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Temporal and spatial variation of larval parasitism in non-outbreaking populations of a folivorous moth

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Abstract In order to assess the role of parasitoids in the regulation of non-outbreaking populations of *Epirrita autumnata*, a geometrid lepidopteran with outbreaking populations in northern Europe, we examined the temporal and spatial variation of larval parasitism in south-western Finland during 6 successive years. The study was carried out on two spatial scales, among trees within sites of about 1 ha and among sites separated by distances of 2–10 km, using experimental and observational approaches respectively. The overall percent parasitism was independent of host density on both spatial scales, while temporally it fluctuated only little. Of the two main parasitoids, the commoner one, *Protapanteles immunis*, showed a variable response to host density on the larger spatial scale and negative density dependence on the smaller scale. Temporally, parasitism caused by this species was independent of host density. Another parasitoid, *Phobocampe bicingulata*, showed positive density dependence on the smaller spatial scale and had a variable response on the larger scale, but exhibited negative density dependence over time. The results of this study caution against drawing conclusions concerning population regulation on the grounds of spatial density dependence alone. Larval parasitoids apparently do not maintain low densities in the *E. autumnata* populations studied. However, they may suppress *E. autumnata* densities to a level low enough for density-dependent mortality factor(s) to become regulating. Among other mortality factors of *E. autumnata*, pupal predation has been found to be temporally positively density-dependent.

Key words Population regulation · Density dependence · Parasitoids · *Epirrita autumnata* · Geometridae

Introduction

Parasitoids have been proposed to regulate insect herbivore populations in many theoretical and empirical studies (e.g. Hassell et al. 1991; Pacala and Hassell 1991; Kidd and Jervis 1997). The consequences of parasitism for the dynamics of host populations vary depending on the temporal and/or spatial response of parasitoids to host density. Sufficiently strong positive, temporally density-dependent parasitism is generally considered to maintain stable low densities. In contrast, delayed density dependence may generate cyclical dynamics of the host population (reviewed by Berryman 1996). Recent models suggest that stability may also be affected by variation in mortality related to spatial density (Stewart-Oaten and Murdoch 1990; Hassell et al. 1991; but see Dempster and Pollard 1986; Mountford 1988). Moreover, both Roland (1994) and Kidd and Jervis (1997) suggest that even if not itself regulating, parasitism may suppress densities of host populations sufficiently to allow regulation by other, density-dependent, mortality factor(s). However, in spite of considerable theoretical advances, the relative role of different mechanisms which potentially contribute to stable host densities in natural populations is still unclear. In particular, there have been very few field studies which examine the dependence of parasitism on both spatial and temporal density simultaneously (Stewart-Oaten and Murdoch 1990).

Most attention has been devoted to outbreaking rather than stable insect populations. A common but probably insufficient approach to determining the role of parasitoids in population regulation has been to compare levels of parasitism at endemic and epidemic densities of outbreaking populations. The populations of *Epirrita au-*

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tumnata (Bkh.) (Lepidoptera: Geometridae) are cyclical, with outbreaks in northern and mountainous Fennoscandia (Tenow 1972; Haukioja et al. 1988; Bylund 1995). In contrast, although widely distributed in forested areas over the Holarctic, the species is not known to reach outbreak densities elsewhere. Because of its dual population dynamics, *E. autumnata* is especially suitable for studying factors that may cause stability and on the other hand those that may lead to outbreaks and/or cyclicity.

The reasons for the contrasting population dynamics of *E. autumnata* are not clear, partly because the extensive studies that have been carried out have concentrated largely on outbreaking populations. In northern Fennoscandia, delayed inducible resistance of host trees (e.g. Haukioja 1990; Ruohomäki et al. 1992) and parasitism (Ruohomäki 1994; Bylund 1995; Kaitaniemi and Ruohomäki 1999) have been proposed to contribute to the cyclical population dynamics, but the mechanisms which assure stable densities elsewhere have received less attention (but see Tanhuanpää et al. 1999).

The purpose of this study was to examine the extent to which larval parasitoids contribute to the stable population dynamics of *E. autumnata* outside the outbreak range, in southwestern Finland. It was assumed that a contribution to the regulation of *E. autumnata* populations would occur if overall parasitism is temporally positively density-dependent. As the paper is focused on stable populations, our analyses are concentrated on direct temporally density-dependent effects. To evaluate the possibility of drawing conclusions concerning the role of parasitism in population regulation on the ground of mere spatial density dependence, the relationships between spatial and temporal variation of parasitism were studied during 6 successive years. The regulatory role of spatially density-dependent parasitism without a corresponding temporal response is more sensitive to system-specific features (e.g. the biology of parasitoids and hosts). Since the crucial significance of spatial scales has frequently been emphasized (Heads and Lawton 1983; Ray and Hastings 1996; Kidd and Jervis 1997), the study was carried out on two spatial scales. Finally, we discuss ways in which the life-history traits and other biological features of the parasitoids may affect the variation in parasitism found in *E. autumnata* populations.

Material and methods

Study species

E. autumnata, the autumnal moth, is a holarctic geometrid with a univoltine life cycle. The females lay their eggs in physically protected micro-sites during the autumn. The eggs overwinter and hatch in the spring. The solitary cryptic larvae feed on deciduous trees and shrubs. The larval stage lasts for 1–1.5 months and consists of five instars. Pupation occurs in the ground before midsummer, and the adults eclose in the beginning of autumn.

Earlier studies of *E. autumnata* have revealed that both larvae and pupae serve as hosts for various hymenopterous parasitoids (Haukioja et al. 1988; Ruohomäki 1994). However, pupal parasitoids are rare in southwestern Finland (Tanhuanpää et al. 1999). We studied parasitoids that utilize the early larval stages of *E. autumnata*. There were six such species: *Protapanteles immunis* (Haliday), *Cotesia jucunda* (Marsh.), *Aleiodes gastritor* (Thunb.) (Braconidae), *Phobocampe bicingulata* (Grav.) (Ichneumonidae), *Eulophus ramicornis* L. (Eulophidae), and a rare egg-larval parasitoid *Copidosoma chalconotum* (Dahlman) (Encyrtidae). All except the last two are solitary.

P. immunis was found to be the most common parasitoid, accounting for more than half of the total parasitism. It is a tiny (2.5–3.5 mm) bivoltine parasitoid. The species is a generalist, also known to parasitize the larvae of other geometrids (Tobias 1986). The second most common parasitoid, *Ph. bicingulata*, is a univoltine species with a body size of 5–7 mm. Some other studies suggest that parasitoids of this genus are generalists (Humble 1984; Ruohomäki 1994; Kerslake et al. 1996). The third species, *C. jucunda*, is taxonomically and ecologically close to *P. immunis*, being similarly a bivoltine generalist in southwestern Finland. In our study area, where *E. autumnata* is most likely not the main host species for this parasitoid, *C. jucunda* seems to parasitize retarded *E. autumnata* larvae. The other parasitoid species were rare.

Study area and sites

The 6-year study (1994–1999) was conducted in a forested area about 20–30 km northeast of Turku (60°15′N, 22°25′E) in southwestern Finland. The collection of *E. autumnata* larvae was carried out within an area of about 60 km^2. This study area was divided into 60 squares of 1×1 km, from among which squares for altogether 15 study sites were randomly selected. However, in two cases that resulted in two adjacent squares others were reselected. Within the 1×1 km squares, the sites for collection were selected in easily accessible plots. The study sites were mainly characterized by mixed coniferous forests, dominated by *Pinus sylvestris* L. and/or *Picea abies* (L.) Karsten, and birches in the understory; always *Betula pubescens* (Ehrh.) and at some sites also *B. pendula* (Roth.).

Sampling

To determine the spatial and temporal distribution of parasitism, larvae of *E. autumnata* were collected from all study sites. The sampling scheme was chosen to facilitate an analysis on two spatial scales. On a larger scale, larvae were collected from sites separated by distances of 2–10 km (15 sites in 1994–1996; 12 sites in 1997–1999). About 30 larvae were collected from each site, the area examined being about 1 ha. The collections were conducted at a time when one half of the larvae had reached their 4th instar. At this stage, most of the parasitism had already occurred, but the parasitoids had not yet emerged. Only larvae found on the main host plants of *E. autumnata*, *B. pubescens* and *B. pendula*, were sampled. The branches and leaves inspected for this purpose were at a height of not more than about 3 m.

On the smaller scale, the spatial distribution of parasitism was studied experimentally using host density manipulation. This density increase experiment was carried out in 1994–1997 at two to four sites each year, most of the sites being repeated in successive years. To create between-tree differences in larval density, important for assessing the ability of parasitoids to aggregate in trees with high host densities, the number of *E. autumnata* larvae was artificially increased in 20 individual birch trees at each site by introducing eggs from a laboratory culture in early spring. The hatched larvae settled on the trees, and the resulting densities considerably exceeded the natural background densities: non-manipulated trees yielded at most two larvae per tree, while in experimental trees of the same size the number of larvae per tree always exceeded this, usually ranging from five to several dozen larvae. All the trees were 1–1.8 m in height, separated by distances of 5–10 m. To avoid dispersal of larvae other than by ballooning, the birches chosen for the study were ones that had no contact with other trees. Later, during the sampling, a maximum of four larvae (except for 1994, with 20) were collected from each “density-increase” tree, while at the same time samples of natural larvae (26–41 in 1995–1997, 13–32 in 1994) were taken from the same sites, at distances of 15–50 m around the experimental trees. All the larvae collected were reared in the laboratory until the parasitoids emerged or unparasitized larvae pupated or died.

Larval density

Simultaneously with collection, the natural densities of *E. autumnata* at the study sites were estimated. As an estimate of natural population density, an index of relative larval density was used (the number of larvae found per 10 min). This index has been previously used in other studies of this system (Ruohomäki and Haukioja 1992; Ruohomäki 1994; Ruohomäki et al. 1997; Tanhuanpää et al. 1999) and of others (e.g. Roland and Taylor 1997). In the case of *E. autumnata*, this index has been shown to correlate positively with more precise tree- and site-specific density estimates (Kaitaniemi et al. 1999). To avoid differences in searching efficiency, the larval counts were always performed by the same person. The searching time varied among sites, and was highest in sites with the lowest larval density. During the search, larvae were observed on birch foliage at a height of 0.5–3 m. No individual birch tree was inspected for more than 20 s.

Statistical methods

On the temporal scale, the relationship between parasitism and host density was studied using linear regression analysis. The year-specific average parasitism rate was used as the dependent variable. The parasitism rate was calculated by dividing parasitized larvae by the total number of larvae collected, but omitting those which died of other causes than parasitism (*c.* 10% of larvae). Since the individuals of *P. immunis* and *C. jucunda*, which died before emerging as adults, were not separated in the early years of the study, these two species were pooled for the analyses. However, the proportion of the latter species was sufficiently small not to affect the results: for example, in 1998 and 1999, when both emerged and unemerged parasitoids were determined, the inclusion of *C. jucunda* in the analyses scarcely changed the trend in the association between host density and parasitism caused by *P. immunis* alone.

On the larger spatial scale, the dependency of the parasitism rate on host density was again studied using linear regression analysis. Site-specific parasitism rate was used as the dependent variable. To examine the relationship between larval parasitism and host density in the density increase experiment, logistic analysis was used, applying the SAS procedure GENMOD with the binomial distribution and logit as the link function (SAS Institute 1995). The probability of parasitism was used as the dependent variable. As there was no reason to expect differences in parasitoid behavioral responses among years and sites, a sample collected from any site in any year was treated as an independent case. Accordingly, case (1, 2,...,12) and host density (with two values: natural sample, density increase sample) were used as the explanatory variables in the analyses.

Results

Temporal density dependence

The average overall percent parasitism of *E. autumnata* across the study sites was surprisingly stable among years, fluctuating only between 27.9% and 35.2% (Table 1) despite considerable within-year variability in parasitism between sites, and among-year variability within sites (with the coefficients of variation of the overall parasitism ranging from 23% to 71%). At the same time, the variability in larval density was much larger (Table 1). However, the among-year relationship between overall percent parasitism and host density was negative and not significant (Fig. 1a). Thus there was no indication that parasitoids acted in a regulatory way in the *E. autumnata* populations studied. This was also true for the two main parasitoids analysed separately. The percent parasitism by *P. immunis* was relatively stable (16.9–26.5%) (Table 1), while the percent parasitism by *Ph. bicingulata* was more variable and much lower (0.4–7.7%) than that of *P. immunis*. Neither *P. immunis* nor *Ph. bicingulata* showed a temporally positive association between parasitism and host density: the former species caused density-independent mortality, while the latter showed negative density dependence (Fig. 1b, c).

Study sites which were sampled during 5 or 6 successive years were analysed separately as well. In 8 sites of 11, the association between host density and overall percent parasitism was weak with r^2<0.08. Two sites tended to show a stronger negative association, but they were far from significant (r^2=0.56, *P*=0.14 and r^2=0.26, *P*=0.30). Only at one site was the association positive, but again not significant (r^2=0.50, *P*=0.12). Analysing *P. immunis* and *Ph. bicingulata* separately, the responses to host density remained highly variable with both negative and positive associations represented at different sites.

Spatial density dependence

On the larger spatial scale, i.e. in comparisons between study sites, overall percent parasitism was independent

Table 1 Parasitism and relative larval densities of *Epirrita autumnata* presented as average percentages over study sites

Parasitoid species	Study year					
	1994	1995	1996	1997	1998	1999
Protapanteles immunis[a]	23.4	23.7	26.5	23.3	24.9	16.9
Phobocampe bicingulata	4.8	0.4	2.7	5.5	7.7	4.8
Cotesia jucunda[a]	0.7	2.4	1.6	2.6	1.6	3.3
Aleiodes gastritor	0.0	0.0	0.2	0.0	0.0	0.0
Copidosoma chalconotum	1.0	0.3	2.6	0.3	1.1	2.9
Eulophus larvarum	0.0	2.2	0.0	0.0	0.0	0.0
Overall percent parasitism±SD	30.0±13.4	29.0±12.1	33.7±9.4	31.7±9.0	35.2±13.9	27.9±4.9
Relative larval density±SD	3.7±1.7	5.3±2.8	4.2±1.9	4.4±1.7	3.5±1.3	4.7±2.3

[a] In 1994–1997, the individuals of the closely related *P. immunis* and *C. jucunda* which did not emerge to adults were not separated, and they were treated as *P. immunis*. Therefore, the percent parasitism of *C. jucunda* is somewhat underestimated (and *P. immunis* overestimated); however, the correction does not exceed ±1–2%.

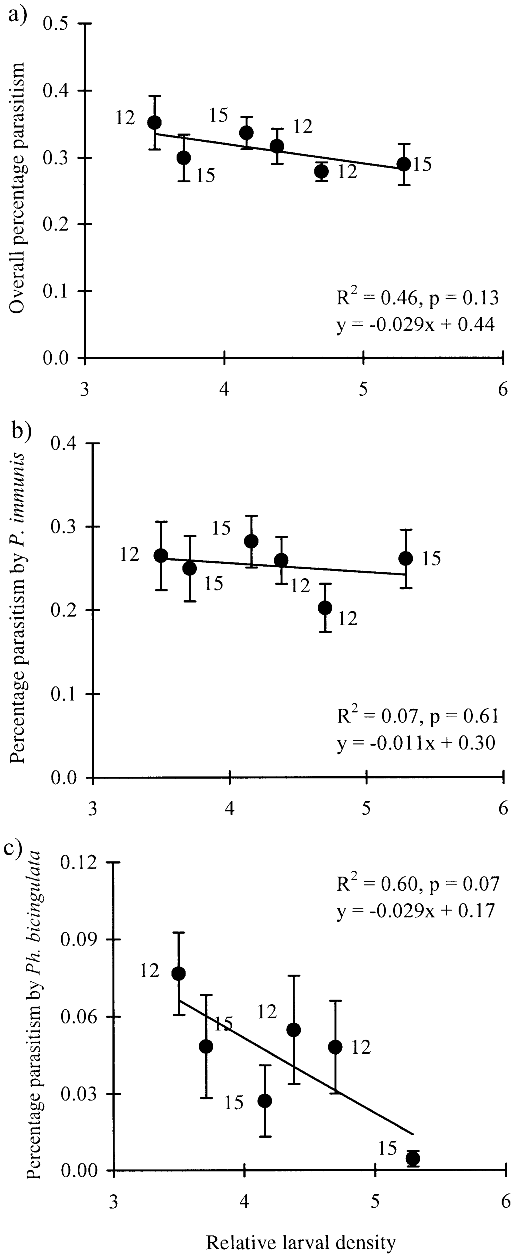

Fig. 1a–c Association between the average rate of parasitism by *Protapanteles immunis* and *Phobocampe bicingulata* for the current year (±SE) and the average host density of the same year. The number of sites studied each year is given

Table 2 Results of logistic analyses examining the effect of host density on the parasitism rate in the density manipulation experiment

Source	*df*	χ^2	*P*
Overall parasitism[a]			
Case	11	57.53	0.0001
Host density	1	0.04	0.85
Case×Host density	11	36.32	0.0001
Parasitism caused by *P. immunis*[b]			
Case	11	50.37	0.0001
Host density	1	6.69	0.001
Case×Host density	11	19.57	0.052
Parasitism caused by *Ph. bicingulata*[c]			
Case	2	2.15	0.34
Host density	1	11.39	0.0007
Case×Host density	2	12.15	0.002

[a] Dispersion estimate (deviance divided by the degrees of freedom) for data used in logistic analyses: deviance/*df*=1.23

[b] Deviance/*df*=1.16

[c] Deviance/*df*=0.88

of host density in most years with the exception of 1995 when the association between host density and percent parasitism was negative (Fig. 2). Both *P. immunis* and *Ph. bicingulata* showed no consistent pattern on this spatial scale (Fig. 3). In 1995 and 1997 mortality caused by *P. immunis* was negatively density-dependent, while in other years it was independent of host density. The association between host density and percent parasitism of the larger species, *Ph. bicingulata*, was positive in 1994, 1996 and 1997 but slightly negative in 1998 and 1999 (Fig. 4). In 1995 *Ph. bicingulata* was practically absent: only two larvae were parasitized by this species. The significant negative association between the overall percent parasitism and host density in 1995 was thus mostly based on the negative density dependence displayed by *P. immunis*. The other parasitoid species were rare (Table 1).

To study parasitism on the smaller spatial scale, i.e. in the density increase experiment, logistic analysis was applied. Host density had no effect on overall parasitism (Table 2). The significance of the case×host density interaction indicates that the relationship between host density and overall parasitism was variable among cases. The difference between the average percent parasitism of natural samples and that of density-increased trees was negligible (Fig. 5).

The relationship between parasitism by *P. immunis* and host density was negative and significant (Table 2), since the larvae collected from natural samples suffered higher levels of parasitism than larvae from density-increase samples (Fig. 5). Only in 3 cases out of 12 was percent parasitism found to be slightly higher in density-increase trees. However, the marginally significant case×host density interaction (Table 2) implies considerable variability among cases.

For *Ph. bicingulata* the effect of host density was positive and significant (Table 2): parasitism was higher in trees in which host density was artificially increased (Fig. 5). However, as in *P. immunis*, this effect varied among cases, as indicated by the significant interaction between case and host density (Table 2). The analysis was based on 3 cases out of 12 where the incidence of parasitism was sufficient to allow a meaningful analysis. To confirm the results obtained with only three cases, a logistic analysis was conducted with all cases pooled, including those cases in which the low incidence of parasitism did not allow their separate analysis. The results of the latter analysis supported those based on three cases: host density had a significant effect on parasitism

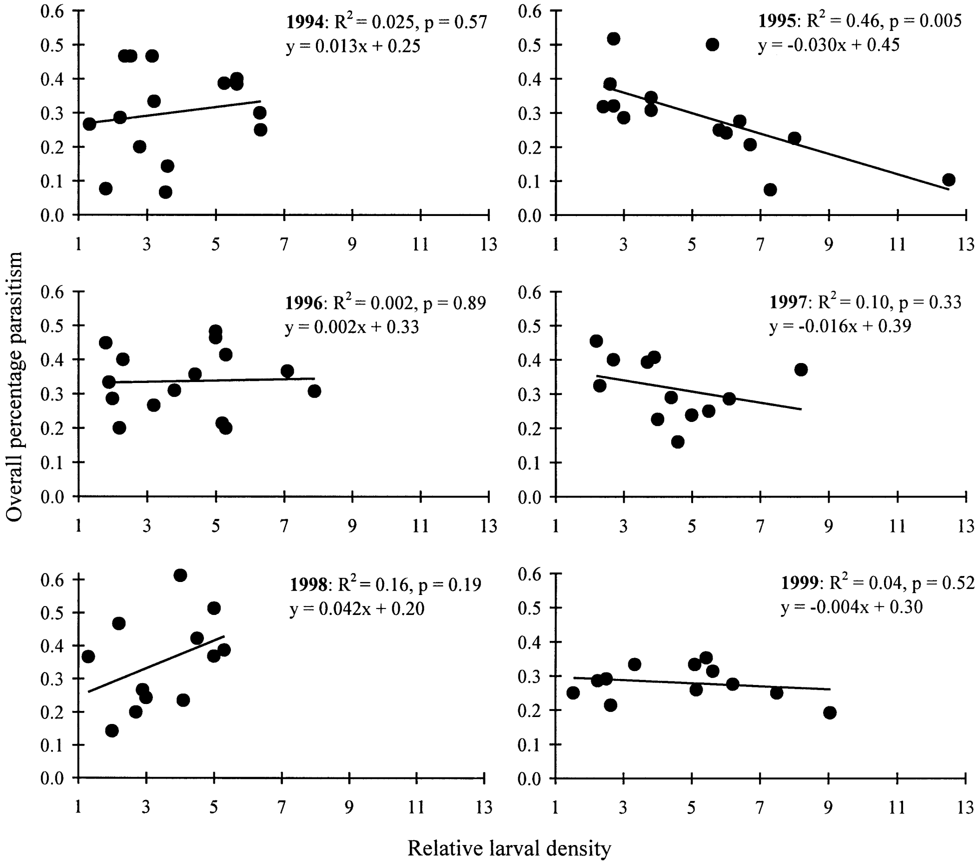

Fig. 2a–f Relationship between overall parasitism rate and density of *Epirrita autumnata* in study sites for six years

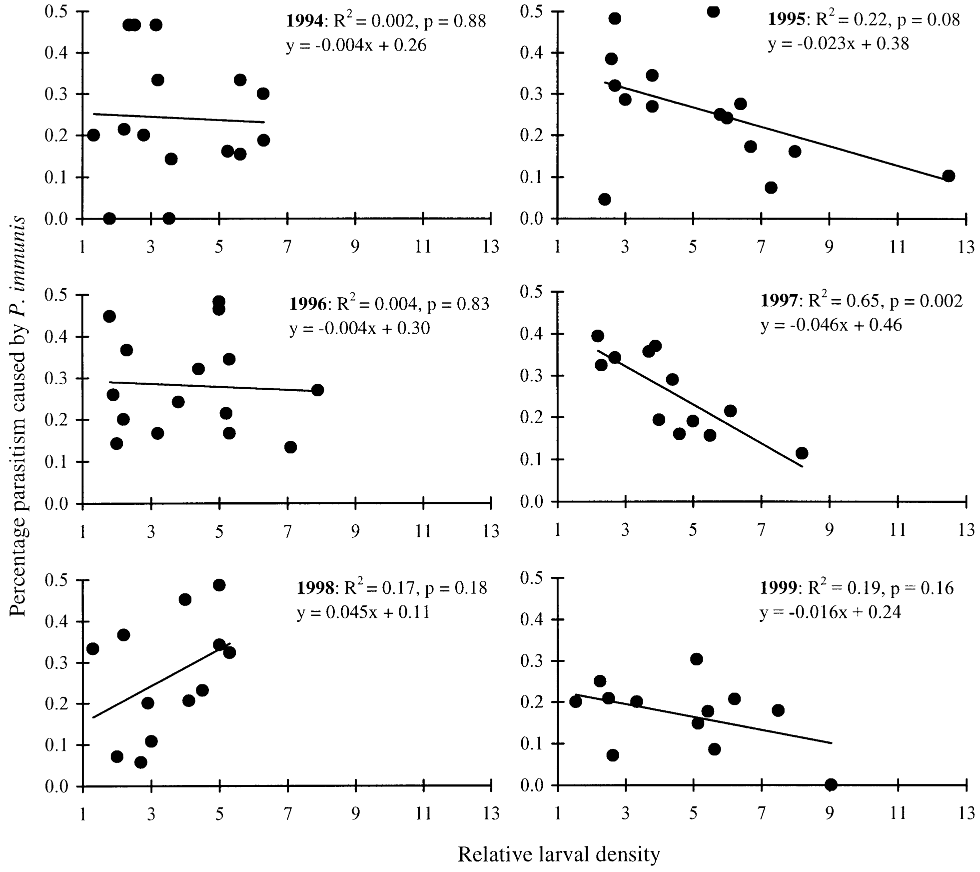

Fig. 3a–f Relationship between rate of parasitism by *P. immunis* and density of *E. autumnata* in study sites for six years

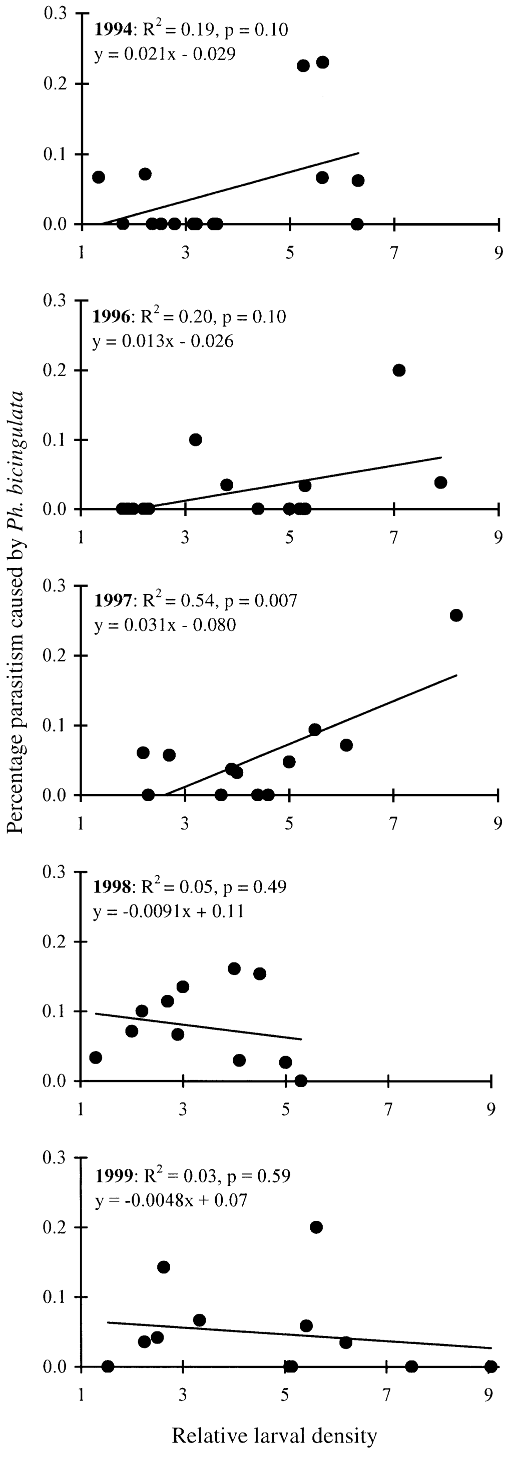

Fig. 4a–e Relationship between rate of parasitism by *Ph. bicingulata* and density of *E. autumnata* in study sites for five years. In 1995, only two individuals of this parasitoid were found

caused by *Ph. bicingulata* (χ^2=11.63, *df*=1, *P*=0.0007). However, as on the larger scale, the positive density dependence of *Ph. bicingulata* was again masked by the negative density dependence of the more common *P. immunis*, resulting in overall parasitism being independent of host density.

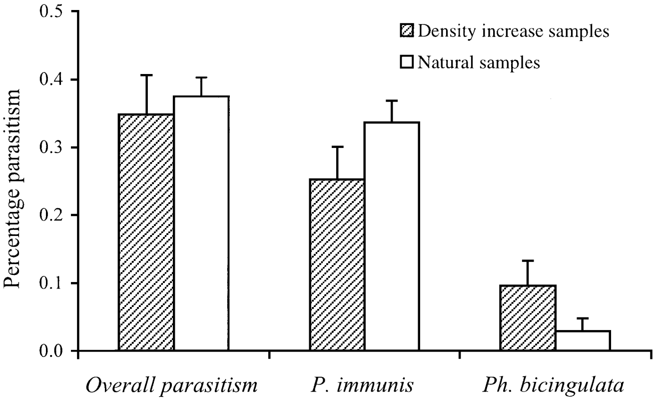

Fig. 5 Average (±SE) parasitism rate of natural larvae and those collected from density-increased trees

Discussion

Temporal and spatial variation in parasitism

The incidence of density dependence in natural systems is dependent on spatial scale (Heads and Lawton 1983; Rothman and Darling 1991; Ray and Hastings 1996). On smaller scales, density dependence may result from the active behavioural responses of parasitoids to host density. In comparisons of sites distant from one another, on the other hand, behavioural aggregation has less importance. Instead, the relationship between parasitism and host density may be shaped by local semiautonomous population dynamics (Walde and Murdoch 1988). Further, the distribution of parasitism in a landscape depends substantially on the biological features of both hosts and parasitoids. In this context, factors suggested as playing a crucial role include the mobility and voltinism of hosts and parasitoids and the degree of specialization of parasitoids (Walde and Murdoch 1988; Jones et al. 1994). The patterns of parasitism caused by different parasitoid species can therefore be expected to be very different. Thus, the characteristics of the host-parasitoid system should be known in order to understand the variation of parasitism in field populations. These aspects are illustrated by the results of the present study.

The variation in the percent parasitism of *E. autumnata* caused by *P. immunis* may be largely influenced by the biological features of this parasitoid species. First, due to its small body size, *P. immunis* presumably has low mobility. The ability of this parasitoid to respond adequately to varying host abundance in space is thus restricted. This is supported by the negative density dependence detected on the smaller spatial scale: the percent parasitism was higher among low-density natural larvae. Secondly, as *P. immunis* is a generalist, utilizing at least some other geometrids as hosts (Tobias 1986), it is more likely to respond to overall host densities than to that of a single host species. This may explain the absence of positive density dependence observed on the larger spatial scale: the abundance of *E. autumnata* most probably does not reflect the overall abundance of hosts suitable for *P. immunis*. Third, *P. immunis* apparently has a bivoltine life cycle, and hosts other than the univoltine *E. autumnata* have to be attacked in the second generation. Since the availability of hosts may then be completely different, an adequate temporally density-dependent response to *E. autumnata* by this parasitoid is unlikely.

The larger size of *Ph. bicingulata* and its univoltine life cycle are probably the major features contributing to the positive spatial density dependence detected on the smaller scale. However, since parasitism by *Ph. bicingulata* accounted on average only 14% (2–22% in different years) of total parasitism, its impact on the overall percent parasitism was small: a positive response to host density by *Ph. bicingulata* was masked by a negative response of *P. immunis*, causing density-independent parasitism on the smaller spatial scale.

Regulation of host densities

There is a general consensus that strong enough positive density-dependent parasitism without a time-lag stabilizes the population dynamics of the host. Moreover, most conclusions concerning the regulatory role of parasitism have been based upon temporal relationships between parasitism and host density (Kidd and Jervis 1996). In the *E. autumnata* populations studied, however, parasitism showed no temporally positive density dependence: the association between host density and the overall parasitism rate was slightly negative. Taken separately, no parasitoid species showed a tendency towards a stabilizing influence: parasitism by *Ph. bicingulata* was negatively associated with host density and that by *P. immunis* independent of host density. Temporal relationships between host density and parasitism rates within single sites were highly variable without any obvious trends. Therefore, the relatively stable densities of *E. autumnata* in southwestern Finland are unlikely to be explained by larval parasitism.

During the last decades, the importance of spatial heterogeneity in parasitism has also been stressed. Hassell et al. (1991) proposed that host densities may be stabilized both by spatially density-dependent and density-independent parasitism (see also Ives 1992), provided that the parasitism is sufficiently heterogeneous among patches (the $CV^2>1$ rule). In a companion article, Pacala and Hassell (1991) also introduced a method for estimating the regulatory potential of spatial heterogeneity in parasitism from field data. However, this procedure involves many restrictions as to the systems where it can be applied. The method requires a patchy habitat; in addition, the parasitoids must effectively be specialists on a single host species, and both hosts and parasitoids must have discrete life cycles. Our system, like many others, does not satisfy these requirements, and the role of spatial variation in parasitism in these natural systems therefore remains an open question. With regard to population regulation, more generally applicable theoretical evaluations are needed, on the basis of which the regulatory potential of spatial heterogeneity in overall parasitism rate can be assessed. Along with further theoretical advances, there still appears to be a need for field studies examining both spatial and temporal aspects of parasitism, in order to allow for empirical generalizations in the context of population regulation. In one study of the few in which both aspects have been considered, Ferguson et al. (1994) showed in *Lymantria dispar* that spatially density-dependent parasitism does not necessarily lead to temporal density dependence in parasitism. Unfortunately, there is almost no information about the conditions (biological features of hosts and parasitoids, spatial scale) under which spatial density dependence leads to a corresponding temporal response. Thus the study of Ferguson et al. (1994), as well as our own results obtained with *E. autumnata* populations, cautions against a straightforward interpretation of any spatial density dependence detected as a factor regulating host populations. The present study shows that even within the same system the connection between spatial and temporal density dependence may vary among parasitoid species.

Even where the impact of parasitoids is temporally density-independent, they may act as an important cofactor in the regulation of the host population, as pointed out by Roland (1994) as well as Kidd and Jervis (1997). Density-independent parasitism may suppress host numbers sufficiently to allow other density-dependent mortality factors to become regulating. For example, Roland (1994) showed that density-independent parasitism reduces the numbers of the geometrid *Operophtera brumata* to a level at which density-dependent pupal predation by generalists can hold the population at a low equilibrium density. His calculations showed that even a percent parasitism of 12–14% may be sufficient to maintain host densities at a level where predators start to regulate.

In southwestern Finland, parasitism alone is apparently unable to regulate *E. autumnata* populations, but in interaction with temporally density-dependent mortality factors it still may contribute to regulation. As in *O. brumata*, positive temporal density dependence has been found in pupal predation of *E. autumnata* (Tanhuanpää et al. 1999). However, factors affecting survival at each life-history stage need to be considered in order to infer the mechanisms which maintain densities of populations of *E. autumnata* or any other species at a low level.

While the vast majority of herbivorous insects have never been reported to outbreak, most studies concerning population regulation have concentrated on outbreaking insect species. Thus little information is available on the factors that continuously maintain low herbivore densities. There is contradictory evidence concerning the role of parasitoids in the dynamics of different herbivore species. For example, Cappuccino (1992) studied the nature of population stability in a non-outbreaking tephritid fly, and found that parasitism does not explain low densities in this species, since only mortality in the early larval stages, partly caused by a defensive reaction of the host plant, showed temporal density dependence. On the other hand, a study by Gould et al. (1992) showed that the low-level densities of populations of a whitefly are maintained only in the presence of parasitoids. However, a large proportion of studies concerning parasitoids' role in population dynamics of herbivorous insects has been focused on managed crop systems which are often characterized by simple habitat and food-web structures. Hawkins et al. (1999) showed that such systems are more likely to experience top-down control by parasitism than are those in natural ecosystems. Therefore, extrapolating conclusions about parasitoids' regulatory role in agroecosystems to explain their importance in natural ecosystems should be done cautiously. Our study indicates that the role of parasitoids may vary even within a species: the significance of parasitoids in contributing to cyclic dynamics of *E. autumnata* populations in northern Fennoscandia (Ruohomäki 1994; Bylund 1995; Kaitaniemi and Ruohomäki 1999) does not imply that they are responsible for maintaining low densities in populations outside the outbreak range. Thus, before generalizations can be drawn as to the role of different kinds of parasitoids in preventing insect outbreaks, a greater number of careful studies are needed to assess the regulatory potential of parasitoids in non-outbreaking species.

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