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# Seasonal and site specific variation in the component community structure of intestinal helminths in *Apodemus sylvaticus* from three contrasting habitats in south-east England

M.A. Abu-Madi<sup>1,3</sup>, J.M. Behnke<sup>2\*</sup>, J.W. Lewis<sup>1</sup> and F.S. Gilbert<sup>2</sup>

<sup>1</sup>School of Biological Sciences, Royal Holloway, University of London, Egham, Surrey, TW20 0EX, UK: <sup>2</sup>School of Biological Sciences, University Park, University of Nottingham, Nottingham, NG7 2RD, UK: <sup>3</sup>Department of Applied Sciences, Faculty of Technology, Qatar University, PO Box 2713, Doha, Qatar

## Abstract

Seasonal fluctuations in the prevalence and abundance of infection with intestinal helminths were studied in *Apodemus sylvaticus* (wood mouse,  $n = 399$ ), from three contrasting habitats in southern England, to test the hypothesis that both intrinsic (host sex, age) and extrinsic (season, site) factors influence parasite species richness and abundance. Five species of helminths were recovered but only one of these (*Capillaria murissylvatici*) was site-specific (Dungeness). Total species richness was therefore 5 at Dungeness and 4 at the other two sites. Mean species richness was 1.4, but in adult mice there was a pronounced difference between the sites, and an independent highly significant effect of season. *Syphacia stroma* and *Corrigia vitta* both showed marked differences between sites in respect of prevalence and abundance of infection. *Capillaria murissylvatici* was encountered at Dungeness mostly in the spring whereas seasonal changes in abundance of *S. stroma* were consistent across all three sites. Seasonal fluctuations in the abundance of *Catenotaenia pusilla* were compounded by differences between sites. Host sex was not a significant factor in any species, although *a posteriori* analysis of *S. stroma* worm burdens for the Isle of Wight site revealed a moderate local sex effect. Overall the principal determinants of variation in helminth burdens were the extrinsic factors, site and season.

## Introduction

Seasonal changes in the abundance of parasitic helminths in wild rodents are well documented in the UK (Montgomery & Montgomery, 1988, 1989), but have seldom been analysed by rigorous statistical analysis with other factors (e.g. age, sex and site) taken into account. Helminth species richness, prevalence and mean

abundance in wood mice (*Apodemus sylvaticus*) have been reported to vary between different sites (Lewis, 1968; O'Sullivan *et al.*, 1984), but with the exception of the studies of Montgomery & Montgomery (1990) and Abu-Madi *et al.* (1998), no previous studies have compared helminth fauna of wood mice between sites across the same complete set of seasons in the UK (but see Webster & MacDonald, 1995 for helminths of wild *Rattus norvegicus* in the UK and Kinsella, 1974; Mollhagan, 1978; Martin & Huffman, 1980; Boggs *et al.*, 1991 for helminths of *Sigmodon hispidus* in the USA).

Abu-Madi *et al.* (1998) showed that for *Heligmosomoides*

\* Author for correspondence.

Fax: 0115 9513251

E-mail: jerzy.behnke@nottingham.ac.uk

*polygyrus*, the dominant intestinal parasite of wood mice in the UK, seasonal patterns and site-specific factors were the major determinants of variation in worm burdens and prevalence of infection. Host sex played little overall role, although statistical interactions involving site and sex were detected. In the present study we extend our earlier work by testing the hypothesis that intrinsic (host sex and age) and extrinsic (season and site of capture) factors play a major role in determining species richness, prevalence and abundance of helminths, predicting specifically a marked effect of site of capture.

## Materials and methods

### Collection of mice and parasites

The study sites utilized in this project were the same as those reported previously at Dungeness in Kent (Grid reference, 074183), the grounds of Royal Holloway, University of London, Egham, Surrey (Grid reference, 993693) and on the Isle of Wight (Grid reference, 523882). A comprehensive description of these sites is given by Abu Madi *et al.* (1998), together with the procedures employed for trapping and ageing mice, and at autopsy. Similarly, the numbers of animals of each sex and age group, sampled at the three sites across four seasons were summarized in the same publication.

### Statistical analysis

The prevalence (percentage of mice infected in each subset), mean abundance of infection (= mean worm burden of each subset, including uninfected animals,  $\pm$  standard error of the mean) and the frequency distribution of each species were calculated. The negative binomial exponent  $k$  was estimated using maximum likelihood procedures based on Elliott (1977). The goodness of fit to the negative binomial distribution was tested by  $\chi^2$ . Prevalence was analysed by maximum likelihood

techniques based on log linear analysis of contingency tables implemented by the software package, Statgraphics Version 7, as described previously (Abu-Madi *et al.*, 1998). A minimum sufficient model was generated, for which the likelihood ratio of  $\chi^2$  was not significant, indicating that the model was sufficient in explaining the data. Parasite abundance was analysed by GLIM (General Linear Models), after  $\log(x+1)$  transformation, using a model with normal errors as reported previously (Crawley, 1993; Wilson & Grenfell, 1997; Abu-Madi *et al.*, 1998; Behnke *et al.*, 1999).

## Results

### *Apodemus sylvaticus*

A total of 399 *A. sylvaticus*, 210 males and 189 females, were trapped from the three sites as reported previously (Abu-Madi *et al.*, 1998) of which 40.4% ( $n=161$ , 55 males and 106 females) were classed as juveniles. Dungeness yielded 185, Egham 133 and the Isle of Wight 81 mice in total.

### Total species richness

Five species of helminths were recovered (table 1) and 322 mice (80.7%) carried at least one of these species. *Heligmosomoides polygyrus* was most common, followed by *S. stroma*. *Corrigia vitta* and *Capillaria murissyloatici* were both comparatively rare: *C. murissyloatici* was recorded solely at Dungeness whereas *Corrigia vitta* was rare in both Dungeness (1 out of 185 mice) and Egham (2 out of 133 mice) in comparison to the Isle of Wight (prevalence 22.2%). Thus total species richness was 5 in Dungeness, and 4 in each of the other two sites.

### Mean species richness

The overall mean number of helminth species harboured per host was  $1.4 \pm 0.05$ , with a variance to mean

Table 1. Prevalence, range and mean abundance of infection by host sex and sexes combined. Data from all three sites and both age groups are pooled ( $n=399$ ).

Species	Host sex <sup>1</sup>	Prevalence	Range	Mean abundance $\pm$ S.E.M.
<i>Heligmosomoides polygyrus</i>	M	80.0	0–126	17.5 $\pm$ 1.7
	F	70.9	0–105	10.8 $\pm$ 1.3
	C	75.7		14.3 $\pm$ 1.1
<i>Syphacia stroma</i>	M	42.4	0–700	47.9 $\pm$ 7.8
	F	37.6	0–320	22.2 $\pm$ 3.9
	C	40.1		35.7 $\pm$ 4.5
<i>Capillaria murissyloatici</i>	M	3.3	0–8	0.12 $\pm$ 0.05
	F	1.6	0–1	0.02 $\pm$ 0.01
	C	2.5		0.07 $\pm$ 0.03
<i>Catenotaenia pusilla</i>	M	23.3	0–20	1.3 $\pm$ 0.2
	F	12.7	0–20	0.7 $\pm$ 0.2
	C	18.3		1.0 $\pm$ 0.15
<i>Corrigia vitta</i>	M	5.7	0–25	0.37 $\pm$ 0.16
	F	4.8	0–25	0.33 $\pm$ 0.16
	C	5.3		0.35 $\pm$ 0.11

<sup>1</sup>M, male; F, female; C, sexes combined.

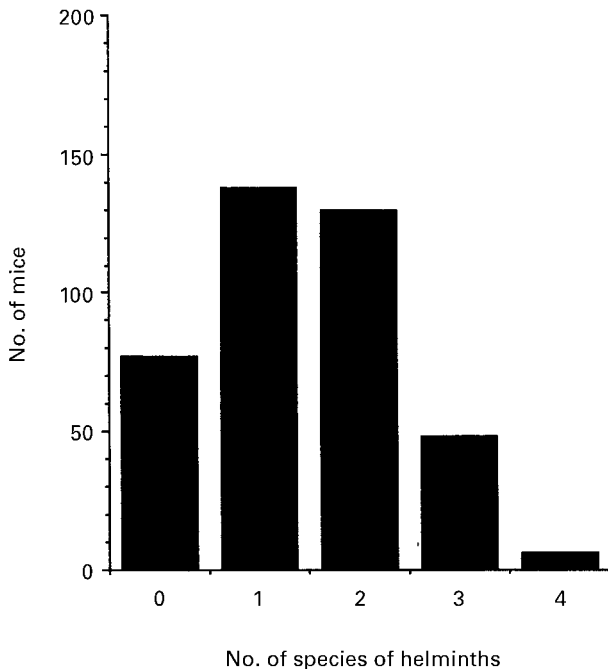


Fig. 1. Frequency distribution of *Apodemus sylvaticus*, according to the number of helminth species harboured.

ratio of 0.68 indicating a positive binomial distribution as shown by the frequency distribution in fig. 1. Analysis of the data for adult animals by GLIM (+ normal errors) revealed that there were no significant interactions, the main effect of host sex was not significant and only site and season affected the number of helminth species harboured. The similarity of the significant seasonal effect across all three sites is clearly apparent in fig. 2 (the main effect of season,  $F_{3,233}=20.578$ ,  $P<0.001$ ), with a peak in the winter and spring and lower values in the summer and autumn. Mean species richness also varied significantly between the sites (main effect of site,  $F_{2,232}=38.642$ ,  $P<0.001$ ), with the highest value at the Isle of Wight ( $2.56 \pm 0.10$ ), intermediate in Egham ( $1.79 \pm 0.08$ ) and lowest at Dungeness ( $1.15 \pm 0.08$ ).

The data for juvenile mice could not be analysed reliably because of some missing subsets, but the summary statistics show that in respect of site of capture, mean species richness followed the same pattern as in adults (Isle of Wight  $1.79 \pm 0.13$ , Egham  $1.21 \pm 0.11$  and Dungeness  $0.64 \pm 0.08$ ). Seasonal changes (fig. 2) again showed much the same pattern as that in adults although, with some exceptions, mostly lower values were obtained throughout.

#### *Syphacia stroma*

The combined data-set (juveniles + adults) fitted the negative binomial distribution, although not closely ( $\chi^2=10.68$ ,  $df=6$ ,  $P=0.098$  and  $k=0.128 \pm 0.013$ ). For juvenile males,  $k=0.041 \pm 0.013$ , but this subset could not be tested for goodness of fit because there were too few degrees of freedom. For juvenile females,  $k=0.122 \pm 0.028$  and

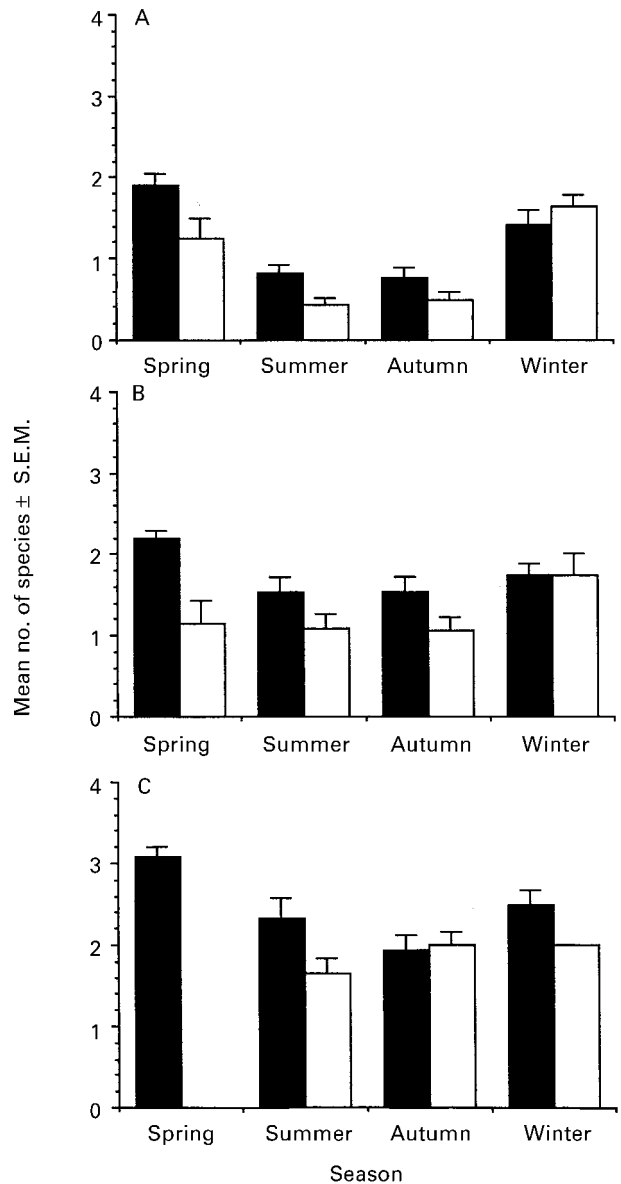


Fig. 2. Variation in species richness (mean number of helminth species harboured) by site (A, Dungeness; B, Egham; C, Isle of Wight), season and age (adults filled in columns, juveniles open columns).

$\chi^2=0.22$ ,  $df=1$ ,  $P=0.65$  indicating a good fit to the negative binomial distribution. Among adults, males showed significant departure from the negative binomial distribution with  $\chi^2=8.11$ ,  $df=3$ ,  $P=0.043$ , but females fitted well with  $\chi^2=1.54$ ,  $df=1$ ,  $P=0.213$  ( $k=0.133 \pm 0.031$ ). When analysed by site, with age, sex and season combined in each case, the data-sets from Dungeness ( $k=0.063 \pm 0.019$ ,  $\chi^2=0.26$ ,  $df=1$ ,  $P=0.619$ ) and the Isle of Wight ( $k=0.582 \pm 0.095$ ,  $\chi^2=0.86$ ,  $df=2$ ,  $P=0.656$ ) both conformed to the negative binomial distribution, but that from Egham did not ( $\chi^2=7.63$ ,  $df=2$ ,  $P=0.022$ ). Moreover, the latter did not fit the Poisson distribution

Table 2. Summary statistics for *Syphacia stroma* infections in *Apodemus sylvaticus* by site and host sex.

Site	No. of mice	Prevalence (%)	Mean intensity $\pm$ S.E.M.	Variance	Index of Dispersion <sup>1</sup>	Range
Dungeness						
Male	89	18.0	4.5 $\pm$ 1.4	170.8	37.6	0–73
Female	96	16.7	1.9 $\pm$ 0.8	65.3	33.7	0–69
Egham						
Male	70	40.0	29.9 $\pm$ 7.7	4108.9	137.6	0–337
Female	63	42.9	34.1 $\pm$ 8.9	5010.5	147.1	0–320
Isle of Wight						
Male	51	88.2	148.2 $\pm$ 25.5	33041.2	223.0	0–700
Female	30	93.3	62.0 $\pm$ 12.7	4825.0	77.8	0–300
All sites						
Male	210	42.4	47.9 $\pm$ 7.8	12695.3	265.2	0–700
Female	189	37.6	22.2 $\pm$ 3.9	2939.2	132.5	0–320

<sup>1</sup> I = Variance/mean ratio.

( $\chi^2 = 985.5$ ,  $df = 5$ ,  $P < 0.0001$ ). This variation in conformity to the negative binomial distribution precluded further analysis by ANOVA with negative binomial errors.

Overall, 160 mice (40.1%) were infected with *S. stroma* (89 male (42.4%) and 71 female (37.6%)). Analysis of the prevalence of infection in adult mice in respect of three factors, site (3 levels), season (4 levels) and sex (2 levels) gave a minimum sufficient model incorporating the effect of sex, and two interaction terms, season  $\times$  infection, and site  $\times$  infection (The likelihood ratio of  $\chi^2$  was 47.752 with 35  $df$ ,  $P = 0.074$ ). Thus, among the adult mice there were significantly more males ( $n = 155$ ) than females ( $n = 83$ ) (table 2) and the prevalence of infection varied significantly between sites, showing significant but similar seasonal changes at all three sites. Prevalence was clearly lowest at Dungeness (fig. 3), where only 20 of 94 (21.3%) adult mice harboured *S. stroma*, intermediate in Egham and markedly higher at the Isle of Wight site where 51/57 (89.5%) adult mice were infected. At all three sites

prevalence was highest in the winter and spring, falling to varying degrees in summer and autumn. Among juvenile mice, prevalence followed a similar pattern with the lowest value for Dungeness (13.2%), intermediate at Egham (31.9%) and the highest on the Isle of Wight (91.7%). As with adult mice, prevalence at the Isle of Wight site was high among juveniles throughout the year, the apparent dip in spring being attributable only to no animals sampled in that season.

Statistical models of abundance of infection, incorporating age, also proved difficult to interpret because of missing data subsets. We therefore confined the analysis to adult mice only. The full factorial model (table 3) shows that of the three factors entered, host sex was the least important, with no significance associated with the main effect of sex, nor any interactions involving sex. Nevertheless, at the Isle of Wight site the mean abundance was higher among male mice in all four seasons and we therefore analysed this data subset *a posteriori* (log [x + 1]

Table 3. Statistical analysis of the factors affecting the abundance of infection with *Syphacia stroma* in adult *Apodemus sylvaticus* by site, sex and season, through a 3-way ANOVA with normal errors.

Source of variation <sup>1</sup>	Change in deviance <sup>2</sup>	Degrees of freedom	Scale parameter	Scaled deviance*	P
Season	99.68	3	3.052	10.887	<0.001
Site	270.9	2	3.803	35.617	<0.001
Sex	2.475	1	2.658	0.931	NS
Sex $\times$ season	5.581	3	2.640	0.705	NS
Site $\times$ season	20.14	6	2.658	1.263	NS
Site $\times$ sex	9.996	2	2.650	1.886	NS
Site $\times$ sex $\times$ season	6.449	6	2.629	0.409	NS

The full model deviance was 569.27 with a scale parameter of 2.673.

NS, Not significant.

<sup>1</sup> Worm burden data were normalized by log (x + 1) transformation because a negative binomial distribution could not be fitted to the data.

<sup>2</sup> Change in deviance following the removal of the combination specified in 'source of variation' column from the full factorial model. We begin by removing the 3-way interaction, followed by the 2-way interactions. The remaining main effects, however, were removed to assess the change in deviance but then replaced before proceeding further.

\* Scaled deviance is a measure of the contribution of the factor specified under the column labelled 'source of variation' to explaining the variation in the data. It is calculated by fitting an analysis of variance with normal errors through GLIM and is distributed as *F*.

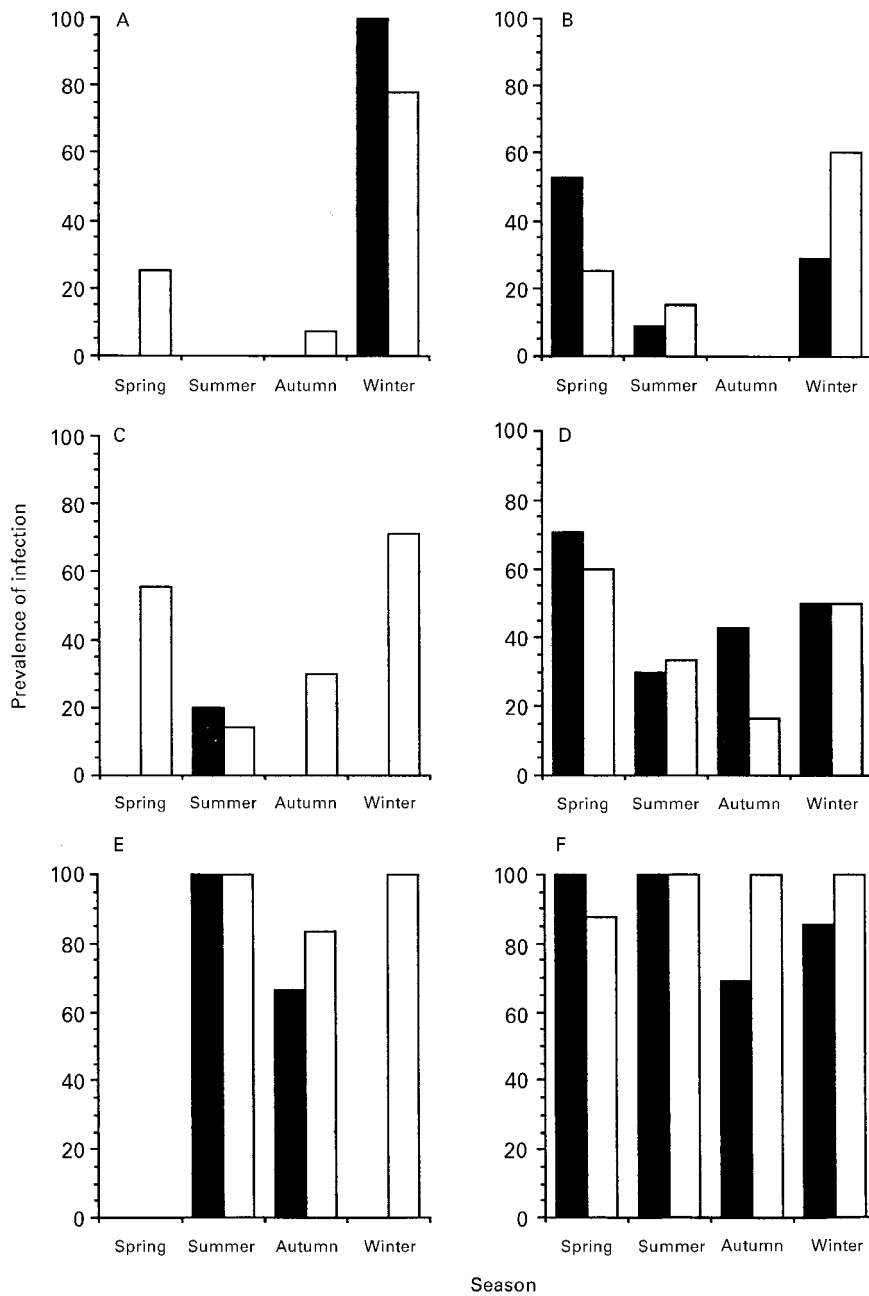


Fig. 3. Seasonal variation in the prevalence of infection with *Syphacia stroma* in *Apodemus sylvaticus* across three habitats (A and B, Dungeness; C and D, Egham; E and F, Isle of Wight) and by host age (juveniles A, C and E; adults B, D and F) and host sex (males filled in columns, females open columns).

transformed worm burdens) through a 2-way ANOVA with season and sex as factors: there was a moderate significant effect of sex ( $F_{1,53}=5.74$ ,  $0.025 > P > 0.01$ ), although this has to be viewed as a rough guide and not a rigorous test. None of the other interactions in the full model were significant but both of the remaining main effects had high significance associated with them. The site effect arose because mean abundance was highest

on the Isle of Wight and lowest at Dungeness (fig. 4, table 2). The significant seasonal effect indicated annual fluctuations in parasite burden which broadly followed the same pattern at each site: highest mean abundance was detected in spring and then fell to a low in summer and autumn before rising again in the winter. The minor site-specific differences in this pattern (the seasonal pattern was least evident in Egham; the rise towards

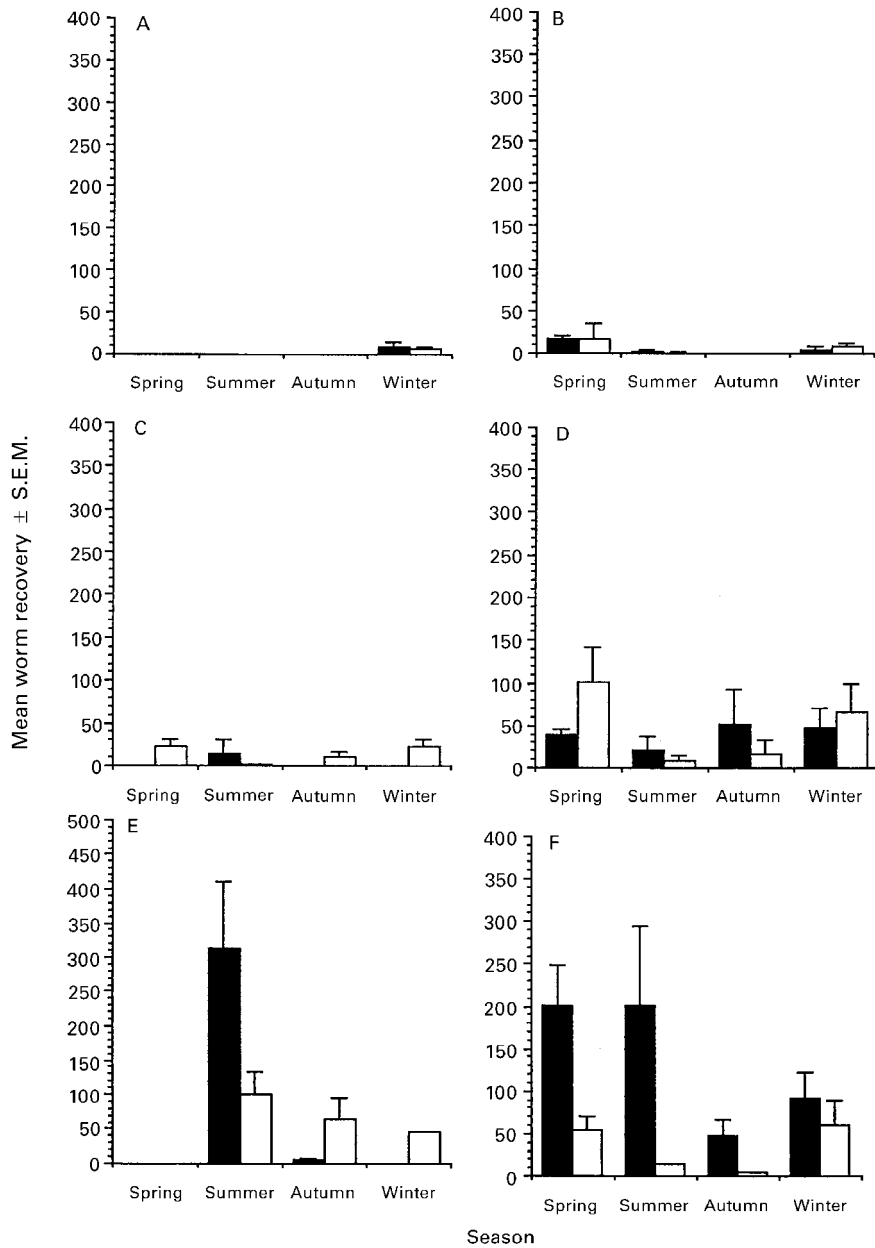


Fig. 4. Seasonal variation in the mean abundance of infection with *Syphacia stroma* in *Apodemus sylvaticus* across three habitats (A and B, Dungeness; C and D, Egham; E and F, Isle of Wight) and by host age (juveniles A, C and E; adults B, D and F) and host sex (males filled in columns, females open columns).

winter was least apparent in Dungeness) were not strong enough to generate significant interaction terms. As with prevalence of infection, the pattern was broadly similar among juvenile mice.

#### *Catenotaenia pusilla*

Seventy three mice (juveniles + adults) harboured *C. pusilla* (18.3%) with a overall mean of  $0.99 \pm 0.147$  and a variance/mean ratio of 8.71, but the distribution did not

conform to the negative binomial ( $k=0.079 \pm 0.011$ ,  $\chi^2 = 11.16$ ,  $df = 4$ ,  $P = 0.025$ ).

In the combined data-set (table 1) males showed a higher overall prevalence than females but few juvenile mice were infected with this species ( $n=12$ ) and among adult mice prevalence also appeared to be higher in male mice (males = 29.0%, females = 19.5%). However, analysis of prevalence in adult mice generated a minimum sufficient model with only two terms, host sex and the interaction between site, season and infection (Likelihood

Table 4. Variation in the mean abundance and prevalence of infection with *Catenotaenia pusilla* in adult mice by site and season.

Season	Site					
	Dungeness		Egham		Isle of Wight	
	Mean $\pm$ SEM	%	Mean $\pm$ SEM	%	Mean $\pm$ SEM	%
Spring	0.04 $\pm$ 0.04	4.3	4.6 $\pm$ 1.1	51.9	2.1 $\pm$ 0.7	65.2
Summer	0.11 $\pm$ 0.11	2.9	3.4 $\pm$ 1.1	38.5	1.9 $\pm$ 1.3	22.2
Autumn	0.25 $\pm$ 0.15	12.5	0.23 $\pm$ 0.17	15.4	0.07 $\pm$ 0.07	6.6
Winter	0.92 $\pm$ 0.61	25.0	1.6 $\pm$ 0.7	25.0	1.6 $\pm$ 0.8	40.0
Combined	0.23 $\pm$ 0.10	8.5	2.8 $\pm$ 0.5	36.1	1.4 $\pm$ 0.4	38.6

Data from both sexes has been combined because no significant sex difference was detected. For statistical analysis see text.

ratio  $\chi^2 = 25.279$ ,  $df = 23$ ,  $P = 0.336$ ). The absence of a sex  $\times$  infection interaction indicated that the sex difference was not significant. The interaction between site, season and infection arose because prevalence was lower at Dungeness (table 4) and showed a contrasting seasonal pattern with those at Egham and the Isle of Wight, where prevalence was highest in spring and then fell in the summer and autumn before rising again in the winter. At Dungeness, prevalence was low in spring and summer but rose in the autumn and winter.

Analysis of abundance of infection revealed a similar picture. There was a significant interaction between season and site ( $F_{6,230} = 2.908$ ,  $0.01 > P > 0.005$ ) and the main effects of site ( $F_{2,232} = 12.123$ ,  $P < 0.001$ ) and season ( $F_{3,233} = 3.776$ ,  $P = 0.01$ ) were both significant. The highest mean abundance of infection was observed at Egham (table 4) and the lowest at Dungeness.

#### *Capillaria murissylvatici*

This species was only detected in Dungeness in a total of ten mice. Nine of these were from the spring cohort, seven were males and nine were adults. No further analysis was feasible.

#### *Corrigia vitta*

Twenty one mice (juveniles + adults) carried *C. vitta* and the majority (18, sixteen adults and two juveniles) were from the Isle of Wight. Analysis of prevalence among adult mice revealed three terms for the minimum sufficient model: host sex and the interactions between site  $\times$  season, and site  $\times$  infection (Likelihood ratio  $\chi^2 = 39.15$ ,  $df = 32$ ,  $P = 0.18$ ). Prevalence among adult mice from the Isle of Wight was significantly higher (28.1%) than from the other two sites (2.3% at Egham and 0% at Dungeness).

A similar picture emerged for abundance of infection. Only the main effect of site was significant ( $F_{2,232} = 15.965$ ,  $P < 0.001$ ). The mean abundance at the Isle of Wight site was  $2.1 \pm 0.7$ , that for Egham was  $0.2 \pm 0.14$  whereas no adult mice carried *C. vitta* at Dungeness.

### Discussion

The key conclusion from the analysis presented in this paper is that the mean helminth species richness was poorest at Dungeness and highest at the Isle of Wight, supporting our prediction that site of capture would have

a major qualitative and quantitative influence on helminth parasite worm burdens in wood mice. Perhaps surprisingly, total species richness was highest at Dungeness but this was because the rarest species recorded in this study, *Capillaria murissylvatici*, was only recovered from a few mice at Dungeness and not at all from mice at the other sites. The same species has been seen previously at Egham, although in *Clethrionomys glareolus* rather than in *A. sylvaticus* (Lewis & Twigg, 1972). Total species richness is known to be dependent on sampling effort (Walther *et al.*, 1995) and in our study Dungeness provided the most mice. Additionally, it is possible that *C. glareolus* at Dungeness provided a heavier reservoir of this species but these hosts were not studied by us.

Our statistical analysis revealed a significant site effect in four of the five species of helminths in our study. Thus with the exception of *Capillaria murissylvatici*, all the other helminths, whether dependent on direct transmission (*S. stroma*), transmission via free-living larval stages (*H. polygyrus*) or dependent on one (*Catenotaenia pusilla*) or two (*Corrigia vitta*) intermediate hosts, were less abundant at Dungeness. Clearly, there are features of the extreme environment at this site which are not conducive for transmission of parasites. Abu-Madi *et al.* (1998) suggested that the acid soil in the pH range 4.0–5.8, may be a factor impairing efficient transmission of *H. polygyrus* in this site and other studies reveal that the acid environment has a profound effect on the diversity of invertebrates (Morris & Parsons, 1991). Dungeness is famous for the high diversity of its insects (Morris & Parsons, 1991), especially its bumblebees (Williams, 1989), probably coupled with low abundance of most species.

In contrast, wood mice from the Isle of Wight yielded the heaviest worm burdens of *H. polygyrus*, *S. stroma* and *C. vitta*, and this from a site in which the fewest hosts were trapped. The question then arises as to why mice from the Isle of Wight were generally heavily infected? One explanation may reside in the fact that in this site wood mice were confined to the hedgerows in-between arable land, essentially in semi-isolated island habitats. It is a common pattern for such island habitats to show low species richness but high species abundance, a phenomenon termed 'competitive release' (Begon *et al.*, 1990). As with other small mammal species, hedgerows are an important part of the arable habitat for wood mice, especially during the winter period (Tew, 1994). This would have resulted in the confinement of hosts and



transmission stages of the parasites to the more limited space of the hedgerows with the consequence that both host and transmission stages were more likely to encounter one another. For *Catenotaenia pusilla*, the heaviest intensity of infection was at Egham, a site from which this species has been reported previously but with a lower prevalence (14.6%, Lewis & Twigg, 1972).

Three of the species showed significant seasonal variation in prevalence and abundance. In all three cases (*H. polygyrus*, *S. stroma* and *C. pusilla*) abundance of infection was higher in the winter and spring periods and lower in the summer and autumn. For *S. stroma*, this finding is much in line with other studies in the UK and Eire. Elton *et al.* (1931) reported peak prevalence in October-March (1925–1926) and in January-April (1928). Lewis (1968) found that worm burdens increased in infected adult mice on Skomer from July through to October. Similar seasonal patterns were described by Langley & Fairley (1982) in the West of Ireland, where wood mice showed a peak intensity in December falling to a low in April/May in one year and September in another, O'Sullivan *et al.* (1984) where peak intensity was in February and by Montgomery & Montgomery (1988) who reported peaks varying between autumn, winter and early spring depending on site and year of their study in Northern Ireland. However, contrasting patterns have also been reported: mice trapped in woodland and rough grassland in Aberystwyth had peak worm burdens from June to October, and then lower counts in the winter months (Lewis, 1968). To a large extent, the decline in summer worm burdens is created by juvenile mice, either still uninfected or carrying low worm burdens, entering the adult cohorts. Moreover, in the case of *S. stroma*, with eggs that are fully embryonated and infective within hours of emergence from hosts, transmission is also likely to be enhanced in the winter period when relative densities of wood mice are greater, especially after a good seed crop earlier in the summer (Mallorie & Flowerdew, 1994). Rodent densities will vary substantially between populations, through time or through limited sampling, but, in their analysis of gastrointestinal strongylid nematodes from 19 mammalian species, Arneberg *et al.* (1998) showed that host population density and mean parasite abundance were positively correlated.

The factors likely to underlie seasonal variation in *H. polygyrus* have been discussed recently (Brown *et al.*, 1994; Abu-Madi *et al.*, 1998). Little is known about *C. pusilla* which has been reported previously from the British mainland (Lewis & Twigg, 1972) but is absent from Ireland (Langley & Fairley, 1982; Montgomery & Montgomery, 1988). Transmission is by fleas (*Ctenocephalms* spp.) and it is conceivable that transmission was enhanced in the winter in nests and tunnels because of higher flea and host population densities, but too little is known about this system to offer any further explanations.

Infections with *Corrigia vitta* were rarer than expected, since a higher prevalence was reported in Egham by Lewis & Twigg (1972) and Behnke *et al.* (1999). However, the latter authors also found that the intensity of *C. vitta* infections varied significantly in the autumn period between years. The two infected mice from Egham were

trapped in autumn and, consistent with Behnke *et al.* (1999) both were adults. The majority of infections on the Isle of Wight were also recorded in adult mice (16/18), supporting the idea that this species is more common among older hosts. Although no significant seasonal effect was identified, because overall prevalence was so low, 11 of the 18 infected mice on the Isle of Wight were trapped in spring and three in summer, which is consistent with the data of Montgomery & Montgomery (1988) who recorded winter peaks with this species. Other studies have found prevalence and intensity to be less seasonal (Lewis, 1968; Langley & Fairley, 1982).

Finally, this analysis has established firmly that site-specific differences in the prevalence and abundance of intestinal helminth parasites of wood mice are pronounced, even between locations within relative close proximity, in the same climatic zones. These site-specific effects were demonstrated whilst controlling for other factors known to influence parasite burdens. Seasonal effects were also demonstrated, but only in the case of *S. stroma* was the seasonal effect uncomplicated by interactions with site. Thus, as demonstrated by Abu-Madi *et al.* (1998), seasonal fluctuations in the prevalence and abundance of some helminths may vary significantly between sites. Building on our earlier paper, our results support the conclusion that transmission of helminth parasites is less successful at Dungeness than elsewhere, raising intriguing questions about the ecosystem in this unique environment. The finding that rodents living on arable land in the Isle of Wight have higher helminth burdens has broader implications for transmission of parasites of domestic animals and zoonotic infections, resulting from man-made changes to the natural environment.

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