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Helminth parasitism in the voles *Microtus oeconomus* and *M. miurus* on the North Slope of Alaska: host specificity and the effects of host sex, age and breeding status

Voitto Haukisalmi, Heikki Henttonen & George O. Batzli

Haukisalmi, V., University of Helsinki, Department of Ecology and Systematics, Division of Population Biology, P.O. Box 17, FIN-00014 Helsinki, Finland
Henttonen, H., Vantaa Research Center, Finnish Forest Research Institute, P.O. Box 18, FIN-01301 Vantaa, Finland
Batzli, G. O., Department of Ecology, Ethology and Evolution, University of Illinois, Urbana, IL 61801, USA

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We studied host specificity and the effects of host sex, age, breeding status and habitat on prevalence and intensity of helminths in the tundra vole *Microtus oeconomus* and the singing vole *M. miurus* at Toolik Lake on the North Slope of Alaska. The helminth faunas of the vole species were similar. However, the cestodes *Paranoplocephala omphalodes* and *Hymenolepis horrida* were particularly prevalent in *M. miurus* and *M. oeconomus*, respectively. Host preference was accompanied by a larger body size in the preferred host species, especially in *P. omphalodes*. This together with biogeographic data suggests that the specificity of *P. omphalodes* to *M. miurus* may be due to an intimate phylogenetic association between the host and the parasite. The factors behind the specificity of *H. horrida* to *M. oeconomus* are less obvious. The habitats of voles (wet vs. dry) did not significantly affect the occurrence of the common cestodes. Sex, age and breeding status of voles showed significant interactive effects on the occurrence of *P. omphalodes* and *H. horrida*; these effects were partly different in the two host species. The prevalence of both cestode species was higher in overwintered males than in other subgroups of the host population, probably because of the combined effect of increased exposure and decreased resistance in overwintered males. The pronounced heterogeneity of host populations with respect to helminth infections suggests that the reported patterns of parasite prevalence in small rodents may be severely biased when the host population structure is not considered and that the harmful effects of helminths may differ among the subgroups of the host population.

1. Introduction

During the breeding season, vole populations are heterogeneous with respect to age and breeding condition of individuals. Myllymäki (1969, 1977) introduced the term *functional group* to describe the various subgroups of the vole population, distinguishing reproducing males, reproducing females, subadults and juveniles. In an analysis of helminth population dynamics in the bank vole *Clethrionomys glareolus*, Haukisalmi et al. (1988) showed that the voles representing different functional groups often differed significantly with respect to the infection levels of helminths. For example, two species of nematodes occurred abundantly in overwintered, mature females, but were rare or absent in the other functional groups.

The tundra vole *Microtus oeconomus* and the singing vole *M. miurus* are dominant mammalian herbivores near Toolik Lake, Alaska. These two species differ ecologically (Batzli & Henttonen 1990) and have different biogeographic origins, *M. oeconomus* being Palearctic and *M. miurus* being Beringian. Although the taxonomy of rodent helminths in Alaska has been studied extensively (Rausch 1952, 1957, 1976), there are no quantitative data on helminth parasitism in *M. oeconomus* and *M. miurus*, except for a report on helminths of *M. abbreviatus* (closely related with *M. miurus*) on the St. Matthew Islands (Rausch & Rausch 1968).

We describe here the patterns of helminth parasitism in *M. oeconomus* and *M. miurus* at Toolik Lake, on the North Slope of Alaska. The analysis has two main purposes: 1) to compare the infection levels of helminths in the two host species, and 2) to analyse the effects of habitat, sex, age and breeding status of the preferred host on the occurrence of two common species of cestode. We attempt to explain the observed inter- and intraspecific differences by ecological and physiological mechanisms.

2. Materials and methods

The rodent material, consisting of 219 individuals of *M. oeconomus* and 182 individuals of *M. miurus*, was obtained at Toolik Lake, on the North Slope of Alaska (68°38'N, 149°36'W), during the summer 1984. These species were the most common rodents at Toolik Lake. Other arvicoline species, *Clethrionomys rutilus*, *Lemmus sibiricus* and *Dicrostonyx rubricatus* were much less abundant (Batzli & Henttonen 1990, 1993, Batzli & Lesieutre 1995).

The general features of the area, habitat types, food selection, and population dynamics of voles at Toolik Lake have been described by Batzli and Henttonen (1990) and Batzli and Lesieutre (1991). *Microtus oeconomus* primarily eats monocotyledons and prefers low, wet sites with the sedges *Eriophorum angustifolium* and *Carex aquatilis*. *Microtus miurus* primarily eats dicotyledons and prefers more mesic habitats with a variety of forbs, *Equisetum* and *Salix*.

For analyses of habitat effects on helminth occurrence, the habitats of voles were classified as "wet" or "dry". Because of the different habitat preferences of *M. oeconomus* and *M. miurus*, these categories are not identical between the vole species. For *M. oeconomus* habitat types next to ponds, lakes and streams were classified as wet and those on slopes as dry. For *M. miurus* habitats on lower slopes were considered wet and those on higher slopes or rocky areas dry (habitat types are described in Batzli & Henttonen 1990).

Trapping started on July 4 and finished on September 6. In the beginning, reproductive voles consisted of overwintered animals only. In the late July the first young of the summer entered the breeding population. Because the infection levels of helminths may differ significantly among subgroups of vole populations (Haukisalmi et al. 1988), we divided the hosts into six categories according to sex, age and breeding status: overwintered, mature males (i) and females (ii), summer-born, mature males (iii) and females (iv), and summer-born, immature males (v) and females (vi). Notice that these categories differ from the original concept of Myllymäki (1969) (see Introduction). Throughout the analyses, the six functional groups are presented as a two-way classification by host sex and cohort. The three cohorts are thus overwintered voles (all mature), summer-born immature voles and summer-born mature voles.

Voles were caught with snap traps and dissected during the same day. The small intestine, caecum, body cavity and liver were examined for helminths; stomachs were examined only occasionally because they were preserved for later diet analyses. Helminths were relaxed and washed in water and fixed in 70% ethanol. For specific identification, cestodes and trematodes were stained with haematoxyline and mounted in Canada balsam. Nematodes were cleared in alcohol-glycerine solution. For taxonomy and identification of helminths we follow Rausch (1952, 1976).

To examine the factors affecting the host specificity of helminths, we compared the body length and maximum body width of two common cestodes, *Paranoplocephala omphalodes* and *Hymenolepis horrida*, in the two host species. If possible, measurements of fully gravid cestodes from ten vole individuals of each host species were included in the analyses. If two or more specimens of conspecific cestodes occurred in an individual vole, the mean of the cestodes' body dimensions was used as a representative measurement.

Three-way contingency tables (log-linear models; Fienberg 1970) were used for analysing the effects of host habitat, sex and cohort on the occurrence of two common cestodes in their preferred hosts. Log-linear modelling aims at finding the best, or the most parsimonious, model amongst all acceptable models. Interactions between variables are shown by combined symbols, and lack of interactions by separating the variables with a comma. For example, the model S, CO shows that the frequency of occurrence of a cestode species (O) depends on the host cohort (C), but not on the host sex (S). The selection of the best model is based on comparison of models which do not differ significantly ($P > 0.05$) from the observed data. The fit of the full-order model (SCO) cannot be tested, but the full-order model is accepted if it differs significantly from the model SC, SO, CO which includes all but the highest order interaction. Because the interpretation of full-order models may be particularly difficult, we complemented the analyses with G-tests between sexes (within cohorts) and between cohorts (within sexes). Mann-Whitney tests was used for comparison of helminth intensities (individuals per host) between host species.

3. Results

3.1. Helminth communities and overall infection levels

Helminths recovered from the two vole species (Table 1) included trematodes (one species), cestodes (six species, including the metacestode of *Taenia mustelae*) and nematodes (three species). Except for the rarest species, all helminths occurred in both vole species. In the pooled material, the cestode *Hymenolepis horrida* and the nematode *Syphacia* sp. were significantly more prevalent in *M. oeconomus*, whereas the cestodes *Paranoplocephala omphalodes* and *Anoplocephaloides* c.f.

Table 1. Helminth species, their microhabitats, prevalence (%), mean intensity, its standard deviation (*SD*) and range of intensity in *Microtus oeconomus* and *M. miurus* at Toolik Lake. If the prevalence (χ^2-test) or mean intensity (Mann-Whitney-test) differs significantly ($P < 0.05$) between the vole species, the higher value has been marked with an asterisk. Microhabitats: st = stomach, si = small intestine, c = caecum, l = liver.

	M. oeconomus (*n* = 219)				*M. miurus* (*n* = 182)			
	%	Mean	*SD*	range	%	Mean	*SD*	range
Trematoda								
Notocotylidae								
Quinqueserialis quinqueserialis (c)	9	27.7	51.3	1–224	7	84.8	86.5	1–254
Cestoda								
Anoplocephalidae								
Paranoplocephala omphalodes (si)	6	1.4	0.5	1–2	13*	2.1	1.8	1–8
P. arctica (si)	0	–	–	–	1	1	–	1
Anoplocephaloides c.f. *variabilis*[a] (si)	1	1.5	–	1–2	7*	2.4	2.1	1–9
A. troeschii (si,c)	5	1.1	0.3	1–2	10	1.9*	0.9	1–4
Hymenolepididae								
Hymenolepis horrida (si)	29*	2.9	4.4	1–35	4	2.1	1.6	1–5
Taeniidae								
Taenia mustelae larvae (l)	5	6.2	6.9	1–20	4	2.4	2.1	1–7
Nematoda								
Spiruridae								
Mastophorus muris (st)	0	–	–	–	<1[b]	2	–	2
Oxyuridae								
Syphacia sp. (c)	5*	–[c]	–	–	1	–[c]	–	–
Heligmosomidae								
Heligmosomum sp.(si)	0	–	–	–	<1	1	–	1

[a] The taxonomic position of this species is uncertain, but it closely resembles *Anoplocephalaloides variabilis*, a parasite of pocket gophers *Geomys bursarius* and *Thomomys talpoides* (Rausch 1976).

[b] Found once; real prevalence unknown.

[c] Not counted; usually very abundant (> 100).

variabilis had significantly higher prevalence, and the cestode *Anoplocephaloides troeschi* higher mean intensity, in *M. miurus*. The number of intestinal helminth species per host individual (mean ±*SD)* differed significantly between the host species (Kruskal-Wallis-test: $U = 184.9$, $P = 0.01$), being higher in *M. oeconomus* (0.56 ± 0.64) than in *M. miurus* (0.44 ± 0.75). Only two cestode species, *P. omphalodes* in *M. miurus* and *H. horrida* in *M. oeconomus*, were sufficiently common for the following analyses.

3.2. Body size of cestodes

Body length and width of *P. omphalodes* were distinctly larger in *M. miurus* than in *M. oeconomus*, whereas *H. horrida* showed higher body dimensions in *M. oeconomus* (Table 2). Interspecific differences were highly significant for *P. omphalodes* and approached significance for *H. horrida*.

3.3. Effects of sex, age and breeding status on prevalence

The most acceptable log-linear model for both common cestodes in their preferred host species was the complex full-order model SCO, which indicates that the sex (S) and cohort (C) of host interactively affect the frequency of occurrence (O) of *P. omphalodes* and *H. horrida* (Table 3, Fig. 1). In both cestode species, overwintered males showed higher prevalence than the other functional groups (Fig. 1, Table 4). On the other hand, mature summer-born females showed higher prevalence of *P. omphalodes* than the males of the same age group and immature females. This difference was not observed in *H. horrida*, but immature summer-born females showed higher prevalence of *H. horrida* than males of the same age group. All other comparisons between sexes and between age groups were non-significant.

The occurrence of common cestodes was further complicated by varying vulnerability of mature females (Fig. 2). Non-pregnant, summer-born females of *M. miurus* showed significantly higher prevalence of *P. omphalodes* than pregnant females of the same cohort ($P < 0.01$, Fisher's exact test), but in overwintered females the difference appeared to be reversed ($P = 0.10$). These differences were similar, but clearly non-significant for *H. horrida* in *M. oeconomus* (summer-born: $P = 0.22$; overwintered: $P = 0.62$).

3.4. Effect of habitat on prevalence

The prevalence of the common cestodes in wet habitats tended to be higher (*P. omphalodes*) or lower (*H. horrida*) than in dry habitats (Fig. 3). The two most acceptable models for both species were H, CO and HO, CO (Table 3). Because the higher-order model HO, CO did not differ significantly from the simpler model H, CO, the latter model (without a habitat effect) was selected.

Table 2. Body length and maximum body width (mm) of the cestodes *Paranoplocephala omphalodes* and *Hymenolepis horrida* in *Microtus oeconomus* and *M. miurus*, and the significance of interspecific differences in body dimensions.

	M. oeconomus		*M. miurus*		Significance	
	Mean	*SD*	Mean	*SD*	*t*	*P*
Paranoplocephala omphalodes	(*n* = 10)		(*n* =10)			
Length	172.2	25.3	227.0	19.3	5.4	< 0.001
Width	3.3	0.60	4.9	0.66	5.7	< 0.001
Hymenolepis horrida	(*n* = 10)		(*n* = 7)			
Length	153.0	24.9	127.7	29.0	1.9	0.07
Width	2.3	0.56	1.8	0.45	2.0	0.07

4. Discussion

4.1. Host specificity

Microtus miurus and *M. oeconomus* showed remarkably similar helminth faunas: excluding the rarest species, all helminths were found to parasitize both host species. The infection levels of helminths did, however, differ between the vole species. *Hymenolepis horrida* dominated the intestinal helminth community of *M. oeconomus*, whereas the helminth community of *M. miurus* was dominated by cestodes of the family Anoplocephalidae, particularly *Paranoplocephala omphalodes*.

The demography, density and dynamics of tundra and singing vole populations are similar (Batzli & Henttonen 1990), but their habitat selection and diet differ fundamentally (Galindo & Krebs 1985, Batzli & Henttonen 1990, Batzli & Lesieutre 1991). However, these ecological differences are difficult to match with the known differences in infection levels of helminths because we cannot separate species effects from habitat and diet effects. The interpretation of the observed patterns is further obscured by the fact that the intermediate hosts of these cestodes are poorly known. Oribatid mites (Acari; Gleason & Buckner 1979) and springtails (Collembola; Smirnova 1980) serve as intermediate hosts for anoplocephalid cestodes, but intermediate hosts for *H. horrida* parasitizing arvicoline rodents apparently are unknown. Nevertheless, the lack of clear habitat effects (wet vs. dry habitats) on prevalence of parasite species suggests that ecological factors are not dominant in determining the host preference of cestodes.

Host preference was paralleled by body size differences in common cestodes, especially in *P. omphalodes*: cestode body length and width were higher in the host species with higher prevalence. Since cestode fecundity tends to correlate positively with body size (Roberts 1961, Quinnell 1988), the more frequently infected vole species evidently plays the central role in the maintenance of a cestode species. 'Physiological' preference of cestodes to one of the host species may reflect an intimate coevolutionary history, which has resulted in high compatibility between host and parasite genotypes. According to Rausch (1976), the presence of *P. omphalodes* in *M. abbreviatus* on the St. Matthew Islands in the Bering Sea (Rausch & Rausch 1968) suggests that this cestode and its main hosts (*M. abbreviatus* and *M. miurus*) are Beringian in origin, and were there before *M. oeconomus* spread into eastern Beringia.

Although the body dimensions of *H. horrida* were higher in the preferred host species (*M. oeconomus*), these differences were much less obvious than those of *P. omphalodes*. Cestodes identified as *H. horrida* parasitize several small rodent genera in the Holarctic region (Rausch 1957), but *H. horrida* does not occur in northern Fennoscandia (Haukisalmi 1986) although *M. oeconomus* occurs abundantly there. Thus large body size and high prevalence of *H. horrida* in

Table 3. The best log-linear models and their fit to the observed data (in bold) for associations between the host sex (S) and cohort (C), and occurrence (O) of the the cestodes *Paranoplocephala omphalodes* (host *Microtus miurus*) and *Hymenolepis horrida* (host *Microtus oeconomus*), and between habitat (H), cohort and occurrence of cestodes (males and females combined). Other models relevant for the selection of the best models have also been presented.

P. omphalodes				*H. horrida*			
Model	*df*	*G*	*P*	Model	*df*	*G*	*P*
SCO[a]				**SCO**[a]			
SC,SO,CO	2	11.67	0.003	SC,SO,CO	2	15.66	< 0.001
H,CO	**5**	**4.54**	**0.48**	**H,CO**	**5**	**3.27**	**0.66**
HO,CO	4	2.05	0.73	HO,CO	4	3.22	0.52

[a] The fit of the full-order model cannot be tested, but it is accepted because it differs significantly from the model SC, SO, CO (assuming that *df* = 0, *G* = 0.00 and *P* = 1.00 for SCO).

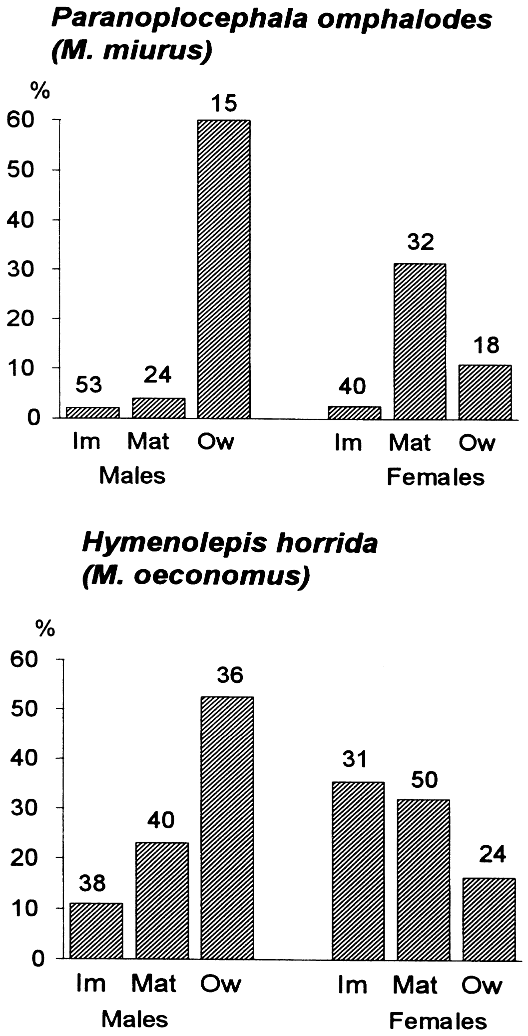

Fig. 1. Prevalence (%) of *Paranoplocephala omphalodes* in *Microtus miurus* and of *Hymenolepis horrida* in *Microtus oeconomus* by sex and cohort of host (c.f. Table 4). Cohorts: Im, summer-born immature voles; Mat, summer-born mature voles; Ow, overwintered mature voles. Sample sizes shown above the bars.

M. oeconomus in northern Alaska suggests local specialization on one of its host species, rather than a phylogenetic association.

4.2. Effects of sex, age and breeding status on prevalence

The present data show that vulnerability of voles to cestode parasitism varies considerably and interactively due to the sex, age and breeding status of hosts. In particular, we indentified three interesting patterns: (i) overwintered males showed higher prevalence than the other functional groups of voles (both cestode species), and (ii) mature summer-born females of *M. miurus* (*P. omphalodes*) and (iii) immature summer-born females of *M. oeconomus* (*H. horrida*) were characterized by higher prevalence than males of the same cohort.

The factors affecting infection levels among subgroups of host population fall in two main categories: exposure and resistance, including the immunological factors.

Exposure

Assuming constant resistance, the degree of exposure should increase with age, but it could also vary due to behavioural differences such as home range size, activity and diet. The differences between host functional groups with respect to diet are poorly known, but it is known that mature voles have larger home-ranges than immature voles, overwintered voles have larger home-ranges than summer-born voles, and mature males have larger home-ranges than mature females (*M. oeconomus*:

Table 4. Significant ($P < 0.05$) pairwise comparisons between the prevalence of the cestodes *P. omphalodes* and *H. horrida* in various functional groups of the host population (c.f. Fig. 1). Frequency of occurence was tested between sexes (within cohorts) and between cohorts (within sexes). Cohorts: ow, overwintered mature voles; imm, summer-born immature voles; mat, summer-born mature voles.

Compared functional groups	*G*	*P*
P. omphalodes in M. miurus		
ow males > ow females	9.26	0.002
ow males > imm males	26.68	< 0.001
ow males > mat males	15.90	< 0.001
mat females > mat males	7.42	0.006
mat females > imm females	12.46	0.001
H. horrida in M. oeconomus		
ow males > ow females	8.46	0.004
ow males > imm males	16.35	< 0.001
ow males > mat males	6.27	0.012
imm females > imm males	6.36	0.012

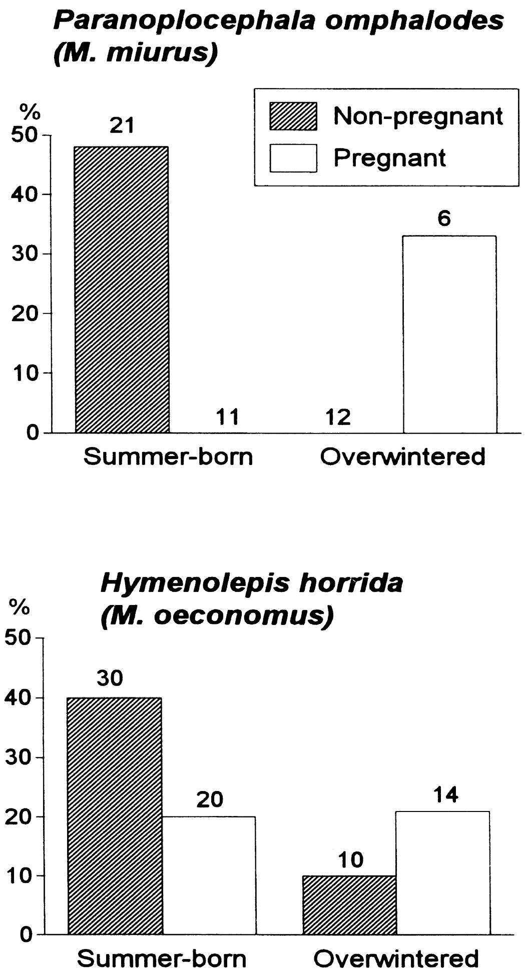

Fig. 2. Prevalence (%) of *Paranoplocephala omphalodes* and *Hymenolepis horrida* in mature females of *Microtus miurus* and *Microtus oeconomus*, respectively by reproductive status (pregnant vs. non-pregnant) and cohort of host. See Fig. 1 for other details.

Tast 1966, Lambin et al. 1992; *M. miurus*: Batzli & Henttonen 1993). Thus we can predict that overwintered males should have higher prevalence than the other functional groups, and this prediction is supported by our data. On the other hand, the prevalence of immature or mature summer-born females exceeded that of the summer-born males and overwintered females, which contrasts the expected pattern. We conclude that age and home-range size alone do not provide a satisfactory explanation for variability in the prevalence of the common cestodes.

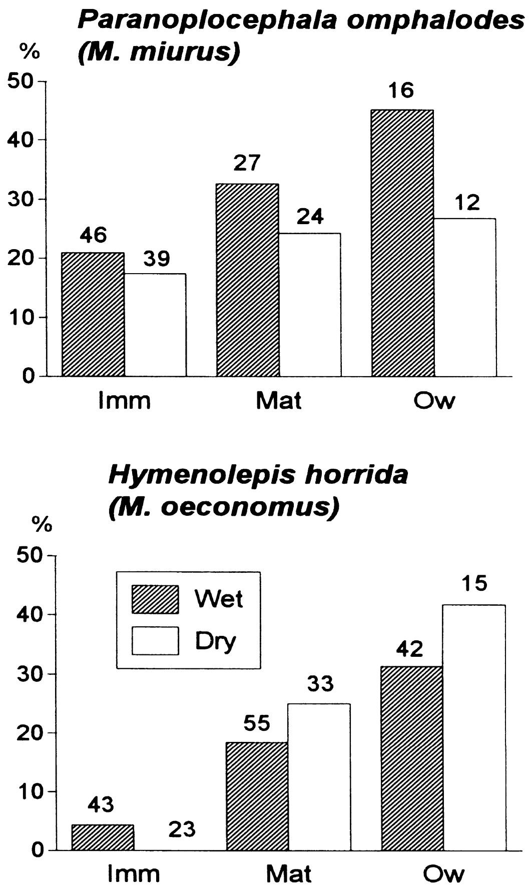

Fig. 3. Prevalence (%) of *Paranoplocephala omphalodes* in *Microtus miurus* and of *Hymenolepis horrida* in *Microtus oeconomus* by habitat (wet and dry) and cohort of host (males and females combined). See Fig. 1 for other details.

Resistance

Sex and stress hormones have a profound effect on the immunological system. Male sex hormones (testosterone) generally decrease resistance to helminth infections, while female sex hormones (oestrogen) often increase resistance (Barger 1993, Molan & James 1984). Furthermore, increased levels of stress hormones (corticosteroids), acting in interaction with high testosterone concentrations, are assumed to impair the resistance of mature males (Folstad et al. 1989, Zuk 1990). These effects suggest that inter-sexual differences in infection level should be evident in mature hosts only, and that mature males should have higher infection levels than mature females. The territoriality of mature *Microtus*-males (Tast 1966, Lambin et al. 1992, Myllymäki 1977) implies severe stress, which should further impair the resistance of this functional group.

However, the data showed that mature summer-born females may be more heavily infected than mature males (*P. omphalodes* in *M. miurus*), and immature hosts may show an inter-sexual difference in prevalence (*H. horrida* in *M. oeconomus*). Empirical evidence thus fails to support the explanations based on immunological factors.

Pregnancy and lactation are reported to decrease females' resistance to helminth infections, probably because of hormonal effects (Barger 1993). The higher prevalence of cestodes, especially *P. omphalodes*, in overwintered pregnant females compared to overwintered non-pregnant females supports this idea. On the other hand, the pattern appeared to be reversed in summer-born females, which may be related to the fact that practically all overwintered females were simultaneously pregnant and lactating, whereas a large proportion of pregnant summer-born females were not yet lactating.

4.3. Conclusions

We conclude that known ecological and immunological differences do not seem to explain the observed variability in cestode parasitism between functional groups. The infection level in a particular functional group is probably modified by several (interactive) factors, including both ecological and immunological ones. For example, the particularly high prevalence in overwintered males may be due the combined effect of increased exposure and decreased resistance. Bearing in mind that in some other host-helminth associations it is the overwintered *females* that show the highest infection levels (Haukisalmi et al. 1988), the search for plausible explanations becomes even more difficult. The complexity and variability of the patterns described above suggest that specific explanations for observed differences between host functional groups cannot be obtained without experimentation.

The heterogeneity and seasonal variability of vole populations with respect to helminth parasitism has important ecological implications. First, reports on overall infections levels in rodents are likely to be severely biased if the heterogeneity of the host population is not taken into account. Second, the differential vulnerability of various subgroups of host population suggests that the possible harmful effects of parasites are not evenly distributed among subgroups of hosts. For example, the rapid disappearance of overwintered voles in late summer may be at least partly due to heavy helminth infections; an extreme example of high mortality due to parasitism in old, reproducing males is described by Lee and Cockburn (1985).

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