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 southwestern 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 immutis*, 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 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-
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 geomtrid 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 mid-summer, 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: *Prospanateles immunis* (Haliday), *Cotesia jucunda* (Marsh.), *Aleioles gastritor* (Thurb.) (Braconidae), *Phobocampe bicingulata* (Grav.) (Ichneumonidae), *Eulophus ramicornis* (Bkh.) (Eulophidae), and a rare endoparasitoid *Copidosoma stenomum* (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 km². 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.