

Larval parasitism in outbreaking and non-outbreaking populations of *Epirrita autumnata* (Lepidoptera, Geometridae)

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Larval parasitism of *Epirrita autumnata* (Borkhausen) was monitored during six years in field samples from within the outbreak range of *E. autumnata* in northern Fennoscandia, and outside it in southern Finland. All parasitoids found were hymenopterans. Six phenologically early species of parasitoids were found in populations within the outbreak range and three species outside the outbreak range. Two late larval parasitoid species were found within the outbreak range, but none outside the outbreak range. In half of the populations within the outbreak range, early larval parasitoids seemed to increase with a time lag. This is consistent with the cyclic population fluctuations of *E. autumnata* there. On a small spatial scale (among trees), however, parasitoids acted without a time lag. Parasitism rates by the early larval parasitoids are probably too low (mean 11%) for early parasitoids alone to keep densities of *E. autumnata* continuously at low levels outside the outbreak range in southern Finland.

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1. Introduction

Parasitoids are often proposed to regulate populations of herbivorous insects (e.g. Podoler & Rogers 1975, Long 1988, see also Price 1987). This is possible if parasitism rate depends positively on host density (23–50% of cases studied, see Lessells 1985, Stiling 1987, Walde & Murdoch 1988). Regulation may or may not involve time lags. Without a time lag parasitoids can produce rapid negative feedback loops, and regulate herbivore density at a low level (see e.g. Andersson & Erlinge 1977, Berryman et al. 1987). Any factor generating time lags, i.e. acting in a

delayed density-dependent way (second-order process), can potentially produce cycles in host density (Royama 1977, Berryman et al. 1987, Myers 1988).

The present study species, the geometrid *Epirrita autumnata* (Borkhausen), is cyclic in northern Fennoscandia (i.e. northern parts of Norway, Sweden, Finland). Outbreaks of *E. autumnata* leading to defoliation of mountain birch forests have occurred at 9 or 10 year intervals during the time period 1862–1968 (Tenow 1972, Haukioja et al. 1988). Data from Abisko, northern Sweden, covering three outbreaks of *E. autumnata*, show delayed density-dependence of

parasitism rates on larval density of *E. autumnata* (Olle Tenow, unpubl.). This suggests that parasitoids can be a factor contributing to the cyclicity in population density of northern *E. autumnata*. In contrast to populations in northern Fennoscandia, those in southern Finland do not reach outbreak densities (see Tenow 1972).

Information on parasitoids of *E. autumnata* has usually been published from single northern localities (see Tenow 1956, 1963, 1972, Jussila & Nuorteva 1968, Nuorteva & Jussila 1969, Nuorteva 1971). No comprehensive information has been published. This study is of the larval parasitoid species associated with *E. autumnata* populations within and outside the outbreak range of *E. autumnata*. I also studied whether parasitism rates are consistent with the cyclic population fluctuation in northern Fennoscandia and whether parasitism rates are high enough in southern Finland, so that parasitism alone is a possible explanation for the continuously low population densities there.

2. Material and methods

The study was conducted during six years (1987–1992). Samples were taken from populations within and outside the outbreak range of *E. autumnata*, i.e. from northern Fennoscandia and from southern Finland, hereafter called northern populations and southern populations, respectively. The geographical origins of population samples are presented in Table 1.

To estimate larval density I searched for larvae at each site by observing birch leaves (cf. Ruohomäki 1992, Ruohomäki & Haukioja 1992). I counted the number of larvae found per time unit (increasing search time with decreasing larval density) and calculated an index of relative larval density (no. of larvae/10 minute search). No individual birch tree was observed for more than 30 seconds.

I collected larvae from the field from birches (*Betula pubescens*), except samples Dm and Dn (see Table 1). In the north birch is represented by the mountain birch (*B. pubescens tortuosa*). Not more than two larvae were collected from the same birch tree. The larvae were brought into the laboratory and they were fed with an excess of

leaves from the plant species from which they had been collected. The mean instar of larvae at the time of collection is shown in Table 1. Although *E. autumnata* has five instars, mean instar is higher in some cases in Table 1, because young, just moulted fifth instar larvae were considered 5.0 instar and older ones, approaching pupation, as >5.0 instar.

In the D population I studied small scale spatial distribution of parasitoids in 1987. This was done by sampling larvae from individual birch trees (10–100 metres apart from each other) from branches whose leaves were counted. Density was determined as the number of larvae per 500 leaves.

Fewer parasitized larvae were collected from southern than from northern populations. The rarefaction method (Krebs 1989) is one appropriate for comparing species numbers between such samples. In the comparison the parasitoids *C. jucunda* and *P. immunis* were combined as one taxon in both southern and northern samples, because it was difficult to separate the two species from each other. In the rarefaction analysis the total number of parasitoid individuals was represented by the number of parasitized *E. autumnata* larvae. Thus, for gregarious species (see Tables 2 and 3) the number of parasitoid adults that emerged from the *E. autumnata* larva was not considered primarily important for the host.

I used Pearson's correlation analysis (see e.g. Sokal & Rohlf 1981) to test whether tree-specific parasitism rate correlates with tree-specific density in *E. autumnata*.

3. Results and discussion

3.1. Parasitoid species and timing of sample collection

Estimates of parasitism rates are sensitive to relative phenologies of the parasitoid and host, as stressed by, for example, Van Driesche (1983) and Gould et al. (1992). Accordingly, in this study larvae collected relatively early (before mean instar four) in northern populations were mainly parasitized by *Apanteles* spp., *Aleiodes gastritor* and *Phobocampe neglecta*, occasion-

ally by *Sinophorus turionus* and *Eulophus larvarum* (Table 2), whereas in southern populations they were parasitized by *Apanteles* spp. and sometimes by *E. larvarum* and by an unidentified species of the superfamily Proctotrupeoidea (Table 3). I call these "early larval parasitoid species"

since they parasitize the host in early instars. Most of them kill the host larva in the fourth or fifth instar (personal observation), but the unidentified proctotrupoid does not do so until the host larva has settled down for pupation. The late parasitoid species (*Zelex deceptor* and *Campoletis*

Table 1. Sample size and mean instar of the *E. autumnata* populations studied. Population codes were given to some populations in other studies (see Ruohomäki 1992, Ruohomäki & Haukioja 1992) and the same codes are used here. Larvae that died before the last instar were excluded. – = place not visited; 0 = no larvae found (low density); (0) = no larvae found (all pupated before collection).

Sample	Number of larvae						Mean instar						Origin
	87	88	89	90	91	92	87	88	89	90	91	92	
Northern													Finland
D	195	11	30	8	25	28	4.0	4.5	3.0	3.0	2.0	3.5	Värriö, 67°44'N, 29°36'E
Dm ^a	86	–	–	–	–	–	4.0	–	–	–	–	–	Värriö, 67°44'N, 29°36'E
Dn ^a	57	–	–	–	–	–	4.0	–	–	–	–	–	Värriö, 67°44'N, 29°36'E
L1	0	0	8	7	25	28			?	3.7	2.5	3.7	Tanhua, 67°30'N, 27°44'E
													Sweden
M1	34	21	27	31	30	30	4.0	3.0	3.0	4.9	3.0	3.2	Sappisaasi, 67°53'N, 21°31'E
L2	13	0	0	1	14	20	3.8			4	3.4	4.0	Vittangi, 67°43'N, 21°34'E
H1	166	27	10	9	10	20	3.5	2.0	2.3	4.5	3.0	3.0	Stenbacken, 68°14'N, 19°35'E
O1	11	13	4	0	10	20	4.0	1.8	2.0		3.1	2.8	Stordalen, 69°18'N, 19°10'E
													Norway
M5	–	52	12	(0)	6	28	–	4.0	3.5	(6)	4.5	3.9	Meby, 68°32'N, 17°30'E
M2	54	28	10	(0)	20	29	4.3	2.5	3.5	(6)	4.7	3.6	Nordkjosbotn, 69°12'N, 19°31'E
M3	27	10	11	–	–	–	3.5	4.3	4.0	–	–	–	Ytre Gåradak, 70°15'N, 25°01'E
L3	0	0	10	–	–	–			4.8	–	–	–	Børselvjellet, 70°20'N, 25°59'E
L4	0	0	8	–	–	–			4.8	–	–	–	Ilfjord, 70°27'N, 27°08'E
M4	28	22	32	12	21	5	3.5	4.8	4.5	5.1	4.1	3.1	Skjærnes, 70°26'N, 27°51'E
L	41	8	27	14	25	20	3.5	5.2	5.0	5.4	4.3	2.9	Boftsa, 70°23'N, 28°10'E
H2	353	28	28	30	0	0	4.0	4.0	4.0	4.1			Hana, 70°14'N, 28°26'E
O	41	27	25	29	17	3	4.0	3.0	3.5	3.8	3.0	2.3	Hana, 70°14'N, 28°29'E
Southern													Finland
NC1	31	21	27	29	24	30	3.8	3.3	3.3	3.4	2.8	3.4	Naantali, 60°26'N, 22°02'E
NC2	15	–	–	–	–	–	3.9	–	–	–	–	–	Lieto, 60°31'N, 22°37'E
NC3	14	–	–	–	–	–	3.8	–	–	–	–	–	Kaarina, 60°24'N, 22°19'E
NC4 ^b	–	–	–	30	–	–	–	–	–	2.2	–	–	Kakskerta, 60°21'N, 22°15'E
NC5 ^b	–	–	–	–	21	–	–	–	–	–	2.9	–	Ruissalo, 60°25'N, 22°10'E
NC6 ^b	–	–	–	–	25	–	–	–	–	–	2.5	–	Reposaari, 61°37', 21°24'E
NC7	–	–	–	–	39	–	–	–	–	–	2.8	–	Irjanne, 61°15'N, 21°43'E
NC8	–	–	–	–	37	–	–	–	–	–	2.9	–	Kallioaronkallio, 61°21'N, 21°40'E
NC9	–	–	–	–	11	–	–	–	–	–	2.5	–	Uotilansuo, 61°17'N, 22°05'E
NC10	–	–	–	–	18	–	–	–	–	–	2.4	–	Näyhälä, 61°17'N, 22°11'E
NC11	–	–	–	–	34	–	–	–	–	–	3.1	–	Levonmäki, 61°15'N, 22°15'E
NC12	–	–	15	–	–	–	–	–	3.8	–	–	–	Orivesi, 61°38'N, 24°12'E
NC13	–	–	19	–	–	–	–	–	3.6	–	–	–	Puuppola, 62°21'N, 25°42'E

^a Sample Dm was collected from bilberries (*Vaccinium myrtillus*) and sample Dn from dwarf birches (*B. nana*); all other samples were collected from birch (*Betula pubescens*).

^b Island population close to mainland.

varians) attack *E. autumnata* larvae most probably when *E. autumnata* is at the fourth instar and kill the host just before its pupation.

More early parasitoid species appear to be associated with *E. autumnata* in the north than in the south (cf. Tables 2 and 3), but the rarefaction

Table 2. Numbers of parasitoids (expressed as number of larvae parasitized) in northern *E. autumnata* populations in 1987–1992. See Table 1 for codes. — Early species: Ap = *Apanteles* spp. (Braconidae) consisting mainly of *Cotesia jucunda* (Marshall), and some individuals of *Protapanteles immunis* (Haliday); Al = *Aleiodes gastritor* (Thunberg) (Braconidae); Ph = *Phobocampe neglecta* (Holmgren) (Ichneumonidae) (a new species for the Finnish and Norwegian fauna, see Jussila 1992); Si = *Sinophorus turionus* (Ratzeburg) (Ichneumonidae); Eu = *Eulophus larvarum* (L.) (Eulophidae), the only gregarious parasitoid of northern *E. autumnata* in this study. Late species: Ze = *Zelex deceptor* Wesmael (Braconidae); Ca = *Campoletis varians* (Thomson) (Ichneumonidae). A blank or – is given when no larvae were found or when the place was not visited, respectively.

Sam- ple	1987 ^a					1988					1989					1990					1991					1992											
	Ap	Al	Ph	Eu	Ze	Ca	Ap	Al	Ph	Eu	Ze	Ca	Ap	Al	Ph	Eu	Ze	Ca	Ap	Al	Ph	Eu	Ze	Ca	Ap	Al	Ph	Eu	Ze	Ca	Ap	Al	Ph	Eu	Ze	Ca	
D	7	5	15	0	0	2	0	0	0	0	3	1	110	1	0	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	2	6	0	0	0	0	
Dm	1	0	8	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
Dn	4	1	2	0	0	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		
L1													4	1	0	0	0	0	5	0	0	0	0	0	0	0	1	0	0	0	0	12	5	0	0	0	0
M1	0	0	7	0	0	0	2	0	1	1	0	1	2	7	1	0	0	0	0	2	0	2	1	0	0	4	0	0	0	0	0	0	9	0	0	0	0
L2	4	1	0	2	0	1												1							4	0	0	0	0	1	3	0	0	0	0	1	
H1	2	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	0	2	0	0	0	0	0	0	1	0	0	0	0	0	
O1	0	0	0	0	0	0	5	0	0	0	0	0	0	1	0	0	0	0							0	0	0	0	0	0	0	0	0	0	0	0	0
M5	–	–	–	–	–	–	0	10	0	0	0	0	0	8	1	0	0	0	–	–	–	–	–	–	1	0	0	0	0	0	0	0	0	1	0	2	
M2	0	5	0	0	3	4	0	4	0	0	0	0	0	6	1	0	0	0	–	–	–	–	–	0	3	0	1	0	0	5	0	0	0	0	0		
M3	4	1	0	0	0	0	2	0	0	0	2	1																									
L3													0	0	0	1	4	0																			
L4													0	0	0	0	0	0																			
M4	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	3	0	0	0	0	1	2	0	0	0	0	0	
L	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	0	0	0	0	0	10	0	1	0	0	0	0	0	0	
H2	4	0	0	0	0	0	1	0	0	0	0	0	9	0	0	0	0	0	12	0	0	2	0	0													
O	0	0	0	0	0	0	6	0	0	0	0	0	3	0	0	0	0	0	10	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	

^a Addition: two larvae parasitized by *S. turionus* in L2.

Table 3. Numbers of parasitoids in *E. autumnata* populations in southern Finland in 1987–1992. — Early species: Ap as in Table 2, Sp. is an unidentified species of the superfamily Proctotrupoidea (gregarious: more than 100 parasitoids pupate within a full-grown host larva; length of adult c. 1.5 mm).

Pop.	1987		1988		1989		1990 ^a		1991		1992	
	Ap	Sp	Ap	Sp	Ap	Sp	Ap	Sp	Ap	Sp	Ap	Sp
NC1	3	1	5	0	3	0	2	2	0	0	1	0
NC2	1	0	–	–	–	–	–	–	–	–	–	–
NC3	0	0	–	–	–	–	–	–	–	–	–	–
NC4	–	–	–	–	–	–	0	0	–	–	–	–
NC5	–	–	–	–	–	–	–	–	0	3	–	–
NC6	–	–	–	–	–	–	–	–	0	0	–	–
NC7	–	–	–	–	–	–	–	–	3	1	–	–
NC8	–	–	–	–	–	–	–	–	5	3	–	–
NC9	–	–	–	–	–	–	–	–	2	0	–	–
NC10	–	–	–	–	–	–	–	–	0	0	–	–
NC11	–	–	–	–	–	–	–	–	2	0	–	–
NC12	–	–	–	–	3	0	–	–	–	–	–	–
NC13	–	–	–	–	5	0	–	–	–	–	–	–

^a Addition: one larva parasitized by *E. larvarum* in NC1.

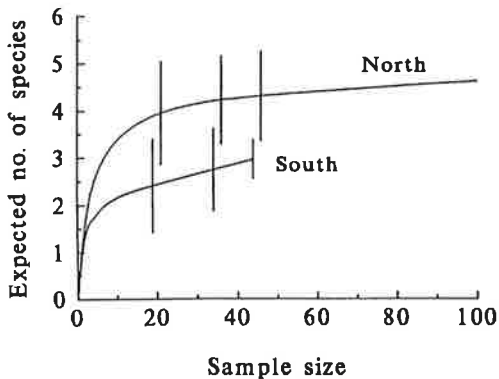


Fig. 1. Rarefaction analysis testing the difference in the number of early parasitoid species between northern (within the outbreak range of *Epirrita autumnata*) and southern (outside the outbreak range) populations. Error bars at three selected sample sizes show two standard deviations.

analysis (two standard deviations overlap in Fig. 1, c.f. Raivio 1989) indicates that the difference is not significant.

I found only one southern larva parasitized by *E. larvarum*. This may be due to phenological reasons, however, because all southern samples were collected before mean instar four. Only in two out of ten northern samples (M1 in 1988 and M5 in 1992) with *E. larvarum*, was the mean instar of *E. autumnata* lower than four at the time of collection. Thus, the species is somewhat intermediate in phenology between the early and late larval parasitoid species of this study, and it was mostly missed in southern populations and its occurrence was probably underestimated in northern samples collected before the mean fourth instar. This conclusion is, however, based on the assumption that the relative phenologies of *E. larvarum* and *E. autumnata* are similar in southern and northern populations.

Perhaps due to early sampling, no late parasitoid species were found in southern *E. autumnata* populations. Hence, whether they really are absent from southern populations remains an open question. I also usually collected the larvae from northern populations before attack by the late parasitoid species and the latter were represented only in a few samples collected late (after mean instar four).

3.2. Generalist vs. specialist parasitoids

Parasitoids can produce time lags (cycles) in the population dynamics of the host, provided that they are so specialized on the host that they collapse with declining host density. Generalist parasitoids are less likely to cause cycles because they can shift host during periods of low density in particular hosts. For the same reason generalist parasitoids may continuously maintain substantial population densities and respond rapidly to an increase in density of a particular host.

This reasoning predicts that at least some parasitoids of *E. autumnata* in northern populations should be specialists if they contribute to the cyclicity there. On the other hand, parasitoids in the south should be generalists to maintain *E. autumnata* continuously at low density level. Limited information available indicates that many of the parasitoid species are generalist (*Aleiodes gastritor*, pers. obs. and C. van Achterberg pers. comm.; *Apanteles* spp., pers. obs. and E. Haeselbarth pers. comm.; *Eulophus larvarum*, S. Vidal pers. comm.; *Zele deceptor*, C. van Achterberg pers. comm.). This is consistent with the population dynamics of southern *E. autumnata*, but not with that of northern *E. autumnata*. However, potentially generalist parasitoids may be forced to near specialism in many subarctic areas since densities of alternative lepidopteran hosts with appropriate phenology are generally low in the north (e.g. Haukioja et al. 1985).

3.3. Parasitism rates and larval densities

In the southern populations the mean percentage parasitism by early larval parasitoids was 11% ($SD = 9.1\%$, max = 26.3%, $n = 18$ samples, see Tables 1 and 3). The relatively low mean parasitism rate suggests that the negative impact of early larval parasitoids on *E. autumnata* populations in southern Finland is not enough, so that parasitism alone could explain the continuously low densities of *E. autumnata*. This cannot be generalized to the parasitism of *E. autumnata* as a whole, because my data do not allow any suggestion about the role of possible late larval or pupal parasitoids. In addition, my results do not

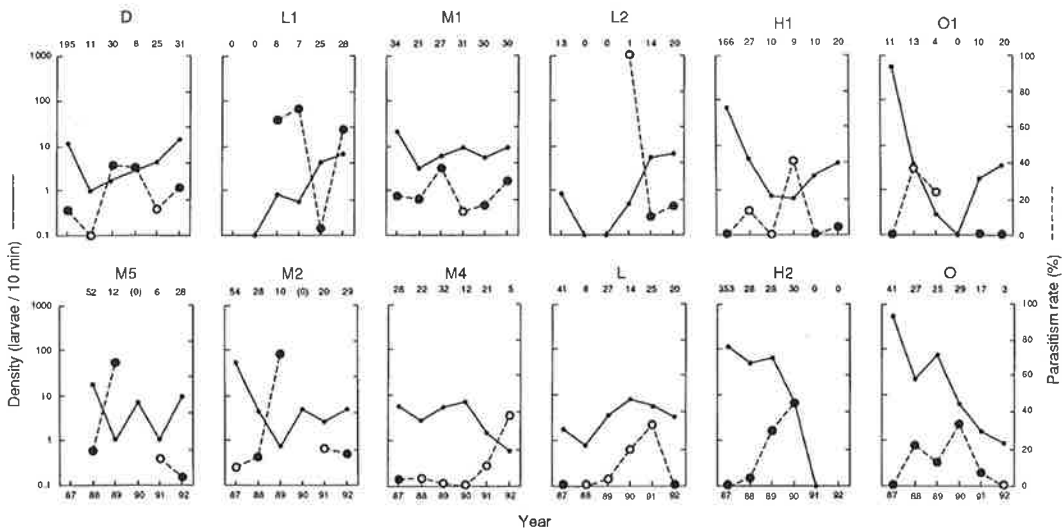


Fig. 2. Change in % parasitism by early larval parasitoids and relative larval density of *E. autumnata* northern populations in 1987–1992. Numbers at the top of each diagram show the number of larvae collected in each year. Parasitism rates indicated by open dots may be biased due to early or late collection time and/or small sample size (cf. Tables 1 and 2).

exclude the potential importance of the early larval parasitoids in contributing with other factors to the low densities of *E. autumnata* in the south. To test this, further investigations are needed.

For the northern populations I plotted the temporal trajectories of *E. autumnata* density and parasitism rates by early larval parasitoids (Fig. 2). Data from only six years did not permit meaningful statistical tests, but for six of the 12 populations the pattern in Fig. 2 suggests delayed density-dependence of parasitism (populations H1, O1, M2, M4, H2, and O; in H1 and O1 parasitism rates in 1988 and 1989 are underestimates, because the sampling was too early (see Table 1), O. Tenow, pers. comm.). Nevertheless, the suggestion of delayed density-dependence is consistent with cyclicity of the northern *E. autumnata* populations and with earlier results (O. Tenow, unpubl.).

Random variation is probable when data from several parasitoid species are pooled and possible species specific responses may be missed (Hassell 1966, but see Stiling 1987). Indeed, in *E. autumnata* different parasitoid species can be associated with different outbreaks (see Tenow 1972). This may result from both *E. autumnata* and parasitoids becoming locally extinct during

the low density phase of the *E. autumnata* cycle (O. Tenow, pers. comm.). Which parasitoid species are important during different high density phases may simply depend on which of them happen to find the high density locality first.

Because of the low number of parasitized larvae in single samples, I did not study the species separately. This may have masked species specific patterns, including phenological differences (see Van Driesche 1983). I reduced the bias by restricting the study of the relationship between the parasitism rate and larval density of *E. autumnata* to the early parasitoid species. Parasitism rates by early species were calculated by excluding larvae which perished before the fifth instar. Consequently, I assumed that the parasitism rate was the same for the larvae that perished before the larval stage from which the parasitoid emerges and for the larvae that survived until the emergence of the parasitoid from the host larva. This may not be automatically justified, because Werren et al. (1992) showed that larvae of *Lymantria dispar* (L.) unparasitized but stung by *Cotesia melanoscela* (Ratzeburg) had a higher mortality rate than unstung control larvae had.

A further potential confounding factor in any study of parasitism in polyphagous herbivorous insects, such as *E. autumnata* (see e.g. Seppänen

1970), is the possibility of variable parasitism among larvae feeding on different host plant species (cf. Bellinger et al. 1988, Werren et al. 1992). In this study, however, parasitism rates by early species in population D in 1987 did not differ among larvae collected from mountain birch (14%), dwarf birch (13%) and bilberry (10%) ($\chi^2 = 0.54$, $df = 2$). Nor were parasitoid species differently associated with plant species ($\chi^2 = 3.3$ for *Apanteles* spp., $\chi^2 = 2.2$ for *A. gastritor* and $\chi^2 = 1.6$ for *Ph. neglecta*; $df = 2$ for all; for numbers of larvae collected and parasitoids found see Tables 1 and 2, respectively).

No signs of delayed density-dependence were found in other populations of Fig. 2 other than those listed above. This may indicate that parasitoids do not act with a time lag in all local populations. Indeed, this was suggested by the positive correlation between tree-specific parasitism rates and *E. autumnata* larval densities in population D in 1987 (Fig. 3).

In studies of spatial density-dependence of parasitoids on host density, it is important to choose the right spatial scale (Hassell 1986, Walde & Murdoch 1988, Rothman & Darling 1990). However, in a review of parasitoid density-dependence in 171 cases, Stiling (1987) did not find consistent differences among spatial scales used in the studies. This is perhaps because scales may vary with parasitoid species due to differential mobility of individuals.

Small scale spatial density-dependence may be caused by parasitoids aggregating at patches of high host density. This is a critical assumption of models on parasitoid-host-interactions (Hassell 1982, Lessells 1985, Murdoch & Stewart-Oaten 1989). I found a positive correlation between *E. autumnata* density and parasitism rate among individual mountain birches (Fig. 3). This suggests aggregation, although parasitism rates may not correlate with the degree of aggregation of adult parasitoids (see Walde & Murdoch 1988). It may also suggest that although northern *E. autumnata* populations are usually considered cyclic, parasitoids in some northern populations can act without a time lag, and provided that the average parasitism rate is sufficiently high, they may keep *E. autumnata* at relatively low densities for long time periods. However, it is also possible that parasitoid behaviour does not vary

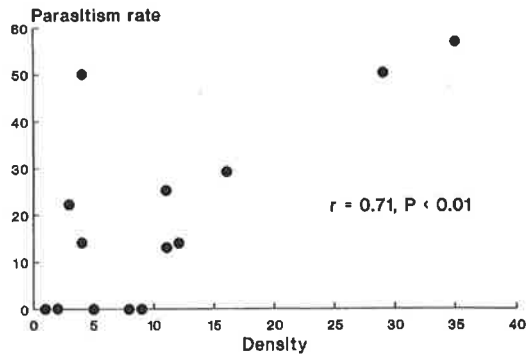


Fig. 3. Correlation of parasitism rate (%) and larval density of *E. autumnata* (no. larvae / 500 leaves) among mountain birch individuals. Parasitism mainly by *Apanteles* spp. and *Ph. neglecta* (see population D in 1987 in Table 2).

spatially, but they occasionally act without a time lag in cyclic populations. Because outbreaks do occur, the control fails after all in northern populations. For example, Haukioja et al. (1988) compared the per-capita growth rate of a pupal parasitoid, *Itamoplex armator* (Vill.) and *E. autumnata*. They concluded that due to the higher potential population growth rate, *E. autumnata* is able of escaping from the parasitoid, when conditions for *E. autumnata* are favourable.

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