DISPERSAL IN PATCHY ENVIRONMENTS: EFFECT ON THE PREVALENCE OF SMALL MAMMAL ECTOPARASITES

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Abstract. Part-time ectoparasites on small mammals disperse via the habitat, while full-time parasites spread throughout the host population by direct contacts between host animals. It is therefore supposed that the effect of the natural environment is different for the two groups. This was studied as differences between observed and expected prevalence, the percentage of the infested host population, during different environmental conditions. Two possible mechanisms of such an effect were analysed, i.e. a) host selection and its change with host frequency and b) parasite migration and reproduction rates as reflected by the frequency distribution patterns on the hosts. As expected the prevalence of full-time ectoparasites (Anoplura and subfamily Laelapinae) could be predicted on the basis of host species frequencies during different environmental conditions, with the exception of one louse species (Hoplopleura acanthopus), because of its restricted distribution. Prediction was not possible for part-time ectoparasites (subfamily Haemogamasinae). Species of the subfamily Haemogamasinae were more catholic in host selection than did species of Anoplura and subfamily Laelapinae. The haemogamasin mites changed host species to a greater extent than did Anoplura and Laelapinae. All haemogamasin mites had short-tailed frequency distribution patterns and all Anoplura and Laelapinae, except Hyperlaelaps microti, had long-tailed frequency distributions.

Parasites are typically living in patchy environments with the favourable habitats, the hosts, surrounded by transition habitats (cf. Dobson and Keymer 1987). In such an environment parasites can either disperse to find new, hopefully better patches or stay and reproduce in an already available patch. The increase rate parameters of the parasite population, birth and immigration, are thus of unequal importantance to dispersing and non-dispersing populations.

Lundqvist (1985) discussed such a dichotomy in the evolution of ectoparasites on small mammals into one group called full-time (FT) parasites reproducing on the hosts and another group called part-time (PT) parasites inhabiting the hosts for only short periods and spending most of their time in the environment off the hosts. This suggested the following notion: PT-parasite populations should be more influenced by the environment of the hosts (the secondary environment, Janion 1983) than FT-parasites, whose conditions are solely set by the hosts. We tested this prediction by measuring the difference between observed and expected prevalence (the percentage of the infested host population) of the ectoparasites in different environments. Two effects of the environmental influence of the ectoparasites population were also studied: changes in a) the host preference and b) the frequency distribution of the parasites on the hosts.

Within the mite family Laelapidae, subfamily Laelapinae represents FT-parasites while subfamily Haemogamasinae represents PT-parasites. Subfamily Hirstionyssinae was placed in between these two life-trait groups by Lundqvist (1985). The Anoplura species are also FT-parasites.

MATERIALS AND METHODS

About 10,000 small mammals were collected in the late summers of 1965—1970 in northernmost Fennoscandia (Finland, Norway and Sweden). Altogether fifteen small mammal species were sampled. The material is described in detail by Hanson et al. (1978) and Lundqvist (1985). In this study the ten most frequent host species (those with more than twenty specimens) will be used.

The ectoparasitic material has previously been reported by Brinck-Lindroth (1972), Edler and Mehl (1972), Edler and Mrciak (1975), Nilsson (1974a, b) and Lundqvist (1985). In this paper we deal only with Anoplura and mites of the family Laelapidae (Table 1).

Table 1. Lice and Laelapidae species with 70 individuals or more collected from small mammals in northernmost Finland, Norway and Sweden in 1965—1970

Species	Males	Females	Juveniles	Sum
Anoplura				
Hoplopleura acanthopus (Burmeister)	372	867	181	1,420
H. edentula Fahrenholz	9,620	20,589	1,283	31,492
Polyplax borealis Ferris	158	510	89	757
P. serrata (Burmeister)	7	67	4	78
Acari				
Eulaelaps stabularis (C. L. Koch)	7	400	0	407
Haemogamasus horridus Michael	42	29	81	152
H. nidi Michael	40	383	50	473
H. nidiformis Bregetova	17	211	5	233
H. ambulans (Thorell)	91	790	81	962
Myonyssus ingricus Bregetova	2	68	0	70
Echinonyssus isabellinus (Oudemans)	516	3,366	380	4,262
E. talpae (Zemskaya)	8	627	2	637
Laelaps clethrionomydis Lange	237	1,936	94	2,267
L. hilaris C. L. Koch	168	4,565	133	4,866
Hyperlaelaps microti (Ewing)	259	945	123	1,327

Study area: The northernmost parts of Finland, Norway and Sweden are surrounded by the Atlantic and the Barents Sea (Fig. 1). Even a slight altitudinal difference gives drastic effects on the climatic conditions at these northern latitudes. Hence, there are relatively mild regions at the Atlantic coast in the west, an inland taiga and coastal tundra close to the Barents Sea in the east.

The area was divided into five regions based on geography, vegetation and small mammal characteristics (Hansson et al. 1978). In region V only 72 mammals were collected; a number considered too small for our analysis. Host and ectoparasite material from this region was used only for calculating the observed prevalence in the total area and in the biotopes.

Region I. The Lofoten and Vesterålen islands. Comparatively mild climate. Sub-maritime birch forests and relatively oligotrophic bog land.

Region II. The Scandinavian mountain range between the Norwegian coastal line and the eastern part of the Lake Torneträsk. Sub-alpine birch forests and oligotrophic mires in the low and middle alpine belt.

Region III. Northernmost Sweden (Vittangi) and northern Finland (Lake Inari). Taiga with spruce and pine forests.

Region IV. Northernmost Finland (Utsjoki) and Norway (Kirkenes), close to the Barents Sea. Sub-alpine forests and eutrophic mires in the low and middle alpine belts.

Region V. The coast of the Varanger peninsula at the Barents Sea, northernmost Norway. Dwarf-shrub communities.

The localities used for trapping were classified according to dominating plants (Table 2).

Prevalence: The observed prevalence of an ectoparasitic species was compared with the expected value. The expected prevalence in a subarea (region or biotope) was calculated from the observed prevalence in the total area and the frequency of the hosts in the subarea. If a parasite population infests 10 % of a certain host species in the total area and the host species constitutes 10 % of the small mammals collected in the subarea, then the expected prevalence will be 1 %.

Thus, the expected prevalence of the species k in the subarea i was calculated as:

$$\frac{1}{100} \times \frac{M}{\sum\limits_{j=1} \left[n_{ij} \times \frac{10,000}{N_i \times 100} \times \frac{m_{jk} \times 100}{N_j} \right]}$$

where:

M = number of host species,

m_{jk} = number of host animals of species j infested by parasite species k,

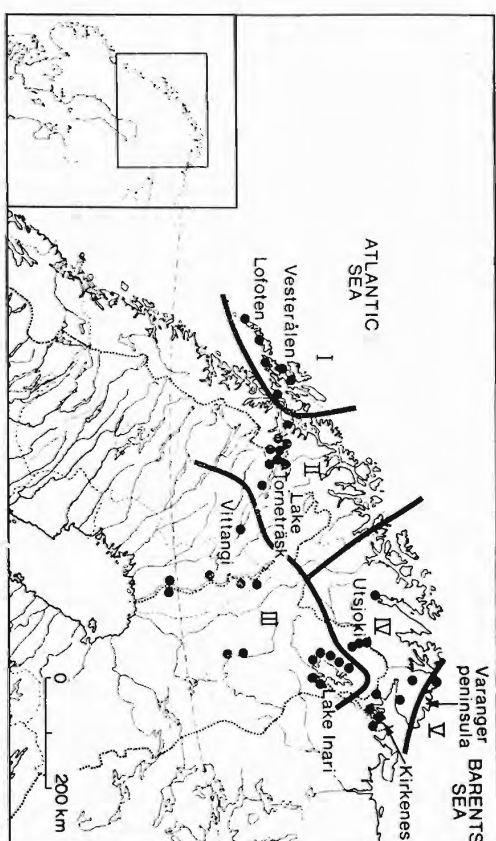n_{ij} = number of host animals of species j in subarea i,

$N_i = \frac{M}{\sum\limits_{j=1}} n_{ij}$, total number of host animals in subarea i,

$N_j = \sum\limits_{i=1}^{S} n_{ij}$, total number of host animals of species j,

S = number of subareas.

The power of this method to predict the observed prevalence was tested by a linear regression analysis. For each of the twelve biotopes and for each of the five regions the observed prevalence was used as the independent variable, and the expected prevalence as the dependent variable and the correlation coefficient was calculated. A high correlation coefficient indicated a good predictability of the method and hence a small environmental influence on the actual prevalence.

Host preference: The percentage of the parasite population found on each host species was calculated and used as a measure of the host preference. A histogram was used to illustrate the numerical distribution of each parasite species, and the abscissa was divided into sections proportional to the percentage of the host species in the region (Figs. 2—4). Thus, the area under the bars became proportional to the percentage distribution of the parasite and the height of the bars indicated the "importance" of the host species to the parasite in the region.

Frequency distribution: For each ectoparasite species, the hosts were classified according to the number of parasites they carried. It was necessary to use a variable class width to get a sufficient number of hosts in each class, since the parasite frequency distribution often was highly aggregated. Thus, the area under each distribution class was ≥ 5. The class width was chosen such that the expected value of each distribution class was ≥ 5. The

Fig. 1. Nothernmost Fennoscandia (= Finland, Norway and Sweden) divided into five regions, I—V, on biogeographic basis (after Hansson et al. 1978). Localities investigated are indicated by dots.

Table 2. Number of host animals collected in 12 biotopes and 5 regions in northernmost Finland, Norway and Sweden 1965—1970

Biotope	Dominating layer	Dominating plant species	I	II	III	IV	V	Sum
1. Poor birch forest	tree	Betula spp. tortuosa	1,638	1,372	286	244	0	3,540
2. Rich birch forest	tree	B. p. tortuosa	1,045	894	42	978	0	2,959
3. Swampy spruce forest	tree	Picea abies	0	0	156	0	0	156
4. Poor pine forest	tree	Pinus silvestris	0	0	453	0	0	453
5. Bilberry-pine forest	tree field	P. silvestris / Vaccinium myrtillus	0	0	208	0	0	208
6. Mixed swampy forest	tree	B. p. tortuosa / P. abies / P. silvestris	0	0	114	25	0	139
7. Willow shrub land	shrub	Salix spp.	0	184	35	0	15	234
8. Migre edge	shrub	B. p. tortuosa / P. silvestris	0	0	0	0	0	0
9. Mire	bottom	Sphagnum spp. / grasses	13	0	20	76	0	109
10. Hay meadow	field	grasses	128	2	16	32	0	178
11. Empetrum heath	field	Empetrum hermaphroditum / Betula nana	0	0	633	223	0	856
12. Close to buildings and refuse tips	shrub	Betula nana	0	38	0	44	57	139
		B. p. tortuosa	0	0	0	0	0	0
		Salix spp.	137	260	42	0	0	439
							sum	9,410

distributions were compared with one another by means of $(r \times k)$ χ^2-tests. A significance level of 5 % was accepted. This method was preferred to comparing arithmetic means by Z-tests or the nonparametric Mann-Whitney U-test, because the prevalence was mostly very low. A low prevalence implies that non-infested although potential hosts strongly contribute to the arithmetic mean.

The frequency distributions of the ectoparasites were all aggregated, with a variance to mean ratio greater than unity. The distributions were therefore tested, by means of χ^2-tests, for conformity with negative binomial and Poisson distributions.

RESULTS

There were significant correlations between observed and expected prevalence in the laelapin mites and two out of three lice species (Table 3). For the third louse, *Hoplopleura acanthopus*, none of the correlation coefficients were significant. Among the haemogamasin mites three out of eight correlation coefficients were statistical significant. In the Hirstionyssinae one species had significant and the other nonsignificant correlation coefficients.

Table 3. Correlation coefficients between observed and expected prevalences of laelapidae mites and lice from northernmost Finland, Norway and Sweden. The total area was subdivided into four regions and the trapping localities into twelve biotopes. Asterisk (*) gives the significance level

Parasites subfamily	species	Correlation coefficients region	biotope
Acari			
Haemogamasinae	Eulaelaps stabularis	0.74	0.25
	Haemogamasus nidi	0.78	0.78**
	H. nidiformis	0.86	0.55*
	H. ambulans	0.93*	0.48
Hirstionyssinae	Echinonyssus isabellinus	0.99**	0.55*
	E. talpae	—0.18	0.44
Laelapinae	Laelaps clethrionomydis	0.95**	0.98***
	L. hilaris	0.96**	0.98***
	Hyperlaelaps microti	0.98**	0.97***
Anoplura			
Hoplopleurinae	Hoplopleura acanthopus	—0.20	0.04
	H. edentula	0.94*	0.54*
Polyplacinae	Polyplax borealis	0.99***	0.87***

Most of the Haemogamasinae species predominated on voles, but two of them were particular in their distribution (Fig. 2). *Eulaelaps stabularis* and *Haemogamasus horridus* prefered shrews. There were also differences in host preferences from one region to another. *H. nidi* was mostly found on *Clethrionomys rufocanus* and *Microtus oeconomus* in the east, but in the west *Microtus agrestis* became an equally important host. *Haemogamasus niddiformis* was found on voles in the three easternmost regions and on shrews only in region II.

Echinonyssus isabellinus was associated with voles and *E. talpae* with the shrew *Sorex araneus* (Fig. 3).

Of the six species of the Laelapinae — Anoplura group, three were found on *Clethrionomys* spp. and three on *Microtus* spp. (Fig. 4). The *Microtus*, but not the *Clethrionomys*, parasites had different main hosts in different regions. 78.8 % of all *Hoplopleura acanthopus* in region II were found on *Microtus agrestis* compared with 85.7 % on *M. oeconomus* in region III. *Laelaps clethrionomydis* and *Hoplopleura edentula* were both found on *Clethrionomys rufocanus* and infrequently on *C. rutilus* and *C. glareolus*. However, none of these two ectoparasites were present in region I, where *C. rufocanus* was absent. Both short- and long-tailed ectoparasites were recognized (Figs. 5—6). All four haemogamasin mites exhibited short-tailed frequency distribution patterns with terminal classes with > 1 or > 2 parasites per host (Fig. 5). Also *Echinonyssus talpae* and *Hyperlaelaps microti* (Fig. 6) had short-tailed frequency distributions. Other
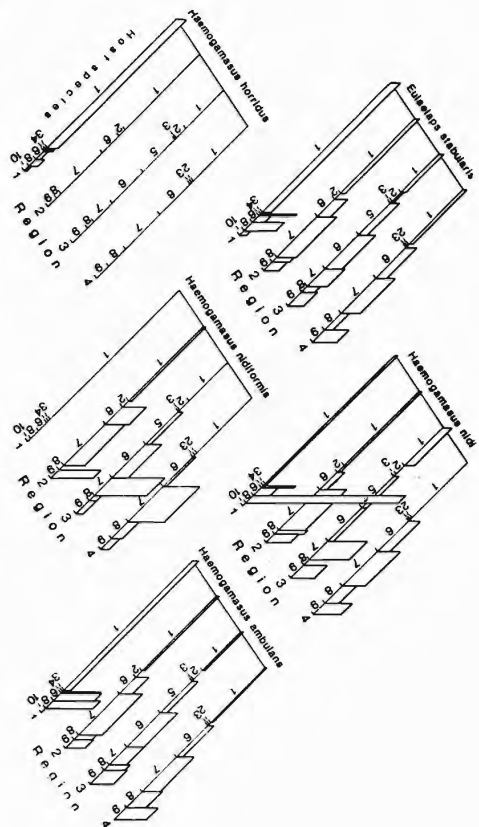
Fig. 2. The numerical distribution of haemogamasinae mites in percent on small mammal host species in four regions in northernmost Fennoscandia. The region axes are divided into sections proportional to the frequency of the host species in that region. The area under each bar is proportional to the percentage of the parasite population found on each host species. The host species are: **1.** Sorex araneus, **2.** S. caecutiens, **3.** S. minutus, **4.** Neomys fodiens, **5.** Clethrionomys glareolus, **6.** C. rutilus, **7.** C. rufocanus, **8.** Microtus agrestis, **9.** M. oeconomus, **10.** Mus musculus.
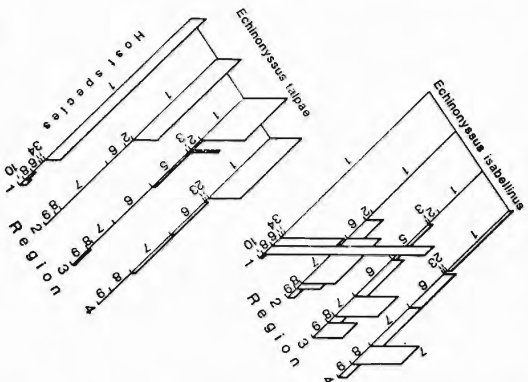
distributions (Fig. 6) were all long-tailed with terminal classes with > 6 (Polyplax borealis), > 10 (Echinonyssus isabellinus, Laelaps clethrionomydis, L. hilaris and Hoplopleura acanthopus) or even > 50 (Hoplopleura edentula). Differences in frequency distribution patterns between regions were found in all species except in Hoplopleura acanthopus which was only found in regions 2 and 3.

The four haemogamasin mites were all less prevalent than expected in localities close to buildings and refuse tips. They were also less prevalent on Empetrum — Betula nana heaths, mires and mire-edges. They were more prevalent than expected on poor birch localities. On other localities, e.g. rich birch forest, poor pine forest and mixed swampy forest, Haemogamasus nidi was in a reversed relationship to the other Haemogamasinae species.
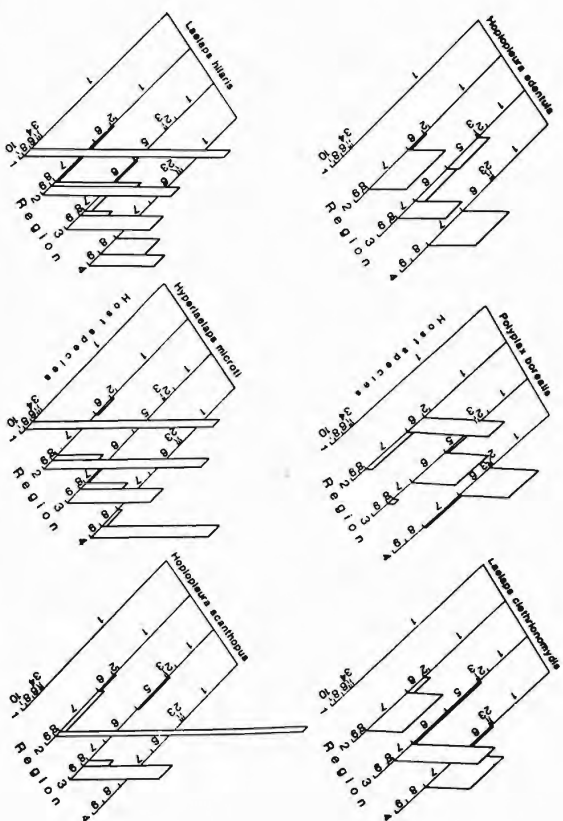
Fig. 3. Numerical distribution of hirstionyssinae mites.

Fig. 4. Numerical distribution of specialists on Clethrionomys spp. and Microtus spp.

Echinonyssus talpae was more prevalent than expected in open localities and in deciduous forests, except hay meadow and rich birch forest. Laelapin mites were often found in expected prevalences and so were two of the three lice species. The one exception was Hoplopleura acanthopus, which was found almost exclusively in three biotopes, viz. poor and rich birch forest and hay meadow. Neither were any lice found in the Empetrum — Betula nana heath and only in low prevalences in localities close to buildings and refuse tips.

In a few cases only the frequency distribution of the ectoparasites could be described as negative binomial (but see Lundqvist 1985 for a more detailed analysis). In no case did the Poisson distribution describe the observed frequency distribution.

DISCUSSION

Part-time and full-time ectoparasites differ in their use of the host's natural environment. For the FT-parasites it constitutes a pure transition habitat (Stenseth 1983), but is used for reproduction by the PT-parasites. Janion (1983) called it the "secondary habitat", a term that might be used without implicit ranking.

We considered the host frequency when calculating the expected prevalence of a parasite population (cf. Methods). A high correlation coefficient between expected and observed prevalences therefore indicates a low influence of the secondary environment on the parasite population. Such a high correlation coefficient was postulated in the Introduction for laelapin mites and low correlation coefficients for haemogamasin mites. This was found to be the case when the effect of regions and biotopes on the prevalence was tested. The effect of biotopes was slightly more pronounced (lower correlation coef-
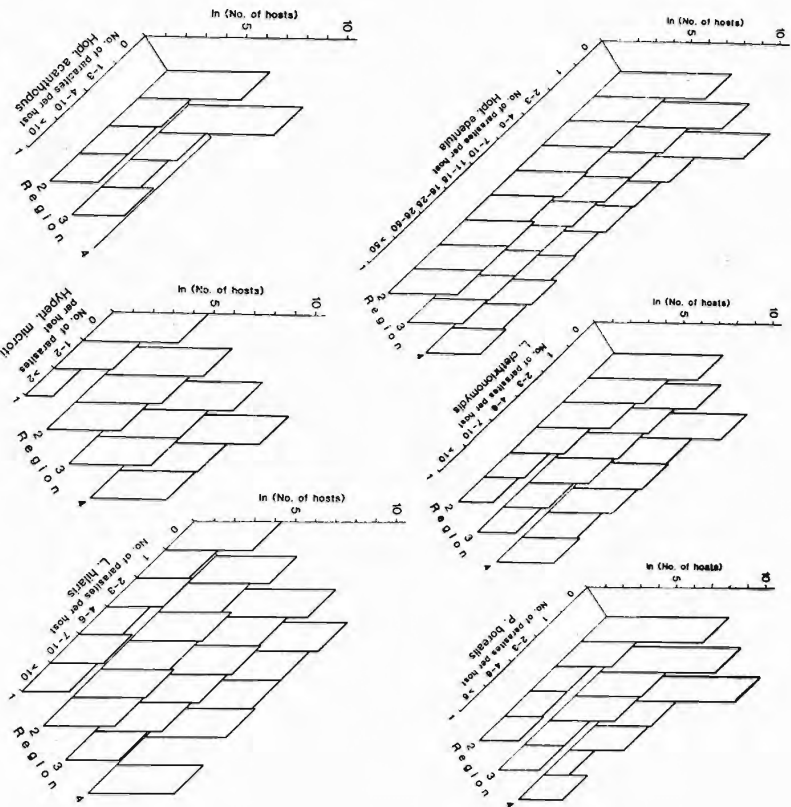
Fig. 5. Frequency distribution of haemogamasine and hirstionyssinae mites on small mammal hosts in four regions in northernmost Finland, Norway and Sweden. Hosts are classified according to their ectoparasitic burden.

ficients in Table 3) than that of regions, but both were lower than for Laelapinae and Anoplura. The conceivable mechanism behind such an influence is probably found in the transmission (immigration — emigration) and reproductive rates of the parasites (Anderson and May 1978). Haemogamasin mites are mainly nest inhabitants (Mrciak et al. 1966). Generally, they find the hosts in the nests. Laelapin mites are host dwelling and are seldom met with off the host. The main way of transfer for the laelapin mites is therefore by direct contact between host animals, e.g. when suckling, mating or socially touching. Lundqvist (1985) put Anoplura and Laelapinae into the same life-trait group and they could hence be only slightly influenced by the secondary environment. This was not contradicted by our results — except for the louse *Hoplopleura acanthopus*.

The immigration rate of a PT-parasite can be increased by increasing the number of possible host species. The transmission as well as the reproduction rates are reflected in the frequency distribution pattern of the parasite on the hosts (Randolf 1975, Anderson 1976). The haemogamasin mites were more catholic and opportunistic in
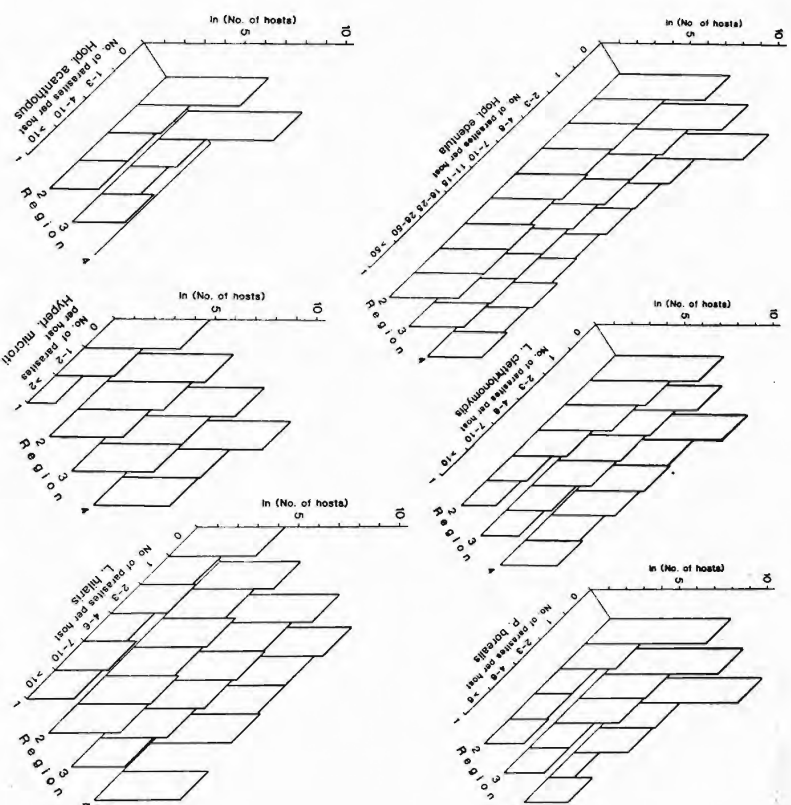

Fig. 6. Frequency distribution of specialists on *Clethrionomys* spp. and *Microtus* spp.

their host selection. Switching from one host species to another was observed, leading to an infestation of the host species in proportion to their frequency in the region. Laelapin mites had a more restricted host selection and switching between host species was less common. The Anoplura species were similar to the Laelapinae in this respect.

All haemogamasin mites had short-tailed frequency distributions, and the laelapin mites, except *Hyperlaelaps microti*, and the Anoplura had long-tailed. There were differences in the frequency distribution patterns between regions. The reproduction of both Haemogamasinae and Laelapinae mites were seasonal in Central Sweden (Edler 1972) and South Sweden (Edler 1973). Artz (1975) showed that there is a seasonality in incidence of the lice *Hoplopleura acanthopus* and *H. edentula* in northern Germany. We interpret the observed regional differences in our investigation as originating from different seasonality due to climatic conditions in the regions.

All observed frequency distributions were highly aggregated and most of them were polymodal. **They** did not fit to negative binomial nor Poisson distributions. Lundqvist (1985) considered this an effect of the heterogeneous host material. By subdividing

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the host populations into groups like "females" or "adult females" alone, groups of hosts were found, of which the ectoparasites were distributed according to negative binomial distribution. Looking for such mono-modal distributions among host populations can be a method of designating groups with common parasitic invasion and extinction rates.

The louse *Hoplopleura acanthopus* did not follow the Anoplura scheme as concerns *Microtus* spp. occurred in all regions. This species was found only in regions 2 and 3, while its main hosts, *Microtus* spp. occurred in all regions. A parasite distribution restricted to a part of the host's range makes the expected prevalence low. This property of the method used made the difference great between observed and expected prevalences, but it does not explain why the difference was restricted to certain inland regions and biotopes.

Резюме. Непостоянные эктопаразиты мелких млекопитающих распространяются посредством местообитания, с другой стороны постоянные паразиты через популяции хозяев. Поэтому предполагают, что влияние природной среды в этих двух группах разное. Это изучалось как разница между наблюдаемой ожидаемой превалецией, процент инфестированых хозяинов в популяции в разных условиях среды. Два возможных механизма такого влияния хозяинов были анализированы, т. е. а) селекция хозяина и ее изменением в зависимости от встречаемости хозяев и б) миграция паразитов в репродуктивный индекс отражающийся в дистрибуции встречаемости хозяев. Как ожидали, превалентный индекс постоянных эктопаразитов (Anoplura и подсемейство Laelapinae) могла быть предсказана на основе встречаемости видов в разнообразных условиях среды, за исключением одного вида вши (Holoplopleura acanthopus) из-за ограниченной дистрибуции. Превалению не было возможно предсказать для непостоянных эктопаразитов (подсемейство Haemogamasinae). Виды подсемейства Haemogamasinae были более строго связаны с селекцией хозяинов более чем Anoplura и подсемейство Laelapinae. Клещи Haemogamasinae меняли вид хозяина более чем Anoplura и Laelapinae у Haemogamasinae был обнаружен узкий диапазон распределения и у всех Anoplura и Laelapinae за исключением Hyperlaelaps microti широкий диапазон распределения.

ДИСПЕРСИЯ В РАЗНООБРАЗНОЙ СРЕДЕ: ВЛИЯНИЕ НА ПРЕВАЛЕНЦИЮ ЭКТОПАРАЗИТОВ МЕЛКИХ МЛЕКОПИТАЮЩИХ

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FLUORESCENCE-MICROSCOPIC VIZUALIZATION OF CHITIN STRUCTURES IN EGG SHELLS OF ASCARIS LUMBRICOIDES

Egg shells protecting the embryo against the effects of the outer environment form in fertilized eggs of *Ascaris lumbricoides*. One of the layers of the egg shells is the chitin protein complex. Chitin is a polysaccharide consisting of molecules of N-acetyl-D-glucos-amine bound in β position by 1,4-glycosidic bond.

One of the direct methods for the detection of chitin is the method of its fluorescence microscopic vizualization by means of the derivative of stilbene-disulfonic acid, Blankophore (Bayer). The principle of this fluorochrome is the specific bond of this fluorochrome to the compounds of hexapyranose type, e.g. chitin, which radiates in a yellow-green colour in the blue excitable light.

The method was verified in our laboratory on pathogenic fungi and was found to be very sensitive (Hejlímánek M., 1987: Diagnostic staining of fungi with Blankophore (in Czech). Čs. dermat., in press).

The method was used for the detection of the chitin layer formation in egg shells of *Ascaris lumbricoides*. A series of semithin sections of eggs (100—120 nm) were prepared for electron microscopy (fixation in 2% OsO_4, in 0.1 M phosphate buffer, pH 7.2). The epoxy-resin was removed from the sections by a lye-alcohol method (Lane B. P., Europa D. L., 1965: J. Histochem. Cytochem. 13: 579). The sections were then put into a saturated solution of NaOH in absolute alcohol. After 1 h they were taken out and left to drip on filter paper. Slides with the sections were dipped four times for 5 min into absolute alcohol and again left to drip. Then they were put into phosphate buffer at pH 7 for 5 min, washed three times in distilled water and put into phosphate buffer, pH 4. Then the samples were washed at pH 4. Then the samples were washed with a solution of 0.2 g of Blankophore in 100 ml of 0.5 % NaOH for 5 min, washed in water and observed either directly in water or after transfer through an alcohol series and embedding into Canada balsam. Fluoval (Zeiss, Jena) microscope with ex-citable filter BG12 and barrier filter OG 1 was

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