Ann. Zool. Fennici 31:263–269
Helsinki 15 July 1994

ISSN 0003-455X

Helminth parasitism does not increase the vulnerability of the field vole *Microtus agrestis* to predation by the Ural owl *Strix uralensis*

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Received 13 October 1993, accepted 6 January 1994

We studied the vulnerability of mature, overwintered field voles *Microtus agrestis* to predation by the Ural owl *Strix uralensis* by comparing helminth parasitism and other characteristics of prey individuals collected from nests and field. The vulnerability of field voles was affected by the sex of voles, males being the most vulnerable prey. The probability of individual voles being captured by owls was not increased either by infections of the common helminth species or by high overall infection levels. By contrast, the prevalence of the nematode *Syphacia nigeriana* in female hosts was lower in nest samples than in field. This indicates that owls hunted preferentially or had high hunting success in open habitats with sparse vegetation, where *S. nigeriana* was rare. Alternatively, females with low foraging activity had simultaneously a low risk of being captured by owls and a high risk of being infected with *S. nigeriana*.

1. Introduction

Prey individuals infected by parasites often have a higher probability of being captured by predators than uninfected individuals (Holmes & Bethel 1972, Dobson 1988). The most pronounced cases of increased vulnerability in parasitized prey concern invertebrates infected with helminth larvae. For example, laboratory and field studies have shown that larval acanthocephalans drastically change the behaviour of isopod and amphipod intermediate hosts, and that such altered behaviour exposes the infected hosts to avian predators (Holmes & Bethel 1972, Moore 1983). Because predators serve as final hosts for these parasites, the ability of acanthocephalans to increase vulnerability of intermediate hosts enhances their transmission. As expected, increased vulnerability of vertebrate hosts

has frequently been shown to be due to infections by transmission stages of parasites (van Dobben 1952, Brassard et al. 1982, Milinski 1985, Hoogenboom & Dijkstra 1987), but seldom due to infections by adult parasites (Hudson et al. 1992).

We here analyse the role of helminth parasitism in the vulnerability of the field vole *Microtus agrestis* to predation by the Ural owl *Strix uralensis*, by comparing two samples of mature, overwintered voles, one consisting of voles snap-trapped in field and the other of voles collected simultaneously from owl nests. In addition to the helminth data, we describe the sex ratios and pregnancy rates of voles, since these factors may also be associated with vulnerability to avian predation (Beacham 1979, Korpimäki 1985, Halle 1988), and therefore confound the comparison of infection levels between nest and field samples. Furthermore, we examine the spatial variation in infection levels and vole characteristics among field samples.

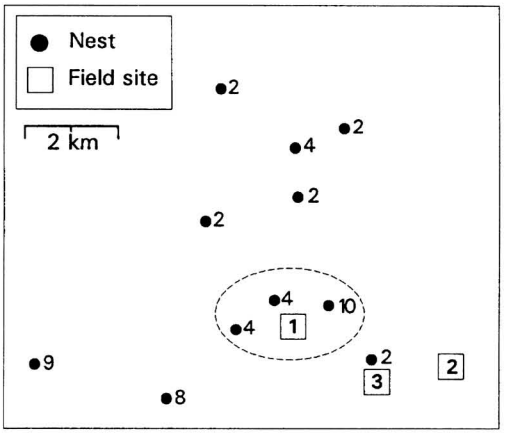

Fig. 1. Location of nests and field trapping sites (1–3). Dashed line denotes the field site and the surrounding nests included in a separate analysis (Fig. 3). Number of voles obtained from each nest is indicated beside the symbol. For sizes of field samples, see Fig. 4.

2. Materials and methods

2.1. Vole and helminth material

The vole material was obtained in connection of studies on the ecology of the Ural owl, conducted since the late 70's in Päijät-Häme, southern Finland (Pietiäinen 1988, 1989). During seven days in early May in 1985 we collected field voles ($n = 49$) from occupied owl nest-boxes and snap-trapped voles simultaneously in the surrounding areas ($n = 124$; Fig. 1). All voles were overwintered, breeding individuals and our study period coincided with the first pregnancy in females. Voles were collected from 11 Ural owl nest-boxes (2–10 voles per nest), and replaced by laboratory mice. The snap-trapping of field voles was performed at three separate sites, one or two nights with 131–150 traps per site. Sites 1 and 2 were old fields, whereas site 3 consisted primarily of a clear-cutting with sparse vegetation. The density of field voles, expressed as the number of voles caught during the first night per 100 traps, was high at sites 1 (26.0) and 2 (28.2), but much lower at site 3 (8.0).

In addition to the information on sex and reproductive status, each vole was examined for endoparasites. The body cavity and liver were searched for encysted larvae of tapeworms, and the alimentary tract (stomach, small intestine and caecum) for adult helminths. Parasites were stored in 70% ethanol for later identification. The specific determination of larval tapeworms was based on the number and shape of rostellar hooks (Verster 1969). Adult tapeworms were stained in haematoxylin and identified according to Tenora & Murai (1980). Nematodes were identified according to Genov (1984) after clearing them in glycerine-alcohol. Earlier faunistical and ecological data on helminths of field vole in Finland are provided by Tenora et al. (1983) and Haukisalmi (1986).

2.2. Statistical methods

The dependence between the occurrence of various helminth species and other characteristics of voles (sex, origin from nest or field, and field site) was analysed by three-dimensional contingency tables (log-linear models). Log-linear modelling aims to find the most parsimonious model that fits the observed data. For example, the model H,SO indicates that the sex ratio of voles (S) depends on the origin of voles (O), but the occurrence of a particular helminth species (H) does not depend on either of these variables. Savolainen & Vepsäläinen (1988)

describe the criteria of selecting the best model and provide an example of effective use of multiway contingency tables.

In addition to the prevalence of helminth species, we present data on overall infection levels of helminths, i.e., the number of helminth species and the number of cestode individuals per host (excluding the larval cestodes). The overall abundance of nematodes was not analysed, since the nematode assemblage was dominated by a single species, *Syphacia nigeriana* (Table 1). To analyse the effects of sex, origin and field site on overall infection levels, two-way analyses of variance were performed on rank-transformed data.

In comparisons of infection levels between nests and field, we combine the data for various nests and field sites. Nest and field site-specific analyses are not possible, because the owls' use of prey patches is unknown, and because the number of voles per each nest was small. However, we performed a separate analysis for field site 1 and three surrounding nests (Fig. 1) to study the occurrence of helminth species in a more homogeneous data set.

3. Results

3.1. Vole characteristics

The sex ratio of voles differed between the combined nest and field samples. The proportion of males was significantly higher ($\chi^2 = 6.4$, $P = 0.01$) in nests (73%) than in field (52%), and the proportion of pregnant females was higher in nests (77%) than in field (54%), but not significantly so ($\chi^2 = 2.3$, $P = 0.13$). The sex ratio of voles did not show significant variation among field sites ($\chi^2 = 1.5$, $P = 0.48$, df = 2), but the proportion of pregnant females varied strongly among sites ($\chi^2 = 38.7$, $P < 0.001$, $df = 2$).

3.2. Helminths

Field voles harboured six species of adult cestodes, two species of larval cestodes and three species of nematodes (Table 1). The most prevalent helminth species were the cestodes *Paranoplocephala gracilis, Anoplocephaloides dentata* and *Anoplocephaloides* sp., and the nematode Syp*hacia nigeriana*. The data of the other, rare helminth species (<10%) will not be analysed further.

3.3. Occurrence of common helminths

The log-linear models for all common helminths (Fig. 2) included an interaction between the sex ratio and origin of voles (SO), and indicated that males were over-represented in the nest sample. The model for *A. dentata* also included the effect of host sex on helminth occurrence (HS), and showed that prevalence was higher in males. The complex full-order model for *S. nigeriana* (HSO) indicates

Table 1. Helminth species of the field vole *Microtus agrestis*, microhabitats and prevalence (%) of helminths, and mean number of helminth individuals per infected host.

	Micro-habitat	%	Mean ± *SD*
Cestoda			
Paranoplocephala omphalodes	small intestine	8	1.4 ± 0.5
P. gracilis	small intestine	15	1.3 ± 1.0
Paranoplocephala sp.	small intestine	2	1.0 ± 0
Anoplocephaloides dentata	small intestine, caecum	33	1.9 ± 1.3
Anoplocephaloides sp.	small intestine	16	2.0 ± 1.3
Hymenolepis asymmetrica	small intestine	0.6	2
Taenia mustelae (larva)	liver	5	2.4 ± 3.1
T. taeniaeformis (larva)	liver	2	2.0 ± 1.4
Nematoda			
Heligmosomoides laevis	small intestine	9	10.5 ± 10.9
Heligmosomum costellatum	small intestine	1	2.5 ± 2.1
Syphacia nigeriana	caecum	32	29.4 ± 10.9

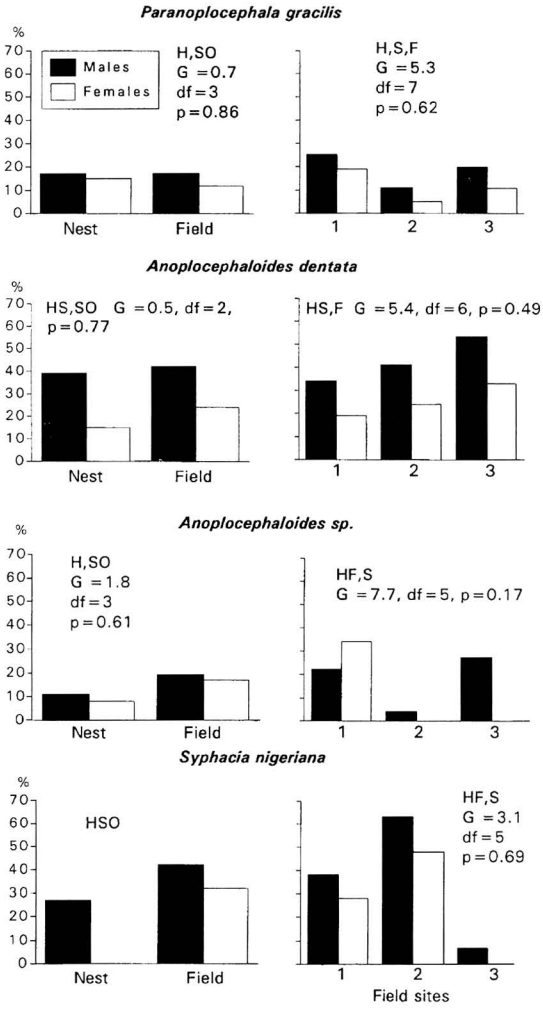

Fig. 2. Prevalence (%) of common helminths of field vole *Microtus agrestis* by sex and origin (left), and sex and field site (right) of host. Inserted are the corresponding log-linear models for associations between the occurrence of helminths (H), and sex (S), origin (O, nest/field) and field site (F) of host, and the fit of the models to the observed data. Goodness of fit-test is not possible for the full-order model HSO (*S. nigeriana*). Sample sizes shown in Fig. 4.

that males and females had equal prevalence in field, but females found in nests had lower prevalence than males (in fact, no infected females were found in nest samples). In other words, the infections by *S. nigeriana* were associated with decreased vulnerability to predation in females, but not in males. *Paranoplocephala gracilis* and *Anoplocephaloides* sp. occurred independently of the sex and origin of voles.

The occurrence of *Anoplocephaloides* sp. and *S. nigeriana* depended significantly on field site (interaction HF), their prevalence being lowest at sites 2 and 3, respectively (Fig. 2). Despite this variation, the comparison of prevalences between field site 1 and its three nearest nest samples supports the decreased vulnerability to owls of female voles infected with *S. nigeriana* (Fig. 3). On the other hand, the data for *Anoplocephaloides* sp. (higher prevalence in field) and *P. gracilis* (higher prevalence in nest) shows that their prevalences may also differ between nest and field samples if studied in a more homogeneous material. Because of small sample size, the log-linear modelling of these data (Fig. 3) was, however, not possible.

3.4. Overall infection levels

The number of helminth species per vole was significantly lower in males and females found in nests than in field-caught voles, but the abundance of cestodes was not related to the origin (nests vs. field) of voles (Fig 4, Table 2). However, the unexpectedly low number of helminth species in voles found in nest boxes appeared to be due to the rarity of *S. nigeriana*; exclusion of this nematode resulted in an ANOVA model with no difference between species number of voles from nests and field (origin, $F_{1,169} = 1{,}53$, $P = 0.39$; sex, $F_{1,169} = 15.87$, $P = 0.01$; interaction, $F_{1,169} = 0.06$, $P = 0.86$). Irrespective whether the voles were found in nests or trapped in the field, male hosts showed higher overall infection levels than female hosts.

The number of cestodes varied significantly among field sites (lowest infection level at site 2). Although no significant spatial variation existed in the number of helminth species per host (Table 2), females appeared to harbour fewer species at site 3 than at the other sites (Fig. 4).

4. Discussion

The vulnerability of field voles to predation by Ural owls was affected by the sex of voles, and by the occurrence of the nematode *Syphacia*

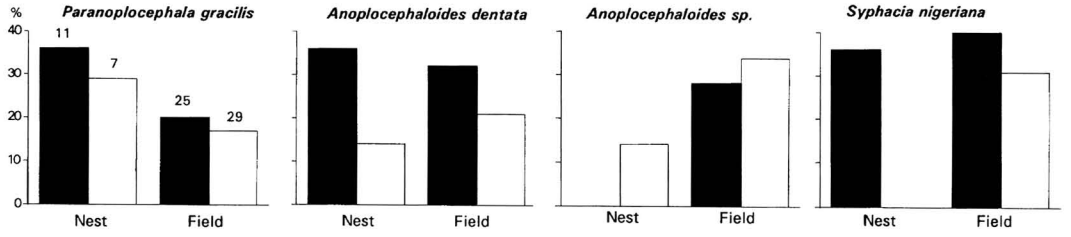

Fig. 3. Prevalence (%) of common helminths of field vole *Microtus agrestis* by sex and origin of host in the material from nest 1 and three surrounding field sites (Fig. 1). Symbols as in Fig. 2. Sample sizes shown above the columns.

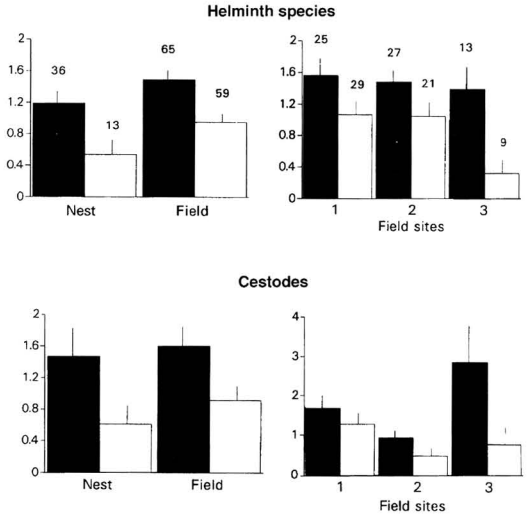

Fig. 4. Number of helminth species and cestode individuals per host (mean±*SE*) in field vole *Microtus agrestis* by sex and origin (left), and sex and field site (right) of host. Samples sizes shown above the columns. Table 2 gives the corresponding test-statistics. Symbols as in Fig. 2.

nigeriana. The dominance of mature males in the diet of avian predators has been explained by high activity and exposure of males (Beacham 1979, Korpimäki 1985). This explanation fits well with the present results, since during the breeding season mature males of *Microtus agrestis* have larger home ranges and are more active than mature females (Myllymäki 1977).

Helminth infections did not increase the vulnerability of field voles to owl predation. The lack of evidence for parasite-induced vulnerability to owl predation is not surprising, because parasites are not expected to affect the vulnerability of their final hosts. In addition, adult helminths rarely are strongly pathogenic (Rees 1967) or able to change the behaviour of their hosts (Dobson 1988). On the other hand, parasites which use birds of prey as their final hosts are capable of altering the behaviour of their arvicoline intermediate hosts (Quinn et al. 1987), thereby increasing their vulnerability to avian predation (Hoogenboom & Dijkstra 1987).

Table 2. A summary of two-way analyses of variance on the number of helminth species and cestode individuals per host (field vole *Microtus agrestis*), using sex and origin (nest/field), and sex and field site as categorical variables. Only field-caught voles were included in the latter analysis.

		Helminth species			Cestodes		
	df	*MS*	*F*	*P*	*MS*	*F*	*P*
Sex	1	27.78	13.38	<0.01	12.16	5.59	0.02
Origin	1	9.32	4.49	0.04	1.69	0.77	0.38
Sex × Origin	1	0.45	0.22	0.64	0.01	0.01	0.94
Error	169	2.08	2.18				
Sex	1	27.90	13.27	<0.01	17.92	8.74	<0.01
Site	2	5.21	2.48	0.09	7.97	3.88	0.02
Sex × Site	2	2.03	0.97	0.38	1.14	0.56	0.57
Error	118	2.10	2.05				

The only evidence of helminths affecting the vulnerability of voles was that the females infected with *S. nigeriana* had a lower risk of being preyed upon than uninfected females. This result was obvious both in the combined data and in the more homogeneous data from a single site. The prevalence of *S. nigeriana* was especially low in the clear-cut site, suggesting that high host density is necessary for its effective circulation, evidently due to direct transmission from host to host (Lewis 1968). Consequently, the rarity of *S. nigeriana* in voles found in nests may indicate owls' preferential hunting or high hunting success in open habitats with sparse vegetation. Other data on infection levels of helminths in nests and field do not, however, consistently support this explanation. The number of helminth species per vole, which did not vary significantly among field sites, was about the same in nest and field samples (excluding *S. nigeriana*). On the other hand, the occurrence of *A. dentata*, and overall abundance of cestodes were high at the clear-cut site, and preferential hunting in open habitats should have lead to higher infection levels of cestodes in voles found in nests, compared to those trapped in the field. Contrary to the expected pattern, the field-trapped and nest-stored voles did not differ with respect to the prevalence and abundance of cestodes.

During the breeding period of owls the predation pressure on voles is high, and any behavioural adaptation by voles to avoid predation would be advantageous. An obvious adaptation of prey to minimise the risk of avian predation is decreased foraging activity (Kotler et al. 1991). McNair & Timmons (1977) have shown that infections by the nematode *Syphacia obvelata* decrease the exploratory activity of mice, an adaptation which is likely to be advantageous to the transmission of *Syphacia*. If *S. nigeriana* were able to decrease the activity of field voles, infected voles would probably be less vulnerable to avian predation than uninfected voles. Assuming that *Syphacia* is not harmful to voles, the ability of *Syphacia* to change the behaviour of field vole females may thus have evolved as a mechanism which simultaneously enhances the transmission of the parasite and decreases the vulnerability of the host to avian predation.

Why is the vulnerability of females, but not that of males, affected by infections with *Syphacia*? This pattern is unexpected, because mature males are more vulnerable to avian predation than females for reasons other than helminth parasitism, and males are thus more likely to show anti-predatory adaptations. The behaviour of mature field vole males, which is characterized by high activity on large territories, contrasts the behaviour of mature females (Myllymäki 1977, Pusenius & Viitala 1993). We hypothesise that decreased vulnerability associated with *Syphacia*-infections is absent in males because of the disadvantages of decreased activity for males' competitive ability and reproductive success.

Acknowledgements. We would like to thank Erkki Korpimäki and Arne Lundberg for critically reviewing the manuscript.

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