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Frequency distributions of helminths in microtine rodents in Finnish Lapland

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Fourteen species of helminths (1 trematode, 7 cestodes and 6 nematodes) parasitic in microtine rodents (*Clethrionomys glareolus, C. rutilus, C. rufocanus, Microtus agrestis,* and *M. oeconomus*) were studied for dispersion patterns and frequency distributions in Finnish Lapland during 1977–1985.

Comparisons between the helminth species revealed that the nematodes, together with a trematode and a larval cestode, were more aggregated than the adult cestodes. The high degree of aggregation in nematodes may be an adaptation to increase the pairing probability of unisexual worms. The differences in the degree of aggregation among nematodes are suspected to be due to the variability of sex-ratios, the severe aggregation characterizing species with markedly female-biased sex-ratios. In addition, the interspecific differences in aggregation among helminths may be explained by ecological factors like differences in dispersal ability and spatial distribution of infective stages.

The seasonal changes in frequency distributions were studied in the dominant helminths of *C. glareolus*, the nematodes *Heligmosomum* spp. and the cestode *Catenotaenia* sp. Most seasonal samples, representing specified age groups of voles, were aggregated, fitting the negative binomial distribution. However, the samples with low prevalence and intensity, or with a small size, agreed with the Poisson, or both with the Poisson and negative binomial, distributions. The degree of aggregation of *Heligmosomum* was higher in male than in female voles, suggesting that individual differences in behaviour, for example in foraging activity, could be one of the causes of aggregation.

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1. Introduction

Almost without exception the observed frequency distributions of parasites within the host population are overdispersed, i.e. the variance is significantly larger than the mean. This means that the majority of the parasite population is aggregated into a small fraction of the host population, and most of the hosts harbour only a few parasites, or none at all (Anderson & May 1978).

The central role of aggregation in the regulation of host and parasite populations has been stressed by Crofton (1971 a, b), Anderson & May (1978) and May & Anderson (1978). Assuming that the host is regulated by the parasite, increasing parasite aggregation has a stabilizing effect on the host-parasite interaction (Anderson & May 1978).

The importance of distribution patterns to the pairing process of unisexual parasites has been established by May (1977), Bradley & May (1978) and Anderson (1981). The aggregation of *Schistosoma* in the definitive host (man) was shown to increase significantly the probability of pairing. However, the effect of aggregation depends on whether the female and male worms are aggregated separately or together (May 1977, Bradley & May 1978). Anderson (1981) demonstrated that the aggregation is beneficial both for monogamous and polygamous parasites.

In most cases the aggregated distributions of parasites can be fitted to the negative binomial distribution, a probability distribution with the advantage of describing the degree of aggregation by a single parameter k. The Poisson distribution has seldom been found to fit parasite populations in the wild, although the distribution of parasites within a homogeneous group of hosts, such as a certain age class, may be random (Anderson & May 1978).

The frequency distributions of parasites have been studied for several natural populations (for references, see Anderson & May 1978). However, with the exception of Li and

Hsü (1951), the frequency distributions have not been analyzed in a multispecies community of parasites. The main purpose of this study is to compare the dispersion patterns and frequency distributions of helminths in a community of several species of parasites and hosts. This could reveal ecological and evolutionary trends in dispersion pattern within a diverse group of parasites with different kinds of life cycles and reproductive patterns. In addition I analyze the relation between the frequency distributions and seasonal dynamics of dominant helminths in pooled and individual seasonal samples.

2. Materials and methods

1329 microtine rodents belonging to five species were examined for helminths in northern Finland during the period 1977–1985. The material consists of the following host species: bank vole *Clethrionomys glareolus* ($N=438$), red vole *Clethrionomys rutilus* ($N=121$), grey-sided vole *Clethrionomys rufocanus* ($N=492$), field vole *Microtus agrestis* ($N=122$) and root vole *Microtus oeconomus* ($N=156$). For species composition and habitat selection of microtine rodents in northern Finland, see Henttonen et al. 1977.

Most of the material (N=1063) was collected at Pallasjärvi (68°03′N, 24°09′E), in the north boreal zone. In addition, 266 grey-sided voles were collected at Kilpisjärvi (69°03′N, 20°49′E), in the orohemiarctic zone (subarctic birch forest).

At Pallasjärvi, the rodent material was obtained by snap trapping in autumn (September, 32% of the material), winter (February, 10%) and spring (May–June, 55%). A small number of voles trapped in April (2%) and July–August (1%) were also included in the material. The seasonal samples monitor the development of a single vole cohort (age group), the members of which are born in the late summer and do not mature until the spring. Accordingly, the mature overwintered and summer born voles have been analyzed separately from the immature voles in autumn samples.

At Kilpisjärvi in 1982 and 1983 the grey-sided voles were trapped only in June, and therefore the material consists of overwintered adults only.

Random samples of voles (sample sizes above) were studied for the presence of helminths in the stomach, intestine, liver and body cavity. The helminths were fixed, stained and mounted as described by Tenora et al. (1983, 1986 a).

3. Systematics and life cycles

The helminths included in this study (14 species) belong to the trematodes (1 species), cestodes (7 species) and nematodes (6 species). Species with a prevalence of less than 1.7% were excluded. The classification of helminths is presented in Table 1.

Table 1. Classification of helminths examined for frequency distributions at Pallasjärvi and Kilpisjärvi (Tenora et al. 1983, 1985 a, b, 1986 a, b).

Class	Family	Species
Trematoda	Notocotylidae	*Notocotylus* sp.
Cestoda	Anoplocephalidae	*Anoplocephaloides dentata*
		A. blanchardi
		Andrya kalelai
		Paranoplocephala omphalodes
		P. gracilis
	Catenotaeniidae	*Catenotaenia* sp.
	Taeniidae	*Taenia tenuicollis* (larva)
Nematoda	Heligmosomidae	*Heligmosomum mixtum*
		H. yamagutii
	Syphaciidae	*Syphacia nigeriana*
		S. petrusewiczi
	Capillariidae	*Capillaria* sp.
	Spiruridae	*Mastophorus muris*

Because of difficulties in specific identification, two closely related nematodes *Heligmosomum mixtum* and *H. yamagutii* were combined. It is possible that the cestode *Anoplocephaloides blanchardi* also represents two different species. The cestode in the *Paranoplocephala omphalodes* group probably belongs to an undescribed species, occurring in *Microtus oeconomus* in northern parts of its range. For details of the taxonomy of rodent helminths in Finland, see Tenora et al. 1983, 1985 a, b, 1986 a, b.

Two different types of life cycle exist in helminths of rodents. In the direct life cycles (nematodes, except *M. muris*) there are no intermediate hosts, and the transmission from host to host is accomplished by free-living larvae (*Heligmosomum*) or eggs (*Syphacia, Capillaria*). In *Heligmosomum*, the eggs are released in faeces, whereafter three larval stages develop. In *Syphacia*, the eggs are thought to be transmitted mainly in contacts between host individuals without any free-living stage; reinfections in a single host individual are also possible. The mode of transmission in *Syphacia* results in high intensities and spatially restricted infections (Lewis 1968). The life cycle of *Capillaria* sp. involves a single free-living stage, the eggs (Kisielewska 1970).

The life cycles of trematodes and cestodes are indirect, i.e. they involve at least one in-

termediate host. The life cycle of the trematode *Notocotylus* sp. is suspected to be like that of other notocotylids: there is only one intermediate host, a mollusc. The definitive host becomes infected by ingesting free-living metacercariae attached to vegetation (Olsen 1962).

The cestodes infecting the voles in the adult stage always have only one intermediate host, an invertebrate. In all anoplocephalid cestodes the intermediate hosts are supposed to be oribatid mites (Stunkard 1941, Gleason & Buckner 1979). The larva is transmitted to the definitive host by ingestion of the intermediate host. Another group of cestodes, including mostly taenids, require rodents as their intermediate hosts. The adult cestodes are parasites of carnivores and birds of prey. The single species studied, *Taenia tenuicollis*, is an obligatory parasite of mustelids, mainly the least weasel (*Mustela nivalis*) and the stoat (*M. erminea*). The intermediate hosts, voles, are infected by eggs, released in the faeces of mustelids.

4. Results

The material was analyzed in three stages, each of them dealing with a specific problem: 1) The interspecific differences in the degree of aggregation among the helminth species were analyzed in the *pooled material* of various host species. 2) The frequency distributions of helminths in relation to their seasonal dynamics were studied in two dominant species — *Heligmosomum* spp. and *Catenotaenia* sp. — in *C. glareolus*. To obtain larger *seasonal samples* the Pallasjärvi material from 1977–1985 was pooled for each season. 3) The dispersion patterns in *individual seasonal samples* of *Heligmosomum* and *Catenotaenia* were examined with reference to the sex of the host, *C. glareolus*. The effect of pooling on the frequency distributions was studied by comparing the pooled seasonal samples with three individual seasonal samples having the largest sample sizes.

Based on the relation between the variance and mean, both randomly dispersed and overdispersed seasonal samples were found in the material. Therefore, two theoretical probability distributions, the Poisson and the negative binomial, were fitted to the data. The negative binomial distribution is defined by two parameters, the mean, m, and the aggregation parameter k. The parameter k was estimated using the three alternative methods described by Bliss & Fisher (1953). If the two simplest methods, based on the variance and zero class of the observed distribution, did not give a sufficiently good estimate of k, then the maximum likelihood method was used.

4.1. Pooled material

As expected, most of the helminths, including all the nematodes, were overdispersed (Table 2). In cestodes there were both overdispersed and randomly dispersed species. *Catenotaenia* and the larval *T. tenuicollis* were always overdispersed, whereas in anoplocephalid cestodes the variance tended to be equal to the mean, with the exception of *P. omphalodes* and *A. kalelai* (host *C. rufocanus*, locality Pallasjärvi). The overdispersion was remarkably severe in the nematodes *Capillaria* sp., *Syphacia petrusewiczi* and *S. nigeriana*, and also in the trematode *Notocotylus* sp. The nematodes ($r=0.83$, $p<0.01$, slope$=1.86$) and the larval *T. tenuicollis* ($r=0.68$, $p>0.05$, slope$=2.38$) had similar regressions (ANCOVA (=analysis of covariance): equality of slopes, $F=0.34$, $p=0.57$; equality of elevation, $F=0.15$, $p=0.93$), being more severely overdispersed than the adult cestodes ($r=0.97$, $p<0.01$, slope$=1.17$) (Fig. 1; ANCOVA: cestodes–nematodes, slopes, $F=4.30$, $p=0.05$; elevation, $F=5.35$, $p=0.01$, *T. tenuicollis*–cestodes, slopes, $F=26.13$, $p=0.00$).

The negative binomial distribution could be fitted to most pooled samples. However, if the observed distribution agreed well with the Poisson, then often $k \to \infty$, and the negative binomial could not be used, as was the case,

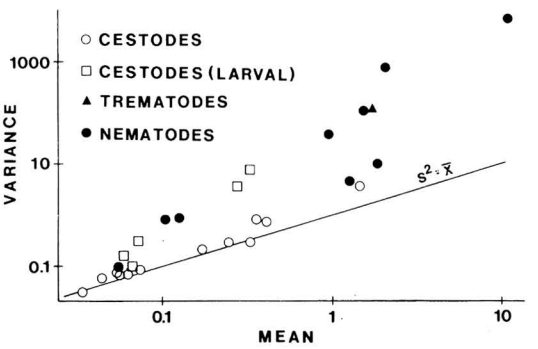

Fig. 1. Dispersion patterns of helminths in various host species (the whole material). Logarithmic scale.

Table 2. Prevalence, dispersion pattern and fit of the observed distribution of helminths to the Poisson and negative binominal distributions in various host species. The whole material. – k = aggregation parameter. Probability of χ^2: *** $p<0.001$, ** $p<0.01$, * $p<0.05$, o $p<0.10$, NS not significant.

Host species Helminth species	N	%	$\bar{x}$	s^2	$s^2/\bar{x}$	Probability of χ^2 Overdisp.	Poisson	Neg. bin.	k
C. glareolus									
Catenotaenia sp.	438	20.5	0.35	0.79	2.26	***	***	NS	0.293
A. kalelai	438	4.3	0.05	0.07	1.40	*	NS	NS	0.108
T. tenuicollis	438	3.6	0.07	0.30	4.29	***	**	NS	0.031
Heligmosomum spp.	438	58.7	1.81	10.05	5.55	***	***	NS	0.609
Capillaria sp.	438	5.7	1.57	105.40	67.13	***	***	NS	0.012
S. petrusewiczi	438	1.8	2.06	782.58	379.89	***	***	NS	0.003
M. muris	359	5.0	0.12	0.85	7.08	***	***	NS	0.032
C. rutilus									
Catenotaenia sp.	121	52.1	1.42	3.61	2.54	***	***	NS	0.479
T. tenuicollis	121	5.0	0.07	0.10	1.43	*	NS	–	$k\rightarrow\infty$
Heligmosomum spp.	121	46.3	1.27	4.25	3.35	***	***	NS	0.612
Capillaria sp.	121	7.4	0.95	34.61	36.43	***	***	NS	0.020
M. muris	89	3.4	0.06	0.10	1.67	***	NS	–	$k\rightarrow\infty$
C. rufocanus, Pallasjärvi									
A. kalelai	226	24.8	0.40	0.70	1.75	***	***	NS	0.447
P. gracilis	226	5.7	0.06	0.07	1.17	NS	NS	NS	0.769
T. tenuicollis	226	2.6	0.06	0.15	2.50	***	*	NS	0.021
M. muris	171	1.7	0.10	1.20	12.00	***	***	–	$k\rightarrow\infty$
C. rufocanus, Kilpisjärvi									
A. kalelai	266	28.2	0.32	0.30	0.94	NS	NS	–	$k\rightarrow\infty$
P. gracilis	266	3.4	0.03	0.03	1.00	NS	NS	–	$k\rightarrow\infty$
T. tenuicollis	309	8.4	0.30	8.31	27.70	***	***	NS	0.042
M. agrestis									
A. blanchardi	122	6.6	0.07	0.08	1.14	NS	NS	–	$k\rightarrow\infty$
P. gracilis	122	18.8	0.24	0.30	1.25	NS	NS	NS	0.845
T. tenuicollis	122	5.7	0.26	3.50	13.46	***	***	NS	0.024
S. nigeriana	122	18.8	10.70	6432.94	601.21	***	***	NS	0.037
M. oeconomus									
Notocotylus sp.	156	5.8	1.65	160.32	97.16	***	***	NS	0.012
A. dentata	156	3.8	0.04	0.06	1.50	NS	NS	–	$k\rightarrow\infty$
A. blanchardi	160	5.0	0.06	0.07	1.17	NS	NS	–	$k\rightarrow\infty$
P. omphalodes	160	13.1	0.17	0.23	1.35	*	NS	NS	0.412

for example, with most anoplocephalid cestodes.

The degree of aggregation, inversely measured by the parameter k, against the overall prevalence of various helminths is shown in Fig 2. In nematodes, there was an expected loglinear correlation ($r=0.95$, $p<0.001$, slope=1.49) between the prevalence and parameter k, the aggregation decreasing as the prevalence increased. Again, the trematode *Notocotylus* sp. and the larval *T. tenuicollis* ($r=0.76$, $p>0.05$, slope=2.38) were associated with nematodes (ANCOVA: nematodes–*T.tenuicollis*, slopes, $F=2.59$, $p=0.15$; elevation, $F=2.28$, $p=0.17$). The adult cestodes were not as severely aggregated as the rest of the helminths, except at high prevalences (ANCOVA: cestodes–nematodes, slopes, $F=9.45$, $p=0.01$, cestodes–*T. tenuicollis*, slopes, $F=16.30$, $p=0.00$). In cestodes, the log linear correlation between the prevalence and the parameter k was not significant ($r=0.38$, slope=0.31).

The comparison between the intensity and degree of aggregation (Fig. 3) revealed no significant correlations. The nematodes ($r=0.04$) were again more aggregated than the cestodes ($r=0.44$) and *T. tenuicollis* ($r=0.81$).

4.2. Seasonal samples

All the seasonal samples of *Heligmosomum* were overdispersed, with the exception of the spring sample of female hosts (Table 3). In *Catenotaenia* there were three autumn

Table 3. Prevalence, dispersion pattern and fit of the observed distribution to the Poisson and negative binomial distributions in seasonal samples of *Heligmosomum* spp. and *Catenotaenia* sp., host *C. glareolus*. mat. = mature voles, imm. = immature voles.

	N	%	$\bar{x}$	s^2	$s^2/\bar{x}$	Probability of χ^2 Overdisp.	Poisson	Neg. bin.	k
Pooled seasonal samples 1977–85									
Heligmosomum									
Autumn (mat.)									
Males	17	76.5	4.12	24.36	5.91	***	NS	NS	0.72
Females	35	68.6	3.23	29.06	9.00	***	***	NS	0.51
Autumn (imm.)									
Males	60	61.7	2.85	24.20	8.49	***	*	*	0.51
Females	42	64.3	1.71	3.72	2.17	***	**	NS	1.17
Winter									
Males	34	79.4	2.09	3.11	1.49	*	o	NS	4.25
Females	35	91.4	2.86	4.83	1.69	**	*	NS	4.13
Spring									
Males	118	50.8	1.06	4.71	4.44	***	**	NS	0.94
Females	72	27.8	0.39	0.63	1.61	NS	NS	NS	0.94
Catenotaenia									
Autumn (mat.)									
Males	17	35.3	0.59	1.13	1.91	*	NS	NS	0.76
Females	35	14.3	0.20	0.28	1.40	NS	NS	NS	0.30
Autumn (imm.)									
Males	60	3.3	0.03	0.03	1.00	NS	NS	–	$k \to \infty$
Females	42	7.1	0.07	0.07	1.00	NS	NS	–	$k \to \infty$
Winter									
Males	34	29.4	0.62	1.82	2.93	***	o	NS	0.33
Females	35	31.4	0.63	1.89	3.00	***	o	NS	0.40
Spring									
Males	118	31.4	0.52	0.94	1.81	***	*	NS	0.62
Females	72	12.5	0.21	0.42	2.00	***	NS	NS	0.16
Individual seasonal samples									
Heligmosomum									
Autumn 1977 (imm.)									
Males	36	61.1	3.22	35.78	11.11	***	**	*	0.45
Females	26	65.4	1.61	3.21	1.99	**	NS	NS	1.43
Winter 1982									
Males	22	81.8	2.14	2.69	1.26	NS	NS	NS	8.16
Females	18	100.0	3.83	5.56	1.45	NS	NS	NS	8.51
Spring 1982									
Males	43	58.1	0.93	1.16	1.25	NS	NS	NS	3.73
Females	19	31.6	0.58	1.48	2.55	***	NS	NS	0.48
Catenotaenia									
Winter 1982									
Males	22	40.9	0.91	2.56	2.81	***	o	NS	0.52
Females	18	27.8	0.50	1.44	2.88	***	NS	NS	0.40
Spring 1982									
Males	43	25.6	0.46	2.19	4.76	***	NS	NS	0.35
Females	19	15.8	0.21	0.29	1.38	NS	NS	NS	0.44

samples, all of them with a low prevalence and intensity, in which the variance was equal to the mean, indicating a random distribution.

In both helminth species the variance to mean ratio, a measure of the degree of overdispersion, varied seasonally (Table 3). In *Heligmosomum*, the ratio tended to follow the intensity and prevalence of the sample; at the highest prevalences (winter), however, the degree of overdispersion was low. Contrary to *Heligmosomum*, the overdispersion in *Catenotaenia* was most severe in the winter

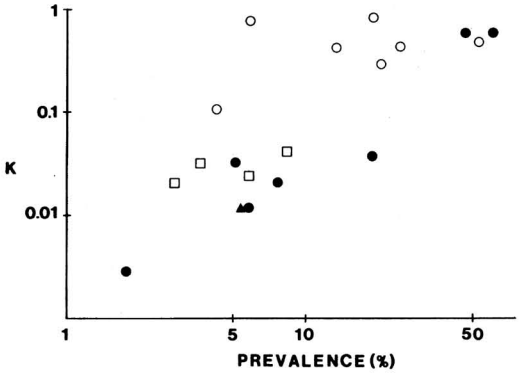

Fig. 2. Relation between the prevalence and aggregation parameter k of helminths in various host species (the whole material). Logarithmic scale. Symbols as in Fig. 1.

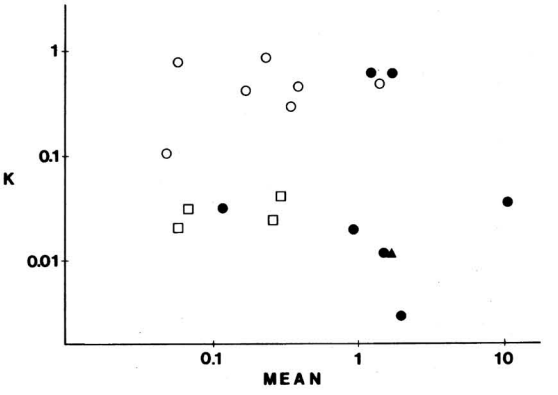

Fig. 3. Relation between the mean and aggregation parameter k of helminths in various host species. Logarithmic scale. Symbols as in Fig. 1.

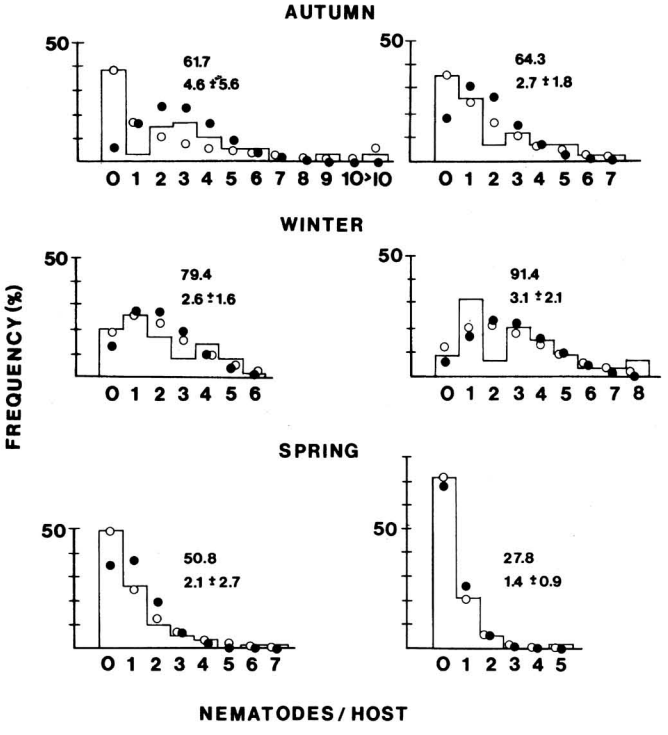

Fig. 4. Observed frequency distributions (histograms) of *Heligmosomum* spp. in seasonal samples of male (left) and female (right) hosts (*Clethrionomys glareolus*). The fitted probability distributions are shown by open (negative binomial) and closed (Poisson) circles. The corresponding prevalence (above) and intensity (below) in infected hosts $\pm SD$ are indicated in figures.

samples.

With the exception of the autumn sample of immature males, all the seasonal samples of *Heligmosomum* agreed with the negative binomial distribution (Table 3). Although some observed data sets could be fitted to the Poisson, the negative binomial always gave a better fit, particularly to the samples with a high prevalence and intensity. Compared with the data on *Heligmosomum*, the observed distributions of *Catenotaenia* agreed better with the Poisson.

Also in the seasonal material the degree of aggregation, measured by the parameter k, depended on the proportion of infected hosts (Table 3). As the prevalence of *Heligmosomum* increased from autumn (immature voles) to winter, k also became larger, indicat-

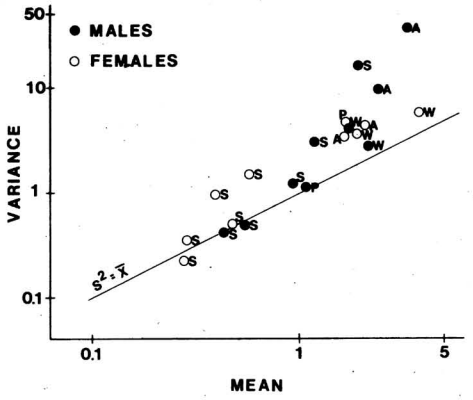

Fig. 5. Dispersion patterns of *Heligmosomum* spp. in individual seasonal samples of *Clethrionomys glareolus*, studied with reference to the sex of the host. Logarithmic scale. A=autumn, W=winter, P=April, S=spring. Voles in this single cohort are immature in A and W, maturing in P, and breeding in S.

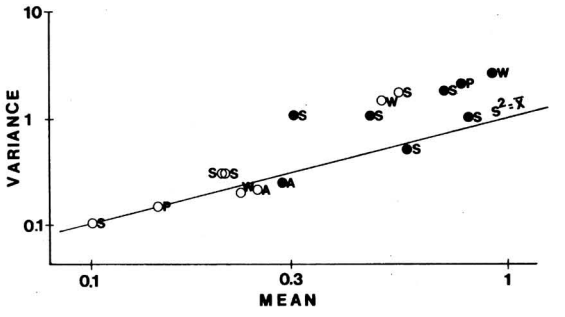

Fig. 6. Dispersion patterns of *Catenotaenia* sp. in individual seasonal samples of *Clethrionomys glareolus*, studied with reference to the sex of the host. Logarithmic scale. Symbols as in Fig. 5.

ing a decline in the degree of aggregation. This was caused primarily by the reduction in the relative size of the zero class; the shape of the distribution in higher classes did not change markedly during that period (Fig. 4). The prevalence of both helminth species declined from winter to spring (maturing voles) with a concomitant increase in aggregation. The spring samples were characterized by high zero classes and reduced size of the higher classes.

4.3. Individual seasonal samples

The dispersion pattern in individual seasonal samples was studied by plotting the variance against the mean. In *Heligmosomum*, the log mean and log variance bore a strong positive correlation; there were, however, differences between the host sexes (Fig. 5). In females, the data points diverged at low intensities from the line of random distribution ($s^2=\bar{x}$), most of the samples being clearly overdispersed. The relation between the mean and variance was log linear ($r=0.94$, $p<0.001$, slope=1.18). In males, the ratio between the variance and mean is first close to unity, but as $\bar{x}>1$, the distribution deviates from random, the variance increasing faster than the mean ($r=0.93$, $p<0.001$, slope =2.10). Thus, in the autumn and spring samples with high intensity, the overdispersion of *Heligmosomum* was more severe in male than in female voles (ANCOVA: slopes, $F=8.06$, $p=0.01$).

In individual seasonal samples of *Catenotaenia*, the relation between the mean and variance was comparable to that of *Heligmosomum* (Fig. 6; males: r=0.71, $p<0.05$, slope= 1.25; females: $r=0.95$, $p<0.001$, slope= 1.71). At higher intensities, however, the variances in males and females were equal (ANCOVA: slopes, $F=0.74$, $p=0.40$; elevation, $F=0.34$, $p=0.79$). Notice that *Catenotaenia* never reaches as high intensities as *Heligmosomum* in *C. glareolus*.

Both the Poisson and negative binomial could be fitted to most data sets in three individual seasonal samples studied for frequency distributions (Table 3). The fit to the Poisson was, however, slightly better in the individual than in the pooled seasonal samples.

5. Discussion

5.1. Dispersion patterns and biology of helminths: pooled material

With regard to the dispersion pattern, two groups of helminths could be distinguished in the whole material. First, all the nematodes, a few cestodes, including the larval *T. tenuicollis*, and the single trematode *Notocotylus* sp, were overdispersed. In the second group, consisting of adult cestodes, the variance tended to be equal to the mean. Similarly, the compari-

son between the prevalence and parameter k revealed that these groups of helminths were characterized by different degrees of aggregation: the adult cestodes, especially anoplocephalids, were less aggregated than the rest of the helminths.

The reproductive success of parasites is determined by two populations: the population of sexually mature parasites in definitive hosts and that of infective larvae (Anderson 1981). The most important reproductive characteristics of sexually mature parasites are the mode of reproduction (unisexual, hermaphrodite), mating habits (monogamous, polygamous) and sex-ratio. The populations of infective larvae (free-living or parasitic) affect the parasite fitness by determining the rate of infection. Clearly, all these factors might have played a significant role in the evolution of distribution patterns of parasites.

The difference between nematodes and cestodes of voles in the degree of aggregation seems to be connected with the mode of reproduction in these helminths. The beneficial effect of aggregation on the pairing probability of unisexual parasites (May 1977, Bradley & May 1978) may have favoured the evolution of predominantly aggregated dispersion patterns in nematodes. The lack of severe aggregation in most adult cestodes is to be expected, because the aggregation does not affect the pairing probabilities in hermaphrodite parasites (Anderson 1981).

In the most prevalent helminth, *Heligmosomum* spp., the degree of aggregation (measured by the parameter k) was as low as in adult cestodes, probably indicating that in common unisexual parasites there has not occurred selection towards higher degrees of aggregation. In common unisexual helminths the probability of pairing is high even if the distribution pattern is random, provided that the worms of different sexes are distributed together (Bradley & May 1978, Anderson 1981).

In nematodes, the degree of aggregation seems to be determined by the sex-ratios. Assuming that the nematodes of voles reproduce sexually, the scarcity of worms of either sex should favour the aggregated distribution patterns, thereby increasing the probability of pairing. The exceptionally high degree of overdispersion in the nematodes *Capillaria* sp., *Syphacia nigeriana* and *Syphacia petrusewiczi* could be an adaptation to their uneven sex ratios; the males of these nematodes, especially those of *Syphacia* spp., are extremely rare. In slightly aggregated *Heligmosomum*, the sex-ratio is much more even than in *Syphacia* and *Capillaria* (Haukisalmi et al., unpubl.).

The infection rate of indirectly transmitted helminths largely depends on the susceptibility of infected intermediate hosts to predation by definitive hosts. The parasitic larvae of many helminths affect the behaviour, or other characters, of the intermediate hosts, making them easier prey to predators (Holmes & Bethel 1972, Moore 1984). Assuming that the probability of an intermediate host being eaten increases with the number of parasites, the aggregated distributions of helminth larvae, for example, of the mustelid parasite *T. tenuicollis*, probably increase their transmission efficiency (see also Pennycuick 1971). The cestode larvae are reported to cause pathological changes in voles (Wiger 1977), but there does not, however, exist any evidence for parasite induced changes in the behaviour of voles. However, it has been shown experimentally that helminth parasites are capable of affecting the exploratory activity and behavioural dominance in male mice (Freeland 1981, Rau 1983 a,b, 1984).

Keymer & Anderson (1979) demonstrated that the aggregated spatial distribution of infective stages of a cestode causes the overdispersion in the intermediate host to be more severe than in the case of random and underdispersed distribution. In the present study, all severely aggregated helminths possess nonparasitic infective eggs or larvae, which indicates that ecological factors, like the spatial distribution of infective stages, may also affect the distribution of helminths in the vole population.

The free-living infective stages of nematodes probably have a more clumped spatial distribution than the motile intermediate hosts of cestodes. The severe overdispersion in the nematodes (*Syphacia* spp.) transmitted mainly in contacts between host individuals may partly be a consequence of the limited dispersal ability of infective stages, the eggs. This also explains the aggregated distribution of the larval cestode *T. tenuicollis*, which is transmitted to voles by eggs, but not that of the trematode *Notocotylus* sp., having both parasitic and free-living larvae.

5.2. Variation in dispersion patterns: seasonal samples

The dominant helminths of *C. glareolus* (*Heligmosomum* spp. and *Catenotaenia* sp.) were mostly overdispersed within specified cohorts of the host population. However, a proportion of the seasonal samples were randomly dispersed or even slightly underdispersed. In both helminth species the dispersion pattern followed the prevalence of the sample. The samples with a low prevalence agreed with the Poisson, or both the Poisson and negative binomial, whereas the samples with a high prevalence could be fitted to the negative binomial distribution only.

These patterns are comparable to the experimental results reported by Anderson et al. (1978). They showed that the frequency distribution of an ectoparasitic trematode in the definitive host was overdispersed even when using a homogeneous host population and a uniform spatial distribution of infective stages. The frequency distribution of the trematode changed from underdispersed, through random, to overdispersed with increasing exposure time. By using a simulation model, the authors concluded that overdispersion in experimental studies was generated by small differences in host susceptibility to infection, probably by differences in host behaviour.

The exposure time (measured by the age of the host) is the most important factor determining the prevalence and intensity of *Heligmosomum* and *Catenotaenia* in the early phases of infection (the first two months in the vole's life) (Haukisalmi et al., unpubl.). Thus, the overdispersion in these helminths is, at least partly, generated by heterogeneity in susceptibility among hosts, the degree of overdispersion increasing with the exposure time. The varying susceptibility may be based on individual differences in host behaviour, for example, in foraging activity. The higher degree of overdispersion of *Heligmosomum* in males in autumn and spring samples supports this interpretation. The role of the spatial distribution and density of infective stages in generating overdispersion in these helminths remains unknown.

The pooling of the individual seasonal samples slightly affected the distribution patterns in *Heligmosomum* and *Catenotaenia*, the Poisson and negative binomial distributions mostly fitting equally well to the individual data sets. This suggests that the heterogeneity was somewhat greater in the pooled seasonal samples than in the individual ones. One obvious reason for this is the higher probability of occurrence of exceptionally heavy infections in larger samples. However, because of the small sample sizes in individual seasonal samples, this result has to be interpreted with caution.

6. Conclusions

The aggregated distribution pattern of parasites, described several times in natural host populations, seems to be an inherent characteristic of most parasite populations. This pattern is created by a variety of factors, most probably by the individual differences in susceptibility to infection, based, for example, on differences in host behaviour and immunity.

The role of ecological and evolutionary factors in bringing about parasite aggregation has been largely ignored, with the exception of the theoretical studies on the pairing probability of helminths by May (1977), Bradley & May (1978) and Anderson (1981). Although the emphasis of this study has not been on the mechanisms producing interspecific differences in the dispersion patterns of helminths (for example, varying behaviour in free-living larvae and intermediate hosts), the results suggest that the comparison between the reproductive biology and dispersion patterns of parasites may elucidate the background of aggregation. I believe that the examination of other multispecies communities of parasites with varying life histories might reveal trends comparable to those observed in helminths of voles.

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