **0·013 &** NS) 0·205 (*P* = **0·002** & NS)	
Cv	–0·12 & 0·16 (*n* = 19, *P* = NS & NS) 0·135 (*P* < **0·001** & **0·045**)	0·12 & 0·24 (*n* = 18, *P* = NS & NS) –0·201 (*P* < **0·001** & 0·15)	0·031 & 0·031 (*n* = 6, *P* = NS & NS) 0·008 (*P* = NS & NS)

*Upper row, Spearman's correlation coefficient r_s for raw data and for residuals from ANOVA.
†Middle row = *n* and *P* for Spearman's test, which are given only for mice that carried at least one specimen each of the species in the pair. No data are given if *n* for single infection with a species of helminth was < 15 and *P* is shown only when < 0·25.
‡Lower row gives the quantitative covariance on $\log_n(x + 1)$ transformed data for all mice (*n* = 399), and *P* for rejection of the null hypothesis calculated with and without subgroup constraints, respectively. No data are given when prevalence was < 10% and values are given only if *P* < 0·25 in one of the tests.
A. murissylvatici is not represented because only 10 mice were infected. Hp = *H. polygyrus*; Ss = *Syphacia stroma*; Cv = *C. vitta*; Cp = *C. pusilla*; NS = not significant.

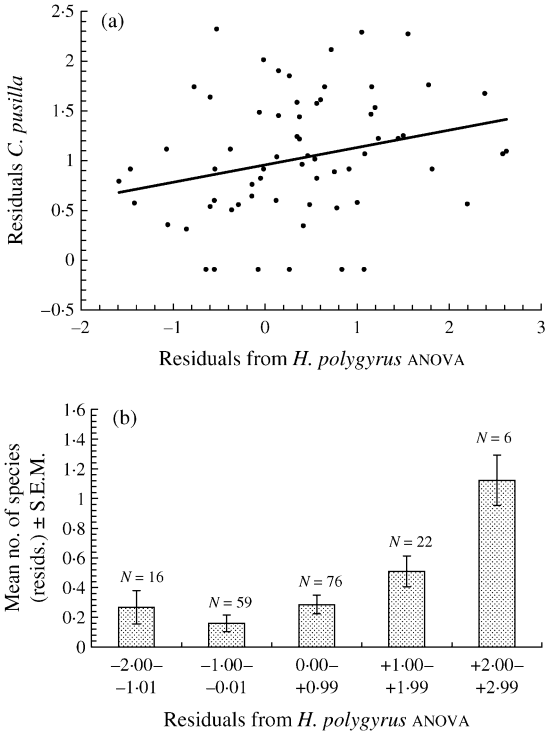

Fig. 4. (A) Quantitative association between *H. polygyrus* and *C. pusilla* (data set 1). Data are expressed as residuals from minimum sufficient ANOVAs of each species (*n* = 68). (B) Mean species richness with other helminths increases with *H. polygyrus* worm burden. The figure shows the mean species richness with helminth species other than *H. polygyrus*, among mice harbouring *H. polygyrus* and at least one other species (*n* = 179). Both variables are residuals from minimum sufficient ANOVAs that have controlled for other factors. Figures above the columns give the sample size.

tests = 14), and in each case only on mice that carried at least one of the two species concerned, revealed that there were no significant associations, neither in the raw data nor among the residuals of ANOVA. The relationship between *H. polygyrus* and *T. muris* was scrutinized carefully: the randomization test had clearly indicated a positive association and there was a suggestion of increasing *T. muris* worm burdens with increasing *H. polygyrus* (mice with < 10 worms, 10–30 worms and > 30 *H. polygyrus* carried mean ± SEM. *T. muris* worm burdens of 2·3 ± 0·6, 2·8 ± 0·9, and 5·9 ± 1·9, respectively).

Does the presence of H. polygyrus *predispose mice to infection with other species?*

We were particularly interested to test the idea that *H. polygyrus* should predispose mice to infection with other helminths because laboratory studies have indicated that in the presence of *H. polygyrus bakeri* other intestinal infections are greatly prolonged in *Mus musculus*. Table 4 summarizes the outcome of multiple correlational analyses on the three variables tested, using both raw data and residuals from ANOVAs (to control for the confounding influence of extrinsic and intrinsic factors), and on three subsets of mice. However, these results have to be interpreted with caution because of the multiple analyses undertaken, which risk Type 1 errors and only *P* < 0·0007 can be accepted as significant.

The relationship between the number of *H. polygyrus* harboured by mice and the total number of other helminth species was highly significant, when the test was conducted on all mice or just on mice with *H. polygyrus* and at least one other species. Similar significant relationships were seen with total worm burdens of other species of helminths, whether expressed as raw totals or percentage totals. However, when site, season, host age and sex were controlled for (by testing the residuals), the correlational coefficients were lower and many were no longer significant. The only relationship to retain significance after implementation of the Dunn–Sidak correction was that between *H. polygyrus* worm burdens

Table 4. Multiple Spearman's Rank correlation analysis of the relationships between abundance of infection with *H. polygyrus* or *S. stroma*, and worm burdens and no. of other helminth species harboured by mice in data set 1

			Variable 1*					
			H. polygyrus			*S. stroma*		
Variable 2†	Type of data‡	Subset of mice§	*n*	r_s	*P*¶	*n*	r_s	*P*
No. of other species	Raw	All mice	399	0·499	< 0·0001	399	0·331	< 0·0001
		subset A	302	0·458	< 0·0001	160	0·183	0·021
		subset B	179	0·446	< 0·0001	148	0·236	0·0042
No. of other species	Residuals	All mice	399	0·123	0·014	399	–0·019	NS
		subset A	302	0·116	0·044	160	0·008	NS
		subset B	179	0·271	0·0003	148	0·001	NS
Total worm burden of other species	Raw	All mice	399	0·472	< 0·0001	399	0·409	< 0·0001
		subset A	302	0·416	< 0·0001	160	0·191	0·016
		subset B	179	0·266	0·0004	148	0·236	0·004
Total worm burden of other species	Residuals	All mice	399	0·014	NS	399	–0·048	NS
		subset A	302	–0·021	NS	160	–0·115	NS
		subset B	179	–0·047	NS	148	–0·124	NS
Worm burden of other species as % of total	Raw	All mice	399	0·504	< 0·0001	399	0·386	< 0·001
		subset A	302	0·471	< 0·0001	160	0·204	0·010
		subset B	179	0·429	< 0·0001	148	0·253	0·002
Worm burden of other species as % of total	Residuals	All mice	399	0·083	NS	399	–0·039	NS
		subset A	302	0·135	0·019	160	–0·044	NS
		subset B	179	0·185	0·014	148	–0·049	NS

*Variable 1 was either *H. polygyrus* or *S. stroma*

†Variable 2 was either total no of additional species (i.e. not counting the species in variable 1), total worm burden of all additional species, or the sum of worm burden data for all additional species, following conversion of the worm burden in each mouse to the percentage of the total number of worms of that species recovered from all mice in that data set.

‡Data were either tested raw or as residuals from minimum sufficient ANOVAS

§Each test was carried out on: (a) all mice; (b) subset A = only mice with at least one representative of either *H. polygyrus* (Hp, where variable 1 was *H. polygyrus*) or *S. stroma* (Ss, where variable 1 was *S. stroma*) (but note that in this subset of data some mice would not have carried other species); (c) subset B = mice with at least one representative of *H. polygyrus* or *S. stroma* and at least one worm of another species.

¶Only $P \leq 0{\cdot}1$ are given.

NS = not significant.

and species richness of other species (number of other helminth species, not individual worms, and excluding *H. polygyrus*) in mice carrying at least one *H. polygyrus* and one other species (Table 4, Fig. 4B). In data set 2, based on fewer mice, no relationship survived as significant when the extrinsic and intrinsic factors were controlled for.

In general correlation coefficients for *S. stroma* were lower and all subsets lost significance when the residuals were tested. In data set 2 there was no indication at all of any significant relationships involving *S. stroma*.

Discussion

Laboratory studies of concurrent infections in rodents utilizing various combinations of helminths have conclusively established that interactions between different species exist, and that they can be a dominant influence on the course of infection with one or both of the interacting species (Christensen *et al*. 1987; Behnke *et al*. 2001a). The most dramatic effects are mediated via the host's immune system, notably when one species elicits a strong immune response leading to the mobilization of powerful nonspecific effectors of resistance with ensuing changes in gut architecture and function. Disruption of the normal intestinal environment can be so marked that other species, concurrently residing in the gut, fail to sustain themselves and are also lost from the host (e.g. *Hymenolepis diminuta* from mice responding to *Trichinella spiralis*; Behnke, Bland & Wakelin 1977). Alternatively, one species may depress the host's intestinal immune system sufficiently to enable other parasites to grow larger, reproduce more successfully and survive longer than they otherwise would [e.g. prolonged survival of *Trichinella spiralis* in mice with *H. polygyrus* (Behnke, Wakelin & Wilson 1978); see Christensen *et al*. (1987) and Behnke *et al*. (2001a) for reviews]. We might therefore, expect to see evidence for either antagonistic or synergistic interactions in wild rodents naturally infected with helminths. In particular, we might expect to see synergistic interactions in wood mice infected with *H. polygyrus*, a core member of the component community, as the closely related subspecies *H. p. bakeri* is known to exert a powerful immunomodulatory effect on the course of other intestinal infections in mice (Behnke 1987). However, in marked contrast to the laboratory studies, hitherto, support from field data for these predictions is weak (Montgomery & Montgomery 1990; Haukisalmi & Henttonen 1998).

While the analyses presented in this paper, in line with earlier studies (Montgomery & Montgomery 1990),

support the co-occurrence of various combinations of helminths, they also show that mostly these depend on context in varying degrees, i.e. on intrinsic and extrinsic factors or their combinations. Overall, without subgroups being taken into consideration, positive co-occurrences of parasites were evident in both data sets and were supported by the Schluter test and the species-richness distributions. The former indicated that for both data sets there was an overall tendency for positive co-occurrence, much as in other intestinal helminth communities (Lotz & Font 1994). In our data sets none of the species ranked as common (Lotz & Font 1994; prevalence > 90%), but equally the communities were not dominated by rare species (prevalence < 10%; two of five in data set 1 and three of nine in data set 2). We therefore had no expectation about whether there would be an excess of positive or negative associations in the two studies. Associations between species at this level, imply that some species co-occur more commonly than expected from overall prevalence data or from the likelihood of infection being entirely random and our analyses demonstrated that both extrinsic and intrinsic factors played a major role in focusing combinations of parasites in specific hosts. Even the species-richness distributions did not differ significantly from a null model that took into account the various subgroups in the data. Among 16 interactions involving combinations of two or more species across both data sets, only one was not confounded by intrinsic or extrinsic factors or additional species of parasites (i.e. *T. muris* and *H. polygyrus* in data set 2). The co-occurrence of *C. pusilla* with *H. polygyrus* was site-dependent, but while differing in extent, in all cases it was in the same direction, with mice harbouring *H. polygyrus* having a greater probability of infection with *C. pusilla*. Therefore, most associations at the level of presence/absence data arose because hosts in certain classes (i.e. years, seasons, sites, age and sex groups) were more likely to carry particular combinations of species than other hosts and not through synergistic interactions between the species. The most likely explanation for these is variation in exposure to infection within subgroups of mice.

Equally, the present analysis does not provide evidence that quantitative interactions between helminths play a dominant role in structuring component communities. Nevertheless, in agreement with our expectations, there was one exception in the quantitative positive association between *H. polygyrus* and the tapeworm *C. pusilla*, supported by both the randomization test with subgroup constraints and by Spearman's test on the residuals of ANOVAs. Quantitative analysis generated a shallow positive gradient but this was more convincing when we controlled for site, season, sex and age effects. Even so, only 68 mice (17% of the sample) carried this combination, and therefore the overall contribution to component community structure was at best modest. To our knowledge, concurrent infections with these two species have not been investigated experimentally, and little is known about the duration of infection with *C. pusilla* or whether it is regulated immunologically. Likewise, the immunomodulatory properties of *H. p. polygyrus*, in contrast to *H. p. bakeri*, have not been investigated, although in the wild *H. p. polygyrus* causes long-lived primary infections in wood mice (Gregory, Keymer & Clarke 1990) and this is consistent with a survival strategy similar to that of its laboratory congener. We were unable to test whether this association existed through an independent data set because in data set 2 wood mice did not carry *C. pusilla*. Indeed none of the published studies on helminths in wild rodents explore exactly this same combination. Kisielewska (1970c) reported co-occurrence between two closely related species in bank voles (*Heligmosomum halli* and *C. pusilla*, although with current nomenclature these species were probably *H. mixtum* and *C. henttoneni*; Tenora & Meszaros 1971; Haukisalmi & Tenora 1993), but claimed a negative quantitative interaction in voles carrying both species. Hobbs's (1980) re-analysis of her data confirmed the positive co-occurrence but failed to substantiate the quantitative interaction. Haukisalmi & Henttonen (1993) detected a number of weak co-occurrences in *C. glareolus* and among these was *H. mixtum* and *Catentaenia* sp. but co-occurrence of these species was not evident in all of their data sets and there was one negative quantitative relationship in the spring subset from one of their study sites at Pallasjarvi.

In data set 2, *T. muris* only occurred in mice with *H. polygyrus* and the quantitative nature of this relationship was supported by the randomization test with subgroup constraints. This may be compatible with the idea that *H. polygyrus* predisposes mice to infection with *T. muris* through its immunomodulatory influence on the host. *T. muris* is known to elicit a strong host response in both laboratory mice and *A. sylvaticus* (Behnke & Wakelin 1973) and interactions between these species are well documented (Jenkins & Behnke 1977; Behnke, Ali & Jenkins 1984). However, further quantitative analysis of our field data by Spearman's test on raw data and on residuals of ANOVA did not substantiate this association, but nevertheless provided some indication that heavier infections with *H. polygyrus* may be associated with heavier infections with *T. muris*.

The detection of quantitative interactions between parasites from observational data is bedevilled by pitfalls, which may generate false significant associations between parasites (Haukisalmi & Henttonen 1998). In our data set 1, mice were trapped in three sites, among which the component communities of helminths varied quite markedly (Abu-Madi *et al*. 1998, 2000). In the Isle of Wight, mice showed a higher prevalence and a greater abundance of both *S. stroma* and *H. polygyrus* than at Dungeness, and the Egham site was intermediate for both species. Thus, the quantitative relationships in raw data (Table 4) might have been generated not by real interactions between the parasites, but rather because the mice came from three sites, the correlations primarily reflecting among-site differences in infections with these species. When we controlled for site, seasonal and other factors, most of the relationships lost significance. Only

those between the residuals of the *H. polygyrus* ANOVA and the ANOVAS of *C. pusilla* and of the number of other species retained significance. Thus with increasing worm burdens of *H. polygyrus*, mice tended to carry heavier infections of *C. pusilla* and more of other species of helminths. Interestingly there was no evidence for such a relationship in *S. stroma*, once the extrinsic and intrinsic factors had been controlled for.

Why then is there such a marked discrepancy between the predictions of laboratory studies and observations from the field? We offer three explanations. First, laboratory experiments have been conducted with relatively high parasite burdens, especially those involving nematode parasites such as *H. p. bakeri* (often 100–300 worms). While individual burdens of *H. p. polygyrus* in excess of 100 worms do occur in the field, they are rare and it is more common for worm burdens to average fewer than 20 per mouse. Such worm burdens rank as low intensity by comparison with laboratory infections and as the immunomodulatory effect of *H. p. bakeri* on concurrent infections with *T. muris* and *T. spiralis* is dose-dependent, and consistently evident only in animals with 100 or more *H. p. bakeri* (Jenkins & Behnke 1977; Behnke *et al*. 1978), it is likely that such effects will only become apparent in a small number of very heavily infected animals. Second, helminth parasites of wood mice, being generally smaller and less bulky than the larger species found in birds and fish (which are often found at higher densities and among which interactions exist), do not occupy as much space within the intestine and may have a lesser impact on the host gut. Third, laboratory experiments are conducted under controlled conditions in which the time frame of events is known precisely. Data based on culled wild animals provide only a snapshot of events in the field, and cover a spectrum of states in which resistance to each of the helminths may vary from complete susceptibility to total resistance. When each of the species comprising the component community is considered, the possibilities become vast. Undoubtedly, interactive events occur within infracommunities in wild rodents, as reflected in studies showing changes in intestinal sites of particular species in the presence of others (Holmes 1961; Lotz & Font 1985; Patrick 1991; Lello *et al*. 2004) and studies showing associations based on prevalence and abundance data in other host–parasite combinations (Bush 1990; Lotz & Font 1991, 1994). However, by comparison with the helminth communities of bats (Lotz & Font 1991, 1994) and birds (Kennedy, Bush & Aho 1986; Bush 1990), our rodent systems can be considered relatively depauperate (Poulin 1996) and quantitative interactions, based on abundance in infracommunities, are difficult to detect. At any one time they probably only concern a small subset of the entire component community.

Finally, the stepwise analysis in this paper sets out a framework for such analyses for the future. It is not primarily concerned with community-wide associations between parasites (i.e. net negative or positive associations, Schluter 1984), although these are the starting point in any analysis of interactions between parasites. Rather we were more concerned with evaluating the extent to which specific combinations of parasites co-occur in the component community of helminths in wood mice, the extent of quantitative interactions with subgroup constraints taken into account, and assessing their overall contribution to the processes that structure component communities of helminths in wild rodents. We conclude that, while combinations of species co-occur mostly in a context-dependent manner, quantitative interactions between species are not a dominant feature of the component communities of helminths in *A. sylvaticus* at our study sites in the south of England, and are unlikely to be major components of the processes that structure such communities. Rather, these communities conform to the isolationist, nonequilibrium type with substantial vacant niches (Holmes & Price 1986) and contrast with the component communities of birds, especially aquatic birds (Bush, Aho & Kennedy 1990), which have dense populations, can be saturated, and in which interactions between parasites are considered to play an important part (Bush & Holmes 1986).

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