Short-term indirect interactions between two moth (Lepidoptera: Noctuidae) species mediated by shared parasitoids: The benefit of being scarce

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Abstract. Despite the impact of parasitoids on insect populations being extensively studied, indirect parasitoid-mediated effects remain rarely documented in natural communities. We examined the influence of shared parasitoids on the interactions between two functionally monophagous moths, Nonagria typhae and Archanara sparganii. The moths showed a considerable variation in terms of relative abundance and the degree of phenological synchrony between the species. On average, parasitism levels caused by shared parasitoids did not differ between the two host species. Relative parasitism levels of the two hosts, however, varied considerably among different samples. Percentage parasitism of the scarcer species, A. sparganii, thus could not be fully explained by that of the dominant species, N. typhae. The results indicated that A. sparganii may 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. The case thus indicates the presence of parasitoid-mediated indirect effects between the coexisting herbivores. The patterns of host use observed in this study are consistent with the scenario of frequency-dependent host use caused by changes in parasitoid behavior. Such a host use by parasitoids is suggested to promote numerical stability and coexistence of the moth species in the system studied.

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). Natural-enemy-mediated indirect effects may arise either through functional (short-term effects) or numerical response (long-term, or transgenerational effects) of the enemy to the prey population. Enemy-mediated indirect effects have been suggested to play a significant role in natural communities affecting community structure and population dynamics of the 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 horizontal, positive 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 behavior 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 herbivorous insects, parasitoids have probably the greatest potential of mediating indirect effects between coexisting 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 behavioral repertoire (host preference, host switching etc.) among parasitoids. Empirical studies on various systems are therefore required to understand how widespread parasitoid-mediated indirect effects may be in natural communities, and which factors influence the expression of such effects. While manipulative studies are necessary to reveal causal relationships, an analysis of correlative data would estimate the range and relevance of the effects in the field.

In the present field study, we demonstrate a pattern consistent with indirect, parasitoid-mediated interactions between a pair of insect herbivores exploiting a common host plant. The species studied are functionally monophagous and their parasitoids lack alternative host species in the study areas. In its relative isolation, the system is thus well suited for examining indirect interactions in the field. We document variation in relative parasitism levels of the two host species, and analyze possible factors
A. sparganii. Known to parasitise some other moths (Rasnitsyn & Siitan, what earlier). All three parasitoids are oligophagous and are also monophagous on the host plant. The pupal period lasts for about one month in late spring / early summer [E. occupator (pers. obs.)] or on fresh 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 one month in both species.

Two principal species of solitary parasitoids, the koinobiont Spilichneumon limnophilus Thomson and the idiobiont Chasmiss paludator Desvignes (Hymenoptera: Ichneumonidae), were found to parasite larvae and pupae of both N. typhae and A. sparganii. A third species, parasitising both moths, Vulgichneumon satorius 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, Exorphes occupator Gravenhorst, parasitises A. sparganii only occasionally (Teder et al., 1999), in most years 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; pers. obs.) and S. limnophilus (pers. obs.]) 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 parasite some other moths (Rasnitsyn & Sitalan, 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 7 consecutive years (1995–2001) in southeastern Estonia. Three habitats differing with respect to Typha distribution pattern were examined. The habitat studied in 1995–1996 was characterized 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 the 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 Emäjõgi River. The third habitat, studied in 1998–2000 was the most heterogeneous where patches of T. latifolia (mostly from 0.01 to 0.05 ha, at small ponds, ditches, or other damp places) were separated by distances of 0.2–1.0 km. This study area was located in an agricultural landscape, close to the Lake Pangodi (58°12’ N, 26°35’ E), 20 km southwest of Tartu. The samples collected from Tartu and Pangodi in 1998 were treated as independent in the analyses.

MATERIAL AND METHODS

Study species

The study system was based on Typha latifolia L. (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, 2002). This study was, however, restricted to the two most abundant species, Nonagria typhae Thunberg and Archanara sparganii Esper (Lepidoptera: Noctuidae). The proportion of other species remained < 1% of all sampled larvae. The species studied are close in feeding biology and phenology (pers. obs.). 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 in 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 one month in both species.

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Data analysis

Levels of parasitism in A. sparganii and N. typhae were analysed with respect to relative abundance of the moths and their relative phenology. 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. Data of such plots were pooled within samples for subsequent analyses. 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 were parasitised by the non-shared E. occupator. Although multiple parasitism of hosts previously parasitised by E. occupator was unlikely in this system, these individuals were re-classified as non-parasitised for the analyses. Such an approach was taken assuming that the shared parasitoids, S. limnophilus and Ch. paludator, presumably make their decisions on relative abundance of the two host species on the basis of overall host density (i.e. parasitised + already parasitised hosts) rather than density of unparasitised hosts.
The rationale of this relative phenology index was in describing the degree of temporal overlap, or co-occurrence of the vulnerable stages of the two host species. This may be relevant in the context of indirect interactions. As predicted by the optimal foraging theory, higher abundance of the preferred host should increase parasitoid's selectivity. Accordingly, when the peaks of vulnerable A. sparganii and N. typhae overlap, more larvae of the preferred host, N. typhae, are available, and thus, a larger proportion of larvae of the less preferred species, A. sparganii, should escape parasitism. In the opposite case, when the phenological distributions of A. sparganii and N. typhae differ, a larger proportion of vulnerable A. sparganii would fall into the period of lesser choosiness of the parasitoids.

Logistic regression analysis (PROC GENMOD; SAS Institute Inc., 1995) was applied to examine whether the distribution of parasitism between A. sparganii and N. typhae differs in the study samples. Binomial probability distribution was assumed, logit was chosen as the link function, DSCALE option was applied to correct for overdispersion. Incidence of parasitism (parasitised/nonparasitised) was used as the response variable, and “sample”, “host species” and “sample x host species” were used as the independent effects. Linear regression was used to examine the effects of relative abundance of the moths and their relative phenological distribution (see above) on their relative distribution of parasitism at the level of sample means. 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. For example, if in a particular sample, 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 on the parasitism levels of A. sparganii. Analogously, relative abundance of the two moths was calculated as the ratio of the numbers of A. sparganii and N. typhae collected in the same sample.

RESULTS

Among the samples studied, parasitism levels were highly variable in both of the moth species. Mean values of total percentage parasitism fluctuated from 5.8% to 38.5% in A. sparganii and from 23.5% to 68.1% in N. typhae (Fig. 1). When only shared parasitoids were considered, percentage parasitism of N. typhae dropped to the range of 7.0% to 33.6%, whereas parasitism of A. sparganii, being caused mainly by shared parasitoids, changed only negligibly (Fig. 1). Variation in the parasitism levels by individual 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 levels of the scarcer species, A. sparganii, tended to covary with those of the dominant species, N. typhae, the correlation presumably being explained by the overall abundance of the parasitoids. A positive and significant association was observed when parasitism by S. limnophilus was analysed (Fig. 2). For parasitism by Ch. paludator no association was observed between the parasitism levels of A. sparganii and N. typhae.
The overall levels of parasitism by the shared parasitoids did not differ between the two moth species (Table 1). In contrast to this "overall equality", parasitism levels were not equal in particular study samples. For example, in 1995 parasitism percentage of *N. typhae* by shared parasitoids exceeded that of *A. sparganii* more than 3 times whereas in 1998 (Tartu - site) *A. sparganii* appeared to suffer from parasitism levels twice higher than *N. typhae* (Fig. 1). The among-sample differences in the relative parasitism of the two host species were statistically confirmed by a highly significant "sample × host species" interaction (Table 1).

One possible factor able to explain these remarkable differences in relative parasitism levels is the variable relative abundance of the host species. Though *A. sparganii* was less abundant in all samples, relative abundance of *A. sparganii* and *N. typhae* considerably fluctuated among samples. The index of relative abundance of the two species (the number of *A. sparganii* divided by the number of *N. typhae*) fluctuated from 0.03 (1996) to 0.49 (2001). Linear regression of mean values indicated that relative abundance of the moths affected their relative parasitism levels. The effect of relative abundance on relative parasitism levels was positive and significant when parasitism by *S. limnophilus* was analysed (Fig. 3).

Another factor that may have differential influence on the availability, and thus, parasitism levels of the two moths, is their relative phenological distribution. Correspondingly, the relative phenology index (see Methods) correlated positively with relative parasitism levels caused by *S. limnophilus* (Fig. 4). Again, the relationship between relative phenology index and relative parasitism levels by *C. paludator* ($R^2 = 0.11$, NS) was also positive but non-significant. Mean values of relative abundance and relative phenology index appeared to be correlated ($R = 0.81$). Unfortunately, a two-way ANOVA examining the effects of relative abundance and relative phenology jointly would not have been statistically meaningful due to small sample size (8 samples).

**DISCUSSION**

The present results revealed a pattern that is consistent with the presence of indirect, parasitoid-mediated interactions between two herbivores. We showed that relative parasitism levels of the two coexisting host species, *A. sparganii* and *N. typhae*, considerably varied among different samples. The present analyses revealed two factors that may contribute to the patterns observed via functional responses of the parasitoids. In particular, relative parasitism levels of the two moths correlated both with relative abundance of the two moths as well as the difference in their phenologies. Although we cannot strictly prove which of the two factors is more important in determination of parasitism levels of *A. sparganii*, the conclusions would be similar: *A. sparganii* appeared to benefit from the presence of *N. typhae*, or in other words, escape parasitism by its relative scarcity. The case is one of very few (see also Bonsall & Hassell, 1997; Müller & Godfray, 1997) providing evidence for indirect interactions in parasitoid-involving systems at a short time-scale (see Holt & Lawton, 1994). Unfortunately, however, the asymmetric distribution of the abundances does not allow us to judge about the symmetry of this interaction (Chaneton & Bonsall, 2000).

**TABLE 1.** The results of logistic regressions (significance tested by type I analyses) examining the differences in the distribution of parasitism between *A. sparganii* and *N. typhae*.

<table>
<thead>
<tr>
<th>Effect</th>
<th>df</th>
<th>$\chi^2$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Incidence of parasitism (0/1)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sample</td>
<td>7</td>
<td>278.8</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Host species</td>
<td>1</td>
<td>1.8</td>
<td>0.19</td>
</tr>
<tr>
<td>Sample × host species</td>
<td>7</td>
<td>39.1</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>
The effect of relative abundance is likely to be explained by the consequences of frequency-dependent changes in host use by the parasitoids. Such a pattern of host use may result either from a host-frequency-dependent change in a) host's anti-parasitoid behaviour, or b) foraging behaviour of the parasitoids (i.e. a change in host preference) (for a review, Sherratt & Harvey, 1993; van Alphen & Jervis, 1996). The mechanisms of different species are unlikely to occur simultaneously with the more abundant host. The present results are consistent with this scenario: smaller differences in the degree of synchrony in hosts’ windows of vulnerability. As parasitoids forage for the hosts in a frequency-dependent manner, the rarer host may reduce parasitism risk by adjusting its vulnerable stage to occur 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. Such a pattern may be seen as another indication of a change in host preference in the system studied.

From the 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 also 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 by adjusting its vulnerable stage to occur 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. Such a pattern may be seen as another indication of a change in host preference in the system studied.

The present system appears to meet the necessary preconditions for switching behaviour to evolve: 1) relative abundance of different prey types should vary either spatially or temporally and 2) predators should be mobile (Cornell, 1976). In the present system, the relative abundance of the two moth species varied among samples; shared parasitoids are extremely mobile and can be met even in very isolated patches (Teder & Tammaru, pers. obs.). Moreover, both moths are quite abundant in absolute terms, they seem to be well suitable for the 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 changes in host preference in the field (see, however, Kato, 1994; Pike et al., 1999), whereas the phenomenon is repeatedly demonstrated under laboratory conditions (Cornell & Pimentel, 1978; Chow & Mackauer, 1991; Drost & Cardé, 1992).

Frequency-dependent host use 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 population dynamics of the scarcer moth, A. sparganii. At lower densities, parasitism levels of A. sparganii appeared to be lower which should allow for A. sparganii populations to increase. As N. typhae populations maintain the density of parasitoids continuously high (N. typhae was the more abundant host species in all samples), 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 (Holt & Lawton, 1993). In the studied system, positively density-dependent parasitism accompanying with a change in host preference allows A. sparganii to increase when rare thus facilitating coexistence of the host species (see also Holt & Kotler, 1987). Mechanisms promoting stability for the populations of N. typhae remain unclear.

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REFERENCES


SKOU P. 1991: Nordens Ugler. Håndbog over de i Danmark, Norge, Sverige, Finland og Island forekommende arter af Herminiidae og Noctuidae (Lepidoptera). Danmarks Dyreliv 20. [in Danish]


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