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Reproductive strategies of ectoparasites on small mammals

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A model of ectoparasitic reproductive strategies is presented. To be successful, an ectoparasite must either disperse to find a new host or stay on one host and produce its progeny during the lifetime of the host. Dispersion is facilitated by utilizing many host species and by waiting for the next host; these strategies prolong the generation time. Staying on the host is facilitated by shortening the generation time. Ectoparasites that repeatedly move on and off hosts are thus expected to have wide host preference spectra and long generation times while sedentary ectoparasites are expected to have narrow host preference spectra and short generation times. Population parameters of 27 ectoparasitic species (fleas, lice, mesostigmatic mites, and one ixodid tick species) on cyclic small mammal populations were investigated and a cluster analysis was performed. Three population parameters proved to be important and could be used to form a base for life-trait grouping of the ectoparasites: (i) the host preference spectra; (ii) the time lag between host and parasite peak abundance; and (iii) the intensity of the infestation. Three groups of ectoparasitic life traits were discernible: (i) species with narrow host preference spectra, no time lag (short ectoparasitic generation time), and major infestation: the Anoplura–Laelapinae group; (ii) species with moderate to wide host preference spectra, 1-year time lag (long parasitic generation time), and minor infestation: the Siphonaptera–Haemogamasinae group; (iii) one species, *Ixodes trianguliceps*, had moderate host preference spectrum, 2-year time lag, and moderate infestation. Ectoparasites, such as trombiculid mites and the tick *Ixodes ricinus*, which are not confined to small mammals, were missing or very rare on the cyclic small mammal populations. This was predicted by the model.

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On trouvera ici un modèle des stratégies de reproduction chez les organismes ectoparasites. Pour survivre, un ectoparasite doit se déplacer pour trouver un nouvel hôte, ou rester sur un hôte et produire toute sa progéniture au cours de la vie de cet hôte. La dispersion est facilitée par l'utilisation de plusieurs espèces hôtes et par l'attente du prochain hôte, deux facteurs qui prolongent la durée d'une génération. Le séjour chez un hôte unique suppose le raccourcissement de la durée d'une génération. Théoriquement, donc, il faut s'attendre à ce que, chez les ectoparasites qui changent d'hôtes de façon répétée, le spectre de préférences d'hôtes soit assez étendu et la durée d'une génération, longue, alors que, chez les ectoparasites sédentaires, le spectre d'hôtes préférés sera assez limité et la durée d'une génération sera courte. Les paramètres démographiques de 27 espèces d'ectoparasites (puces, poux, acariens méso-stigmatiques et une espèce de tique ixodide) ont été examinés chez des populations cycliques de petits mammifères et les résultats ont été soumis à une analyse des groupements. Trois paramètres sont déterminants et peuvent servir de base à la formation de groupes: (i) le spectre des hôtes préférés, (ii) l'intervalle entre l'abondance maximale des hôtes et l'abondance maximale des parasites et (iii) la gravité de l'infestation. Trois groupes d'ectoparasites peuvent être formés d'après ces caractéristiques: (i) les espèces du premier groupe ont un spectre restreint d'hôtes, il n'y a pas d'intervalle entre leur abondance maximale et celle de leurs hôtes (durée d'une génération courte) et les infestations sont considérables: groupe Anoploures–Laelapinae; (ii) chez les espèces du deuxième groupe, le spectre d'hôtes est moyen, il y a un intervalle de 1 an entre l'abondance maximale de l'hôte et celle du parasite et les infestations sont mineures: le groupe Siphonaptères–Haemogamasinae. (iii) Une espèce, *Ixodes trianguliceps*, a un spectre moyen d'hôtes, l'intervalle entre son abondance maximale et celle de son hôte dure 2 ans et les infestations sont moyennes. Les ectoparasites tels les acariens trombiculidés et la tique *Ixodes ricinus*, que ne sont pas restreints aux petits mammifères, étaient absents ou très rares chez les populations cycliques de petits mammifères, ce qui était d'ailleurs prédit par le modèle

[Traduit par la revue]

Introduction

A parasite has three alternatives with regard to reproduction: (i) "here and now," (ii) "here but later," and (iii) "elsewhere and later" (Southwood 1977). The restraints of these options are how long will a specific, suitable patch last? and what are the chances of finding another patch? According to the first two alternatives (without dispersal) the parasite must produce its progeny within the life-span of the host. For successful reproduction, the third alternative postulates that the parasite finds a new host. The chance of doing so comprises at least two elements: (i) a specific host-finding property of the parasite, which is inherited within the species, and (ii) the number of available hosts.

In this paper a simple model for the life traits of ectoparasites on small mammals is formulated. The model is based on the observations that some ectoparasites are one-host parasites, while others have adopted a strategy of recurring host exchange. The strategies are selected for both by evolution within the ectoparasitic population and as a result of host properties and host population characteristics.

Material

The small mammal hosts

About 10 000 small mammals were collected in the summers of 1965–1970 in northernmost Fennoscandia (Finland, Norway, and Sweden) (Fig. 1). The main part of the sampling was performed during the first 3 weeks of August. Multiple-catch live traps (type Ugglan special) were used and emptied in the mornings, except when the traps were set for more than 24 h: then they were emptied also in the evenings. The number of animals collected during daytime was small, usually less than 10% of the total catch (Andersson and Hansson 1966). Collected small mammals were put in separate poly-ethen bags and killed with diethyl ether. Their reproductive status was determined and they were preserved in a mixture of equal amounts of 80% ethanol and 4% formaldehyde. The entire catch comprised 15 small mammal species. However, in this study only 11 species (those with more than 10 specimens) were used (Table 1).

The host populations fluctuated in density during the period. The fluctuations were not synchronous for the shrew *Sorex araneus* and the vole populations over the total area. Low, increase, and peak years were designated on the basis of index trapping (Hansson et al. 1978). Pronounced fluctuations with a 3- to 4-year periodicity of abundance were found for the rodents with peaks in 1966, 1969, and

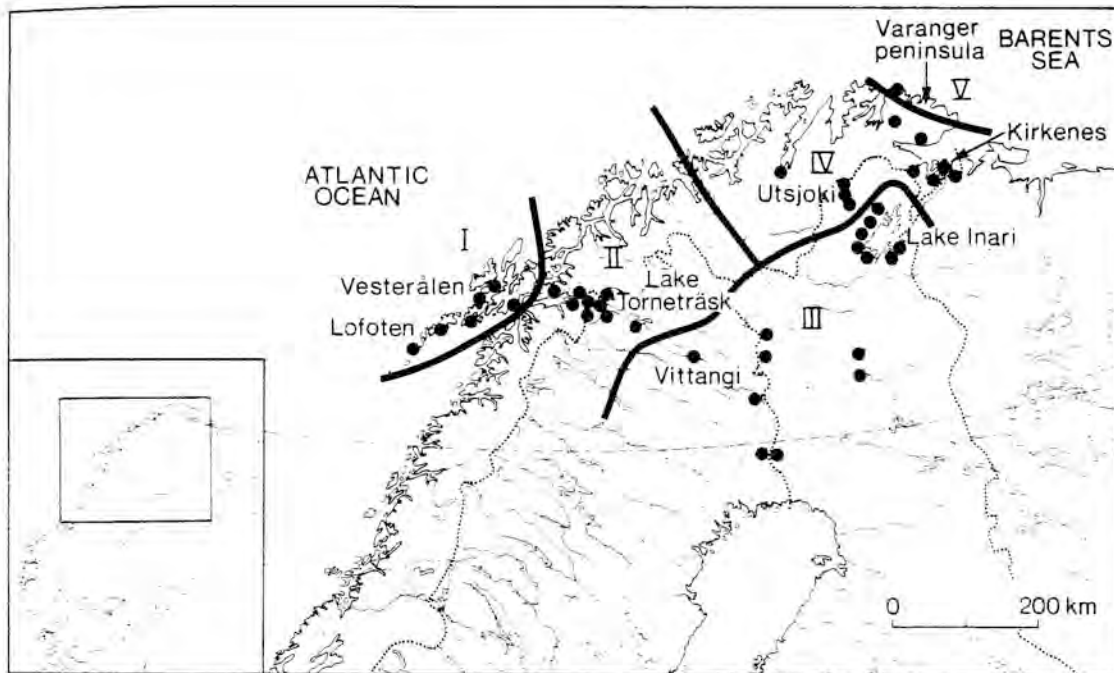


FIG. 1. Northernmost Fennoscandia divided into five regions, I–V, on a biogeographical basis (after Hansson et al. 1978). Localities investigated are indicated by solid circles.

1970 (Table 2). In region IV (Fig. 1) there were peaks in 1965 and 1970, while a peak year was observed in region V only in 1970. Insectivore fluctuations were pronounced only in regions I and II (Table 2).

The ectoparasites

In the laboratory some 67 000 arthropods were removed by hand from the fur of the small mammals. To avoid bias all material was handled by only two people. Further, only the biggest ectoparasites were taken into consideration. Small prostigmatic and astigmatic mites were collected when found but no specific search for them was made.

Ectoparasites were preserved in 80% ethanol and later mounted on microscope slides and identified to stage, sex, and species. In this study 27 ectoparasitic species (those of more than 50 specimens) were used, for a total of 65 583 specimens (Table 3). The ectoparasitic material has previously been reported by Brinck-Lindroth (1972), Edler and Mehl (1972), Edler and Mrciak (1975), Nilsson (1974a, 1974b), and Lundqvist (1985).

The study area

Based on geography, vegetation (Hämet-Ahti 1963), and small mammal characteristics (Hansson et al. 1978) the study area was divided into five regions (Fig. 1).

The model

Parasite generation time

Pielou (1977) defined T as a generation time for populations with nonoverlapping generations:

$$[1] \quad T = \ln R_0 / r$$

where R_0 is the net reproductive rate and r is the intrinsic rate of natural increase. She also gave a definition of the generation time for populations with overlapping generations.

However, in this paper, I will use τ as a symbol for the generation

time of the ectoparasites for both overlapping and nonoverlapping generations, i.e. $T = \tau$. Doing so is justified when r is "small" (Pielou 1977: p. 62).

To reproduce according to alternatives (i) and (ii) in the Introduction, it is necessary that the generation time of the parasite, τ , be shorter than the period during which the patch is favourable for the parasite, H . This can be expressed as an inequality:

$$[2] \quad H/\tau \geq 1$$

where H is the average life-span of a host individual.

Two elements of successful reproduction "elsewhere," according to alternative (iii), can be denoted by m , the intrinsic host-finding property of the parasite, and N_t , the number of hosts at time t . The chance of successful reproduction can then be formulated as follows:

$$[3] \quad p = m \times N_t$$

The parameters H and N_t are properties of the host population and cannot be altered by selection among the parasites.

Estimating the host-finding ability

The host-finding ability of an ectoparasite is represented by m in [3]. The less energy an ectoparasite has to spend to locate a host animal the greater the value of m for that parasite. There are at least three ways for an ectoparasitic species to increase m by means of natural selection: (i) to increase the ability to resist starvation and drought, (ii) to locate the host by means of special adaptations, and (iii) to increase the host spectrum. If any small mammal encountered by a searching ectoparasite can serve as a host, then searching time is shortened. This ability is important when host animals are rare, which is the case during low population density phases. In this paper an index of the host preference spectrum will be used as an estimator of m (see Methods and Discussion sections).

The unpredictability of H and N

In a small mammal population, the life-span of an average individual is highly unpredictable and varies greatly with the time of

TABLE 1. Small mammals examined for ectoparasites

	Males	Females	Juvenile	Subadult	Adult	Postreproductive	Total
Insectivora							
<i>Sorex araneus</i> L.	2465	2084	4089	0	460	0	4549
<i>Sorex caecutiens</i> Laxmann	129	117	222	0	24	0	246
<i>Sorex minutus</i> L.	32	27	43	0	16	0	59
<i>Neomys fodiens</i> (Pennant)	27	20	37	0	10	0	47
Rodentia							
Voies							
<i>Lemmus lemmus</i> (L.)	11	7	2	4	12	0	18
<i>Clethrionomys glareolus</i> (Schreber)	240	213	22	285	135	11	453
<i>Clethrionomys rutilus</i> (Pallas)	664	524	200	523	463	2	1188
<i>Clethrionomys rufocanus</i> (Sundevall)	585	702	364	301	621	1	1287
<i>Microtus agrestis</i> (L.)	216	252	133	126	205	4	468
<i>Microtus oeconomus</i> (Pallas)	226	263	52	316	101	20	489
Mice							
<i>Mus musculus</i> L.	43	42	41	7	37	0	85
Total	4638	4251	5205	1562	2084	38	8889

NOTE: Material taken from five regions in northern Finland, Norway, and Sweden, 1965–1970.

TABLE 2. Population density phases of rodents and shrews in five regions of northern Fennoscandia, 1965–1970 (after Hanson et al. 1978)

	1965	1966	1967	1968	1969	1970
Rodents						
Region I	<i>l</i>	<i>p</i>	<i>l</i>	<i>l</i>	<i>p</i>	<i>l</i>
Region II	<i>i</i>	<i>p</i>	<i>l</i>	<i>l</i>	<i>i</i>	<i>p</i>
Region III	<i>i</i>	<i>p</i>	<i>l</i>	<i>l</i>	<i>i</i>	<i>p</i>
Region IV	<i>p</i>	<i>l</i>	<i>l</i>	<i>l</i>	<i>i</i>	<i>p</i>
Region V	<i>l</i>	<i>l</i>	<i>l</i>	<i>l</i>	<i>i</i>	<i>p</i>
Shrews						
Region I	<i>p</i>	<i>l</i>	<i>l</i>	<i>i</i>	<i>p</i>	<i>l</i>
Region II	<i>p</i>	<i>l</i>	<i>l</i>	<i>l</i>	<i>i</i>	<i>p</i>

NOTE: *l*, low density years; *i*, increasing population; *p*, peak density years.

birth, sex, and fluctuation phase (Myllymäki 1977; Erlinge et al. 1983; Gliwicz 1983). The number of available hosts varies with the season.

Methods

Three variables of parasite–host interactions were studied: (i) B_i , the breadth of the host spectrum where B is the niche breadth as defined by Levins (1968); (ii) $\Delta B = B_{low} - B_{peak}$, the change in breadth of the host spectrum with decreasing host abundance (only the sign of dB/dN was used); (iii) $\Delta x = x_{low} - x_{peak}$, the change in mean number of parasites per host when the host population fluctuates from peak to low density years (only the sign of dx/dt was used).

The breadth of the host spectrum

B_j was used to measure the host preference spectrum on the j th parasite species.

$$[4] B_j = \frac{1}{\sum_{i=1}^k q_i}$$

where k is the number of host species and

$$[5] q_i = (p_{ij})^2 \times (P_T)^{-2}$$

Here p_{ij} is the number of parasites of species j on the i th host species and P_T is the total number of parasites of species j .

This B value illustrates a parasite's host preference spectrum in a

specific situation, given the host species frequencies, and was used to calculate ΔB , the change of host preference spectrum from host peak year to low year.

However, to obtain a B value less dependent on the specific environment (i.e., the frequency of different small mammal species differed between years and regions), a B_c value based on standardized host material was used. This was accomplished by dividing the number of ectoparasites on each host species by the number of hosts. Thus, we can substitute in [4]

$$[6] q_i = \frac{(P_{ij})^2}{N_i} \times (P_T)^{-2}$$

where N_i is the number of hosts of the i th species. The B_c value was calculated over all years.

The mean number of parasites per host

From the variation in the host preference spectrum (B_j), three main categories of host selection among ectoparasites were discernible (Table 3). Category 1 comprised ectoparasites that occurred on one or at most two host species, usually of the same genus. In category 2 were ectoparasites with a broader host spectrum; hosts often belonged to different genera. Two groups were distinguished; category 2.1 comprised the vole ectoparasites (on genera *Clethrionomys* and *Microtus*) and category 2.2 comprised the shrew ectoparasites (on genera *Sorex* and *Neomys*). Ectoparasites of category 3 had no distinct preference and were therefore considered to be generalists.

For calculating the mean number of ectoparasites, \bar{x}_{cat} (cf. Lundqvist 1985), the following formula was used: $\bar{x}_{cat,j}$ = the number of individuals of species j found on hosts preferred by the species/the total number of individuals of host species preferred by parasite species j .

Preferred hosts of ectoparasite species j were defined as those constituting the smallest number of species on which at least 90% of all individuals of species j were found.

When studying changes in \bar{x}_{cat} with changing host abundance only time lags of 1 year could be observed, since the material was gathered by annual collecting.

Cluster analysis

A cluster analysis (BMDP Statistical Software P2M) was performed on the material to form clusters of cases based on more than one variable. Initially every species was considered as a separate cluster. The computer program then joined species and (or) clusters of species in a stepwise process until all species were combined into one cluster. The algorithm used the distance between centroid clusters as a criterion for joining (amalgamating) clusters. The variables used in

TABLE 3. Ectoparasites (species with more than 50 specimens collected) from small mammals in northern Fennoscandia in 1965–1970, arranged according to increasing host preference spectrum

	Taxonomic classification*	n†	B ₁ ‡	ΔB§	Category
<i>Polyplax serrata</i> (Burmeister)	A	78	1.00	—	1
<i>Laelaps clethrionomydis</i> Lange	L	2 267	1.21	±	1
<i>Polyplax borealis</i> Ferns	A	757	1.36	—	1
<i>Myonyssus ingricus</i> Bregetova	M	70	1.41	—	1
<i>Hyperlaelaps microti</i> (Ewing)	L	1 328	1.44	±	1
<i>Hoplopleura edentula</i> Fahrenholz	A	35 009	1.82	—	1
<i>Peromyscopsylla bidentata bidentata</i> (Kolenati)	S	91	1.98	—	1
<i>Laelaps hylaris</i> Koch	L	4 866	2.07	—	1
<i>Hoplopleura acanthopus</i> (Burmeister)	A	1 437	2.12	—	1
<i>Echinonyssus talpae</i> (Zemskaya)	Hi	637	2.53	+	2,2
<i>Palaeopsylla soricis</i> s.l. (Dale)	S	3 381	2.62	—	2,2
<i>Rhadinopsylla integella</i> Jordan & Rothschild	S	68	2.99	—	2,1
<i>Megabothris calcarifer</i> (Wagner)	S	168	3.26	±	2,1
<i>Haemogamasus nidiformis</i> Bregetova	Ha	233	3.34	+	2,1
<i>Hystrihopsylla orientalis orientalis</i> Smit	S	453	3.35	+	3
<i>Peromyscopsylla silvatica</i> (Meinert)	S	330	3.36	+	2,1
<i>Haemogamasus horridus</i> Michael	Ha	152	3.61	—	3
<i>Corrodopsylla birulai</i> (Ioff)	S	811	3.93	—	2,2
<i>Echinonyssus isabellinus</i> (Dudemans)	Hi	4 262	4.04	—	2,1
<i>Amphipsylla sibirica sibirica</i> (Wagner)	S	887	4.64	+	2,1
<i>Amalareus penicilliger pedias</i> (Rothschild)	S	2 282	5.05	—	2,1
<i>Ixodes trianguliceps</i> Birula	I	2 259	5.17	—	3
<i>Megabothris rectangularis</i> (Wahlgren)	S	1 665	5.54	—	2,1
<i>Haemogamasus nidi</i> Michael	Ha	477	5.59	—	3
<i>Ctenophthalmus uncinatus uncinatus</i> (Wagner)	S	242	6.08	—	3
<i>Haemogamasus ambulans</i> (Thorell)	Ha	963	6.37	—	2,1
<i>Eulaelaps stabularis</i> (Koch)	Ha	410	7.34	—	3

NOTE: In this table the subspecific epithets of the fleas are given. Only specific epithets are used in the text and figures.

*A, Anoplura; Ha, Haemogamasinae; Hi, Hirstionyssinae; I, Ixodidae; L, Laelapinae; M, Myonyssinae; S, Siphonaptera.

†Number of specimens.

‡Breadth of host preference spectrum.

§Change in host preference spectrum with crash of host population: +, host spectrum increases; —, host spectrum decreases; ±, no significant change.

||Host preference category: 1, specialist; 2,1, vole ectoparasites; 2,2, shrew ectoparasites; 3, generalists.

this analysis were: (i) B_1 , calculated over all years, (ii) ΔB , (iii) prevalence, and (iv) \bar{x}_{cal} over all years.

Results

The nine narrowest host spectra included all four Anoplura species (Table 3), the four mite species of the subfamilies Laelapinae and Myonyssinae and the flea *Peromyscopsylla bidentata*. The remaining 18 species were mites of the subfamilies Haemogamasinae and Hirstionyssinae, the tick *Ixodes trianguliceps*, and fleas.

In 14 of 22 cases (in the remaining species there was insufficient material for analysis), the host preference spectrum was narrower in low years than in peak years (Fig. 2). Eight of nine category 1 species had restricted host preferences when the hosts became sparse in low years. The changes were, however, very small for two species, *Laelaps clethrionomydis* and *Hyperlaelaps microti*. In categories 2 and 3, species with moderate host spectra, five of seven species had broader host spectra during low density years than during peak years. Ten of the 11 species with the broadest host spectra became restricted by host availability in low years.

Three types of changes in ectoparasitic density from host peak to low years were observed (Fig. 3): (i) a time lag of less than 1 year between the peak of host abundance and the response of the ectoparasites corresponding to an apparently simultaneous peak of host and ectoparasitic abundance; (ii) a

1-year time lag; and (iii) a time lag of 2 or more years between host peak and ectoparasitic response. Because of the low number of hosts during low years only six of the nine specialist species could be analysed. Five of them had a somewhat similar development with low means when the host population was low. Four had, in addition, peak densities in phase with host populations. The louse *Polyplax borealis* and the mite *Laelaps clethrionomydis* both had low densities in host peak years. *Laelaps clethrionomydis* also diverged from the specialist pattern in host low years by being most abundant both 1 and 2 years after the peak year. The densities of the ectoparasites in categories 2 and 3 usually varied less strongly (Fig. 3). In eight of nine flea species there was a more or less pronounced peak of density 1 year after the host peak. The exception was *Ctenophthalmus uncinatus*, which maintained a notably steady population from year to year. The mite species of the subfamily Haemogamasinae (genera *Haemogamasus* and *Eulaelaps*) had the same type of population development as the fleas. The mite *Echinonyssus talpae* (subfamily Hirstionyssinae) was in phase with the population density cycle of its hosts. The tick *Ixodes trianguliceps* had a 2-year time lag between peaks of abundance of host and parasite (Nilsson 1974b). The mite *Echinonyssus isabellinus* seemed to have a 3-year time lag.

A cluster analysis cannot be performed on species for which variables are missing. Therefore only four of the nine species

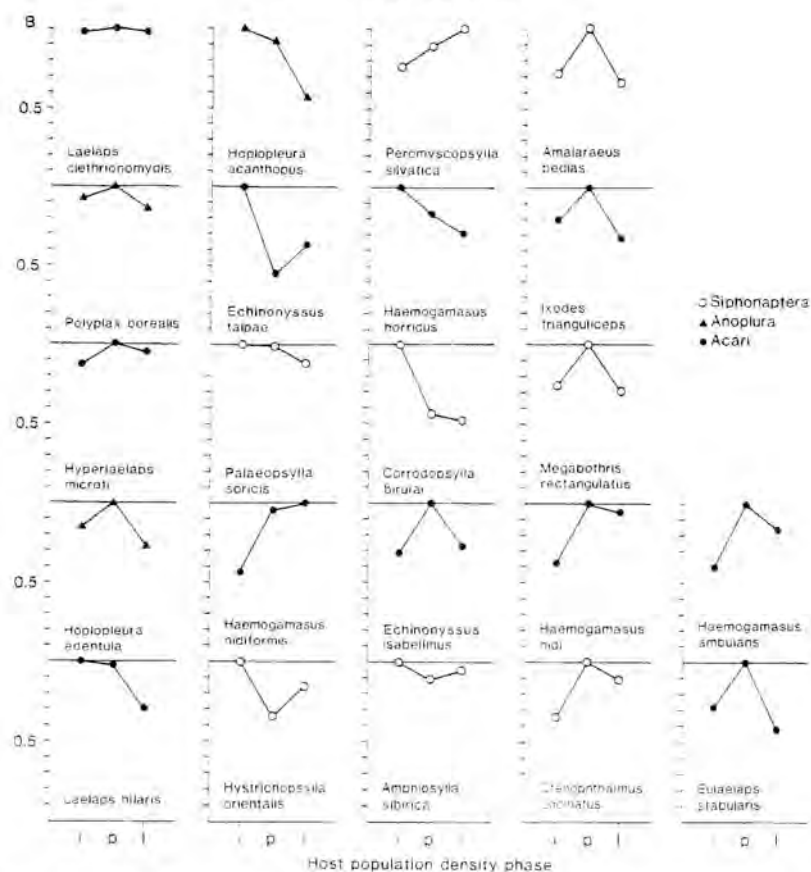


FIG. 2. Changes in the host-breadth spectrum (B) when the host population crashes from a peak year to a low year. The values are standardized so that the largest B value is set to 1 and smaller values are expressed as fractions of the largest; i , increase; p , peak; l , low years.

in category 1 were included. Likewise 1 of the 12 category 2 species was excluded. Four clusters of 18 ectoparasitic species were distinguished (Fig. 4). In addition three species did not fall into any of these clusters. Cluster 1 included two laelapine mites and one flea. It was characterized by narrow host preferences and high infestation values. Clusters 2 and 3 both had broad host preference spectra and low infestation values. Species in cluster 2 had narrowing and in cluster 3 broadening host preference spectra during low years. Cluster 4, like cluster 1, had high infestation values, but differed by having broad host preference spectra. The three remaining species had one extreme parameter value each. *Eulaelaps stabularis* had very broad host preference spectrum. *Laelaps hylaris* was very prevalent, and the louse *Hoplopleura edentula* had a high number of parasites per host.

Life traits

Based on the category classification, the cluster analysis, and the time lag between host and parasite peak density, three groups of life traits were discernible (cf. Table 3 and Fig. 4). These groups comprised different taxa.

The first group was distinguished by a narrow host spectrum, by high or extremely high infestation levels (expressed as mean number of parasites per host and (or) prevalence) and by no time lag between host and parasite abundance. The

group included Anoplura and the subfamily Laelapinae of the mesostigmatic mites.

The second group was the largest and was characterized by moderate to broad host spectra, low infestation, and a 1-year time lag between peaks of density. Species of both host preference categories 2 and 3 belonged to the group, which comprised Siphonaptera and Haemogamasinae species.

The tick *Ixodes trianguliceps* alone constituted the third group; besides being the only tick, *I. trianguliceps* was the only species with a 2-year time lag. This ectoparasite was a generalist (actually the larvae infested shrews and adult voles; see Nilsson 1974b) with low infestation levels and a moderate host spectrum.

Discussion

There is no general correlation between host-finding ability of an ectoparasite, m , and the breadth of the host spectrum, B_c . In many cases the parasites have adapted special means to find special host species. Such a mechanism is known, for example, in the African tick species *Ixodes (Afrixodes) neitzi*. The antelope *Oreotragus oreotragus* uses a secretion for intra-specific communication, but the secretion also attracts ticks (Rechav et al. 1978) resulting in a positive effect on m . In such a case, B_c cannot be used as an estimator of m . However, there

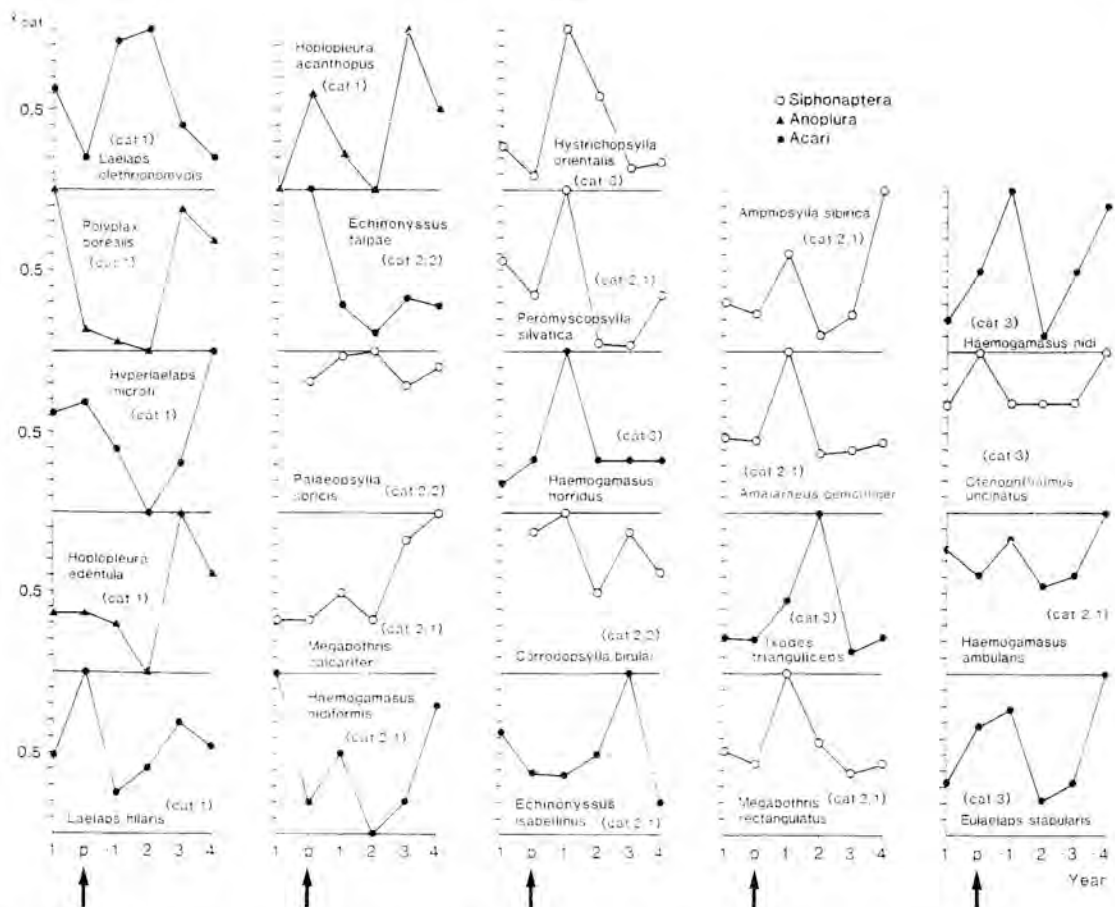


Fig. 3. Changes in x_{cat} when the host population crashes from a peak to a low year. For shrew parasites (category 2.2) the values are from regions I and II, for all other parasites region III is also included. In these areas the shrews had a peak year (p) in 1965 and voles had a peak year in 1966. The values are standardized so that the largest \bar{x}_{cat} value is set to 1 and smaller values are expressed as fractions of the largest.

are no reports supporting the assumption that such particular host-parasite relationships exist in small mammals in Scandinavia. Therefore, in this paper, I have used B_r to estimate the host-finding ability among a limited number of ectoparasitic species living in a restricted habitat.

From [1] we know that the intrinsic rate of natural increase is inversely proportional to the generation time and directly proportional to the logarithm of the net reproductive rate and thereby the realized fecundity (Pianka 1983; p. 109). This means that an increasing generation time must be compensated for by a logarithmically increasing net reproductive rate. Anoplura and Laelapinae are characterized by reduced generation time, τ , and benefit in this way from the direct proportionality between r and $1/\tau$ in [1]. There are but few reports on fecundity of terrestrial ectoparasitic arthropods. The human head louse, *Pediculus humanus* var. *capitis* (L.), produces about 120 larvae per female (Nutall 1917; Brinck-Lindroth et al. 1984). Marshall (1981) gives further data: *Haematopinus eurysternus* (Nitzsch) (worldwide on cattle), maximum of 24 offspring per female and *Haematopinus tuberculatus* (Burmeister) (on buffalo in Asia), mean of 73 offspring per female (maximum of 93). Edler and Solomon (1979) reported

that the laelapine mite *Laelaps agilis* Koch is ovoviviparous. It is likely that this also applies to other *Laelaps* (and probably also *Hyperlaelaps*) species. There is, however, no detailed information on the reproductive output of *L. agilis*.

The second group (Siphonaptera-Haemogamasinae) had typically a 1-year time lag, indicating a longer generation time. This implies that R_0 should be relatively high. Marshall (1981) gives two examples: *Echidnophaga myrmecobii* Rothschild (on small mammals in Australia) produces a mean of 170 offspring per female (maximum of 250) and *Pulex irritans* L., the human flea, produces a maximum of 448 offspring per female. According to Osbrink and Rust (1984) the cat flea, *Ctenocephalides felis felis* (Bouché) lays a life-span average of 158.4 eggs per female (maximum of 432).

It seems that the fleas can bypass the drawback of a high net reproductive rate by producing one or more generations during a reproductive season (G. Brinck-Lindroth, unpublished data; Darskaya and Suvorova 1984). During the reproductive season the generation time is short, 1-3 months (Marshall 1981). In this way the fleas can increase the intrinsic rate of natural increase but still keep the net reproductive rate reasonably low. This phenomenon is known in many other taxa, e.g., aphids

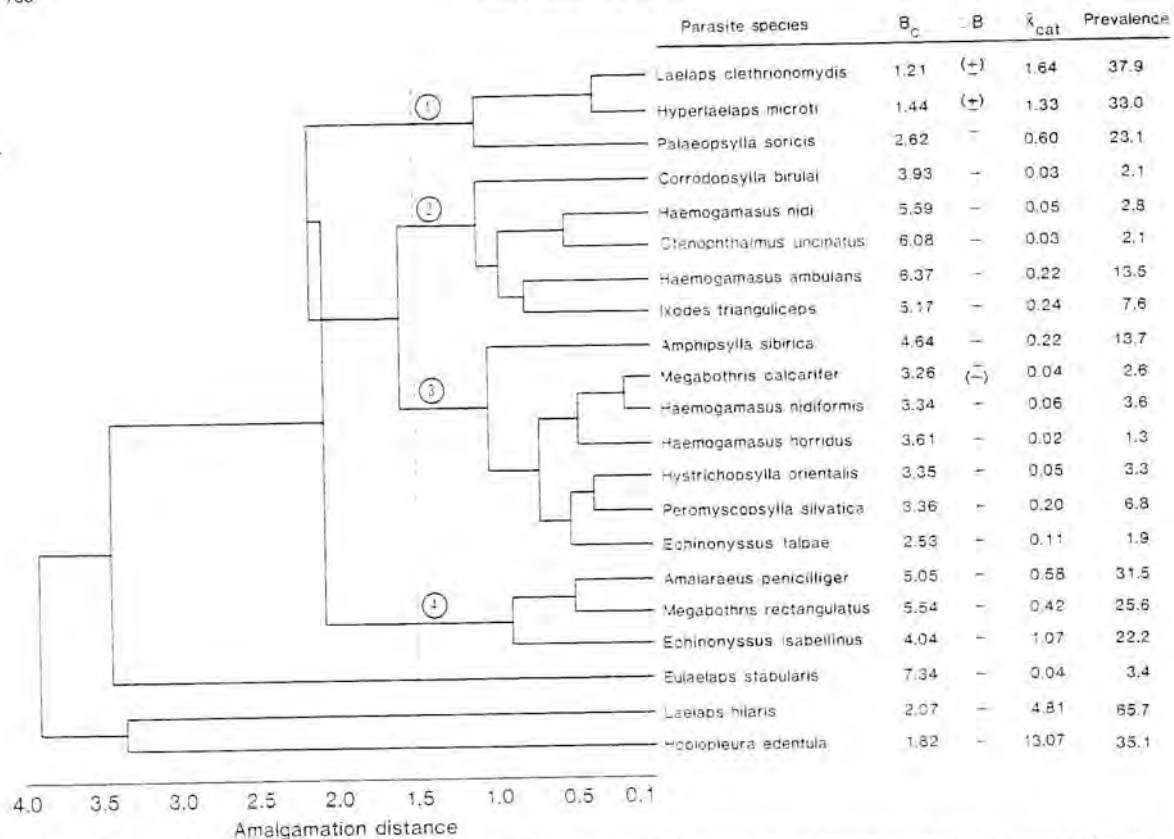


FIG. 4. Cluster analysis employed on 21 ectoparasite species. At an amalgamation distance of 1.5, seven clusters can be distinguished; four are multispecies clusters and three are single-species clusters.

and various other pest insects. Whether it applies to haemogamasine mites is not known.

Ixodes trianguliceps, which in this material constituted the third life-trait group, has a long generation time, several years according to Nilsson (1974b). To compensate for such a long generation time, ixodid ticks usually have a high net reproductive rate. *Ixodes ricinus* (L.) (on small mammals in Europe) lays about 2000 eggs per female (Arthur 1962). The reproductive output of *I. trianguliceps* is not known, but may be less than that of *I. ricinus*, because of its closer association with the small mammal hosts (Nilsson 1978).

The genus *Echinonyssus* (subfamily Hirstionyssinae) was not easily included in this arrangement. The species representing this genus had a moderate host spectrum, like the Siphonaptera-Haemogamasinae group, but differed in that their peak of density was in phase (e.g., *E. talpae*) with the host population, as in the Anoplura-Laelapinae group.

The apparent 3-year time lag in *Echinonyssus isabellinus* may be an artifact due to the 3- to 4-year frequency of the small mammal population cycle.

The life tactics of an ectoparasite should maximize the exploitation of either the host individual or the host population, since these are incompatible. Based on this dichotomy one can distinguish two main trends in the evolution of ectoparasites: representatives of the first stay on the host and reproduce there, while those of the other visit the host for short periods and ovi-

posit their eggs off the host. Reproduction on the host is advantageous when the host individual constitutes a predictable environment, whereas reproduction off the host may be successful when the number of hosts can be forecast based on the present number. In addition, staying on the host minimizes the risk of not finding a host for the next blood meal, while reproduction off the host minimizes the risk of being killed when the host dies. Reproduction on the host deductively leads to iteroparity, reproduction off the host logically to semelparity.

The host population is a patchy environment where the patches are ephemeral. For parasites that reproduce on the host the patchiness may be very real; the transition areas between individual hosts have become uninhabitable. These types of ectoparasites can be called full-time (FT) parasites. Part-time (PT) parasites, then, are those that also include parts of the environment (their host's nests and (or) runways) in their optimal habitats.

An extreme FT parasite has a short average life-span. In this case the host individual as an environment is relatively stable, since $\tau < H$. This is so even if the number of hosts fluctuates. However, by shortening the generation time, the FT parasites become heavily dependent on the host and cannot survive for long away from the host. They are transferred between hosts by direct contact. It is likely that the number of intraspecific encounters between hosts is greater than the number of interspecific encounters. This makes the host spectrum narrow.

An extreme PT parasite, on the other hand, has an enhanced ability to find a new host. For these parasites the habitat is not only the host but also the areas between the hosts. The advantage of this tactic is the reduced risk of the unpredictable and short average life-span of the hosts. But there are at least two disadvantages. First, the PT parasites have to find new hosts, often several times during their lifetime: N_t , the number of hosts at time t , must be sufficiently high ($> 1/m$) and cannot be influenced by selection among the parasites. The number of hosts is, on the contrary, an ecological variable and as such is exposed to rapid alterations, while the host-finding ability is predominantly an evolutionary variable. Optimally, from the parasite's point of view, there should be a correlation between N_t and N_{t+1} , which is not always the case in a cyclic population. Second, increasing the host-finding ability by prolonging the time interval between meals also prolongs the generation time.

Thus, it seems that parasites that concentrate on increasing the ability to find new hosts (PT parasites) are dependent on an ample and predictable access to hosts. Such a steady level cannot be found in a cyclic host population. This suggestion is supported by the fact that the number of trombiculid mites on small mammals decreases towards the north, where the small mammal populations tend to be more cyclic than in the south. Members of this mite family are parasitic only as larvae, while the adults are free-living predators. Similarly, the tick *Ixodes ricinus*, a common ectoparasite throughout Europe, is absent in the north; this species also is heavily dependent on small mammals in its larval stage.

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