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

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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 × 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 × 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

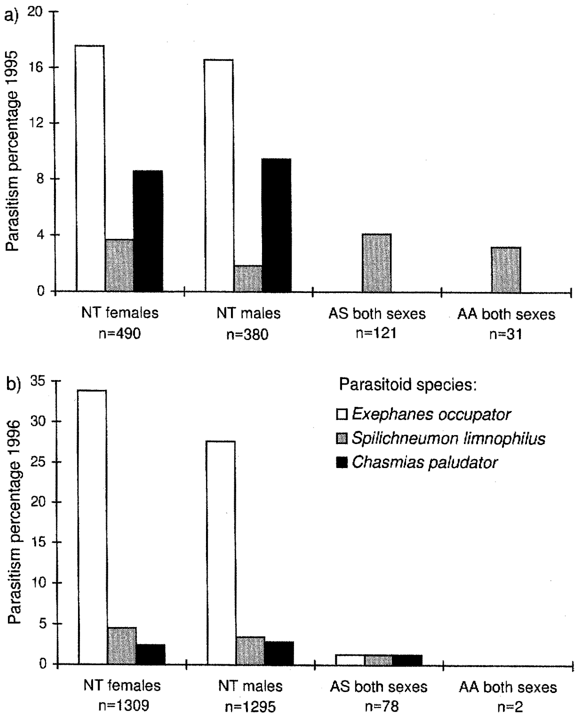

Fig. 1. Parasitism percentages of three noctuid moths (NT – *Nonagria typhae*, AS – *Archanara sparganii*, AA – *Archanara algae*) by different parasitoids in two years.

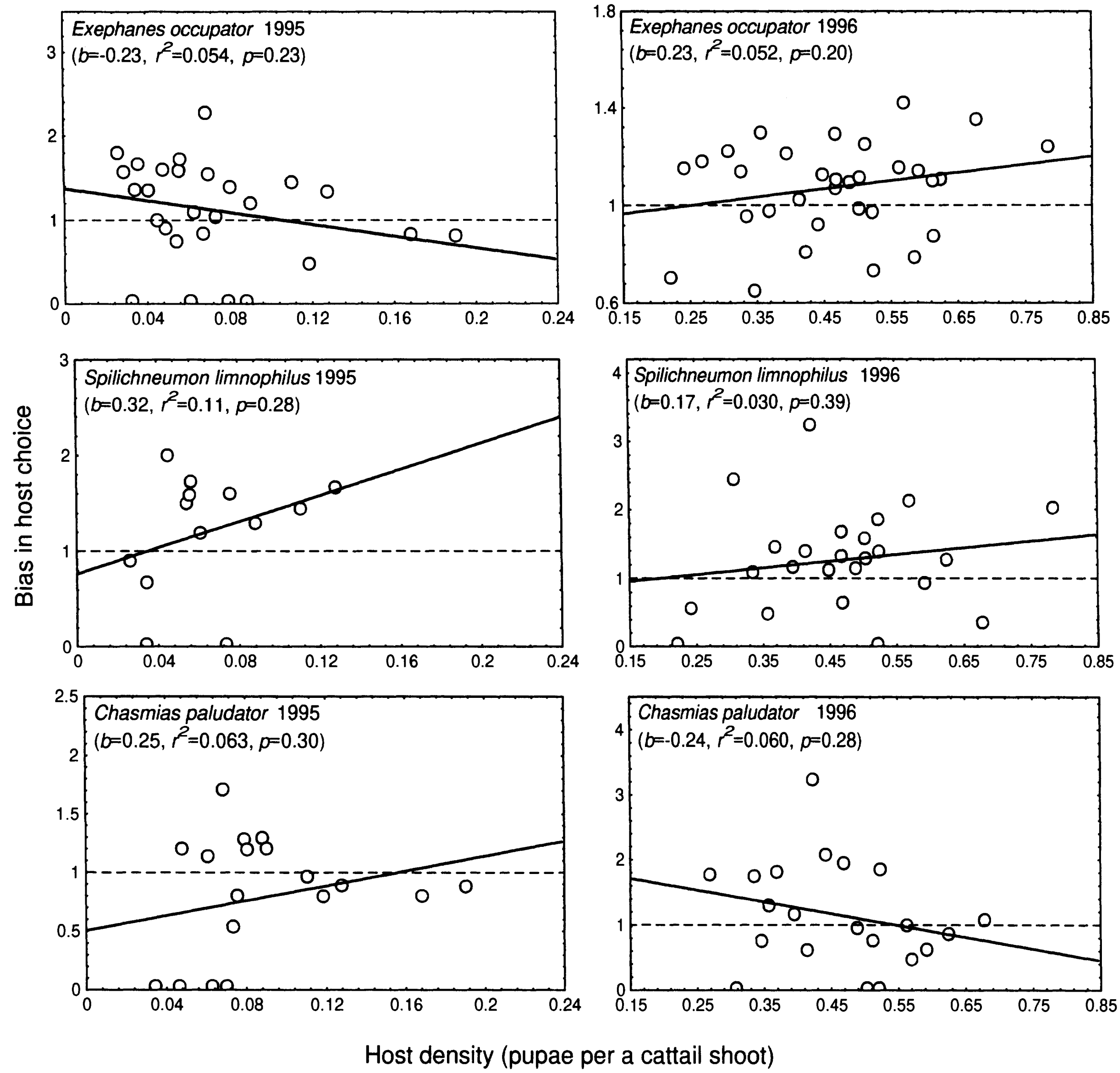

Fig. 2. The relationship between the host density in a plot and intraspecific host choice. The host choice index is calculated as the ratio of [parasitised *Nonagria typhae* females/all parasitised *N. typhae* in a plot] and [all *N. typhae* females/all *N. typhae* in a plot]. If this ratio is equal 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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