DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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DIRECT AND INDIRECT EFFECTS IN HOST–PARASITOID INTERACTIONS: ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES

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PRESS

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is a summary of the following papers which are referred to in the text by the Roman numerals:

I Teder, T., Tammaru, T., Pedmanson, R. (1999) Patterns of host use in solitary parasitoids (Hymenoptera: Ichneumonidae): field evidence from a homogeneous habitat. *Ecography* 22: 79–86.

II Teder, T., Tammaru, T. (2001) Cascading effects of plant vigour on the relative performance of insect herbivores and their parasitoids. *Ecological Entomology*: In press.

III Teder, T., Tammaru, T. Indirect interactions between coexisting herbivorous insects mediated by shared parasitoids: the influence of relative abundance and phenology of the species. Submitted.

IV Teder, T., Tanhuanpää, M., Ruohomäki, K., Kaitaniemi, P., Henriksson, J. (2000) Temporal and spatial variation of larval parasitism in non-outbreaking populations of a folivorous moth. *Oecologia* 123: 516–524.

V Teder, T., Tammaru, T. (2001) Larger larvae of a flush-feeding moth are not at a higher parasitism risk: implications for host life-history. *European Journal of Entomology* 98: In press.

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INTRODUCTION

Parasitoids can be defined as insects that pass their juvenile development feeding on or in the body of their host, usually an immature stage of another insect, eventually killing it. The majority of parasitoids belong to Hymenoptera and Diptera, and comprise about 10% of all metazoan species (Godfray, 1994). Parasitoids are frequently a major source of mortality in herbivorous insects, having thus a strong potential to influence host populations both on the ecological and evolutionary time scales. Because of the applied importance of parasitoids in biological control, a huge number of studies have empirically and theoretically assessed their influence on variation in host abundance (for recent reviews, see Hochberg & Ives, 2000; Hassell, 2000). The most frequently asked questions address the response of parasitoids to temporal and spatial variation in host density and focus on the corresponding consequences on the population dynamics of the host (Waage, 1979; Heads & Lawton, 1983; Gould *et al.*, 1990; Stiling *et al.*, 1991; Connor & Beck, 1993; Jones *et al.*, 1993; Ferguson *et al.*, 1994; Cronin & Strong, 1999).

Some other aspects of parasitoid behaviour, ovipositional decisions at the level of host individuals among them, have been deserved less attention in population ecology. Quite obviously, however, parameters of host choice of parasitoids may strongly shape their effect on host populations. In particular, the exploitation of hosts by parasitoids is frequently non-random: some types of hosts may run a higher risk of being parasitised than others. For example, several studies have shown that parasitoids prefer large hosts to small ones (Bertschy *et al.*, 2000; Fidgen *et al.*, 2000; Karamaouna & Copland, 2000). Among insects, in turn, larger individuals within the species are commonly more fecund (Honěk, 1993). By selectively killing larger hosts, the effect of parasitoids on a host population may thus be stronger than that which can be inferred from simple mortality estimates. This effect, however, may prove to be even more pronounced when females are the larger sex in the host. On the contrary, as shown by Cronin and Gill (1989), the influence of parasitism on the host population may be weaker than expected if males are preferably parasitised. Ovipositional decisions at the individual level may also affect the parasitoid population itself. Producing female-biased sex ratios may affect the rate of increase in parasitoid abundance. Similarly, parasitoids choosing larger hosts for oviposition often achieve a larger body size that, in turn, may correlate with their reproductive success in the field (Bennett & Hoffmann, 1998; Ellers *et al.*, 1998).

The question of the role of parasitoids in shaping the evolutionary dynamics of their hosts has, however, been far less frequently addressed than their ecological role. In the life-history context, there has been a tendency for studies on host–parasitoid interactions to focus their attention on the parasitoid's perspective. In particular, the main question in this context is whether, and how, the exploitation of particular host types affects the life-history traits of the parasitoid — its body size, development time, sex ratio, clutch size, etc. (Brodeur *et al.*, 1998; Fidgen *et al.*, 2000). The complementary question — how do parasitoids thereby affect the life-history of their host? — is rarely asked. The answer to this question is not straightforward. A diverse array of life-history strategies (koinobionts vs. idiobionts, generalists vs. specialists, capital breeders vs. income breeders, egg vs. larval vs. pupal parasitoids, etc.) makes the influence of parasitoids on host life-history sensitive to the parasitoid species assemblage. Moreover, the extent to which different species of parasitoids exhibit specific behavioural phenomena, e.g. host preference and host switching, may further shape the consequences of parasitism. The following example illustrates the potential influence that parasitoids may exert upon host body size. As widely appreciated, in most organisms fecundity selection and sexual selection favour large body size. Given the actual size distribution among insect species, there should be some counterbalancing forces that select against large size (Tammaru, 1997; Blanckenhorn, 2000). Parasitism may constitute such a factor in a number of ways. If parasitism is very high in the growth stage, selection may favour a short development time and a reduced body size as a co-product. However, parasitism may also act against large body size directly, if larger hosts are preferably parasitised.

The influence of parasitoids on host populations may occur via direct and/or indirect effects. Direct effects occur when two species physically interact with each other (e.g. predation, parasitism, interference competition). Interactions between two species are, however, called indirect when the effect of one species on another requires the presence of a third species (Strauss, 1991; Wootton, 1994). Most species in natural communities are involved in a number of direct interactions. Any change in one interacting species pair is therefore likely to affect indirectly also the interactions in several other species pairs. On the other hand, for indirect effects to occur, direct interactions must often already exist. The tight intertwining of direct and indirect effects in the interactions among species makes a good understanding of processes in natural communities possible only when both types of effects are considered.

Two types of mechanisms may underlie indirect effects — an interaction chain and an interaction modification (Wootton, 1994). In systems involving insect parasitoids, the former type has been demonstrated to occur in the form of bottom-up or top-down trophic cascades (Tscharntke, 1992; Preszler & Boecklen, 1996; Roininen *et al.*, 1996; Dyer & Letourneau, 1999), the latter as exploitative (Luck & Podoler, 1985; Müller & Godfray, 1997) or apparent competition (Settle & Wilson, 1990; Bonsall & Hassell, 1997, 1998; Müller & Godfray, 1997). On the whole, however, evidence of most types of indirect effects involving parasitoids is still scarce. For example, in a recent review on apparent competition Chaneton & Bonsall (2000) found only four studies examining parasitoid-mediated interactions between hosts. For exploitative competition between parasitoids, there seems to exist no unequivocal field evidence at all (Hawkins, 2000). The studies on trophic cascades involving parasitoids have concentrated mainly on examining top-down effects while the potential role of bottom-up changes in plant quality has deserved less attention (see, however, Fox *et al.*, 1990; Roininen *et al.*, 1996).

The scarcity of documentation of indirect effects in parasitoid-related studies is somewhat surprising: a large body of circumstantial evidence suggests that indirect interactions in natural communities are not necessarily rare. Some illustrative lines of reasoning are presented below to underline possible indications of indirect interactions.

a) *Trophic cascades.* Variation in food plant quality often has a strong effect on body size of insect herbivores (Roland & Myers, 1987; Kaitaniemi *et al.*, 1999; Lill & Marquis, 2001). Body size of the host insect, in turn, has frequently been shown to determine parasitoid performance — body size, fecundity, development time and survival (Petitt & Wietlisbach, 1993; Sequeira & Mackauer, 1994; Croft & Copland, 1995; Harvey *et al.*, 2000). The direct energetic links in plant–herbivore and herbivore–parasitoid interactions suggest that trophic cascades involving all three trophic levels can also be expected.

b) *Exploitative competition among parasitoids.* Exploitative competition is expected to occur, if one species, reducing the abundance of the shared resource, indirectly reduces the abundance of the coexisting species (Wootton, 1994). In many holometabolous insects, parasitoids comprise an important mortality factor for eggs, larvae and pupae. In such a system, there is a great potential for exploitative competition to occur. For example, egg parasitoids, killing a fraction of host individuals, clearly reduce the number of hosts available for larval and pupal parasitoids. Another indication of the occurrence of exploitative competition is provided by high parasitism rates in herbivorous insects that, at its extreme, may lead to multiparasitism of hosts (Isenhour, 1988; Mackauer *et al.*, 1992; Ueno, 1999).

c) *Parasitoid-mediated interactions between hosts (apparent competition, apparent mutualism, amensal interactions).* Parasitism is often shown to be positively host-density dependent (Gould *et al.*, 1990; Hopper *et al.*, 1991; Connor & Cargain, 1994; Lei & Camara, 1999). Suppose there is a parasitoid attacking several coexisting host species, and responding to total host density. An increase in the abundance of the focal host species leads then to an increase in total host density, and indirectly, to an elevated risk of parasitism for alternative host species.

The aim of this thesis is to contribute to our knowledge concerning the gaps outlined above. In this thesis, I document various direct (I, IV, V) and indirect (II, III) effects in the (plant)–herbivore–parasitoid systems studied, and discuss their consequences on ecological (I, II, III, IV) and/or evolutionary (I, III, V) processes. On the ecological time scale, I refer to both population-level (I, II, III, IV) as well as community-level (I, II, III) outcomes. Wherever justified, the possible behavioural mechanisms underlying the patterns of parasitism observed are discussed (I, III, IV, V). This intends to point out direct links between host–parasitoid population dynamics and the behaviour of the counterparts. The present thesis is based on five field studies conducted on two model systems: 1) the noctuid moths feeding on *Typha latifolia* and their parasitoids (I, II, III), and 2) the geometrid *Epirrita autumnata* (Lepidoptera) and its parasitoids (IV, V).

1. MATERIAL AND METHODS

1.1. Study systems

The model system used in studies I, II and III was based on *Typha latifolia* L. (Typhaceae), a rhizomatous perennial plant up to 3 m in height forming dense stands at damp sites. Larvae of four moth species were found feeding on leaves and stems of *T. latifolia*. Most of the investigations were restricted to the two most abundant species, *Nonagria typhae* (Thunb.) and *Archanara sparganii* (Esp.) (Lepidoptera: Noctuidae). The proportion of the two other species, the noctuids *Archanara algae* (Esp.) and *Helotropha leucostigma* (Hbn.), remained <1% of all larvae (excl. 1995, see I). The species studied are taxonomically close and have a high resemblance in feeding biology and phenology. They overwinter as eggs that hatch in spring. At the beginning of the season, larvae feed on the aerial roots of the host plant, while later they switch to endophytic feeding on the shoots (Galichet *et al.*, 1992). Larvae of *N. typhae* are monophagous on *T. latifolia*, while larvae of *A. sparganii* may also use some other species (Skou, 1991); however, in the studied areas both species were apparently functionally monophagous on *T. latifolia*. At the end of July or at the beginning of August larvae pupate inside the shoot or between the leaves of the host plant. The pupal period lasts for about one month in both species. The short-lived adults do not feed.

Four principal species of solitary parasitoids were found to parasitise larvae and pupae of *N. typhae* and *A. sparganii*: *Exephanes occupator* (Grav.), *Spilichneumon limnophilus* (Thoms.), *Chasmias paludator* (Desv.) and *Vulgichneumon saturatorius* (L.) (Hymenoptera: Ichneumonidae). Other parasitoids accounted for <1% of total parasitism. The most numerous parasitoid of *N. typhae*, *Exephanes occupator*, uses *A. sparganii* only occasionally (I, III). Like their hosts, the studied parasitoids have univoltine life cycles. Adult females overwinter and lay their eggs on young moth larvae in late spring (*E. occupator*; Hinz & Horstmann, 2000; and probably also *S. limnophilus* and *V. saturatorius*) or on fresh pupae in July and August (*Ch. paludator*; Hinz, 1983; Hinz & Horstmann, 1999). Adult wasps emerge from moth pupae more or less simultaneously with unparasitised moths. All four parasitoids are oligophagous and are also known to parasitise some other moths (Rasnitsyn & Siitan, 1981; Hinz & Horstmann, 1999, 2000), which, however, apparently constitute only a minor fraction of hosts in the studied system.

In studies IV and V, *Epirrita autumnata* (Bkh.) (Lepidoptera, Geometridae) and its parasitoids were used as the model system. *E. autumnata* is a medium-sized holarctic lepidopteran known for its tendency to achieve outbreak levels of abundance in northern and mountainous Fennoscandia (Tenow, 1972; Haukioja *et al.*, 1988; Ruohomäki *et al.*, 2000). The populations elsewhere are stable. The reasons for the contrasting population dynamics of *E. autumnata* are, however, not clear. The species has a univoltine life cycle. The eggs overwinter and hatch in spring at the time of bud burst. The solitary, cryptic larvae feed on deciduous trees and shrubs. *E. autumnata* is a typical flush-feeder (= spring-feeder): its larval performance is critically dependent on the phenological stage of the foliage (Ayres & MacLean, 1987; Kaitaniemi *et al.*, 1998; Kause *et al.*, 1999). Larval development lasts for about one month and consists invariably of 5 larval instars (Tammaru, 1998). Pupation occurs in the ground in early June, and the short-lived adults emerge in early autumn.

Larvae of *E. autumnata* are attacked by several hymenopteran parasitoids (Ruohomäki, 1994; Kaitaniemi & Ruohomäki, 1999; and IV, V). The most common ones encountered in the areas studied were the solitary koinobiont species: *Protapanteles immunis* (Haliday), *Cotesia jucunda* (Marsh.) (both Braconidae), *Phobocampe bicingulata* (Grav.) and an unidentified species of *Campoletis* (both Ichneumonidae).

1.2. Study areas

Studies I, II and III are based on the material collected in 6 consecutive years (1995–2000) in southeastern Estonia. Three habitats differing with respect to heterogeneity of the vegetational pattern were examined. The habitat studied in 1995–1996 was characterised by a dense, almost monospecific stand of *T. latifolia.* The vegetation of the habitat examined in 1997–1998 was more heterogeneous with patches of *T. latifolia* and *Carex elata* Bell. ex All. alternating. Both these habitats (with areas of ≈3 and ≈4 ha, respectively) were located in the town of Tartu (58°22' N, 26°45' E), on the flooded meadow of the Emajõgi River. The third habitat, studied in 1998–2000, was much more heterogeneous again with respect to *T. latifolia* abundance: the patches of *T. latifolia* (mostly from 0.01 to 0.05 ha, few patches over 0.1 ha; small ponds, ditches, and other damp places) were separated by distances of 0.2–1.0 km. This study area was located in an agricultural landscape, near Lake Pangodi (58°12' N, 26°35' E), 20 km southwest of Tartu.

Study IV (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 investigations were carried out within an area of about 60 km^2. This study area was divided into 60 squares of 1×1 km, from which squares for a total of 15 study sites were randomly selected. Within the 1×1 km squares, the sites for collection were selected in easily accessible plots. Study V (1998–1999) was carried out in two forested areas outside the range where outbreaks of *E. autumnata* occur: 1) in the area used in study IV, and 2) near the town of Tartu, southeastern Estonia (1999). The experiments were conducted at a total of 12 sites, 4 sites in 1998 (within an area of ≈10 km^2) and 8 in 1999 (within an area of ≈2 km^2). The study sites (IV, V) were mainly characterized by mixed coniferous forests dominated by *Pinus sylvestris* L. or *Picea abies* (L.) Karsten and by birches in the understory: always *Betula pubescens* (Ehrh.) and at some sites also *B. pendula* (Roth.).

1.3. Sampling, measurements and data analysis

Depending on the purpose of each particular study, a correlational (I, II, III), an experimental (V) or a combined (IV) approach was chosen. All the studies were conducted in the field. While laboratory studies are important for revealing the behavioural mechanisms that potentially lead to particular patterns of parasitism, they do not tell us whether a particular behaviour leads to similar patterns under natural conditions. Moreover, the magnitude of the effects detected in the laboratory is not directly comparable with natural background variation. There are a number of parasitoid-related studies in which the results obtained from the field differ substantially from the laboratory results (Jones & Hassell, 1988; Visser, 1994; West *et al.*, 1996; Amarasekare, 2000). On one hand, a behaviour optimal under simple laboratory conditions is not necessarily so in the more complex natural environment. On the other hand, there may exist other, compensatory mechanisms in nature that may mask the patterns caused by parasitoids alone. When studying the consequences of a particular behaviour for ecological and evolutionary processes, the pattern rather than mechanism underlying it appears to be important.

In studies I, II, and III, field populations were sampled to obtain data on the distribution of moths and the levels of parasitism. Sampling was conducted at the end of July and/or the beginning of August, when most of the moths were in the pupal stage. In the habitats located in Tartu, samples were taken from the plots of about 3 × 3 m, while in the most heterogeneous habitat at least 30 individuals per each site (one plot per each site) were sampled. Each year, samples from 12–33 plots (173 in total) were collected. From study plots, moth pupae were collected by inspecting all *Typha* shoots carefully. The pupae were relatively large (2.0–3.5 cm in length), potential pupation sites were limited, and damaged shoots were easily distinguishable from undamaged shoots, so it was possible to collect nearly all pupae from the plots. Pupae were stored in Petri dishes until eclosion of the adult moth or the parasitoid. For *A. sparganii*, collected as exuviae, it was always possible to determine whether a moth or a parasitoid (and nearly always, which of the two parasitoids) had been emerged.

In study IV, sites were sampled to determine the spatial and temporal distribution of parasitism in *E. autumnata*. The sampling scheme was chosen to facilitate an analysis on two spatial scales. On the larger scale, larvae were collected from sites separated by distances of 2–10 km. About 30 larvae were collected from each site, the area examined being about 1 ha. The collections were conducted at the time when 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 not exceeding 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 between 1994 and 1997 at two to four sites annually, most of the sites being repeated in successive years. To create 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 individual small birch trees (20 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 figure, usually ranging from five to several dozen larvae. Later, during the sampling, a maximum of four larvae were collected from each "density-increase" tree, while at the same time samples of natural larvae were taken from the vicinity of the experimental trees. All the larvae collected were reared in the laboratory until the parasitoids emerged or unparasitized larvae pupated. Simultaneously with the collections, natural densities of *E. autumnata* at the study sites were estimated. As the estimate of natural population density, an index of relative larval density was used (the number of larvae found during 10 min).

To determine if parasitoids preferably attack certain larval instars of *E. autumnata*, three separate host choice experiments were conducted (V). At each study site, 16–20 birches (mostly *B. pubescens*, occasionally *B. pendula*), less than two metres in height, separated by distances of less than ten metres were chosen. Laboratory-reared larvae of two different instars were released onto the experimental trees. Three combinations of instars were used: larvae moulting either into the 1) second and third instars (conducted at four sites in 1998), 2) second and fourth instars (four sites in 1999), or 3) third and fourth instars (four sites in 1999). The numbers of larvae of each instar released were equal on each tree (e.g. 5 second and 5 third instar larvae). The host densities used greatly exceeded the natural background densities in the study area. Larvae were exposed to parasitoids for a period corresponding to the duration of about one instar. The experiments were performed at the time when laboratory-reared larvae were approximately of the same age as those in the field. After the exposure period the released larvae were collected and reared in the laboratory until they pupated or a parasitoid emerged.

Besides the parasitism status, indices of body size and development time were recorded in particular studies. For moths, pupal weight, and in some cases, host species, sex or larval instar were used as the indices of their body size (I, II, V). For parasitoids, adult weight or hind tibia length was measured (I, II, V).

To examine the factors affecting the levels of parasitism of different host species (I, III), sexes (I), instars (V), or densities (IV), categorical data analysis or logistic regression were used (CATMOD and GENMOD procedures, respectively; SAS Institute Inc., 1995). Where appropriate, various regression and ANOVA techniques were applied.

2. RESULTS

2.1. Direct interactions

2.1.1. Host-size dependent parasitism (I, V)

The use of the three host species in the *Typha*-based community (*N. typhae*, *A. sparganii* and *A. algae*) by parasitoids was found to be non-random both on the interspecific and intraspecific level (I). All three major parasitoids in this system parasitised the largest species of the three moths, *N. typhae*, in a larger proportion than expected from the relative abundance of the host species (Fig. 1 in I). Moreover, two parasitoids, *E. occupator* and *S. limnophilus*, also showed a non-random host exploitation on the intraspecific level, causing higher mortality among females of *N. typhae*, which is the larger sex in this species. A preference-performance linkage was detected: more frequently used host types were favourable in terms of body size. Parasitoids that emerged from *N. typhae* were larger than those that emerged from *A. sparganii* (Table 4 in I). Analogously, parasitoids that developed in female *N. typhae* achieved larger body sizes than those that developed in male *N. typhae* (Table 3 in I).

In contrast, the field experiment with the aim of studying the effect of larval body size of *E. autumnata* on the risk of being parasitised (V) revealed no evidence of a positively host-size dependent parasitism risk. Rather the opposite was true: smaller larvae suffered higher parasitism (Table 1, 2 in V). In terms of body size and development time, developing in late instars of *E. autumnata*, however, was profitable. In particular, body size of adult parasitoids correlated positively with host size. Additionally, the larger the host, the shorter the development time in *Campoletis* sp.

2.1.2. Host-phenology dependent parasitism (III, V)

The response of parasitoids to host phenology was studied both for *A. sparganii* (III), as well as for *E. autumnata* (V). The phenological distribution of *A. sparganii* relative to that of *N. typhae* was shown to influence its risk of being parasitised (see also 2.2.2, and Table 1, Fig. 4 in III). Exposing different instars of *E. autumnata* to parasitoids may alternatively be interpreted as exposing larvae of different ages to parasitoids (see also 2.1.1). In this context, neither the larvae ahead nor behind the average in development exhibited increased risk of parasitism.

2.1.3. Host-density dependent parasitism (IV)

Temporal and spatial variation of larval parasitism in response to the density of *E. autumnata* was studied. The among-year relationship between larval density and overall levels of parasitism was negative and non-significant (Fig. 1 in IV). Moreover, annual fluctuations of overall levels of parasitism in absolute terms were negligible (Table 1 in IV). Temporal responses of the two main parasitoids, *P. immunis* and *Ph. bicingulata*, on host density were density-independent and negatively density-dependent, respectively (Fig. 1 in IV). On both spatial scales studied, overall levels of parasitism were independent of host density (Fig. 2, Table 2 in IV). On the larger scale, no consistent pattern was found when parasitoids were analysed separately. On the smaller scale, parasitism by *P. immunis* was negatively density-dependent whereas that by *Ph. bicingulata* correlated positively with host density.

2.2. Indirect interactions

2.2.1. Cascading effects from plants to parasitoids (II)

In the studied system, considerable levels of spatial and annual variation in the performance indices were found in all the trophic levels considered. The host plant, *T. latifolia*, varied both in terms of height of shoots and proportion of generative shoots (Fig. 1, 2 in II). This induced a strong cascading effect on the performance of herbivores and parasitoids. In particular, the body size of both *A. sparganii* and *N. typhae* was strongly and positively correlated with the indices of plant vigour (Fig. 3, 4 in II). The body size of parasitoids, in turn, was positively affected by the body size of moths (Fig. 5, 6 in II). The relationships were consistent for all species both among years, and for patches within the years. Moreover, a direct positive link between plant vigour and the size of parasitoids was revealed (Fig. 5, 6 in II). However, the effects of plant vigour on insect size were consistently stronger in the moths than in the parasitoids (Fig. 6 in II).

2.2.2. Parasitoid-mediated interactions between herbivores (III)

If coexisting species share common natural enemies, there exists a possibility for natural-enemy-mediated interactions between these species. The results reported in this thesis are consistent with this scenario indicating the presence of parasitoid-mediated amensalism between *N. typhae* and *A. sparganii*. The moths varied in their relative abundance both among patches and years. Moreover, a considerable variation was documented also in the degree of phenological synchrony of the two species. Parasitism levels of the scarcer species, *A. sparganii*, correlated negatively with its abundance relative to that of *N. typhae* (Table 1, 2, Fig. 2, 3 in III). The abundance of *A. sparganii*, on the contrary, did not affect the risk of parasitism for *N. typhae* (Table 3, Fig. 2, 3 in III). In addition, confirming the idea of the presence of indirect interactions, the smaller the difference in the phenologies of the moths, the lower the risk of parasitism for *A. sparganii* (Table 1, Fig. 4 in III).

2.2.3. Host-mediated interactions between parasitoids

A preliminary analysis (T. Teder, unpubl.) also indicates the presence of a third type of indirect effects in the *Typha*-based system — exploitative competition between the parasitoids. The most abundant parasitoid in this system, *E. occupator*, oviposits on young larvae of *N. typhae*, whereas *Ch. paludator* is a pupal parasitoid. Moreover, *S. limnophilus* is presumed to attack older larvae than *E. occupator*. *E. occupator* thus has a strong potential to reduce the reproductive success of phenologically later parasitoids. The first results confirm this hypothesis. The higher the parasitism levels by the most abundant species, *E. occupator*, the lower the parasitism levels caused by the two other major parasitoids, *S. limnophilus* and *Ch. paludator*. The recorded reduction of percentage parasitism by *E. occupator* from 58% to 6% raised parasitism by other species from 8% to 28%. Analogously, parasitism levels by *Ch. paludator* were negatively correlated with those by *S. limnophilus*.

3. DISCUSSION

3.1. Direct effects and their ecological consequences

In the two natural systems studied, parasitoids were shown to cause considerable levels of mortality among the herbivorous insects (I, III, IV, V). As such, parasitism thus has a potential to strongly suppress the abundance of the host. However, high levels of parasitism *per se* do not necessarily regulate host populations (Kidd & Jervis, 1996). The consequences of parasitism for the dynamics of host populations depend on the temporal and/or spatial responses of parasitoids to host density. Sufficiently strong positive, temporally density-dependent parasitism is generally considered to maintain stable low densities. In the *E. autumnata* populations studied, however, larval parasitism showed no temporally positive density dependence, on the contrary, the association between host density and the total levels of parasitism was found to be slightly negative (IV). Therefore, the relatively stable densities of *E. autumnata* observed in the studied areas are unlikely to be explained by parasitism. However, larval parasitoids may still be an important co-factor in the regulation of *E. autumnata* populations. Relatively high levels of parasitism may suppress host numbers sufficiently to allow other, density-dependent mortality factors to become regulatory (see, e.g. Roland, 1994).

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 parasitism is sufficiently heterogeneous among patches (the $CV^2>1$ rule). A method for estimating the regulatory potential of spatial heterogeneity (Pacala & Hassell, 1991), however, involves various restrictions as to the systems where it can be applied. The system studied, like many others, does not satisfy these requirements, and the role of spatial variation in parasitism in such systems therefore remains an open question. Moreover, Ferguson *et al.* (1994) showed in *Lymantria dispar* that spatially density-dependent parasitism does not necessarily lead to temporal density dependence in parasitism. The present study shows that even within the same system the connection between spatial and temporal density dependence may vary among parasitoid species. The results reported in this thesis, in accordance with the study of Ferguson *et al.* (1994), caution thus against a straightforward interpretation of spatial density dependence as a factor regulating host populations.

Under some circumstances, the effect of parasitism on host populations may be stronger than that which can be inferred from simple life-tables. In the present thesis, parasitism levels of female *N. typhae* were shown to be higher than those of males (I). Killing more females, parasitoids may bias operational sex ratios and reduce the host population's reproductive potential. Mortality estimates not considering host sex may thus underestimate the effect of parasitism on host population dynamics. If based on sex-related differences in host body size, this effect could be much stronger for insects with more strongly pronounced sexual dimorphism. The effects of sex-related risk of parasitism may have been overlooked in many cases due to the practical impossibility of determining the sex of larvae. Parasitoids emerging from host pupae provide a good opportunity for studies on sex-dependent parasitism.

3.2. Indirect interactions and their ecological consequences

Theoretical expectations supported by circumstantial evidence suggest that indirect interactions may be widespread in plant–herbivore–parasitoid systems. For indirect effects to arise, at least three species should be involved in the interaction. The more complex the system, the greater the potential for various direct and indirect effects to occur (see e.g., Müller *et al.*, 1999; Memmott *et al.*, 2000; Rott & Godfray, 2000; Schönrogge & Crawley, 2000). A complicated mixture of direct and indirect effects, however, may make the documentation of a particular indirect effect difficult (Holt & Lawton, 1993). Therefore, a natural system simple in structure and diversity might be a good starting point to study the role of indirect interactions in natural communities. This is the case with the *Typha*-based system used in this study (II, III). Six major species organised on three trophic levels form a relatively isolated system in which major direct links are well-known.

The results reported in this thesis show that even in such a relatively simple plant–herbivore–parasitoid system, all the trophic levels and major species may be significantly interconnected by various indirect effects. In particular, the variation in quality of the host plant, *T. latifolia*, induced strong cascading effects on the performance of higher trophic levels — herbivores and parasitoids (II). Furthermore, the patterns observed indicate that the relationships between the herbivores, *N. typhae* and *A. sparganii*, were affected by shared parasitoids (III). The interactions among major parasitoid species, in turn, were mediated by hosts in the form of exploitative competition (see 2.2.3 in Results; T. Teder, unpubl.).

Indirect effects, when present, are not necessarily reciprocal: the relative strength of the mediated effects may vary for the species involved. In the studied system, the risk of being parasitised for the scarcer species, *A. sparganii* seemed to be affected by its abundance relative to that of the dominant species *N. typhae*, whereas relative abundance of *N typhae* did not influence its risk to be parasitised (III). Non-reciprocal indirect effects were also found in host-mediated interactions among parasitoids. Phenologically later species were competitively inferior with their reproductive success depending on the abundance of the species attacking earlier stages of the host, whereas the opposite is not likely. The non-reciprocal nature of indirect interactions observed in the studied system is consistent with the results of Chaneton and Bonsall (2000). They surveyed 34 studies on terrestrial and freshwater systems to find evidence of enemy-mediated apparent competition. Of these, only 3 studies revealed reciprocal effects between competitors, while 26 studies documented a non-reciprocal interaction (the remaining 5 provided insufficient data to determine the form of interactions).

Indirect interactions in the system studied may have a strong influence on the population dynamics of particular species and the structure of the community. The relative abundance of herbivores and parasitoids on the whole trophic levels may be affected by plant parameters. In particular, the results reported in this thesis showed that the effects of plant vigour on insect size were consistently stronger in moths than in their parasitoids (II). However, to derive conclusions about population dynamics, it is also necessary to examine the dependence of expected realised fecundity on body size in the species involved. In insects, the body size – fitness relationship appears to depend on the presence of adult feeding. The potential fecundity of capital breeders, i.e. species with non-feeding adults, is typically strongly correlated with female body size (Honěk, 1993; Tammaru & Haukioja, 1996; Taylor *et al.*, 1998). In contrast, the relationship between body size and realised fecundity in income breeders (i.e. insects in which adult feeding is crucial for reproduction) is often shown to be less clear (e.g. Karlsson & Wiklund, 1984; Braby & Jones, 1995). The studied moths, *N. typhae* and *A. sparganii*, do not feed as adults, being thus capital breeders. The number of eggs as the index of potential fecundity is therefore presumably a satisfactory measure of their realised fecundity. The parasitoids in this system, on the other hand, represent income-breeding hymenopterans (Hinz, 1983, 1991; T. Teder, pers. obs.). In addition to their dependence on resources for adult feeding, several features common to parasitoids' life-histories may weaken further the relationship between body size and potential fecundity in these insects (Hardy *et al.*, 1992; Ellers & van Alphen, 1997) compared with their capital-breeding hosts. The effects of plant vigour on the fitness of the moths can thus be concluded to be stronger than on that of the parasitoids (II). This implies that the numerical response of the herbivore population to a change in plant quality should exceed the response of the parasitoids. A favourable change in plant vigour should thus lead to a short-term increase in moth densities, and lower levels of parasitism.

The balance of species composition in the specific trophic levels depends obviously on the form of indirect effects: the consequences of reciprocal and non-reciprocal effects may differ strongly. In the system studied, frequency-dependent host use by parasitoids has a strong potential to stabilize *A. sparganii* population dynamics. However, as the indirect effects between the moths were non-reciprocal, such an outcome for *N. typhae* is not expected. Analogously, exploitative competition among parasitoids may have a considerable effect on the abundance of *S. limnophilus* and *Ch. paludator*, but a reversed effect is presumably negligible.

Under some circumstances, the effects of different indirect interactions may be compensatory or enhancive. In the system studied, *E. occupator*, parasitising only *N. typhae*, may potentially change the numerical balance of the moths available for the shared parasitoids, *S. limnophilus* and *Ch. paludator*. As a consequence, the latter parasitoids may then start to exploit more *A. sparganii*. There is, however, no evidence on the actual interplay of indirect effects in this system, and this question may deserve further attention.

3.3. Evolutionary consequences of the direct and indirect effects

Two related species, or two developmental stages of the same species, even if potentially suitable for parasitoids as hosts, do not necessarily exhibit an equal risk of being parasitised. Parasitism risk may vary both phenologically or spatially, or in response to host density. Parasitoids constitute a selective force on host life-history when the risk of being parasitised depends on host life-history traits. The strength of this influence, however, should depend on the relative contribution of parasitoids to the overall mortality of the host.

3.3.1. The effect of parasitism on host body size

In the systems studied, parasitoids have a potential to affect the body size of their host on the evolutionary time scale in the following ways: 1) by parasitising preferably large hosts, and 2) by making the growing stage unsafe. Despite the obvious fitness advantage of parasitising larger hosts, the response of parasitoids to host body size was not straightforward in the systems studied. In the *T. latifolia*-based system, the hosts were parasitised according to their profitability to parasitoids (I). Correspondingly, the incidence of parasitism was higher in the larger host, *N. typhae*, and the larger sex (females). The size-dependent patterns of parasitism suggest that parasitoids may create a selective pressure against large body size in *N. typhae*. Moreover, host-sex dependent parasitism provides a possible mechanism that may select against female-biased size dimorphism in this system. Most hypotheses explain the degree of sexual size dimorphism through intraspecific phenomena — sexual selection, intersexual food competition and reproductive role division (Slatkin, 1984; Hedrick & Temeles, 1989; Shine, 1989; Fairbairn, 1990). However, the results of this thesis suggest that the evolution of sexual size dimorphism may occur also via interspecific interactions.

In *E. autumnata*, on the contrary, small rather than large larvae exhibited an elevated risk of being parasitised (V). Differential parasitism in the larval stage is thus not likely to be the factor able to balance the strong fecundity advantage of large size (Tammaru, 1998) in this species. However, high levels of parasitism in the growing stage *per se* may contribute to a selection against large size. According to the slow-growth/high-mortality hypothesis, longer developmental periods frequently increase the risk to be predated (parasitised) (Loader & Damman, 1991;

Häggström & Larsson, 1995; Benrey & Denno, 1997). Tanhuanpää *et al.* (1999, 2001) showed that daily survival in the larval stage is the lowest in the life-cycle of *E. autumnata*. Mortality of larvae, attributable to parasitoids alone (Ruohomäki, 1994, IV, V) may reach levels that exceed mortalities in other stages. Selection should thus favour short developmental times, and reduced body size as a co-product.

3.3.2. The effect of parasitism on host phenology

Host individuals of different ages are often not equally vulnerable to parasitoid attacks (Briggs & Latto, 1996, Benrey & Denno, 1997). In *E. autumnata*, however, neither the larvae that were ahead nor behind the average in development escaped parasitism (V). These results complement those of Kaitaniemi and Ruohomäki (1999), who showed that the flight period of most *E. autumnata* parasitoids exceeds the larval period of the host: larvae reared outside the normal time schedule did not escape parasitism. Combined with the results of the present study, this observation allows us to exclude parasitism as an important selective force acting on the timing of larval development in *E. autumnata*. The need to synchronise larval development with suitable host plant phenology is apparently a much stronger determinant of the optimal hatching date of the larvae (Ayres & MacLean, 1987; Kaitaniemi *et al.*, 1998).

Indirect interactions may also appear to be important in shaping phenological switches. Parasitism of *A. sparganii* was shown to depend on the relative phenological distribution of *A. sparganii* and *N. typhae*. Parasitism may thus have a selective influence on the timing of the life-cycle in *A. sparganii*.

3.3.3. The effect of parasitism on host dispersing abilities

If in some patches of a suitable habitat hosts exhibit an elevated risk of parasitism the individuals with better dispersing abilities would have a selective advantage. In the system studied (III), *A. sparganii* has a survival advantage from being rare in relation to *N. typhae*. This should favour selection of females dispersing their offspring in patches with low incidence of conspecifics (see also van Baalen and Sabelis, 1993; Nagelkerke *et al.*, 1996; Hunter & Elkinton, 2000). This might explain why *A. sparganii* has not evolved towards reduced female flight ability, which is typical for most capital-breeding lepidopterans (Tammaru & Haukioja, 1996). The density-independent levels of parasitism in *E. autumnata*, on the contrary, suggest that parasitism does not constitute a selective pressure on dispersal abilities in this species (IV, V).

To sum up:

The results of the work reported in the present thesis show how diverse the processes and effects involved in herbivore–parasitoid interactions may be. In particular, the results indicate that the often ignored indirect effects may well equal direct effects in their magnitude, and, presumably, in their ecological and evolutionary significance. A two-species approach to host–parasitoid interactions may thus not be sufficient. Moreover, this thesis highlights the need to carefully consider the life-history parameters of both hosts and their natural enemies before reaching any conclusions about the ecological or evolutionary consequences of their interactions.

SUMMARY

Parasitoids are insects that pass their juvenile development feeding on or in the body of their host, eventually killing it. Because of the applied importance of parasitoids in pest control, their response to temporal and spatial variation in host density has been extensively studied. The role of parasitoid behaviour, ovipositional decisions at the level of host individuals among them, has deserved less attention in population ecology. In the life-history context, it is well-known how the exploitation of particular host types affects the life-history traits of the parasitoid. However, the potential of parasitoids in shaping the evolutionary dynamics of its host has been considered far less.

The aim of the work reported in this thesis was to contribute to our knowledge concerning the gaps outlined above. Various direct and indirect effects were documented in the (plant)–herbivore–parasitoid systems studied, and their consequences on ecological and evolutionary processes were assessed. The research reported was conducted on two model systems: 1) the noctuid moths feeding on *Typha latifolia* and their parasitoids and 2) the geometrid *Epirrita autumnata* (Lepidoptera) and its parasitoids. Depending on the purpose of each particular study, a correlational, an experimental, or a combined approach was used.

Larval parasitism showed no temporally positive density dependence in the *E. autumnata* populations. Therefore, the relatively stable densities of this species in the studied areas are unlikely to be explained by parasitism. The results reported in this thesis showed that the connection between spatial and temporal density dependence may vary among parasitoid species even within the same system. Spatial density dependence should thus be cautiously interpreted as an indication of regulation in host populations.

The results indicate that the often ignored indirect effects may well equal direct effects in their magnitude, and, presumably, in their ecological and evolutionary significance. Even in the relatively simple plant–herbivore–parasitoid system studied, a number of different indirect effects were found. The variation in the quality of the host plant, *T. latifolia*, induced strong, cascading effects on the performance of higher trophic levels — herbivores and parasitoids. The patterns observed also indicated parasitoid-mediated relationships between the herbivores, and host-mediated interactions among major parasitoid species. The mediated effects were non-reciprocal with respect to their strength. Indirect interactions in the system studied were shown to have a potentially strong influence on the population dynamics of particular species and on the structure of the community. A two-species approach to host–parasitoid interactions may thus not be sufficient.

The influence of parasitoids on host life-history was variable in the systems studied. In the *T. latifolia*-based system, the incidence of parasitism was higher in the larger host and the larger sex (females). In *E. autumnata*, on the contrary, small rather than large larvae exhibited an elevated risk of parasitism. The size-dependent

patterns of parasitism suggest that parasitoids may create a selective pressure against large body size in *N. typhae*, but not in *E. autumnata*.

In the *T. latifolia*-based system, parasitism of the scarcer species, *A. sparganii*, was shown to depend on the relative phenological distribution of the two moths. Parasitism may thus have a selective influence on the timing of the life-cycle in *A. sparganii*. In *E. autumnata*, neither the larvae that were ahead nor behind the average in development escaped parasitism. This observation allows us to exclude parasitism as an important selective force acting on the timing of larval development in *E. autumnata*.

A survival advantage of *A. sparganii* due to being rare in relation to *N. typhae* should favour selection for females dispersing their offspring in patches with low incidence of conspecifics. The density-independent levels of parasitism in *E. autumnata*, on the contrary, suggest that parasitism does not constitute a selective pressure on dispersal abilities in this species.

KOKKUVÕTE

Otsesed ja kaudsed efektid peremees–parasitoid-süsteemides: ökoloogilisi ja evolutsioonilisi tagajärgi

Parasitoide võib määratleda kui putukaid, kes vastsena parasiteerivad teiste putukate erinevatel arengujärkudel, põhjustades lõpuks peremeeslooma surma. Enamus parasitoide kuulub kiletiivaliste (*Hymenoptera*) ja kahetiivaliste (*Diptera*) seltsidesse, moodustades hinnanguliselt umbes 10% hulkraksete liikidest. Parasitoidid on herbivoorsete putukate üks peamisi suremust põhjustavaid tegureid ja seega võib neil olla potentsiaalselt suur mõju peremeesliigile nii ökoloogilises kui ka evolutsioonilises ajaskaalas.

Peamiselt rakenduslikel kaalutlustel on viimastel aastakümnetel põhjalikult uuritud, mil viisil parasitoidid reageerivad peremehe populatsiooni arvukuse varieerumisele ajas ja ruumis ning kuidas see mõjutab peremehe populatsioonidünaamikat. Seevastu on palju vähem teada, millist mõju avaldavad peremees–parasitoid-süsteemi dünaamikale parasitoidi käitumuslikud otsused peremehe isendi tasandil. Evolutsioonilises plaanis on palju tähelepanu pööratud sellele, kuidas erinevat tüüpi peremeesisendite kasutamine mõjutab parasitoidide elukäiguparameetreid. Hoopis harvemini on aga hinnatud parasitoidide osa peremeesliigi elukäiguparameetrite, nagu keha suurus, arengu kestus jne., kujunemises. Eeldatavasti võib sõltuvalt uuritava parasitoidiliigi elukäigustrateegiast ning käitumisest vastav mõju liigiti märkimisväärselt erineda. Üldise teooria loomine eeldab siiski suurema hulga erineva elukäiguga parasitoidiliikide mõju uurimist.

Parasitoidid võivad peremehe populatsiooni mõjutada otseselt või kaudselt. Otsese vastasmõjuga on tegemist siis, kui kahe liigi isendid mõjutavad üksteist füüsiliselt. Kaudse vastasmõju puhul interakteeruvad kaks liiki kolmanda liigi vahendusel. Otseste ja kaudsete vastasmõjude tihe läbipõimumine võimaldab looduslikes kooslustes toimuvaid protsesse mõista paremini siis, kui arvestatakse mõlemat tüüpi interaktsioone. Kahe liigi kaudne vastasmõju võib toimuda kahel viisil — vastasmõjuahelana (*interaction chain*) või modifitseeritud vastasmõjuna (*interaction modification*). Parasitoididega seotud uurimustes esindab esimest tüüpi kaudseid vastasmõjusid troofiline kaskaad (*trophic cascade*), teise tüübi näitena võib tuua ressursikonkurentsi (*exploitative competition*) ja vahendatud konkurentsi (*apparent competition*). Juhuslikku laadi tõendite põhjal võib oletada, et kaudsed vastasmõjud on parasitoididega seotud interaktsioonides vägagi laialt levinud.

Käesolevas doktoritöös dokumenteeriti mitmesuguseid otseseid ja kaudseid vastasmõjusid taim–herbivoor–parasitoid-süsteemides ning hinnati nende ökoloogilisi ja evolutsioonilisi tagajärgi. Erilist tähelepanu pöörati eespool toodud lünkadele meie teadmistes. Töö viidi läbi kahe loodusliku mudelsüsteemi näitel. Uuriti laialehisel hundinuial (*Typha latifolia* L.) toituvaid kaldaöölasi (*Noctuidae*, *Lepidoptera*) ja neil parasiteerivaid käguvaablasi (*Ichneumonidae*, *Hymenoptera*) (I, II, III) ning harilikku hallavaksikut (*Epirrita autumnata*, *Geometridae*, *Lepidoptera*) ja selle parasitoide (IV, V). Sõltuvalt üksikuurimuse eesmärkidest rakendati kas korrelatiivset, eksperimentaalset või kombineeritud lähenemist.

Mõlemas uuritud süsteemis põhjustasid parasitoidid peremehe populatsioonis kõrge suremuse. See siiski ei tähenda, et parasitoidid reguleerivad peremehe populatsiooni arvukust: selleks peab parasitism sõltuma ajaliselt peremehe populatsiooni tihedusest. Hallavaksiku puhul vastavat seost ei leitud, mistõttu parasitismil ilmselt stabiliseerivat mõju peremehe populatsioonidünaamikale ei ole. Viimastel aastakümnetel on väideldud selle üle, kas ka tihedusest ruumis sõltuv parasitism võiks reguleerida peremehe arvukust. Käesolevas töös uuriti parasitismi sõltuvust hallavaksiku tihedusest nii ruumis kui ka ajas ja seega oli võimalik hinnata nende sõltuvuste omavahelisi seoseid. Tulemused näitasid, et peremehe tiheduse ja parasitismi seosed ruumis ei pruugi viia sarnastele tulemustele ajas. Seega tuleks käesoleva töö tulemuste alusel ettevaatlikult suhtuda võimalusse ennustada peremehe populatsiooni reguleeritust parasitoidide poolt ruumiliste seoste põhjal.

Käesolev töö näitab, et kaudsed vastasmõjud võivad kooslustes oma tugevuselt ja eeldatavasti ka ökoloogiliselt ja evolutsiooniliselt tähtsuselt olla võrdsed otseste vastasmõjudega. Isegi suhteliselt lihtsas taim–herbivoor–parasitoid-süsteemis, leiti terve rida erinevaid kaudseid vastasmõjusid. Varieeruvus toidutaime kvaliteedis vallandas tugeva troofilise kaskaadi, mõjutades nii liblikate kui ka parasitoidide kohasust. Kahe peamise liblikaliigi suhteid mõjutasid parasitoidid, liblikad omakorda vahendasid parasitoidide omavahelisi vastasmõjusid. Töö tulemused näitavad, et kaudsed vastasmõjud võivad avaldada tugevat toimet süsteemi populatsioonidünaamikale ja koosluse struktuurile. Kaheliigiliste peremees–parasitoid-süsteemide uurimine võib seega osutuda populatsioonitiheduse kõikumiste seletamisel ebapiisavaks.

Parasitoidide potentsiaalne mõju peremeesliigi elukäiguparameetritele näib uuritud mudelsüsteemides erinevat. Hundinuial põhinevas süsteemis oli liigiti parasitismitase kõrgem suuremal peremeesliigil (suur-kaldaöölane), ka liigisiseselt parasiteeriti suuremat sugupoolt, s.o. emaseid sagedamini kui isaseid. Seevastu hallavaksiku puhul oli parasitismitase kõrgem pigem väiksematel röövikutel. Seega võib peremehe kehasuurusest sõltuv parasitism põhjustada valikusurve keha suuruse evolutsioonilise kasvamise vastu suur-kaldaöölase puhul, hallavaksiku puhul aga mitte. Ühtlasi võib parasitism olla mehhanismiks, mis evolutsioonilises ajaskaalas vähendab suur-kaldaöölase sugulist dimorfismi.

Vähem arvuka liigi (hele-kaldaöölane) parasitismitase oli seda väiksem, mida vähem tema fenoloogia erines dominantliigi (suur-kaldaöölane) fenoloogiast. Seega võib parasitism mõjutada hele-kaldaöölase elutsükli ajastust. Hallavaksiku puhul parasiteeriti enam-vähem võrdselt nii neid röövikuid, kes olid arengus ette jõudnud, kui ka neid, kes olid arengus maha jäänud. Selle põhjal võib oletada, et hallavaksiku arengutsükli ajastuses ei ole parasitism oluliseks valikuteguriks.

Mida väiksem oli hele-kaldaöölase arvukus suur-kaldaöölase suhtes, seda väiksem oli hele-kaldaöölase risk saada parasiteeritud. Valik peaks seega soosima emaseid, kes paigutavad oma järglased laikudele, kus on vähem liigikaaslasi. Hallavaksiku parasiteeritus tihedusest ei sõltunud, mistõttu võib arvata, et sellel liigil parasitism ei tekita valikusurvet levimisvõimele.

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Patterns of host use in solitary parasitoids (Hymenoptera, Ichneumonidae): field evidence from a homogeneous habitat

Tiit Teder, Toomas Tammaru and Rein Pedmanson

Teder, T., Tammaru, T. and Pedmanson, R. 1999. Patterns of host use in solitary parasitoids (Hymenoptera, Ichneumonidae): field evidence from a homogeneous habitat. – Ecography 22: 79–86.

We detected a significant inter- and intraspecific host preference on the level of individual host use in a system, in which three moth species (Lepidoptera: Noctuidae), feeding on a cattail *Typha latifolia*, are parasitized by three solitary parasitoid species (Hymenoptera: Ichneumonidae). The biology of the host species is similar but they exhibit remarkable inter- and intraspecific variance in body size. All the parasitoid species preferred the largest host species in this system whereas other host species were used only occasionally. We found that parasitoids which emerged from females of the preferred host species were larger than those which developed in males of the same species. Accordingly, two of the parasitoid species had a significant within-host-species preference: females of the largest moth species were used more often than males. No dependence of the preference pattern on host density was found. This pattern of host use is discussed in the light of the switching theory and the optimal host selection theory. Our results indicate that non-random host use by parasitoids may have significant effects on host populations and communities, and forms a potential selective factor against large body size in herbivorous insects. Unlike the majority of ichneumonid wasps, these three parasitoid species have no remarkable female-biased sexual size dimorphism. In accordance with the predictions of Charnov's sex allocation theory for this case, we did not observe any significant host quality dependent biases in sex allocation: there was no association between host sex and parasitoid sex, neither did parasitoid sex ratio differ between years with different host quality.

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The individual fitness of a hymenopterous parasitoid has often been found to be dependent on its body size (King 1987, van den Assem et al. 1989, Heinz and Parrella 1990, Petersen and Hardy 1996). A larger body size often implies higher fecundity and longevity for females, and better competitive abilities, mobility and longevity for males (Godfray 1994). Parasitoid body size is commonly positively correlated with host body size. Therefore, one may expect a strong selection on the behavioural mechanisms of host search and choice. Optimal host selection theory predicts then that a parasitoid prefers larger hosts for oviposition, whenever there is a possibility for choice (Iwasa et al. 1984). This prediction is supported by a great deal of evidence from experiments with laboratory populations (e.g., Jones 1982, van den Assem et al. 1989, Brault 1991). Furthermore, theory predicts that the degree of selectivity, and resulting pattern of host use should be relative, it should depend on host density (van Alphen and Vet 1986).

However, attempts to test these predictions in the field are scarce. Due to the complexity of natural habitats, different factors often preclude host choice between different host species (van Alphen and Vet

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1986, Schmid-Hempel and Schmid-Hempel 1996). Moreover, it is often practically impossible to obtain unbiased samples for natural systems. Here we report on a study of a system highly appropriate for exploring patterns of host use on the level of host-individuals. The study area – relatively homogeneous in vegetation and topography – is inhabited by three potential host species, which are similar in phenology and feeding biology, but have a considerable difference in size. This provides the possibility to investigate host use on the level of host species selection. In addition, hosts also exhibit a considerable intraspecific size difference: on average, females of all host species are larger than males. Thus, the fitness of a female parasitoid may depend on host use on the interspecific as well as the intraspecific level. Accordingly, the primary aim of the present study was to test for the presence of non-random patterns of host use by parasitoids, predicted by the theories of behavioural optimisation, in a natural system. Our ultimate intention was to evaluate the ecological and evolutionary significance of this non-random host use for populations and communities of host species.

Furthermore, ichneumonid parasitoids have a haplodiploid sex determination system that provides the possibility of differential sex allocation. There are numerous observations that solitary parasitoids tend to lay male eggs in smaller and female eggs in larger host specimens. Charnov et al. (1981) and Charnov (1982) hypothesised that females benefit more from being larger than males. Accordingly, parasitoid species usually exhibit a female-biased sexual dimorphism in body size (Hurlbutt 1987). However, many species of the subfamily Ichneumoninae, including all our study species, have a reversed pattern of sexual size dimorphism, or none at all. This provides an opportunity to investigate whether this affects host quality dependent sex allocation in these parasitoids, a phenomenon potentially involved in numerical host-parasitoid interactions (Hassell et al. 1983, Comins and Wellings 1985).

Material and methods

The study system

The study was carried out near the town of Tartu (58°22'N; 26°45'E), Estonia, on the flooded meadow of the Emajõgi river. In spring, the area is flooded by the river; the water recedes by the end of May. The study area has a quite homogeneous vegetation typical for regularly flooded meadows in northern Europe. The dominant species in the vegetation is a cattail – *Typha latifolia* L. (Typhaceae), a perennial helophyte (i.e. a plant growing in soil saturated with water) which forms dense stands of 1–3 m in height. *Solanum dulcamara* L., *Cicuta virosa* L., *Glyceria maxima* Hartm., *G. fluitans* L., *Carex elata* Bell. ex All., *Epilobium palustre* L. and some other plants are common. Large stands of *C. elata* and *Phragmites australis* Cav. border the study area.

The study embraces moths feeding on *T. latifolia* and the parasitoids of these moths. The moths were represented by three related species – *Nonagria typhae* Thunb., *Archanara sparganii* Esp. and *A. algae* Esp. (Lepidoptera: Noctuidae). The phenology and feeding biology of all three moth species are similar. All the species are univoltine, they overwinter as eggs, which start to develop in spring. At the beginning of the season, young instars feed on the aerial roots of cattails, later they switch to feeding endophytically on the shoots of the plant (Galichet et al. 1992). Usually, one larva damages more than one shoot. Larvae pupate at the end of July or at the beginning of August, in *A. sparganii* and *A. algae* the pupal period starts on average about a week earlier than that of *N. typhae*, and lasts about a month in all species. Pupation takes place inside the shoot or between the leaves of the host plant. *Nonagria typhae* is reported to be monophagous on cattails, *Archanara* species may also use some other plants (Skou 1991). However, in our study area both *Archanara* species were apparently functionally monophagous on cattails. All these moths are common herbivores on cattails in Estonia (unpubl.).

All three moth species can be parasitised by three solitary larval-pupal ichneumonid wasps (Hymenoptera: Ichneumonidae) from the subfamily Ichneumoninae: *Exephanes occupator* Grav., *Spilichneumon limnophilus* Thoms. and *Chasmias paludator* Desv. A few other parasitoids were found but their proportion of the total number remained < 1%.

Like their hosts, the parasitoid species are univoltine. The adult females overwinter and lay their eggs at the end of May and at the beginning of June (known for *E. occupator*), when young larvae of all host species can be found together feeding on cattail shoots (unpubl.). Adults of all parasitoid species are very mobile and search for hosts actively. The adult wasps emerge from moth pupae more or less simultaneously with unparasitised moths. None of these species is monophagous, they parasitize all the moth species included in this study as well as some others (Rasnitsyn and Siitan 1981). The larvae of some other moths were occasionally found in our study area but they were obviously too rare (< 0.5%) to influence the host choice or sex allocation of the parasitoids.

The adult body size of the males of parasitoid species is similar (*E. occupator*) or even larger (*S. limnophilus* and *C. paludator*) than that of the females (Table 3).

Sampling methods

The material for this study was collected from 32 sample plots of 4 × 4 m in 1995 (moth abundance was low) and 33 sample plots of 3 × 3 m in 1996 (moth abundance was high) in an area of 300 × 100 m. As the study area was homogeneous in vegetation, the plots were systematically selected along transects at 20 m intervals. From these plots, moth pupae were collected by carefully inspecting all cattail shoots. As the pupae were relatively large (2–3.5 cm in length), potential pupation sites were limited, and damaged shoots were easily distinguishable from undamaged shoots, we believe that we managed to collect nearly all pupae from the plots. The pupae were weighed and kept in Petri dishes until the eclosion of the adult moth or parasitoid.

The collections were carried out between 24 July and 2 August in 1995 and between 4 August and 13 August in 1996, so that the moths were in the same phenological phase. In the beginning of the collecting period, we also found some moth larvae, which were reared in the laboratory until pupation. The total number of collected moth pupae in the main study area was 1022 in 1995 and 2684 in 1996. To test the predictions of the switching theory, we looked for relatively isolated patches outside the main study area, where the density of *Archanara* species could be higher than that of *N. typhae*. We found one patch with a dominance of *Archanara* species which was sampled as plots in the main area.

In the course of collecting, we counted all live cattail shoots in order to calculate the number of moths in relation to the number of cattail shoots, which might be a more appropriate density estimate than the number of moths per unit area. The length of hind tibia as an index of body size was measured in parasitoids. Also, the sex of all parasitoid and moth individuals was determined using external characters of pupae and adults.

Data analysis

First, we evaluated various system variables relevant in the present context – host abundance in different years, parasitoid body size as a function of its sex and host type, and host consumption by parasitoids. This was needed to find out whether the parasitoids do benefit from appropriate host choice in this system, which may be seen as a precondition for behavioural optimization to evolve. To study patterns of host use and sex allocation and sex ratio on the intraspecific level, log-linear analysis was applied (SAS CATMOD, Anon 1994). When studying host use patterns, year (1995, 1996), host sex (male, female), and parasitism (yes, no) were used as categories; year, host sex, and parasitoid sex (male, female), when testing for biased sex allocation; and year and parasitoid sex, when studying parasitoid sex ratio. Saturated models were fitted first, and a stepwise simplification was performed.

The moth pupal weight was standardized to the weight at the pupation date using a regression obtained from laboratory rearings. However, the average correction was small (< 3.5%). Larvae and pupae dead from other reasons than parasitism were omitted from the data analysis. As the proportion of dead larvae was relatively small (< 4.5% of all host individuals), these deaths have no confounding influence on our conclusions.

Results

Host abundance and body size

In 1995, the moth abundance was much lower than in 1996, the average numbers of moth pupae per 100 live cattail shoots were 7.8 and 44.7 specimens, respectively (2.0 and 8.8 pupae 1 m^{-2}, pooled over species, Table 1). The pupae of *N. typhae* are considerably larger than the pupae of the other two species. The pupae of both *Archanara* species have about the same weight. In addition, there is a significant sexual size dimorphism in all three species with females being heavier than males. The moth pupae weighed significantly less in 1996 than in 1995 (Table 1).

Host consumption by parasitoids

Developing parasitoids from different species consumed their hosts differently. *Exephanes occupator* used almost the whole content of the host pupa, causing more than

Table 1. Host densities in different years expressed as the number of moths per 100 cattail shoots and results of the two-tailed t-tests for comparing host pupal weight averages in 1995 and 1996 (only unparasitised pupae in calculations).

Host species and sex	Host density		Weight average (g) and standard deviation		DF	t-value	p
	1995	1996	1995	1996			
Nonagria typhae ♀♀	3.70	21.13	0.941 ± 0.150	0.718 ± 0.114	945	24.87	0.00
N. typhae ♂♂	2.87	20.90	0.674 ± 0.088	0.545 ± 0.079	955	20.21	0.00
Archanara sparganii ♀♀	0.45	0.60	0.543 ± 0.079	0.430 ± 0.075	97	7.27	0.00
A. sparganii ♂♂	0.29	0.61	0.393 ± 0.043	0.362 ± 0.067	79	2.17	0.03
Archanara algae ♀♀	0.12	0.02	0.414 ± 0.073	–	–	–	–
A. algae ♂♂	0.08	0.02	0.326 + 0.065	–	–	–	–

Table 2. Host consumption by studied parasitoids in 1995 (EO – *Exephanes occupator*, CP – *Chasmias paludator*, SL – *Spilichneumon limnophilus*) expressed as the average weight of parasitised pupae as a percentage of the average weight of unparasitized pupae. The percentages were similar in 1996. The numbers of studied pupae (parasitised/total number) are given in parentheses.

Host species and sex	Parasitoid species		
	EO	CP	SL
Nonagria typhae ♀♀	29.0% (n = 86/490)	92.0% (n = 42/490)	62.4% (n = 18/490)
N. typhae ♂♂	31.6% (n = 63/380)	88.9% (n = 36/380)	58.8% (n = 7/380)
Archanara sparganii ♀♀♂♂	–	–	75.4% (n = 5/121)
Archanara algae ♀♀♂♂	–	47.4% (n = 1/31)	73.7% (n = 1/31)

a 3-fold decrease in the weight of the host pupae. *Chasmias paludator* consumed only a small part of its host, whereas *S. limnophilus* was in an intermediate position among studied parasitoids (Table 2). Such a difference is probably the result of differences in the beginning of host consumption – *E. occupator* starts its development earlier in the host life cycle than other parasitoids.

Parasitoid body size

Body size of adult parasitoids depended on host species and sex. The adults of all parasitoids (both males and females), which emerged from the pupae of female *N. typhae*, were larger than those parasitoids, which developed in male moths of the same species (Table 3). For *S. limnophilus*, we had sufficient material to compare specimens emerged from *N. typhae* and *A. sparganii* + *A. algae*. The parasitoid body size difference was significant for female *S. limnophilus*, and marginally significant for males (Table 4). Therefore, there was a selective advantage of appropriate host choice in the study system, and non-random patterns of host use could be expected.

Host use

All three parasitoid species appeared to prefer *N. typhae* as a host species. *Archanara sparganii* and *A. algae* were parasitized only occasionally with the exception of *S. limnophilus* in 1995 (Fig. 1). However, all three host species were potentially acceptable, i.e. development to adulthood was possible in all host species for all parasitoid species (we have no data on, whether *E. occupator* has successfully developed in *A. algae*) (Fig. 1 and unpubl.).

In the single isolated patch with dominance of *A. algae* (84 specimens of *A. algae*, 11 of *A. sparganii*, and 22 of *N. typhae*), both *S. limnophilus* and *C. paludator* used only *A. algae*, the parasitism percentages were 19.0 and 23.8, respectively. However, as in the main study area in 1995, *E. occupator* parasitised only *N. typhae*.

Further, we studied pattern of host use on the intraspecific level in *N. typhae* whereas both the *Archanara* species were too rarely oviposited to facilitate a meaningful statistical analysis of within-species patterns. Host use was studied using log-linear analysis (SAS CATMOD, Anon 1994). The three-factor interaction term between year, host sex and parasitism was non-significant for all the studied parasitoid species. Thus, although host densities had about a 4.8-fold difference in 1995 and 1996, no corresponding difference in host use was discovered. Thereafter, the significance of two-factor interactions was tested with the main interest concentrated on the 'host sex × parasitism' interaction term. The models including all two-factor interactions fitted well for *E. occupator* ($G = 1.08$, $DF = 1$, $p = 0.30$) and *S. limnophilus* ($G = 0.37$, $DF = 1$, $p = 0.54$) whereas models with the 'host sex × parasitism' interaction term excluded did not fit ($G = 12.51$, $DF = 2$, $p = 0.002$ and $G = 6.14$, $DF = 2$, $p = 0.047$, respectively). Therefore, we conclude that *E. occupator* and *S. limnophilus* had a significant preference for female *N. typhae* (Fig. 1). The preference for female hosts, detected in the data pooled over the study plots, was also confirmed by comparisons between plots. There were significantly more plots (both years pooled since there was no difference in host use between years) with a female-biased preference in *E. occupator* ($\chi^2 = 5.92$, $DF = 1$, $p = 0.015$) and *S. limnophilus* ($\chi^2 = 7.41$, $DF = 1$, $p = 0.006$). For *C. paludator*, the model without the 'host sex × parasitism' interaction term fitted well ($G = 0.99$, $DF = 2$, $p = 0.61$), and there was thus no reason to assume dependence of parasitoid host use on host sex.

Study plots were also compared to discover whether host use was dependent on host density in space. The degree of preference for females was density-independent for all parasitoids in both years (Fig. 2).

Parasitoid sex allocation and sex ratio

To study, whether there were any biases in parasitoid sex allocation in the *N. typhae* as host, a log-linear analysis was performed. For *E. occupator* and *S. limnophilus*, the saturated models including a three-way interaction term between year, host sex and parasitoid sex were not justified, since the models with two-way interactions fitted well (G = 1.94, DF = 1, p = 0.16; G = 0.51, DF = 1, p = 0.48, respectively). The subsequent analysis showed that *E. occupator* and *S. limnophilus* had no significant tendency to allocate either female or male offspring preferably to either female or male *N. typhae* as the two-way models without the 'host sex x parasitoid sex' interaction term were sufficient (*E. occupator*: G = 4.61, DF = 2, p = 0.10; *S. limnophilus*: G = 1.17, DF = 2, p = 0.56). *Chasmias paludator* had laid more female eggs in female hosts in 1995, whereas the opposite was true in 1996. The between-year difference was significant ($\chi^2 = 9.59$, DF = 1, p = 0.002). However, we find that without additional data, it is premature to discuss the possible reasons for this peculiar pattern.

Although the overall parasitoid sex ratio was slightly female-biased for all species in both years (varied from 1.1 to 1.5, see also Table 5), there was no significant difference between years, since two-way models without the 'year x parasitoid sex' interaction term fitted well (*E. occupator*: G = 1.19, DF = 1, p = 0.28; *S. limnophilus*: G = 0.02, DF = 1, p = 0.88; *C. paludator*: G = 0.89, DF = 1, p = 0.35).

Discussion

Host species selection in parasitoids is not commonly based on decisions on the level of choosing between individuals belonging to different host species which are simultaneously available: host selection is usually restricted to habitat or patch choice (van Alphen and Vet 1986). Moreover, the availability of different host species may be asynchronous. This is not the case in our system as the larvae of the three host species, *N. typhae*, *A. sparganii* and *A. algae* are vulnerable for parasitoids to large extent simultaneously in a relatively homogeneous habitat. Therefore, our study provided a possibility to test some predictions of the theory of optimal host use in a natural system. Furthermore, our results enabled us to obtain estimates of the ecological, and potentially, evolutionary significance of the behavioural mechanisms of individual host choice for populations and communities of the host species.

We showed that in such a system parasitism rate was markedly different among host species: *N. typhae*, the most abundant, and simultaneously, the largest species was clearly preferred as host. Our results are consistent with the two main theories predicting possible patterns of host use. According to the switching theory, parasitoid attacks concentrate on the most abundant species of potentially acceptable hosts as this will increase the searching efficiency (Cornell 1976, Cornell and Pimentel 1978). According to the optimal host selection theory, female parasitoids choose hosts in a way which maximizes the expected fitness of progeny (Iwasa et al. 1984). As suggested by the optimal host selection theory, all parasitoids preferred *N. typhae* as the largest host species, whereas the two smaller species were parasitized only occasionally. Accordingly, parasitoid size (and probably fitness) was, indeed, positively correlated with host body size. However, this pattern can be explained by the switching theory as well, since *N. typhae* was the most abundant species. We found some evidence for switching from the patch, where *A. algae* was the dominant species. Following the predictions of the switching theory, *S. limnophilus* and *C. paludator* parasitized exclusively *A. algae* in this patch, despite the other two host species being available. However, *E. occupator* still used only *N. typhae* for oviposition here. Probably, both species of *Archanara* were suboptimal for its development, and they were rejected regardless of their density.

Host use was non-random on the intraspecific level as well. Both *E. occupator* and *S. limnophilus* showed a statistically significant preference for females of *N. typhae*. This preference pattern is well-interpretable within the framework of the optimal host selection theory. The females of *N. typhae* were larger than the males, and the parasitoids emerged from female *N. typhae* were larger as well. However, the third parasitoid species, *C. paludator*, was unselective on the intraspecific level. The reason may lay in the different degrees of host consumption by the studied parasitoids. *Exephanes occupator* consumed almost the whole content of *N. typhae* pupae, *S. limnophilus* used most of a pupa, while *C. paludator* emerged from pupae always containing unconsumed parts of the host, independent of the sex of the host. This may imply that *C. paludator*

Table 3. Comparison of mean hind tibia lengths (as an estimate of body size) of parasitoids, which emerged from female or male *Nonagria typhae* in 1995. The patterns in 1996 were not qualitatively different.

Parasitoid species and sex	Mean hind tibia length (mm)		t-value	DF	p
	N. typhae ♀♀ as hosts	*N. typhae* ♂♂ as hosts			
Exephanes occupator ♀♀	0.365 ± 0.018	0.353 ± 0.011	3.19	68	0.002
E. occupator ♂♂	0.359 ± 0.018	0.344 ± 0.018	2.22	34	0.033
Spilichneumon limnophilus ♀♀	0.309 ± 0.013	0.308 ± 0.007	0.18	13	0.864
S. limnophilus ♂♂	0.401 ± 0.013	0.377 ± 0.032	2.67	20	0.015
Chasmias paludator ♀♀	0.344 ± 0.010	0.326 ± 0.020	4.11	45	<0.001
C. paludator ♂♂	0.363 ± 0.013	0.352 ± 0.008	3.22	42	0.002

Table 4. Comparison of mean hind tibia lengths of *Spilichneumon limnophilus*, which emerged from *Nonagria typhae* or *Archanara sparganii*+*Archanara algae* in 1995. The patterns in 1996 were not qualitatively different.

Parasitoid species and sex	Mean hind tibia length (mm)		t-value	DF	p
	N. typhae as hosts	*Archanara* sp. as hosts			
Spilichneumon limnophilus ♀♀	0.308 ± 0.012	0.287 ± 0.016	3.58	22	0.002
S. limnophilus ♂♂	0.392 ± 0.020	0.375 ± 0.024	1.96	33	0.059

profits less from host choice on the intraspecific level than do the other two parasitoids: both female and male *N. typhae* provided enough food for their larval development. However, interpretation of the detected sex-dependent parasitism rate as originating from active preference for females as larger host items is justified only if the sexual dimorphism in the host is present already in young larvae, i.e. at the time when parasitising actually occurs. We do not have such an information for *N. typhae*, but results with some other moths (e.g. Tammaru 1998) suggest that this may well be the case.

Importantly, irrespective of exact behavioural mechanisms which have led to observed patterns, our results convincingly indicate that non-random host use by parasitoids can have measurable effects on host populations. Sex-dependent mortality rates bias operational sex ratios. Killing more females, parasitoids may reduce the reproductive potential, and thereby affect the dynamics of the host population more than it can be inferred from simple mortality estimates. If based on sex-related differences in host body size, this effect could be much stronger for insects with more strongly pronounced sexual dimorphism. Therefore, this observation may have a practical significance for control of some forest pests, like lymantriid moths, for example. The effects of sex-related parasitism rate might have been overlooked in many cases due to practical impossibility of sexing larvae, and parasitoids emerging from host pupae provide a good opportunity for studies on sex-dependent parasitism.

Furthermore, size-dependent parasitism rate has a potential to create a selective pressure against large body size in herbivorous insects. Interestingly, as the preference of larger hosts has a relative nature (Godfray 1994), we see here a possibility for a specific selection against female-biased size dimorphism. These effects may be important when considering the surprisingly non-trivial question of which forces preclude a continuous evolutionary increase in female body size in insects (Leimar 1996, Tammaru 1998), despite a common strong positive correlation between female body size and fecundity (Honěk 1993).

Observed non-random patterns indicate a potentially strong impact of parasitoids on composition of the herbivore community. The smaller and less numerous *Archanara* species largely avoided parasitism, which was a significant source of mortality in the dominant herbivore, *N. typhae*. The tendency of the parasitoids to specialize on the most abundant host, revealed in experiments (Murdoch 1969, Cornell and Pimentel 1978), and supported by the present study, has a potential to maintain diversity of the lower trophic level.

Following the optimal host selection theory, one may derive a prediction that lower host densities promote lower selectivity in host use (van Alphen and Vet 1986). Therefore, we expected that the patterns of host use on the intraspecific level were different in 1995 and 1996, considering the remarkable difference in host densities. However, parasitism patterns were year-independent for all parasitoids. We suggest that host densities could have been high enough to allow for differential host selection in both years. In addition to yearly differences in moth densities, there was also a within-year spatial heterogeneity in host densities. A corresponding pattern of host use was not discovered here either: the level of parasitoid preference for females of *N. typhae* was

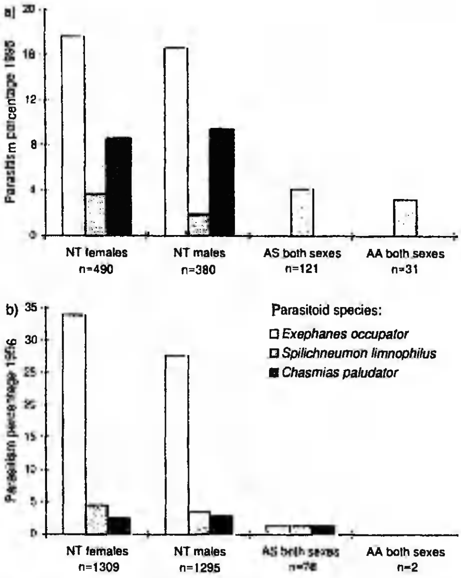

Fig. 1. Parasitism percentages of three noctuid moths (NT – *Nonagria typhae*, AS – *Archanara sparganii*, AA – *Archanara algae*) by different parasitoids in two years.

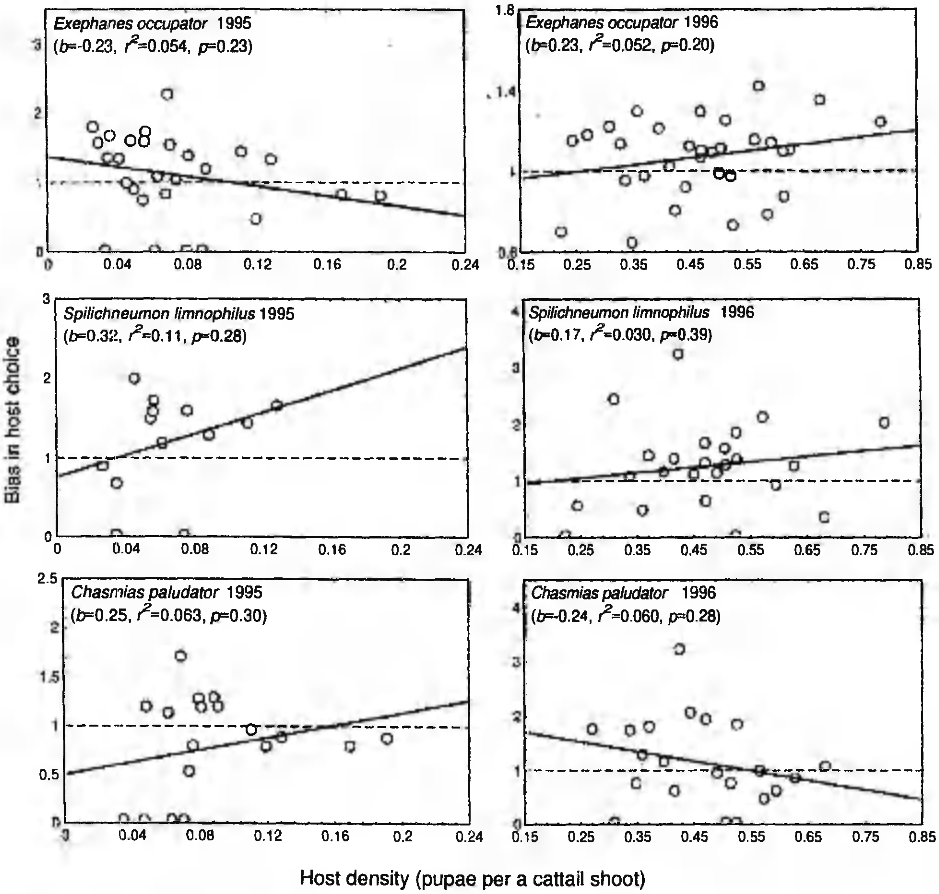

Fig. 2. The relationship between the host density in a plot and intraspecific host choice. The host choice index is calculated as the ratio of [parasitised *Nonagria typhae* females/all parasitised *N. typhae* in a plot] and [all *N. typhae* females/all *N. typhae* in a plot]. If this ratio is equal to unity, no preference to either host sex was detected in the plot. Host density in a plot is expressed as the number of hosts per cattail shoot.

independent of host density in a plot. The explanation may be linked to the high mobility of the studied parasitoids. In this case, the degree of selectivity of parasitoids is probably determined on a spatial scale much larger than the distances between patches. Therefore, we predict that density-dependence of selectivity may have ecologically significant effects for parasitoids with lower mobility, or in the cases of lower absolute host density.

No biased sex allocation, a pattern often observed in parasitoids, was found in our study. Data from numerous studies suggest that being larger is more important for female fitness. This is a likely explanation for the corresponding pattern of sexual size dimorphism: female parasitoids are commonly larger than males (Hurlbutt 1987). Accordingly, various authors have observed that more female offspring emerges from larger hosts and more males from smaller hosts (e.g. Heinz and Parrella 1990, Brault 1991). In our study, female parasitoid eggs were not preferentially laid in the larger female hosts, there was even a slight but statistically nonsignificant opposite tendency (Table 5). In our parasitoid species, sexual dimorphism is minimal (*E. occupator*) or even male-biased (*S. limnophilus* and *C. paludator*). This suggests that fitness consequences of size may be similar for both sexes. Consequently, the observed patterns of sex allocation in these species provide support to the view (van den Assem et al. 1989)

Table 5. The sex ratios (males/females) of studied parasitoids as dependent on host sex. The sex ratio values are followed by the number of parasitised hosts studied (in parentheses).

Parasitoid species and year	Parasitoid sex ratio	
	N. typhae ♀♀ as hosts	*N. typhae* ♂♂ as hosts
Exephanes occupator (1995)	0.91 (n = 86)	0.70 (n = 63)
E. occupator (1996)	0.77 (n = 427)	0.73 (n = 341)
Spilichneumon limnophilus (1995)	1.00 (n = 18)	0.40 (n = 7)
S. limnophilus (1996)	0.76 (n = 58)	0.63 (n = 44)
Chasmias paludator (1995)	0.56 (n = 56)	1.50 (n = 55)
C. paludator (1996)	1.13 (n = 32)	0.42 (n = 37)

that sex differences in fitness functions of body size is the reason for biased offspring sex allocation where observed. Returning to the framework of estimating ecological consequences of optimisation of host use, these results imply that host-dependent biases in sex ratios of parasitoids is not a factor involved in numerical host-parasitoid interactions in systems like ours (compare, Hassell et al. 1983, Comins and Wellings 1985). This is directly supported by the observation that overall sex ratio (all males/all females) of all parasitoid species was year-independent, despite the considerable yearly difference in pupal sizes of hosts.

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CASCADING EFFECTS OF VARIATION IN PLANT VIGOUR ON THE RELATIVE PERFORMANCE OF INSECT HERBIVORES AND THEIR PARASITOIDS

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ABSTRACT

1. Consequences of variation in food plant quality were estimated for a system consisting of two monophagous noctuid herbivores and three ichneumonid parasitoids.

2. In a natural population, pupal weights of the herbivores in this system, *Nonagria typhae* and *Archanara sparganii*, were found to be highly variable. Pupal weights increased strongly and consistently with the increase in the vigour of the host plant, *Typha latifolia*, providing support for the plant vigour hypothesis. Correspondingly, as the moths do not feed as adults, a strong, positive correlation between host vigour and fecundity of the herbivores would be expected.

3. There were strong and positive relationships between adult body sizes of the parasitoids and the sizes of their lepidopteran hosts. Moreover, a direct positive link between plant quality and parasitoid size was documented.

4. For all three parasitoids, cascading effects of plant quality on body size were weaker than for the herbivores. Differences in the importance of adult feeding and oviposition behaviour suggest that dependence of fitness on body size is also weaker in the parasitoids than in the moths. It is therefore concluded that the numerical response of the herbivore population to a change in plant quality should exceed the corresponding response in the parasitoids.

5. The results of this work imply that variation in plant variables may affect performance of different trophic levels to a different extent. It is suggested that the importance of adult feeding for the reproductive success (capital vs. income breeding strategies) in both herbivores and parasitoids is an essential aspect to consider when predicting responses of such a system to changes in plant quality.

Key words. Adult feeding, *Archanara*, body size, cascading effects, Ichneumonidae, *Nonagria*, population dynamics, *Typha latifolia*.

INTRODUCTION

Trophic cascades can be defined as strong interactions within food webs that influence system properties and embrace at least two trophic links (Pace *et al.*, 1999). Both bottom-up and top-down trophic cascades may influence community-level processes and population dynamics of single species (Polis & Strong, 1996; Polis *et al.*, 2000; Sinclair *et al.*, 2000). In terrestrial ecosystems, one of the most universal bottom-up cascades is based on plants

(Price, 1992). In particular, heterogeneity in food plant quality has a strong potential to affect body size in herbivorous insects (Hunter & Price, 1992; Price, 1992). In turn, body size of an adult insect is frequently a good predictor of life-history parameters (e.g. fecundity, longevity, and survival) that have direct relevance to population dynamics (Honěk, 1993; Nylin & Gotthard, 1998; but see Leather, 1988). Most data on the effects of plant quality on insect performance come from laboratory studies, however less is known about the range of food plant-induced size variation in natural herbivore populations (e.g. Roland & Myers, 1987; Kaitaniemi *et al.*, 1999). Moreover, the question of whether vigorous or stressed plants provide a more favourable food source for insect herbivores remains controversial (Koricheva *et al.*, 1998). While manipulative studies are necessary to reveal causal connections, correlative analyses assessing the scope of the effects in the field are of no less importance.

Cascading effects of variation in plant resources may extend to the performance of the third trophic level, parasitoids and predators (Price *et al.*, 1980; Duffey *et al.*, 1986; Faeth, 1994; Turlings & Benrey, 1998). Among these, parasitoids are expected to be particularly sensitive to variation in the quality of their insect hosts because of their tight developmental coupling with host insects. This is supported by numerous laboratory studies that have shown the influence of host diets on parasitoid development and body size (Bloem & Duffey, 1990; Barbosa *et al.*, 1991; Bourchier, 1991; Werren *et al.*, 1992). The effect of host diet on body size of insect parasitoids is commonly mediated by host size (e.g. Petitt & Wietlisbach, 1993; Heinz, 1996; Teder *et al.*, 1999), however there is a limited amount of information on the range of host- and plant-quality-dependent variations in parasitoid body size in natural populations. Moreover, little is known about which of the two counterparts, the host or the parasitoid, is affected more strongly by changes in plant quality. This question becomes important when considering the dynamics of a host–parasitoid system: an increase or decrease in plant quality may affect host and parasitoid numbers to a different extent.

The work reported here on natural populations documents a strong positive correlation between pupal weight of lepidopteran herbivores and vigour of their host plant, *Typha latifolia*. Further, it is shown that parasitoid body size depends on the pupal weight of the herbivore and, directly, on the characteristics of the plant. The relative strength of plant quality effects on herbivore and parasitoid fitness and population dynamics is discussed considering their adult feeding strategies.

MATERIAL AND METHODS

Study area and organisms

The study examining tritrophic interactions in a natural plant–herbivore–parasitoid system was conducted from 1995 to 1998 near Tartu, southeastern Estonia (58°22'N, 26°45'E). Study areas were located on the flooded meadow of the Emajõgi river where water usually recedes by the end of May. In order to assess the effects of both temporal and spatial variation in plant characteristics on insect performance, two habitats somewhat different with respect to homogeneity of growth conditions and abundance of a cattail, *Typha latifolia* L. (Typhaceae), were examined. The habitat studied in 1995–1996 was characterised by quite homogeneous vegetation with *T. latifolia* dominant. Other plant species, *Solanum dulcamara* L., *Cicuta virosa* L., *Glyceria maxima* Hartm., *G. fluitans* L., *Carex elata* Bell. ex All., and *Epilobium palustre* L., were common but formed a minor part of the plant cover. In 1997–1998, a more heterogeneous habitat with patches of *T. latifolia* and *C. elata* alternating was examined. The two study areas were separated by a distance of ≈ 300 m.

The study system was based on *T. latifolia*, a rhizomatous perennial helophyte (i.e. a plant growing in soil saturated with water) forming dense stands up to 3 m in height. The larvae of four moth species were found to feed on leaves and stems of *T. latifolia*, however the study was restricted to the two most abundant species, *Nonagria typhae* Thunb. and *Archanara sparganii* Esp. (Lepidoptera: Noctuidae), the other species being too scarce to allow a meaningful analysis (< 1% of all larvae). The phenology and feeding biology of these two taxonomically close univoltine species are similar. They overwinter as eggs that hatch in spring. Larvae feed on the aerial roots of the host plant at the beginning of the season, switching to endophytic feeding on the shoots later (Galichet *et al.*, 1992). One individual therefore usually feeds on more than one shoot during the larval period. Larvae of *N. typhae* are reported to be monophagous on *T. latifolia* while larvae of *A. sparganii* may also use some other species (Skou, 1991), however in the studied areas, both species were apparently functionally monophagous on *T. latifolia.* At the end of July or the beginning of August, larvae pupate inside the shoot or between the leaves of the host plant. The pupal period lasts for about a month in both species. Because adults of both *N. typhae* and *A. sparganii* do not feed, the potential fecundity of the females of these species should be determined largely by their weight at eclosion.

Three principal species of solitary parasitoid were found to parasitise larvae and pupae of *N. typhae* and *A. sparganii*: *Exephanes occupator* Grav., *Spilichneumon limnophilus* Thoms., and *Chasmias paludator* Desv. (Hymenoptera: Ichneumonidae). Other parasitoids accounted for < 1% of total parasitism. Like their hosts, studied parasitoids have univoltine life cycles. Adult females overwinter and lay their eggs on young moth larvae in late spring (*E. occupator*; T. Teder, pers. obs.; and probably also *S. limnophilus*) or on pupae in July and August (*Ch. paludator*; Hinz, 1983). Adult wasps emerge from moth pupae more or less simultaneously with unparasitised moths. All three parasitoids are oligophagous and are also known to parasitise some other moths (Rasnitsyn & Siitan, 1981), which, however, apparently constitute only a minor fraction of hosts in the studied system. All three parasitoids show a preference for *N. typhae*, the larger of the two host species (Teder *et al.*, 1999).

Sampling and measurements

Field populations were sampled to obtain data on the extent of natural variation in plant vigour, as well as body sizes of moths and parasitoids. Sampling was conducted at the end of July and/or the beginning of August in 4 consecutive years. Each year, 20–33 plots of 2 × 2 m, 3 × 3 m, or 4 × 4 m (depending on larval abundance in the particular year) were sampled. In the area with the homogenous habitat, plots were selected systematically along transects at 20 m intervals in an area of ≈ 300 × 100 m. In the area with the heterogeneous habitat, ≈ 200 × 200 m in size, plots were selected so as to obtain samples from patches with variable heights of *T. latifolia*. As indices of plant vigour, the total number of live shoots on each plot, the proportion of generative shoots (in 1997), and a height index of *T. latifolia* were recorded for every plot. This was done simultaneously with insect collections. To eliminate the influence of outlying plant individuals, the height index was obtained by measuring the height of about the 15th highest vegetative shoot in the plot. Using such a simple method was justified by the limited within-plot variation in the height of the shoots, which was exceeded considerably by the variation among plots and years (Fig. 1). Moreover, the height index used correlated strongly and positively with two other indices of vigour — plant biomass and proportion of generative shoots (Fig. 2, see also Results). Moth pupae were collected from the study plots by inspecting all the cattail shoots carefully. The pupae were relatively large (2.0–3.5 cm in length), potential pupation sites were limited, and damaged shoots were easily distinguishable from undamaged shoots, so it was possible to collect nearly all pupae from the plots. The number of pupae collected each year varied from 1022 to 2684, the average number of pupae per study plot being 45. Pupae were stored in Petri dishes until eclosion of the adult moth or parasitoid.

Weight of live pupae was used as an index of the moths' body size. Weight of parasitoids was determined in two ways. In 1997 and 1998, dry weight of adult parasitoids was measured. Comparable weight indices of parasitoids originating from 1995 and 1996 could not be obtained in a similar way because, in 1995 and 1996, the emerged parasitoids had not been weighed in the year of collection, and different conditions of preservation had apparently affected their weights. Estimates of dry weight for these parasitoids were therefore calculated using the regression of weight of parasitised pupae on dry weight of corresponding adult parasitoids in 1997 (*E. occupator* females: $R^2 = 0.47$, males: $R^2 = 0.59$; *S. limnophilus* females: $R^2 = 0.55$, males: $R^2 = 0.72$; *Ch. paludator* females: $R^2 = 0.27$, males: $R^2 = 0.26$). Such a method could be used as the parasitoid pupae embraced a considerable proportion of the volume of host pupae. Furthermore, the applicability of this transformation was confirmed by measuring the hind tibia length of a sample of emerged parasitoids: in all parasitoid species, there was a positive relationship between the weight of parasitised pupa and this linear measure of body size ($p < 0.001$ for all species), and the slopes did not differ between years with different host quality (ANCOVA: p = NS for all year × pupal weight interaction terms, average sample size = 65 per species). A representative sample of moths was used for estimating fecundity as a function of body size. For this purpose, eclosed female moths were kept in Petri dishes until they died, their abdomens were then dissected, and chorionated eggs were counted.

Data analysis

The levels of natural variation in plant performance and insect body sizes, and the relationships between them, were studied by two complementary approaches. First, patterns of temporal variation were studied on the basis of yearly means. Second, high variance in plant vigour in 1997 allowed analysis based on spatial variation.

In the within-year analyses, plot-specific averages of respective variables (e.g. average pupal weight of *N. typhae* males collected from one plot) were used as independent observations in regressions. In the among-year comparisons, the regressions were based on mean values of plot averages in study years. Weights of parasitoids were corrected for sex using a linear regression of plot means, and, thereafter, sexes were pooled to increase sample sizes in corresponding analyses. The analyses examining herbivore–parasitoid relationships are based on the most numerous herbivore of the system, *N. typhae*, and its parasitoids. The number of parasitoids that emerged from *A. sparganii* was too low for the analyses.

The relationship between pupal weights of moths and corresponding adult weights of parasitoids was estimated at the level of plot means to compare the relative sensitivity of moths and parasitoids to environmental variation in the studied plots. As both variables contained random variation, type I regression was an inappropriate technique to derive a functional relationship, so a type II regression had to be used (Sokal & Rohlf, 1995; see also e.g. Fairbairn, 1997). The type II regression was performed by calculating the first principal component (PRINCOMP procedure; SAS Institute Inc., 1995). This line is fitted by finding the minimum of the sum of squared deviances from the regression line, measured perpendicular to the line. Prior to the analyses, weights of studied parasitoids and moths were standardised by dividing them by species- and sex-specific means.

To compare the effects of *T. latifolia* vigour on sizes of moths and parasitoids directly, a corresponding ANOVA design (MIXED procedure; SAS Institute Inc., 1995) was applied to the 1997 within-year data. Species, sex, and plot were used as classification variables. The model contained weight as the dependent variable and species (moth, parasitoid), sex (male, female), height of shoots, and two interaction terms (species × height of shoots, species × sex) as independent effects. The interaction term plot × species was treated as a random effect.

RESULTS

Variation in the vigour of *T. latifolia*

There was considerable among-year variation in performance in the studied stands of *T. latifolia*. The average height of vegetative shoots ranged from 1.0 m in 1996 to 2.2 m in 1995 (Fig. 11). Spatial variation within the study area was highest in 1997, when the height in the study plots ranged from 0.85 to 1.85 m (average ± SD = 1.52 ± 0.28 m^2), with the variation being notably lower in other years. The height of shoots correlated positively with another variable related to plant performance, proportion of generative shoots (Fig. 2a), which also showed considerable plot-to-plot variation (0–36%) in 1997. In addition, the height of shoots was a good indicator of the above-ground biomass per unit area (Fig. 2b). Height of shoots can thus be considered an uncontroversial measure of vigour in *T. latifolia*.

Water conditions, highly variable both spatially and among years, formed an obvious factor responsible for observed variation in *T. latifolia*: the performance of plants was clearly poorest in the dry year, 1996, when the stand was not flooded in spring. Similarly, the high within-year variation in 1997 was apparently related to variable water conditions in the study area.

Variation in the body size of the moths

The studied herbivores, the moths *N. typhae* and *A. sparganii*, showed a high level of variation in the body size, with notable differences in moth pupal weights among years (ANOVA: *N. typhae* females: d.f. = 3, $F = 43.3$, $p < 0.001$; males: d.f. = 3, $F = 27.0$, $p < 0.001$; *A. sparganii* females: d.f. = 3, $F = 7.2$, $p < 0.001$; males: d.f. = 3, $F = 1.2$, $p =$ NS). In 1995, females of *N. typhae* were 1.3 times heavier and females of *A. sparganii* 1.2 times heavier on average than in 1996. In 1997 and 1998, moths were of intermediate size (Fig. 3). There was about a 3.2-fold weight difference between the smallest and largest females of *N. typhae* in 1997 (average ± SD = 0.83 ± 0.15 g) when spatial variation in the system was the highest. For female *A. sparganii*, the corresponding difference was 2.4-fold (average ± SD = 0.44 ± 0.07 g). The range of variation for males was of similar magnitude. Significant differences were also detected consistently in average moth sizes at the level of studied plots: the smallest and largest plot averages for females of *N. typhae* and *A. sparganii* differed 1.9 and 1.7 times respectively (Fig. 4).

Relationships between plant performance and moth size

Among years, the correlations between height of shoots and pupal weight of moths were all strongly positive with the exception of male *A. sparganii* (Fig. 3). Within-year comparisons confirmed the among-year results: in 1997, when variation in performance of *T. latifolia* among patches was highest, there was a significant, positive association between height of *T. latifolia* and pupal weight for both sexes of *N. typhae* and for female *A. sparganii* (Fig. 4). Once again, however, the pupal weight of male *A. sparganii* did not depend on the height of shoots (Fig. 4). These trends were similar for the proportion of generative shoots (*N. typhae* females: $R^2 = 0.34, p < 0.001$, males: $R^2 = 0.38, p < 0.001$; *A. sparganii*, females: $R^2 = 0.22, p < 0.05$, males: $R^2 = 0.01, p =$ NS). In other years within-year variation in 0food plant performance was lower. Still the associations between pupal weights and height of shoots were all positive though not significant.

Effect of host size on parasitoid size

Within-year comparisons in 1997 showed positive relationships between pupal weights of *N. typhae* and weights of its parasitoids: larger parasitoids came from plots with larger *N. typhae* (Fig. 5a-c). The association was significant for *E. occupator* and *Ch. paludator* but not for *S. limnophilus*. Similar results were obtained when year averages were compared: in years with larger hosts, all three parasitoids achieved a larger size on average (Fig. 6a-c). Differences among years in body size were significant in male *E. occupator* (ANOVA: d.f. = 3, $F = 5.41, p < 0.01$), female *Ch. paludator* (d.f. = 2, $F = 7.83, p = 0.001$) and *S. limnophilus* (d.f. = 3, $F = 3.53$, $p < 0.05$), and almost significant in females of *E. occupator* (d.f. = 3, $F = 2.65, p = 0.053$). These results are in good agreement with those of an earlier study of the system (Teder *et al.*, 1999), which demonstrated that parasitoids emerging from *N. typhae* were larger on average than those that developed on the smaller host species, *A. sparganii*. Moreover, while female *N. typhae* were larger than males by

≈ 30%, parasitoids emerging from females attained larger sizes than those that developed from males (Teder *et al.*, 1999).

Effect of plant vigour on parasitoid size

Variation in height of *T. latifolia* had a substantial influence on the adult size of parasitoids (presumably mediated by host size). Within-year comparisons showed significant positive associations between plant vigour and adult size of *E. occupator* (Fig. 5d) and *Ch. paludator* (Fig. 5e). A positive response to plant vigour was also observed in *S. limnophilus* but the association was not significant (Fig. 5f). Among-year comparisons gave similar results: both sexes of all three parasitoids showed a positive response to plant vigour, the associations being strongest in males and females of *E. occupator* and females of *Ch. paludator* and *S. limnophilus* (Fig. 6d-f).

Comparison of body size variation in moths and parasitoids

Indices of plant vigour (height of shoots and proportion of generative shoots) had a positive influence on the size of both moths and their parasitoids, however the slopes of all regression lines (type II) estimating the relationship between pupal weights of moths and adult weight of parasitoids showed values below unity (Fig. 5a-c and 6a-c). This indicates a weaker relative response of parasitoids to environmental variation across the study plots: e.g. a 10% increase in moth weight corresponded to less than a 10% increase in parasitoid weight. Within-year comparisons accorded well with among-year results (Figs 5a-c and 6a-c).

Additionally, an ANOVA was used (see Methods) to compare the effect of plant variation on moth and parasitoid body size directly. All the parasitoids consistently exhibited a weaker response to changes in plant quality than did *N. typhae* moths; the effect attained significance for the most numerous parasitoid, *E. occupator* (interaction between height of shoots and species: d.f. = 646, $t = -2.41$, $p < 0.05$).

Effect of body size on fecundity in moths and parasitoids

It was possible to assess potential fecundity in the studied moths but not in the parasitoids. In the moths collected as pupae in the field, body size and the number of eggs were correlated strongly and positively: a twofold difference in pupal weight caused a slightly less than twofold difference in the number of eggs (Fig. 7). Ovaries of studied parasitoids start developing after overwintering with the increase in temperature (Hinz, 1983). No eggs could therefore be found in the abdomens of females that emerged in the autumn. All three parasitoids are synovigenic: their eggs mature throughout adult lives.

DISCUSSION

Performance of *T. latifolia*, both when measured as height of shoots and proportion of generative shoots, was found to vary widely both spatially and temporally. This is in accordance with earlier studies showing that performance of *T. latifolia* is sensitive to various environmental factors, e.g. shading (Grace & Wetzel, 1981) and water depth (Grace & Wetzel, 1982). The high variability in host plant quality induced strong cascading effects on performance of higher trophic levels — herbivores and parasitoids. The indices of food plant vigour and body sizes of studied moths were found to be correlated strongly and positively (Figs 3 and 4), thereby supporting the plant vigour hypothesis (Price, 1991). The influence of plant parameters was consistent both among years and among patches within a year. Moreover, the responses of the two herbivores were notably similar. It is thus concluded that host plant vigour represents a major and predictable determinant of moth performance in the studied system. A positive correlation between plant vigour and herbivore performance is, however, not ubiquitous (Mattson & Haack, 1987, and references therein). The strong positive correlations observed in the present study can presumably be ascribed to the high growth rate of *T. latifolia* (Prach & Wade, 1992; T. Teder and T. Tammaru, pers. obs.). Fast-growing plant species generally have lower levels of defence against herbivores than do plants with a slow growth rate; positive effects of plant vigour are thus more likely to occur (Herms & Mattson, 1992; Loehle, 1996; Zangerl *et al.*, 1997).

Price *et al.* (1980) stressed that studies on population dynamics of herbivorous insects should, in addition to plant-herbivore interactions, consider three-trophic-level cascading phenomena. The work reported here demonstrates that the size of both moths (Figs 3 and 4) and parasitoids was related positively to plant vigour (Figs 5d-f and 6d-f). As far as population dynamics is concerned, however, the relative extent of this effect on the two trophic levels is what matters. This study showed that the effects of plant vigour on insect size were consistently stronger in moths than in their parasitoids (Figs 5a-c and 6a-c). As such, this difference does not necessarily imply similar biases in reproductive potentials as the effect of body size on fitness may vary among taxa. To derive conclusions about population dynamics, it is also necessary to examine the dependence of expected realised fecundity on body size in the species involved.

In insects, the body size–fitness relationship appears to depend on the presence of adult feeding. The potential fecundity of capital breeders (vs. income breeders; terminology first used by Drent & Daan, 1980), i.e. species with non-feeding adults, is typically correlated strongly with female body size (Istock, 1967; Honěk, 1993; Tammaru & Haukioja, 1996; Taylor *et al.*, 1998). The strength of this relationship is apparently based on two complementary mechanisms. First, in a non-feeding adult, reproductive potential is limited by the resources accumulated during the larval stage (≈ pupal weight). Second, due to relatively simple reproductive behaviour and short life-time of capital breeders, there tends to be a straightforward link between potential and realised fecundity in those insects (Tammaru & Haukioja, 1996; Tammaru *et al.*, 1996). In contrast, the relationship between body size and realised fecundity in income breeders (i.e. insects in which adult feeding is crucial for reproduction) is often shown to be less clear (e.g. Karlsson & Wiklund, 1984; Braby & Jones, 1995). The fecundity of these insects depends primarily on resources available for adults rather than weight at eclosion. Long adult life and complex reproductive behaviour of income-breeding insects further obscure the physiological link between large size and fecundity in complex environments: realized fecundity may be very different from potential fecundity (Leather, 1988; Tammaru & Haukioja, 1996).

The studied moths, *N. typhae* and *A. sparganii*, do not feed as adults, being thus capital breeders. The number of eggs as the index of potential fecundity is therefore presumably a satisfactory measure of their realised fecundity. The parasitoids in this system, on the other hand, represent income-breeding hymenopterans (Hinz, 1983, 1991; T. Teder, pers. obs.). In addition to dependency on resources for adult feeding, several features common to parasitoids' life histories may weaken further the relationship between body size and potential fecundity in these insects compared with their capital-breeding hosts (Hardy *et al.*, 1992; Ellers & van Alphen, 1997). If the period when hosts are vulnerable to parasitoid attacks is short, the relationship between body size and realised fecundity is presumably weakened as parasitoids have to share time between feeding, searching for hosts and ovipositing. Moreover, the realised fecundity of parasitoids depends critically on the encounter rates with suitable hosts, the distribution of which may vary both spatially and temporally. A straightforward link between resource level and reproductive success can thus be expected in capital breeders, the things being quite different in income breeders. Such a difference can have consequences for community and population dynamics: bottom-up regulation is more likely in capital breeders.

Weaker plant quality–body size and body size–fitness relationships suggest that, in terms of fitness, the studied parasitoids gained less from an increase in plant vigour than did the moths. This implies that the numerical response of the herbivore population to a change in plant quality should exceed the response of the parasitoids. Thus, a favourable change in the quality of *Typha* should, in the short term, lead to increased population densities of the moths and lower total parasitism rates. This study showed that in *T. latifolia* substantial and rapid changes in vigour are possible: in the years of 1995 and 1996 there was a more than twofold difference in height of shoots. A direct documentation of the effects of plant quality on the transgenerational dynamics of the insect community would, however, require longer time series.

Tammaru and Haukioja (1996) discussed factors that may explain the relatively frequent occurrence of eruptive dynamics in capital-breeding herbivorous insects compared with income breeders. The work reported here hints at a possible additional explanation for this tendency. If a capital-breeding herbivore is attacked by an income-breeding parasitoid(s), a rapid increase in plant quality may affect herbivore fitness to an extent where its population may escape the regulation by parasitoids. This would be the case due to a weaker corresponding numerical response of the parasitoid population to plant quality. The results thus imply that adult feeding in both herbivores and their parasitoids may be an important aspect to consider in the population dynamics of host–parasitoid systems in general. This logic may well be reversed in a system where an income-breeding herbivore is attacked by a capital-breeding parasitoid: a change in plant quality may then have a stronger effect on the reproductive potential of the parasitoid population.

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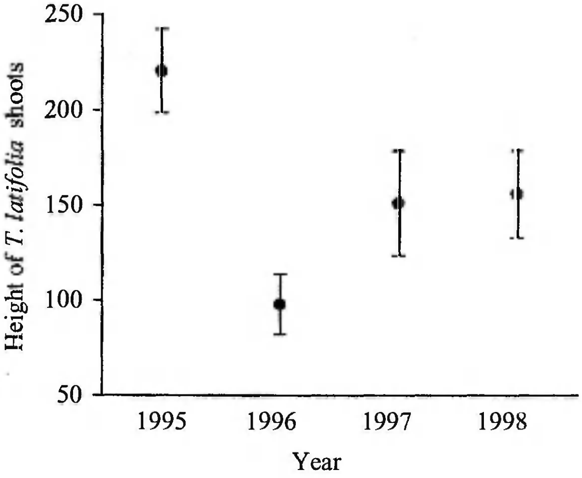

Fig. 1. Among-year variation in the height of *T. latifolia* shoots. Error bars indicate SD.

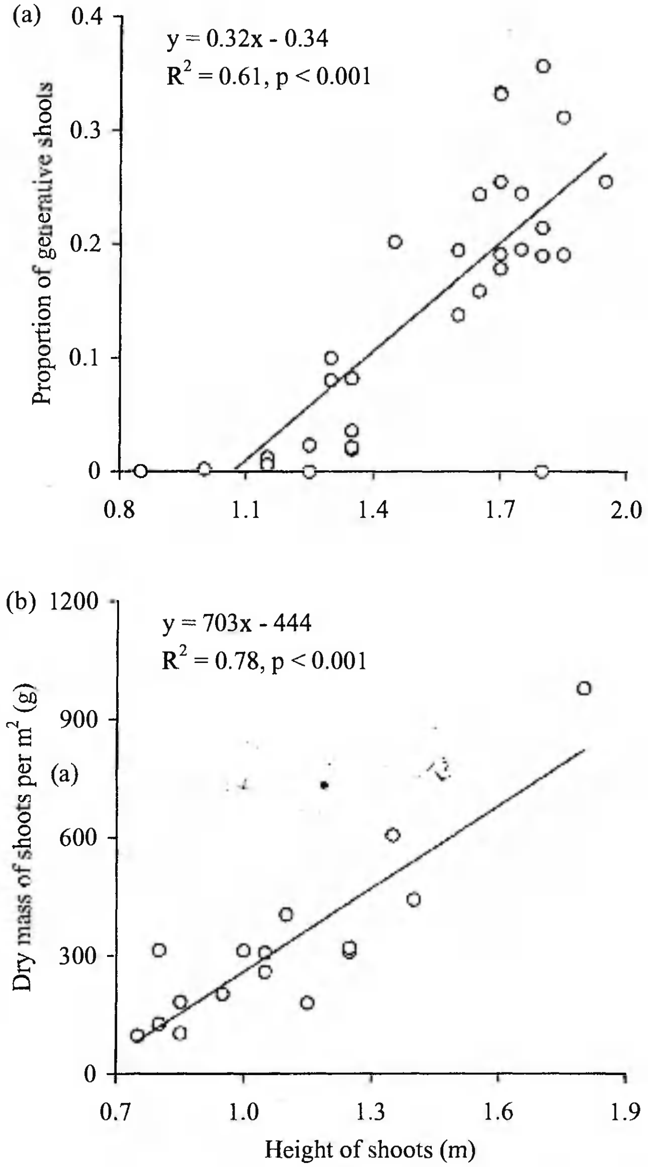

Fig. 2. (a) The relationship between height of *T. latifolia* shoots and proportion of generative shoots in plots in 1997 and (b) the relationship between height of *T. latifolia* shoots and their dry biomass per m^2 (samples were taken from the studied stand in 1997).

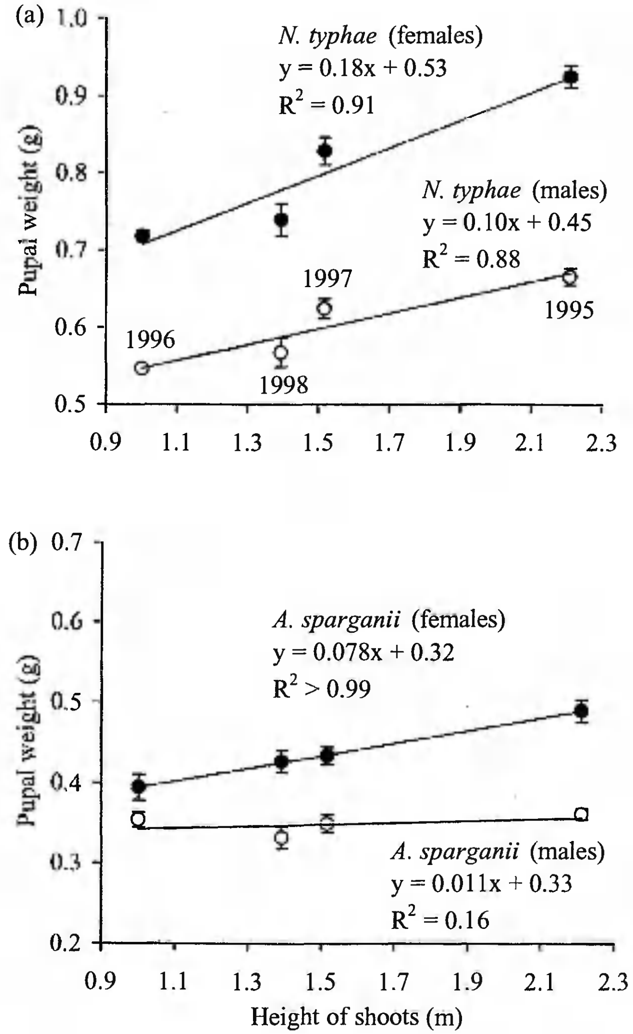

Fig. 3. Among-year relationships between height of *T. latifolia* shoots and pupal weight of the herbivores (a) *N. typhae* and (b) *A. sparganii*. Each point represents the mean value of plot averages in 1 year. Error bars indicate SE. Statistics are for type I regression.

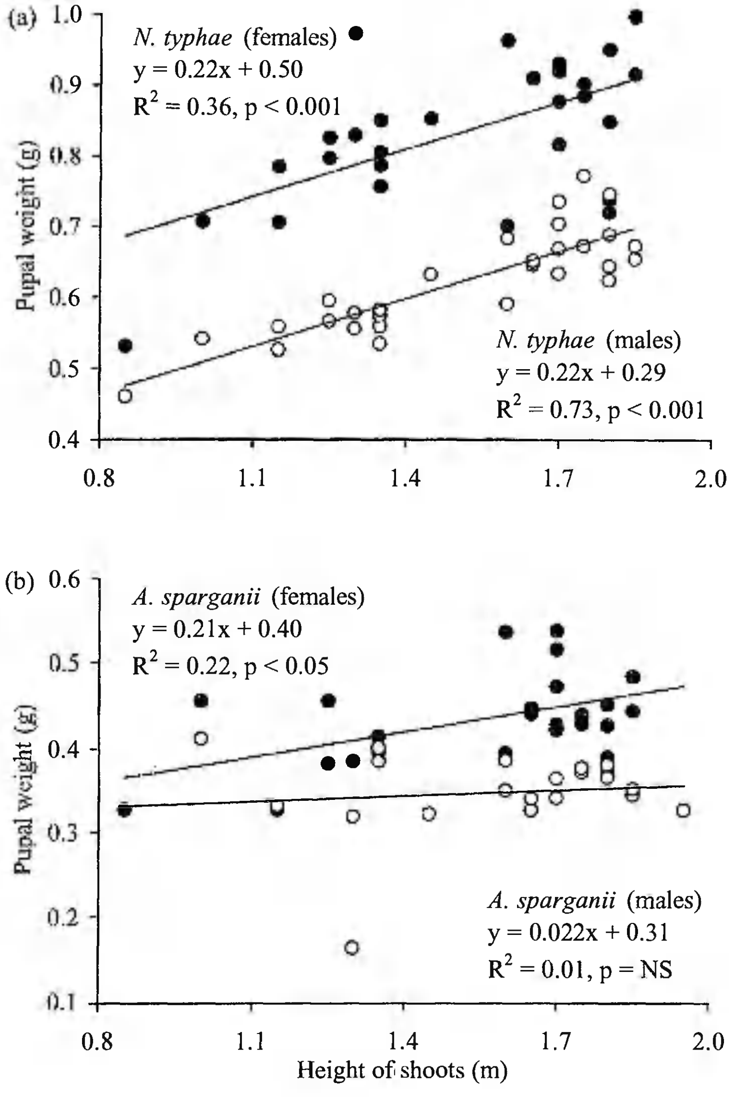

Fig. 4. Within-year (1997) relationships between height of *T. latifolia* shoots and average pupal weight of (a) *N. typhae* and (b) *A. sparganii*. Each point represents one study plot. Statistics are for type I regression.

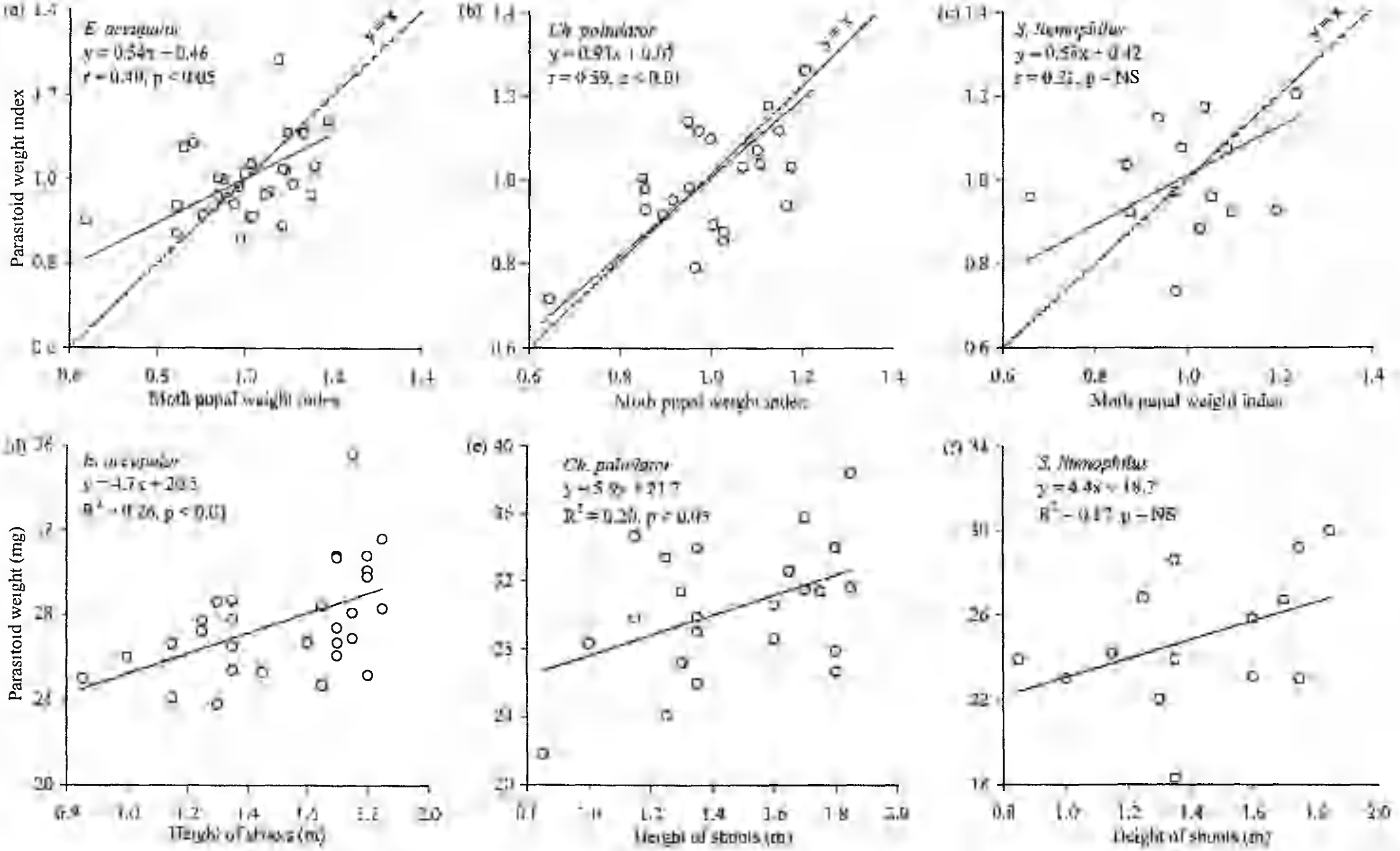

Fig. 5. (a - c) Within-year (1997) relationships between pupal weight of *N. typhae* and dry adult weight of studied parasitoids. Pupal weight and parasitoid weight are expressed in relation to the overall mean of the respective variable. The solid lines and equations correspond to type II regressions, r and p values are those of Pearson correlations. The dashed lines presented for reference would correspond to equal relative increase in weights with environmental conditions improving. (d - f) Within-year relationships between height of *T. latifolia* shoots and dry adult weight of studied parasitoids. Statistics and equations are for type I regression. Each point represents one study plot.

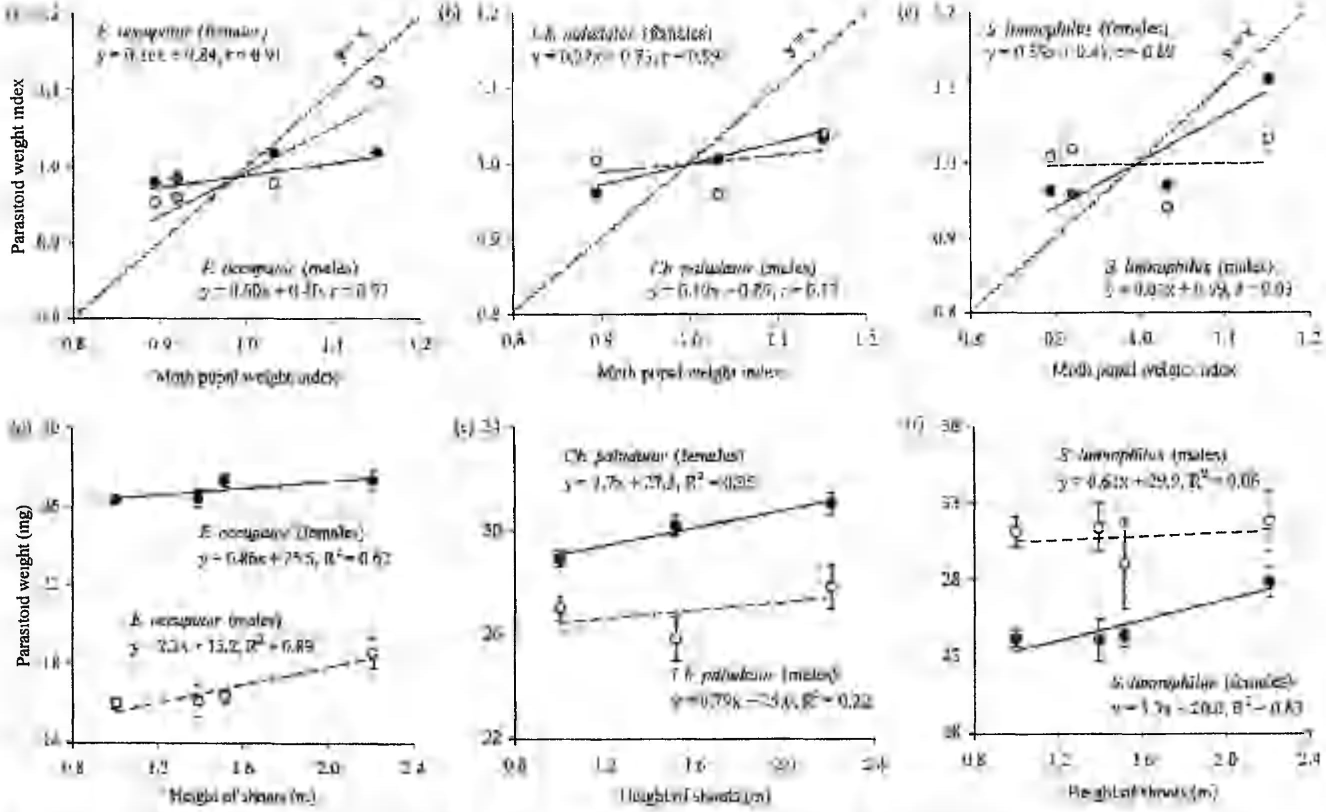

Fig. 6. (a – c) Among-year relationships between pupal weight of *N. typhae* and dry adult weight of studied parasitoids. Each point indicates a mean value of plot averages in the respective year. Pupal weight and parasitoid weight are expressed in relation to the mean value of the study years. The solid (●, females) and dashed lines (○, males) and equations correspond to type II regressions. r and p values are those of Pearson correlations. The diagonal lines (y = x) presented for reference would correspond to equal relative increase in weights with environmental conditions improving. (d – f) Among-year relationships between height of *T. latifolia* shoots and dry adult weight of studied parasitoids. Statistics and equations are for type I regression. Each point represents 1 study year. Error bars indicate SE of plot means.

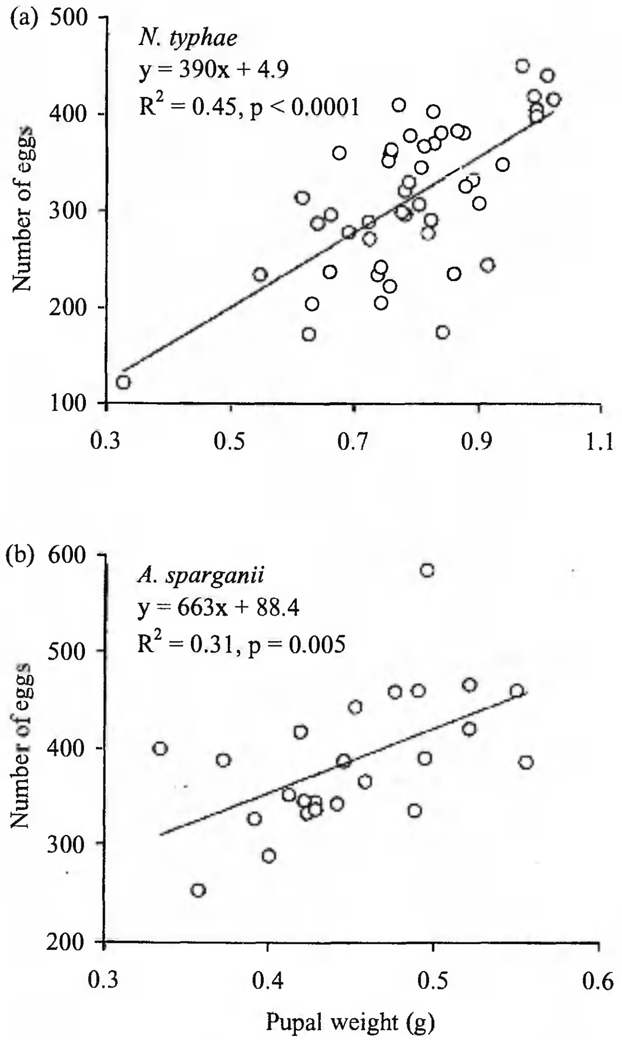

Fig. 7. Relationships between pupal weight and number of eggs in studied moths (N = 48 for *N. typhae*, N = 24 for *A. sparganii*).

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INDIRECT INTERACTIONS BETWEEN INSECT HERBIVORES MEDIATED BY SHARED PARASITOIDS: THE INFLUENCE OF RELATIVE ABUNDANCE AND PHENOLOGY OF THE SPECIES

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ABSTRACT

Despite the impact of parasitoids on insect populations being extensively studied, parasitoid-mediated indirect effects remain scarcely documented in natural communities. The aim of this work was to examine the influence of shared parasitoids on the interactions between two functionally monophagous moths, *Nonagria typhae* and *Archanara sparganii*. The moths showed a considerable spatial and temporal variation in terms of relative abundance and the degree of phenological synchrony between the species. Levels of the parasitism also varied considerably, percentage parasitism of the scarcer species, *A. sparganii*, was not proportional to that of the dominant species, *N. typhae*. *A. sparganii* appeared to benefit from the presence of *N. typhae*. In particular, both low relative density as well as high phenological synchrony with *N. typhae* reduced parasitism levels in *A. sparganii*. Percentage parasitism of the dominant species, *N. typhae*, on the contrary, was not affected by the presence of *A. sparganii*. The results remained qualitatively consistent both when total parasitism or parasitism by single parasitoid species was considered. The patterns of host use observed in this study are consistent with the scenario of frequency-dependent host use caused by changes in parasitoid behaviour (host switching). Frequency-dependent host use by parasitoids is suggested to promote numerical stability and coexistence of the species in the system studied. Parasitism may also have a selective influence on *A. sparganii* life-history favouring dispersal and shaping timing of development..

Key words: apparent competition, apparent mutualism, indirect amensalism, coexistence, indirect effects, host switching, Ichneumonidae, Noctuidae.

INTRODUCTION

An interaction between two species is called indirect when the effects of one species on another are mediated by some third species (Strauss, 1991; Wootton, 1994). Indirect effects may arise either through the functional (short-term effects) or the numerical response (long-term, or transgenerational effects) of the natural enemy. Short-term apparent mutualism may arise as a consequence of predator's satiation: functional response of the natural enemy may become saturated as prey densities increase (Holt, 1977; Abrams & Matsuda, 1996). Short-term apparent competition, in turn, is expected when the functional response of the natural enemy on the increase of one host species leads to a higher mortality rate of the coexisting species. For apparent competition to occur, the natural enemy should be prey-limited and respond to the total density of the victim species (Holt, 1977, 1987; Bonsall & Hassell, 1999). Asymmetric indirect interactions assume that prey species vary in some aspects essential for the interaction, e.g. in vulnerability, quality, feeding biology or phenology (Chaneton & Bonsall, 2000).

Enemy-mediated indirect effects have been suggested to play a significant role in natural communities affecting community structure and population dynamics of species involved (Jeffries & Lawton, 1984; Holt & Lawton, 1994; Müller & Godfray, 1999). However, the empirical evidence on such effects is still scarce (Bonsall & Hassell, 1999; Chaneton & Bonsall, 2000). In a recent review, Chaneton & Bonsall (2000) found as few as 21 studies addressing questions about, or interpreting results, in the context of apparent competition. The evidence on apparent mutualism and positive, non-reciprocal indirect effects in communities is even more scattered and comes mainly from herbivore-mediated interactions between plants (Houston *et al.*, 1993; Olofsson *et al.*, 1999).

Interspecific interactions between coexisting herbivorous insects can be mediated both by lower (host plant) and higher (natural enemies) trophic levels. While host-plant-mediated effects are usually mutually negative (resource competition), the type and strength of indirect interactions mediated by shared predators or parasitoids are less obvious. The outcome — are the interactions mutually positive (apparent mutualism), mutually negative (apparent competition), or non-reciprocal (indirect amensalism) — is suggested to depend on various factors, e.g. foraging behaviour of the natural enemies, relative feeding habits or competitive abilities of victim species (Jeffries & Lawton, 1984; Holt, 1987; Holt & Kotler, 1987; Holt & Lawton, 1994; Abrams *et al.*, 1998).

In the case of coexisting herbivorous insects, parasitoids have probably the greatest potential of mediating indirect effects between species. The type and strength of parasitoid-mediated indirect interactions are presumably sensitive to the composition of parasitoid community. This is because of a high diversity of life-histories (e.g. koinobionts vs idiobionts, ectoparasitoids vs endoparasitoids) and diverse behavioural repertoire (host preference, host switching etc.) among parasitoids. Empirical studies on various systems are therefore required to understand how widespread may parasitoid-mediated indirect effects be in natural communities, and which factors influence the expression of such effects.

In the present field study, we demonstrate a pattern consistent with parasitoid-mediated amensal interactions between a pair of insect herbivores exploiting a common host plant. Studied species are functionally monophagous and their parasitoids lack alternative host species in the study areas. In its relative isolation, the system is thus well suitable for examining indirect interactions in the field. We analyse possible factors that influence the expression of indirect interactions in this system. For this purpose, we compare species-specific levels of parasitism with respect to relative abundance and phenology of the host species. Finally, we discuss possible consequences of the detected indirect interactions on the population dynamics and the life-history of particular moth species, and community structure.

MATERIAL AND METHODS

Study species

The study system was based on *Typha latifolia* (Typhaceae), a rhizomatous perennial plant up to 3 m in height forming dense stands in damp sites. Larvae of four moth species have been found feeding on leaves and stems of *T. latifolia* (Teder *et al.*, 1999; Teder & Tammaru, 2001). This study was, however, restricted to the two most abundant species, *Nonagria typhae* Thunb. and *Archanara sparganii* Esp. (Lepidoptera: Noctuidae). The proportion of other species remained < 1% of all sampled larvae. Studied species are close taxonomically and have a high resemblance in feeding biology and phenology. They overwinter as eggs that hatch in spring. At the beginning of the season larvae feed on the aerial roots of the host plant, while later they switch to endophytic feeding on the shoots (Galichet *et al.*, 1992). One larva usually feeds on more than one shoot during its development. Larvae of *N. typhae* are monophagous on *T. latifolia*, while larvae of *A. sparganii* may also use some other species (Skou, 1991), however, in the studied areas both species were apparently functionally monophagous on *T latifolia*. At the end of July or at the beginning of August larvae pupate (*A. sparganii* somewhat earlier than *N. typhae*) inside the shoot or between the leaves of the host plant. The pupal period lasts for about month in both species. The short-living adults do not feed.

Two principal species of solitary parasitoids, the koinobiont *Spilichneumon limnophilus* Thoms. and the idiobiont *Chasmias paludator* Desv. (Hymenoptera: Ichneumonidae), were found to parasitise larvae and pupae of both *N. typhae* and *A. sparganii*. A third species parasitising both moths, *Vulgichneumon saturatorius* L., was rare in most years. These three species were treated as the *shared parasitoids* in the analyses. The most numerous parasitoid of *N. typhae*, *Exephanes occupator* Grav., parasitises *A. sparganii* only occasionally (Teder *et al.*, 1999): in most years of this study no individual *A. sparganii* was parasitised by this species. Other parasitoids, treated here as *non-shared*, accounted for <1% of the total parasitism. Like their hosts, studied parasitoids have univoltine life cycles. Adult females overwinter and lay their eggs on moth larvae in late spring / early summer (*E. occupator*; Hinz & Horstmann, 2000; and probably also *S. limnophilus* and *V. saturatorius*) or on fresh pupae in July and early August (*Ch. paludator*; Hinz, 1983; Hinz & Horstmann, 1999). Adult wasps emerge more or less simultaneously with unparasitised moths (*E. occupator* somewhat earlier). All three parasitoids are oligophagous and are also known to parasitise some other moths (Rasnitsyn & Siitan, 1981; Hinz & Horstmann, 1999, 2000) which, however, apparently constitute only a minor fraction of hosts in the habitats studied.

Study areas

This work was conducted in 6 consecutive years (1995–2000) in southeastern Estonia. Three habitats differing with respect to heterogeneity of the vegetation pattern were examined. The habitat studied in 1995–1996 was characterised by a dense, almost monospecific stand of *T. latifolia*. The vegetation of the habitat examined in 1997–1998 was more heterogeneous with patches of *T. latifolia* and *Carex elata* Bell. ex All. alternating. Both these habitats (with areas of ≈3 and ≈4 ha, respectively) were located in the town of Tartu (58°22' N, 26°45' E), on the flooded meadow of the Emajõgi River. The third habitat, studied in 1998–2000 was still much more heterogeneous with respect to *T. latifolia* abundance: the patches of *T. latifolia* (mostly from 0.01 to 0.05 ha, few patches over 0.1 ha; small ponds, ditches, and other damp places) were separated by distances of 0.2–1.0 km. This study area was located in an agricultural landscape, in the surroudings of the Lake Pangodi (58°12' N, 26°35' E), 20 km southwest of Tartu. The samples collected from Tartu and Pangodi in the year of 1998 were treated as independent (different 'years') in the analyses at the level of yearly means.

Sampling

Field populations were sampled to obtain data on the distribution of moths and the levels of parasitism. Sampling was conducted at the end of July and/or the beginning of August, when moths were in the pupal stage. A variable fraction of *A. sparganii* pupae (2–51%) had eclosed by the day of collection. Similarly, a variable, but relatively small fraction of *N. typhae* specimens (4–21%) were collected as larvae. The fractions of individuals collected before or after the pupal period in a particular year were treated as indices reflecting the phenology of the species (see below for details). Each year, samples from 12–33 plots (173 in total) were collected; in the habitats located in Tartu, samples were taken from the plots of 2 × 2 m, 3 × 3 m or 4 × 4 m (depending on larval abundance in the particular year), while in the most heterogeneous habitat at least 30 individuals per each site (one plot per each site) were sampled. From study plots, moth pupae were collected by inspecting all shoots carefully. The pupae were relatively large (2.0–3.5 cm in length), potential pupation sites were limited, and damaged shoots were easily distinguishable from undamaged shoots, so it was possible to collect nearly all pupae from the plots. The number of pupae collected in one year varied from 356 to 2684 (6935 individuals in total; 745 *A. sparganii* and 6190 *N. typhae*). Pupae were stored in Petri dishes until eclosion of the adult moth or the parasitoid. For *A. sparganii* individuals collected as exuviae, it was always possible to determine whether a moth or a parasitoid (and nearly always, which of the two parasitoids) had been emerged. The fate (parasitised / unparasitised) of the specimens (mainly *N. typhae*) that died in the laboratory in the early pupal stage could not be determined; they were thus omitted from calculations and analyses (5–10% of specimens per year).

Data analysis

Relative levels of parasitism in *A. sparganii* and *N. typhae* were analysed with respect to relative abundance of the moths and their relative phenological distribution. As the purpose of this study was to examine parasitism-mediated indirect effects, all the calculations and analyses were restricted to plots in which both *A. sparganii* and *N. typhae* were found. For the same reason, only parasitism caused by *shared* parasitoids was considered in the analyses. In *A. sparganii*, shared parasitoids accounted for most of the parasitism. In contrast, for *N. typhae* a considerable fraction of individuals parasitised by the non-shared *E. occupator* were re-classified as non-parasitised for the analyses. The dependent variable, *relative parasitism* of the two host species was expressed as the ratio of the fractions of parasitised *A. sparganii* and

N. typhae per sample (or per year, in the among-year comparisons). For example, if in a particular plot, percentage parasitism of *A. sparganii* was 12% and that of *N. typhae* was 30%, the corresponding index of relative parasitism was 12 / 30 = 0.4. The use of this relative measure was chosen to eliminate the effect of overall parasitoid abundance. Analogously, *relative abundance* of the two moths implies the ratio of the numbers of *A. sparganii* and *N. typhae* collected from one plot, or in the same year.

To derive an index describing annual differences in phenology of the two moths, the study years were ranked according to 1) the percentage of adults among *A. sparganii* (found as exuviae) on the day of sampling, and 2) the percentage of larvae among *N. typhae* on the day of sampling. The value '1' was assigned to the year of the highest proportion of adults among *A. sparganii*, and to the year of the lowest proportion of larvae among *N. typhae*, both these ranks indicating the earliest phenologies. Accordingly, the value '7' indicated the latest phenologies. The *relative phenology index* for a particular year was calculated by subtracting the rank of *A. sparganii* from the corresponding rank of *N. typhae*. The larger was the index obtained in this way, the larger was the difference in phenological distributions of the two species.

Linear regression and ANOVA were used to examine the relationships at the level of yearly means. Logistic regression was applied to study the association between relative abundance of the moths and parasitism levels at the level of study plots (PROC GENMOD; SAS Institute Inc., 1995). Binomial proportion (parasitised moths / total number of moths, collected from one plot, the moth species were treated separately) was used as the response variable. Binomial probability distribution was assumed, logit was chosen as the link function, DSCALE option was applied to correct for overdispersion. Relative abundance of the moths was used as the independent variable. Two alternative models applied to the same data set were fitted, one with, and another without, study year as an additional factor. Due to small sample sizes, a calculation of relative phenology indices for the individual plots would have been meaningless, therefore no plot-level analyses examining the association between relative phenology and parasitism levels were performed.

RESULTS

Relative abundance of *A. sparganii* and *N. typhae* was highly variable both among years and patches within years. The annual index of relative abundance of the two species (the number of *A. sparganii* divided by the number of *N. typhae*) fluctuated from 0.03 to 0.46. *A. sparganii* was also nearly always less abundant than *N. typhae* on particular study plots: only 6.9% of samples (12 out of 173) comprised more *A. sparganii* than *N. typhae*. In 24.3% of samples (42 out of 173), no *A. sparganii* was found, while *N. typhae* was always present. The levels of parasitism varied both between the host species and within the species. Annual values of the total percentage parasitism fluctuated from 5.8% to 38.5% in *A. sparganii* and from 23.5% to 68.1% in *N. typhae*, *A. sparganii* being always less parasitised than *N. typhae* (Fig. 1). When only shared parasitoids were considered, the percentage parasitism of *N. typhae* dropped to the range of 7.0% to 33.2%; parasitism of *A. sparganii* changed only negligibly as it was caused mainly by shared parasitoids (Fig. 1). Variation in the parasitism levels by particular parasitoid species was also considerable (e.g. parasitism by *S. limnophilus* fluctuated from 2.6% to 19.2% in *N. typhae* and from 1.4% to 22.1% in *A. sparganii*).

Parasitism in *A. sparganii* was not wholly explained by parasitism levels of *N. typhae*, so additional determinants had to be involved. Linear regression analysis of annual mean values indicated that relative parasitism of the moths (shared parasitoids only, see methods) appeared to depend on their relative abundance (Fig. 2a). The relationships between relative abundance of the moths and percentage parasitism of particular species (Fig. 3) suggest that this effect can predominantly be ascribed to the variation in parasitism levels of *A. sparganii*, not *N. typhae*. A higher proportion of *A. sparganii* thus implies a higher parasitism risk for this species, while it does not imply a reduced parasitism risk for *N. typhae*. The effect of relative abundance on relative parasitism levels by particular parasitoid species consistently coincided with the overall trends (significant in the case of *S. limnophilus*; Fig. 2b-c). Relative phenology index correlated positively with relative parasitism levels caused by *S. limnophilus* (Fig. 4b). The association between relative phenology index and relative parasitism levels by all shared parasitoids and *Ch. paludator* were also positive but non-significant (Fig. 4a, 4c). Additionally, a two-way ANOVA was performed to examine the effects of relative abundance and relative phenology on relative parasitism jointly. Both variables appeared to have a significant effect on relative parasitism when all shared parasitoids were considered (Table 1).

In a complementary approach, a logistic regression analysis at the level of study plots confirmed that the incidence of parasitism in *A. sparganii* depended on relative abundance of the moths (Table 2). The effect of relative abundance on the total parasitism by shared parasitoids was positive and significant (Table 2). When parasitoid species were considered separately, relative abundance affected significantly parasitism by *S. limnophilus* (*d.f.* = 1, $\chi^2 = 11.1$, $p = 0.005$). In alternative models with the effect of study year removed, the focal relationships were qualitatively consistent but not quite significant (total parasitism: *d.f* = 1, $\chi^2 = 2.7$, $p = 0.1$; parasitism by *S. limnophilus*: *d.f.* = 1, $\chi^2 = 3.6$, $p = 0.058$). There was thus no conclusive evidence of the associations at the level of spatial variation independent of the among-year effects. For *N. typhae*, the effect of relative abundance on parasitism was non-significant both when total parasitism by shared parasitoids (Table 3) or parasitism by single species was considered.

The incidence of parasitism in *N. typhae* by the *pupal* parasitoid, *Ch. paludator*, might be somewhat underestimated because of the presence of moth larvae in the samples. This may lead to a potential systematic error when analysing the effects of phenology: the earlier the phenology, the larger the effect of the underestimation. It may be easily seen, however, that such an effect could create a negative correlation only while we saw a positive one.

DISCUSSION

The present results revealed a pattern that indicates the presence of indirect interactions in the form of parasitoid-mediated amensalism between two herbivores. The moths, *N. typhae* and *A. sparganii*, coexist in their habitat and share a common food plant. The species varied in their relative abundance both among patches and years. Moreover, the two hosts exhibited a considerable annual variation in the degree of phenological synchrony. Parasitism levels of the more abundant species, *N. typhae*, did not depend on relative abundance or phenology of the two species. Parasitism of the scarcer species, *A. sparganii*, on the contrary, being yearly highly variable, correlated both with relative abundance of the two moths as well as their relative phenology index. *A. sparganii* appeared thus to benefit from the presence of *N. typhae*. The present results can be seen as complementary to the findings of Teder and Tammaru (2001), who showed another form of indirect interactions in this system, a bottom-up trophic cascade, having a strong potential to influence population dynamics in *T. latifolia*-based tritrophic assemblages. The present study further emphasises the significance of considering indirect effects in natural communities.

The expression of indirect interactions in relation to relative abundance is likely to be explained by the consequences of a frequency-dependent host use by the parasitoids. Such a pattern of host use may result either from the host-frequency dependent changes in a) host's anti-parasitoid behaviour, or b) foraging behaviour of the parasitoids (i.e. host switching) (for a review, Sherratt & Harvey, 1993; van Alphen & Jervis, 1996). The mechanisms of the first type are unlikely in the present system: given the solitary, concealed life-style of the studied moths, an increase in the density hardly has a chance to change their defensive behaviour. Host switching in parasitoids is a more likely explanation. In the system studied switching might arise as a consequence of host-composition dependent changes in parasitoid experience: the higher the *A. sparganii* density, the greater the possibility for parasitoids to learn stimuli deriving from this species.

The studied system appears to meet the necessary preconditions for switching behaviour to evolve. In particular, relative abundance of different prey types should vary either spatially or temporally; predator should be mobile and use sensory systems for detecting prey from a distance (Cornell, 1976). In the present system, the relative abundance of the two moths varied both among patches and years; shared parasitoids are extremely mobile and can be met even in very isolated patches (T. Teder & T. Tammaru, pers. obs.). The latter pattern implies that parasitoids obviously use some sensory mechanisms to find host patches and concealed larvae and pupae of these moths. Moreover, both moths are quite abundant in absolute terms, they seem to be well suitable for both parasitoids, and their feeding biologies and phenologies are similar. Parasitoids are thus faced with an actual choice of different host species, and switching may appear to be favoured in this system. Such a complex of preconditions is seemingly rarely fulfilled in most natural systems as reflected by rare documentation of host switching in the field (see, however, Kato, 1994; Pike *et al.*, 1999), while repeatedly demonstrated under laboratory conditions (Cornell & Pimentel, 1978; Chow & Mackauer, 1991; Drost & Cardé, 1992).

Frequency-dependent host selection has been suggested to have significant consequences for the structure and dynamics of multispecies communities by promoting stability and coexistence of the species (Holt & Lawton, 1993; Bonsall & Hassell, 1999; Hassell, 2000). One of the most obvious consequences of parasitism in the studied system is its potential to stabilize *A. sparganii* population dynamics. Since the parasitoids exploited *A. sparganii* in a positively density-dependent manner, at lower densities parasitism levels appeared to be low, which should allow for *A. sparganii* populations to increase. As *N. typhae* populations maintain the density of parasitoids continuously high, the response of parasitoids to an increase in *A. sparganii* density occurs without a delay, a mechanism widely appreciated as promoting stable population dynamics in the host (Hassell, 2000). Host switching is potentially also a mechanism facilitating coexistence of the host species: coexistence of a pair of host species is possible only when either of them can increase when rare (Holt & Kotler, 1987). In the studied system, positively density-dependent parasitism accompanying with host switching provides such a mechanism for *A. sparganii*. Mechanisms promoting stability for the populations of *N. typhae* remain unclear.

From parasitoids' point of view, the relative abundance of a pair of hosts is not necessarily determined by their absolute numbers: host individuals of different ages are rarely equally vulnerable to parasitoid attacks (Briggs & Latto, 1996; Benrey & Denno, 1997). The risk of parasitism for the coexisting hosts might thus depend on the degree of synchrony in hosts' windows of vulnerability. If parasitoids forage for the hosts in a frequency-dependent manner, the rarer host may reduce parasitism risk being vulnerable to parasitoids simultaneously with the more abundant host. The present results are consistent with this scenario: smaller differences in the phenological distributions of the two hosts implied a reduced parasitism risk for *A. sparganii* (but not for *N. typhae*). Such a pattern may be seen as another indication of host switching in the studied system.

The observed patterns suggest that parasitism may have a selective influence on *A. sparganii* life-history. A survival advantage from being rare in relation to *N. typhae* should favour selection for females to disperse their offspring in patches with low incidence of conspecifics (see also van Baalen and Sabelis, 1993; Nagelkerke *et al.*, 1996; Hunter & Elkinton, 2000). Such a strategy should be advantageous for females as long as there are enough low-density patches (Nagelkerke *et al.*, 1996). In the studied system, density-dependent parasitism (and, presumably, other factors) maintain *A. sparganii* density at the level, where dispersing progeny could seemingly be adaptive: *A. sparganii* density was in nearly all patches lower than *N. typhae* density. This might explain why *A. sparganii* has not evolved towards reduced female flight ability, as it is typical for most capital-breeding lepidopterans (Tammaru & Haukioja, 1996). Additionally, parasitism, dependent on the relative phenology of the hosts, has potentially a selective influence on the timing of life-cycle in *A. sparganii*. The individuals being vulnerable at the peak of window of vulnerability of *N. typhae*, gain a survival advantage.

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Table 1. Results of two-way ANOVA (type III sums of squares) examining the effect of relative abundance of *A. sparganii* and *N. typhae* and their relative phenology index on the relative levels of parasitism. The response variable was percentage parasitism at the level of annual means.

Effect	*df*	*SS*	*F*	*p*
Total parasitism caused by shared parasitoids				
Relative abundance of the two moths	1	1.75	18.2	0.01
Relative phenology index	1	0.81	8.4	0.04
Error	4	0.38		
Parasitism caused by S. limnophilus				
Relative abundance of the two moths	1	0.04	0.6	0.46
Relative phenology index	1	0.59	10.1	0.03
Error	4	0.24		
Parasitism caused by Ch. paludator				
Relative abundance of the two moths	1	16.0	6.0	0.07
Relative phenology index	1	7.5	2.8	0.17
Error	4	10.8		

Table 2. Results of logistic regressions (significance tested by type I analyses) examining the effect of the relative abundance on the parasitism levels in *A. sparganii*. Two alternative models applied to the same data set were fitted with a) percentage parasitism of *N. typhae* as an additional factor, and b) year and percentage parasitism of *N. typhae* as the additional factors. The response variable was percentage parasitism at the level of study plots.

Effect	*df*	χ^2	*p*
Total parasitism caused by shared parasitoids [a]			
Corresponding percent parasitism of *N. typhae*	1	17.1	<0.001
Relative abundance of the two moths	1	5.6	0.02
Total parasitism caused by shared parasitoids (year as an additional factor) [b]			
Year	6	62.5	<0.001
Corresponding percent parasitism of *N. typhae*	1	8.0	0.005
Relative abundance of the two moths	1	2.7	0.1

Dispersion estimates (deviance divided by the degrees of freedom) for data used in logistic analyses: [a]Dev./DF = 1.20; [b]Dev./DF = 1.53

Table 3. Results of logistic regressions (significance tested by type I analyses) examining the effect of the relative abundance on the parasitism levels in *N. typhae*. Two alternative models applied to the same data set were fitted a) with no additional factors, and b) with year as an additional factor. DSCALE option is used to correct overdispersion (SAS Institute Inc., 1995). The response variable was percentage parasitism at the level of study plots.

Effect	*df*	χ^2	*p*
Total parasitism caused by shared parasitoids			
Relative abundance of the two moths	1	1.5	0.2
Total parasitism caused by shared parasitoids (year as an additional factor)			
Year	6	73.4	<0.001
Relative abundance of the two moths	1	0.3	0.6

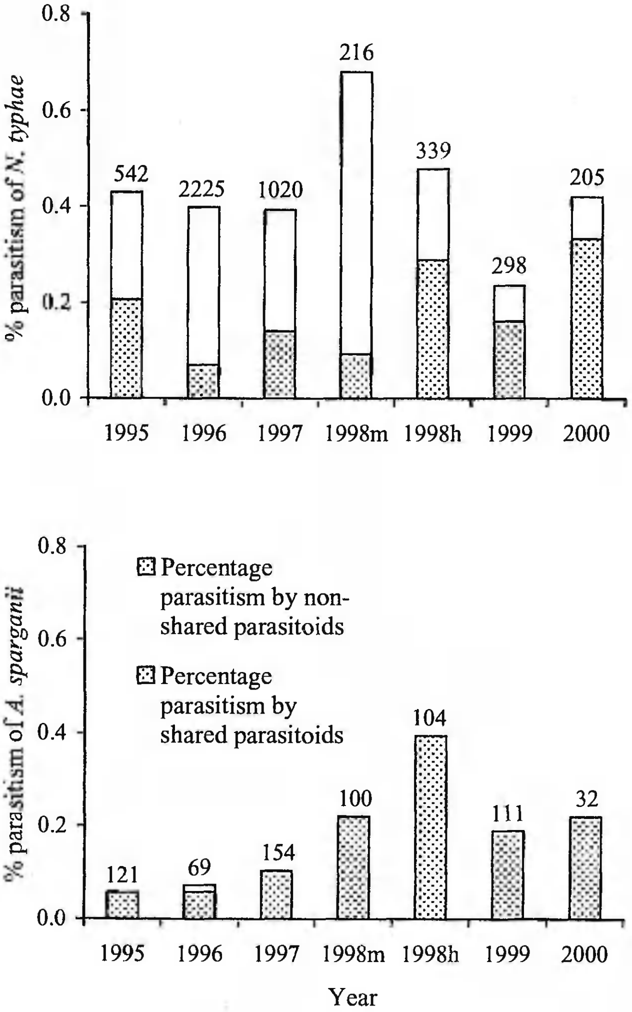

Fig. 1. The levels of shared and total parasitism in *A. sparganii* and *N. typhae* in the study years (1998m - samples collected in Tartu, 1998h - samples collected in Pangodi, see text for details). Sample sizes are presented above the bars.

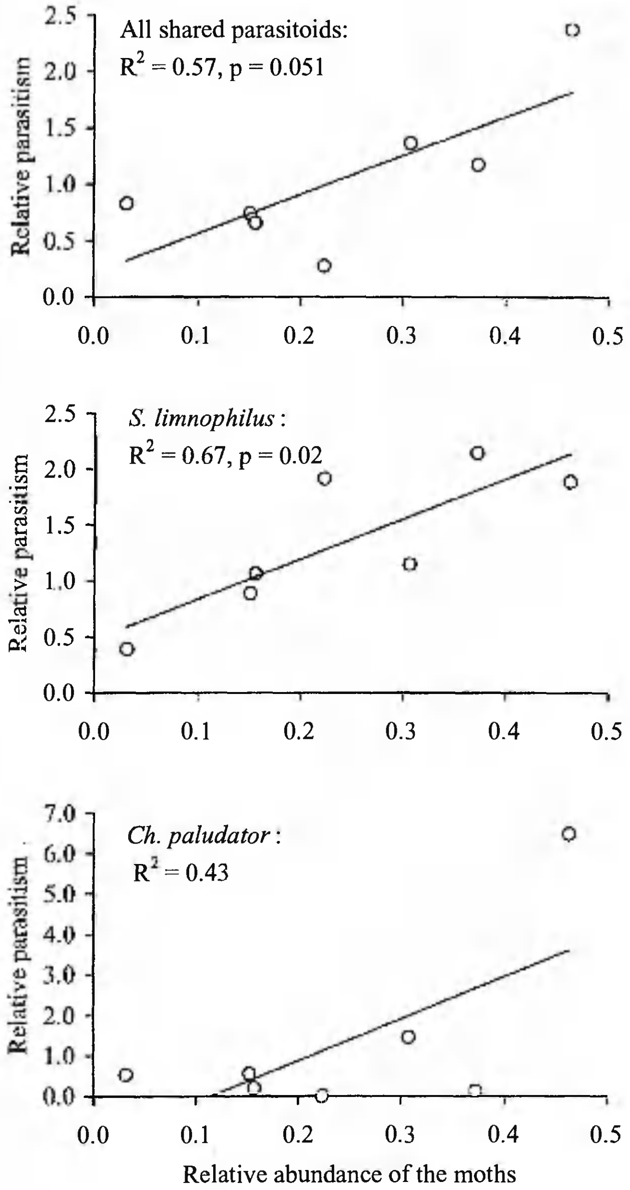

Fig. 2. The relationships between relative abundance of the moths (the ratio of the numbers of *A. sparganii* and *N. typhae* collected in the same year) and relative parasitism (the ratio of the fractions of parasitised *A. sparganii* and *N. typhae* per year) at the level of annual means. A *p*-value for *Ch. paludator* would be meaningless due to obvious heteroscedasticity.

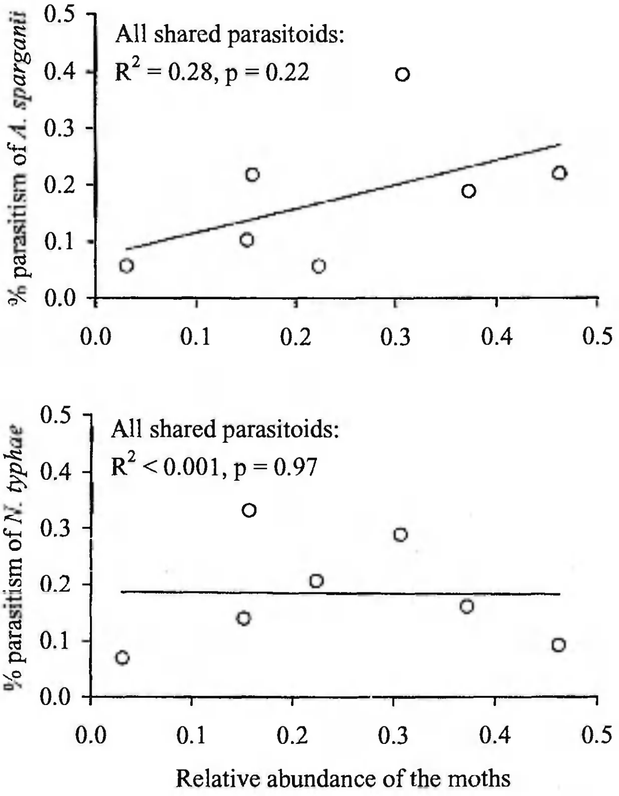

Fig. 3. The relationships between relative abundance of the moths and percentage parasitism of *A. sparganii* and *N. typhae.*

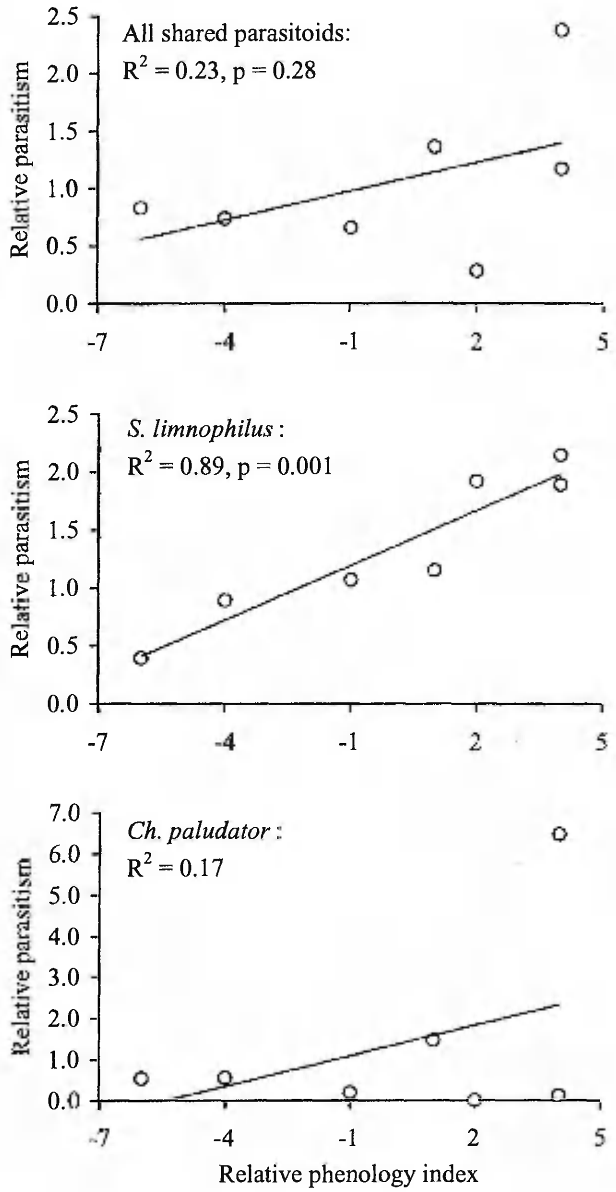

Fig. 4. The relationships between relative phenology index (the larger the index, the larger the difference in phenological distributions of the two species) and relative parasitism (the ratio of the fractions of parasitised *A. sparganii* and *N. typhae* per year) at the level of annual means. A p-value for *Ch. paludator* would be meaningless due to obvious heteroscedasticity.

IV

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Temporal and spatial variation of larval parasitism
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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 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 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%.

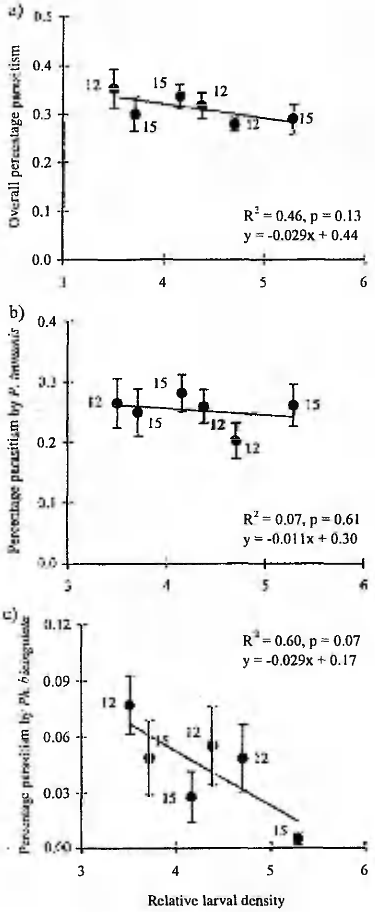


Fig. 1a–c Association between the average rate of parasitism by *Protapanteles immunis* and *Phobocampe bicingulata* for the current year (±SE) and the average host density of the same year. The number of sites studied each year is given

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

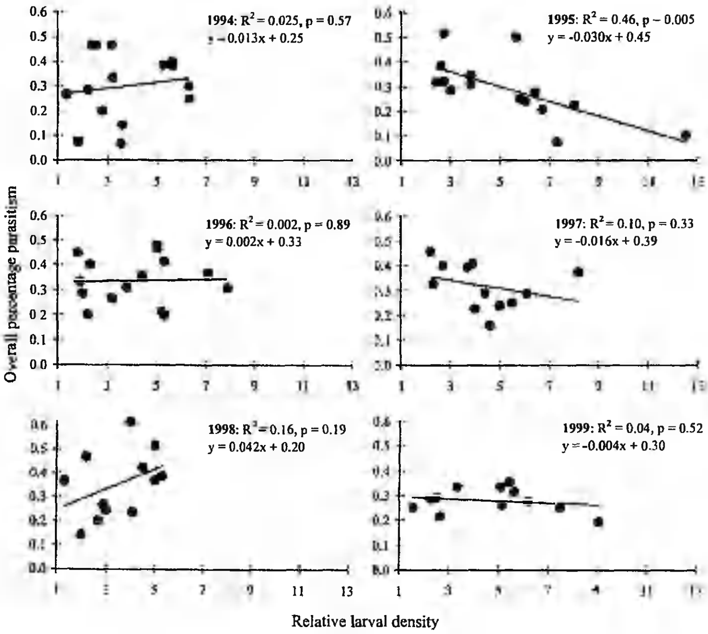
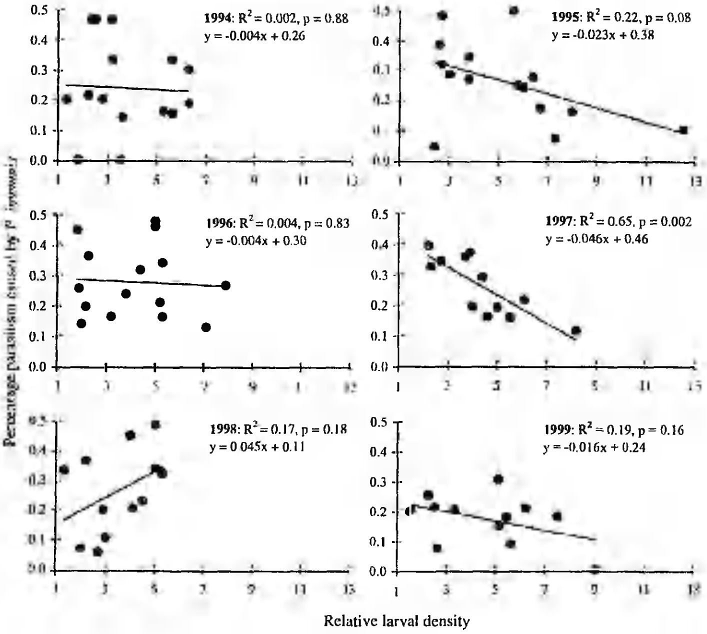


Fig. 3a–f Relationship between rate of parasitism by *P. immunis* and density of *E. autumnata* in study sites for six years



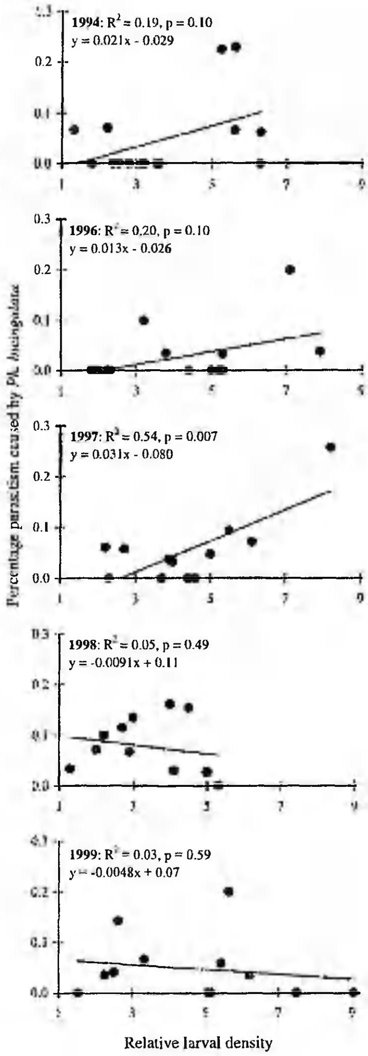


Fig. 4a–e Relationship between rate of parasitism by *Ph. bicingulata* and density of *E. autumnata* in study sites for five years. In 1995, only two individuals of this parasitoid were found

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.

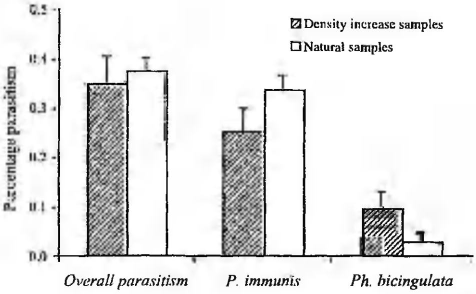


Fig. 5 Average (±SE) parasitism rate of natural larvae and those collected from density-increased trees

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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LARGE LARVAE OF A FLUSH-FEEDING MOTH, *EPIRRITA AUTUMNATA* (LEPIDOPTERA, GEOMETRIDAE) ARE NOT AT A HIGHER RISK OF PARASITISM: IMPLICATIONS FOR MOTH'S LIFE-HISTORY

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ABSTRACT

The effect of larval body size of *Epirrita autumnata* (Lepidoptera, Geometridae) on the risk of parasitism was studied in a field experiment. The experiment involved three pairwise exposures of different larval instars to parasitoids. Three hymenopteran species were responsible for most of the parasitism. Parasitism risk was found to be host-instar independent. This result was consistent across parasitoid species and experiments. The results suggest that host use by larval parasitoids cannot constrain selection for larger body size in *E. autumnata*. However, high mortality due to parasitism may select for a short developmental period (the slow-growth / high-mortality hypothesis), and smaller body sizes as a by-product. A strong selective effect of parasitism on the timing of larval development in *E. autumnata* is also unlikely. The larger was the host, the larger was the adult size of the parasitoid and the shorter its development time (for one species). We suggest that the lack of a preference-performance linkage in the system studied may be related to the time stress associated with the short phenological window of host vulnerability.

Key words: body size, parasitism risk, parasitoids, phenology, preference-performance linkage, life-history, *Epirrita autumnata*, Geometridae.

INTRODUCTION

In insects, fecundity is often strongly correlated with the body size of the female (Honěk, 1993). Such a correlation implies a persistent selection for large adult size. We are thus justified in asking what selective forces balance this obvious fecundity advantage, and prevent a continuous evolutionary increase in insect body size. The answer is intuitively related to elevated mortality risks, but it is not necessarily a trivial one (Leimar, 1996; Tammaru, 1998). In particular, for *Epirrita autumnata* (Borkhausen) (Lepidoptera: Geometridae), an optimality analysis (Tammaru, 1998) showed that realistic values of constant, *body-size independent* larval mortality rates and seasonal changes in host plant quality are insufficient to explain why these insects do not grow larger by prolonging their larval growth. However, if large larvae are more likely to be killed, the resulting *positively body-size dependent* mortality might be the ecological factor capable of balancing the fecundity advantage of large body size.

Parasitoids are often one of the main causes of mortality in herbivorous insects, and affect various ecological traits of their hosts. The traits affected include food plant preference (Ohsaki & Sato, 1990, 1994; Björkman *et al.*, 1997), and timing of life-history switches (McGregor, 1996). Numerous laboratory experiments, and some field studies have shown that parasitism risk may depend on host body size, and the dependence being often mediated via behavioural responses of the parasitoids (e.g. van Alphen & Drijver, 1982; Nealis, 1990; Sait *et al.*, 1997). Either small or large hosts may experience a higher risk of parasitism in different host–parasitoid systems; adaptive explanations for these patterns are largely based on differences in parasitoid life-histories, especially koinobiosis and idiobiosis (Harvey, 1996, Harvey *et al.*, 2000; Strand, 2000). Host-size dependent parasitism is usually discussed from the parasitoid's perspective, while the importance of this phenomenon in shaping the life-history of the host has received markedly less attention (see, however, Solbreck *et al.*, 1989; Teder *et al.*, 1999).

To assess the role of parasitism as a selective agent acting on host body size, we conducted field experiments and recorded the incidence of parasitism of different sized larvae of *E. autumnata*. We asked if the risk of size-dependent parasitism could balance the high fecundity advantage of large female size (Tammaru *et al.*, 1996). In addition, the design of the experiments enabled us to assess whether parasitism affected the phenology of the herbivore. Finally, we briefly discuss whether parasitoids benefit from size-selective use of the host in the system studied, and propose an explanation for the observed patterns of size selectivity.

MATERIAL AND METHODS

Study species

Epirrita autumnata, the autumnal moth, is a medium-sized holarctic lepidopteran known for its tendency to achieve outbreak levels of abundance in northern and mountainous Fennoscandia (Tenow, 1972; Haukioja *et al.*, 1988; Ruohomäki *et al.*, 2000). The populations are stable elsewhere. The species has a univoltine life cycle. The eggs overwinter and hatch in spring. The solitary, cryptic larvae feed on deciduous trees and shrubs. *E. autumnata* is a typical flush-feeder (= spring feeder): its larval performance is critically dependent on the phenological stage of the foliage (Ayres & MacLean, 1987; Kaitaniemi *et al.*, 1998; Kause *et al.*, 1999). Larval development lasts for about one month and consists invariably of 5 larval instars (Tammaru, 1998). A 5th instar larva may reach ≈40 mm in length and 150 mg in weight, the size gain per instar being roughly two-fold for length, and four-fold for weight. They develop relatively synchronously, but larvae of two or three different instars may still occur at the same time. Pupation occurs in the ground in early June, and the adults emerge in early autumn.

Larvae of *E. autumnata* are attacked by several hymenopteran parasitoids (Ruohomäki, 1994; Kaitaniemi & Ruohomäki, 1999; Teder *et al.*, 2000). The most common encountered in the present study were the three solitary koinobiont species: *Protapanteles immunis* (Haliday) and *Cotesia jucunda* (Marsh.) (both Braconidae), and an unidentified species of *Campoletis* (Ichneumonidae). The two former species (2.5–3.5 mm in length) are bivoltine generalists parasitising various geometrids (Tobias, 1986). Their development from oviposition to pupation (i.e. emergence from host larvae) takes about 3 weeks. The body length of the *Campoletis* sp. is 6–8 mm, and irrespective of the host instar parasitised, it always emerges from the prepupa of its host.

Study areas and sites

The two-year (1998–1999) experimental field study was carried out in two forested areas outside the range where outbreaks of *E. autumnata* occur: 1) about 20–30 km northeast of the town of Turku (60°15'N, 22°25'E), southwestern Finland (1998), and 2) near the town of Tartu (58°22'N; 26°45'E), southeastern Estonia (1999). The experiments were conducted at a total of twelve sites, four sites in 1998 (within an area of ≈10 km^2) and eight in 1999 (within an area of ≈2 km^2). Most of the study sites were mixed coniferous forests, dominated by *Pinus sylvestris* L. or *Picea abies* (L.) Karsten with birches (*Betula pubescens* (Ehrhart) and also *B. pendula* (Roth) in some sites) growing in the understory.

Experiment design

To determine if parasitoids preferably attack certain larval instars of *E. autumnata*, three separate host choice experiments were conducted. At each of the 12 study sites, 16–20 birches (mostly *B. pubescens*, occasionally *B. pendula*), 1–1.8 m in height, separated by distances of 5 to 10 m, were chosen. Laboratory-reared larvae of two different instars were released onto the experimental trees. Three combinations of instars were used; larvae moulting either into the 1) second and third instars (conducted at four sites in 1998), 2) second and fourth instars (four sites in 1999), or 3) third and fourth instars (four sites in 1999). The numbers of larvae of each instar released were equal on each tree (e.g. 5 second and 5 third instar larvae). The total number of larvae used in the three experiments was 1452. In each experiment, two densities were created, with ten (5+5) and four larvae (2+2) on 40% and 60 % of the trees, respectively. These host densities correspond to those during minor and moderate outbreaks of *E. autumnata*, and greatly exceeded the natural background densities in the study area. Using two different densities was motivated by the original idea, which was to study the effects of host density, as an additional factor, on size-selectivity in host use. However, a subsequent data analysis showed that larval density did not affect the patterns of parasitism. For the sake of clarity of presentation, we do not incorporate this factor in the further analyses.

Larvae were exposed to parasitoids for a period corresponding to the duration of about one instar (7–8 days). The experiments were performed at the time when laboratory-reared larvae were approximately of the same age as those in the field. After the exposure period, the released larvae were collected and reared in the laboratory until they pupated or a parasitoid emerged. For the parasitoids the dates of emergence and the length of hind tibia, as measure of body size, were recorded. Parasitoid size was used to assess the profitability of different host instars for the parasitoids.

Data analysis

To determine if risk of parasitism differed for different larval instars, the data were analysed using generalised linear models (SAS PROC GENMOD, SAS Institute Inc., 1995). Parasitism status of a host (parasitised/unparasitised) was treated as the binary dependent variable, instar (second and third; second and fourth; third and fourth instars in the respective analyses) and study site as the categorical independent variables. Binomial distribution was assumed and logit was used as the link function. In additional analyses, parasitism caused by the most common species of parasitoids was considered separately. Finally, an analogous analysis of the total parasitism was performed with the data from the three experiments combined. Larval instar was then coded on the relative binary scale (younger instar / older instar) in each particular experiment, irrespective of the instars involved.

Larvae that were not recovered from the field (44% of the larvae, pooled over study sites and experiments) and those that died in the laboratory before pupation or emergence of a parasitoid (about 10 % of the larvae) were not included in the statistical analyses. To analyse the effect of host instar on adult body size of parasitoids, a two-way analysis of variance was applied, with parasitoid sex as an additional factor. Student t-test was applied to test the effect of host instar on parasitoid development time.

RESULTS

Distribution of parasitism among larval instars

Parasitism rate was highly variable between study sites, varying from a few to about 75 percent. Species composition of the parasitoids was also very different (Table 1). Parasitism risk was host-instar independent when parasitoids were given a choice between second and third instar larvae (Table 1a, 2a). Consistently, the percentage parasitism by each of the two dominant parasitoids (*C. jucunda* and *P. immunis*)was not different between instars ($DF = 1, \chi^2 = 0.03, p = 0.87$, and $DF = 1, \chi^2 = 1.96, p = 0.16$, respectively). Other parasitoids were present in numbers too low for a meaningful analysis.

The most numerous parasitoid in the Estonian experiments, *Campoletis* sp., showed no preference for a particular host instar, neither when second and fourth instars, nor when third and fourth instars were simultaneously exposed ($DF = 1, \chi^2 = 0.16, p = 0.69$, and $DF = 1, \chi^2 = 1.27, p = 0.26$, respectively). Other parasitoids were too scarce to analyse separately. The levels of total parasitism did not differ significantly between instars in the experiment in which second and fourth instars were exposed to parasitoids (Table 1b, 2b). However, there was a slightly lower level of total parasitism of fourth instar larvae when they were exposed with third instar larvae (Table 1c, 2c). This difference was due to parasitoids other than *Campoletis* sp. (a few *C. jucunda* among these).

Consistently, an analysis of the data pooled over the experiments did not support the notion that the larger larvae are more likely to be parasitised, rather the reverse. The corresponding tendency, however only approached statistical significance (Table 2d). Calculated for the entire data set, 23.6% of the younger vs 20.0% of the older larvae were parasitised (N=725). The 95% confidence limits of the ratio of these values (lower 0.89, upper 1.56, SAS PROC FREQ CLI option) gives a simple but illustrative power estimate of this analysis.

Effect of host instar on parasitoid development

Body size of the offspring of *Campoletis* sp. significantly increased with host instar (two-way ANOVA with parasitoid sex as an additional factor: $F_{2,62} = 8.20$, $p < 0.001$; all three pairwise contrasts between instars were significant; sites pooled). The average lengths of the hind tibia of parasitoids from second, third and fourth instars were 1.87, 1.94 and 1.98 mm, respectively. Similarly, body size of *C. jucunda* significantly increased with host instar (one-way ANOVA: $F_{1,16} = 7.10$, $p = 0.02$; females only, only one male emerged). The average lengths of the hind tibia of *C. jucunda* that developed in the hosts' second and third instars were 0.99 mm and 1.02 mm, respectively. The number of *C. jucunda* emerging from fourth instar hosts was too low for analysis. Most individuals of *P. immunis*, the third most common parasitoid, failed to emerge from their cocoons. The effect of host instar on their body size could thus not be estimated.

Host instar strongly affected developmental period in *Campoletis* sp. but not in *C. jucunda* or *P. immunis*. In *Campoletis*, exact timing of parasitoid emergence could not be recorded due to the below-ground pupation of the host. However, irrespective of the host instar parasitised, parasitoid larvae invariably emerged from host prepupae. This allows us to conclude that parasitising a younger instar larva would add an extra week to the parasitoid's development time. In contrast, there was no effect of host instar on the parasitoid's development time in the remaining two species (*C. jucunda*: $t = 0.44$, $DF = 29$, $p = 0.67$; *P. immunis*: $t = 0.09$, $DF = 11$, $p = 0.93$).

DISCUSSION

There was no evidence of a positively size-dependent parasitism risk in *E. autumnata*. The only experiment where a significant difference in parasitism rates was detected, suggested the opposite: the smaller larvae suffered more parasitism (Table 1, 2c). A combined analysis of the effects of host size on the incidence of parasitism also indicated a greater risk for the smaller larvae rather than *vice versa* (Table 2d). Risk of larval parasitism is thus not likely to balance the strong fecundity advantage (Tammaru et al. 1996) of large size in females of *E. autumnata*.

However, even if mortality due to larval parasitism cannot alone provide a sufficient adaptationist explanation for body size in *E. autumnata*, parasitoids may still be a factor determining the cost of large adult size. According to the slow-growth/high-mortality hypothesis, longer developmental periods often imply higher vulnerability to predation and/or parasitism (Loader & Damman, 1991; Häggström & Larsson, 1995; Benrey & Denno, 1997). In terms of daily survival, the larval stage is definitely the most vulnerable one in the life cycle of *E. autumnata* (Tanhuanpää *et al.*, 1999, 2001). Mortality of larvae attributable to parasitoids may reach levels (Ruohomäki, 1994; Teder *et al.* 2000, and this study) that exceed mortalities in other stages of the life cycle combined. This should favour short developmental periods.

In contrast to parasitism, large larvae may be at a greater risk of bird predation than small. In particular, Tanhuanpää et al. (2001) showed that mortality due to bird predation was considerably higher during late instars than early instars. However, the design of these experiments does not allow the separation of the effects of time and size: larger larvae occurred later in the season when, e.g., the foraging activity of birds could have been higher. The effect of other principal predators, ants and spiders, was shown to be spatially restricted and presumably of less importance.

The present study also suggests that parasitism creates no significant selective pressure on the phenology of the larval stage in *E. autumnata*. In particular, our experiments may be alternatively interpreted as exposing larvae of different *ages*. In this context the results suggest that neither the larvae that are ahead nor behind the average in development suffer from increased levels of parasitism. These results complement those of Kaitaniemi and Ruohomäki (1999) who showed that the flight period of most *E. autumnata* parasitoids exceeds the larval period of the host: larvae reared outside the normal time schedule did not escape parasitism. Combined with the results of the present study, this observation allows us to exclude parasitism as an important selective force acting on the timing of larval development in *E. autumnata*. The need to synchronise larval development with suitable host plant phenology is apparently much stronger determinant of the optimal hatching date of the larvae (Ayres & MacLean, 1987; Kaitaniemi *et al.*, 1998).

Parasitoids appeared to benefit from developing in late instars of *E. autumnata*: body size of adult parasitoids was positively correlated with host size. Additionally, *Campoletis* sp. showed considerable host-instar dependent variation in development time. Both these variables have important fitness consequences: body size is frequently a good indicator of fecundity (Harvey *et al.*, 1994; Sequeira & Mackauer, 1994; Ellers *et al.*, 1998), while a short development time may imply reduced risk of mortality during preimaginal stages (Price, 1972; Slansky, 1986; Godfray, 1994). The latter is apparently true for *E. autumnata* parasitoids as well: high predation rates of moths during the larval stage (Tanhuanpää *et al.*, 2001) imply a high mortality risk for juvenile parasitoids. However, different profitabilities of parasitising differently-aged larvae did not lead to a preference–performance linkage, a phenomenon demonstrated in numerous laboratory studies on insect parasitoids (e.g. van Alphen & Drijver, 1982; Liu *et al.*, 1984 and Liu, 1985; Hopper, 1986).

Parasitoids may use suboptimally sized hosts for a variety of reasons, e.g. because of their size-dependent apparency (van Alphen & Drijver, 1982) or behavioural defence (van Alphen & Drijver, 1982; Brodeur *et al.*, 1996; Harvey, 1996; Chau & Mackauer, 2000), or age-dependent survival in hosts (especially koinobiont parasitoids: Driessen *et al.*, 1991; Sequeira & Mackauer, 1994; Brodeur & Vet, 1995). Although this study did not address the question of the causes of the non-selective host use, we would like to highlight a potential explanation specific to the system studied. In particular, the larvae of flush feeders like *E. autumnata* pass quickly and synchronously through the larval stage. The parasitoids of these moths are thus likely to be time- rather than egg-limited and the resulting time-stress should favour lower selectivity (cf. Jaenike, 1990; Mayhew, 1997, for examples with herbivorous insects). Moreover, in *E. autumnata*, high levels of larval parasitism (Teder *et al.*, 2000, and this study) suggest strong intra- and interspecific exploitative competition among parasitoids that further contributes to the ephemeral character of the resource for parasitoids. This, in turn, should select for high oviposition rates, and reduced selectivity as a correlated response.

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Table 1. Percentage parasitism of two simultaneously exposed larval instars of *E. autumnata*. Sample sizes refer to the numbers of larvae recovered (by instar) and used in the analyses.

Site (sample size)	Percentage parasitism by *Campoletis* sp.		Percentage parasitism by *P. immunis*		Percentage parasitism by *C. jucunda*		Total percentage parasitism	
a) 2nd and 3rd instars (Finland, 1998)								
	2nd	*3rd*	*2nd*	*3rd*	*2nd*	*3rd*	*2nd*	*3rd*
1 (41/41)	–	–	2.4	2.4	–	–	2.4	2.4
2 (34/48)	–	–	17.6	8.3	–	–	17.6	8.3
3 (36/39)	–	–	–	–	38.9	43.6	38.9	43.6
4 (44/49)	–	–	2.3	0.0	2.3	0.0	4.5	0.0
b) 2nd and 4th instars (Estonia, 1999)								
	2nd	*4th*	*2nd*	*4th*	*2nd*	*4th*	*2nd*	*4th*
5 (12/26)	–	–	8.3	0.0	8.3	3.8	16.7	3.8
6 (9/27)	22.2	18.5	11.1	0.0	11.1	0.0	44.4	18.5
7 (8/14)	12.5	50.0	–	–	12.5	0.0	25.0	50.0
8 (8/28)	75.0	60.7	–	–	12.5	3.6	87.5	64.3
c) 3rd and 4th instars (Estonia, 1999)								
	3rd	*4th*	*3rd*	*4th*	*3rd*	*4th*	*3rd*	*4th*
9 (39/43)	2.6	4.7	–	–	2.6	0.0	7.7	4.7
10 (37/41)	18.9	12.2	–	–	–	–	24.3	12.2
11 (23/34)	47.8	29.4	–	–	8.7	2.9	60.9	35.3
12 (14/30)	35.7	36.7	–	–	–	–	57.1	40.0

Table 2. Results of analyses of the effect of host instar (relative size in d) — see text) on the incidence of total parasitism.

Source	*DF*	χ^2	*p*
a) 2nd and 3rd instars			
Site	3	62.96	<0.001
Instar	1	0.54	0.46
b) 2nd and 4th instars			
Site	3	36.38	<0.001
Instar	1	1.99	0.16
c) 3rd and 4th instars			
Site	3	46.62	<0.001
Instar	1	6.77	0.009
d) All experiments combined			
Experiment	2	30.13	<0.001
Size	1	3.55	0.06

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Zooloogia ja Botaanika Instituut, teadur (2000–)

Teadusorganisatsiooniline tegevus

Eesti Loodusuurijate Seltsi liige
Jakob von Uexkülli Keskuse liige
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Teaduspublikatsioonid

(1) Teder, T., 1998. Limited variability of genitalia in the genus Pimpla (Hymenoptera: Ichneumonidae): inter- or intraspecific causes? *Netherlands Journal of Zoology* 48: 335–347.
(2) Teder, T., Tammaru, T., Pedmanson, R., 1999 Patterns of host use in solitary parasitoids (Hymenoptera: Ichneumonidae): field evidence from a homogeneous habitat. *Ecography* 22: 79–86.
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(5) Teder, T., Tammaru, T., In press. Cascading effects of plant vigour on the relative performance of insect herbivores and their parasitoids. *Ecological Entomology*.

Uurimistoetused

1995: ETF grant nr. 1645 ("Lukk-võti mehhanismi kehtimisest käguvaablastel (*Hymenoptera, Ichneumonidae*) ja alamsugukond *Tryphoninae* (*Hymenoptera, Ichneumonidae*) liigiline koosseis Eestis")
1996–1997: ETF grant nr. 2147 ("Peremees–parasitoid-süsteemi erinevaid populatsiooniökoloogilisi tahke endofaagsete öölaste (*Noctuidae*) ja neil parasiteerivate käguvaablaste (*Ichneumonidae*) näitel")
1998–1999: *Kone Säätiö* stipendium teadustööks Turu Ülikoolis
1998–2000: Tartu Ülikooli doktorandi teadustöö stipendium nr. DBGZH0628

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