Ecological Entomology (2003) **28**, 500–502

SHORT COMMUNICATION

Does parasitoid attack strategy influence host specificity? A test with New World braconids

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Abstract. 1. Parasitoid attack strategy has been divided into two broad categories, koinobiosis and idiobiosis, based on the arrest of host development and the intimacy of larval contact. Koinobionts allow the host to continue developing and larvae usually feed within the host body, whereas idiobionts stop host development and larvae usually feed externally.

2. Comparisons of host ranges from rearings of parasitoids from specific host communities have shown that koinobionts are more host specific than idiobionts. These tests suggested that parasitoid attack strategy influenced specialisation in parasitoid–host interactions within certain host communities.

3. To determine whether this pattern was consistent within a single parasitoid lineage that utilises hosts from many different communities, the host ranges of koinobiont and idiobiont braconid genera of the New World were compared. Koinobiont genera utilised fewer host families than idiobionts, suggesting that parasitoid attack strategy may direct the evolution of host specificity throughout the evolutionary history of parasitoid lineages.

Key words. Braconidae, host range, idiobiosis, koinobiosis, specialisation.

Introduction

Parasitoids represent one of the most prevalent lifestyles on earth, second only to phytophagous insects, their major hosts. Parasitoids are best known from the parasitic Hymenoptera but occur also in other insect orders such as the Diptera, Coleoptera, Lepidoptera, Neuroptera, and Trichoptera (Eggleton & Bradshaw, 1992; Godfray, 1994). As the name implies, parasitoids have been characterised more like parasites even though they end up killing their hosts like predators. Based on the parasite-like portion of their life history, Askew and Shaw (1986) proposed that parasitoids should be divided into two major groups depending on the effect on host development and the intimacy of contact between parasitoid larvae and host individuals. Parasitoids that initially allow their host to continue developing after oviposition are termed koinobionts; those that kill or paralyse their hosts permanently at the time of oviposition are termed idiobionts. Most koinobionts are also endoparasitoids, whose larvae live and feed within the host body. In contrast, idiobionts are typically ectoparasitoids and feed from the outside surface of their hosts.

This categorisation represents a major advance in identifying processes that are likely to direct the evolution of parasitoids in general. In particular, Askew and Shaw (1986) predicted that koinobiont parasitoids should have a narrower host range than idiobionts because of selection to circumvent functioning host defences. They presented data on parasitoids that attack arboreal leaf-mining communities in Great Britain and showed that, on average, koinobionts attacked 1.5 host families whereas idiobionts attacked 4.2 host families. Subsequent tests with parasitoids of lepidopteran leaf miners on oaks (Sato, 1990), leaf miners in tropical communities (Memmott *et al*., 1994), and forest Lepidoptera in Canada (Sheehan & Hawkins, 1991) supported the hypothesis that koinobionts are more host-specific than idiobionts.

The koinobiont/idiobiont dichotomy has the potential to be a very informative hypothesis for understanding the evolution of parasitoid taxa (Hawkins, 1994). For example, koinobiont lineages may have a greater propensity to be specialised over evolutionary time than idiobionts. Previous tests used data on host ranges from rearings of taxonomically diverse parasitoids from specific host communities, but there have been no tests of this hypothesis within a single parasitoid lineage. Host-use patterns among parasitoid

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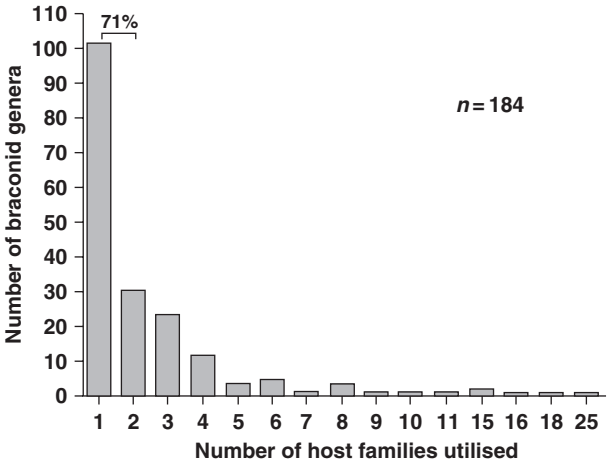

Fig. 1. Frequency distribution of host family use for the braconid genera of the New World. Seventy-one per cent of the genera utilise one or two host families.

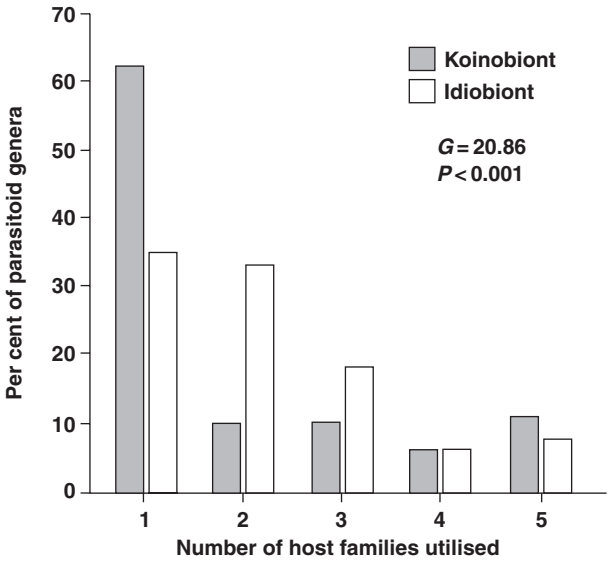

Fig. 2. Comparison of host-use patterns of koinobiont and idiobiont genera of the New World Braconidae. A greater proportion of koinobiont genera uses only one host family.

genera of the Braconidae in the New World were used to test whether the koinobiont/idiobiont hypothesis is supported at higher taxonomic levels. Specifically, the following questions were addressed: (1) Are most braconid genera host specific; do they utilise relatively few host families? (2) Does parasitoid attack strategy influence this host specificity; do koinobionts have a narrower host range than idiobionts? Although far from being a complete data set, the taxonomy and host-use patterns of New World Braconidae represent the best data set available to test the koinobiont/idiobiont hypothesis at higher taxonomic levels.

Materials and methods

Host-use data for braconid genera were taken from two sources. The work of Wharton *et al.* (1997) was used as the primary source of data. This volume lists the known braconid genera and subfamilies in the New World and the host families utilised. For each genus, the number of parasitoid species, host families utilised, and the parasitoid attack strategy (koinobiosis or idiobiosis) were recorded. In instances where host use or the number of species was ambiguous, Marsh (1979) was consulted as a secondary source. Parasitoid species that were indicated as introduced to the New World were not included in the analysis. Of the 404 New World genera listed by Wharton *et al.* (1997), host-use data were collated for 184 genera; of these, data on host use and number of parasitoid species were available for 166 genera.

The effect of parasitoid attack strategy on host range was analysed in three ways. (1) The proportion of koinobiont and idiobiont genera that utilise one, two, three, four, and five or more host families were compared using a *G*-test (Sokal & Rohlf, 1995). (2) Host-use data from all 184 genera were used in a Wilcoxon two-sample test to test for differences in host range between koinobionts and idiobionts. (3) Linear regression was used to examine the effect of the number of parasitoid species/parasitoid genera on host range for the 166 genera for which there were data for both variables. This analysis determined whether increased sampling (i.e. more parasitoid species surveyed) increased the host range for a genus. Based on this analysis, ordinal logistic regression was used to determine the effect of parasitoid attack strategy on host range while controlling for the number of parasitoid species within a genus. All statistical analyses were performed using JMP 3.2.1 (SAS Institute Inc., 1998).

Results and discussion

The host range of some braconid genera can be quite broad, however 71% of the 184 genera utilised only one or two host families (Fig. 1). The distributions of the proportion of koinobiont and idiobiont genera utilising one, two, three, four, and five or more host families differed (Fig. 2). Sixty-two per cent of the koinobiont genera utilised just one host family in comparison with 34% of the idiobiont genera. Similarly, individual koinobiont genera utilised significantly fewer host families than did idiobiont genera (Chi-square 5.28, $P < 0.05$). The median number of host families utilised by koinobiont genera was one, compared with a median of two for idiobiont genera. This difference in host use was upheld even after correction for sampling effort. Increasing the number of parasitoid species surveyed for a genus increased the host range significantly (Fig. 3). Incorporating this finding into a logistic regression with parasitoid attack strategy and number of parasitoid species as factors, however, still resulted in significant differences in koinobiont and idiobiont host ranges (attack strategy: Nparm = 1,

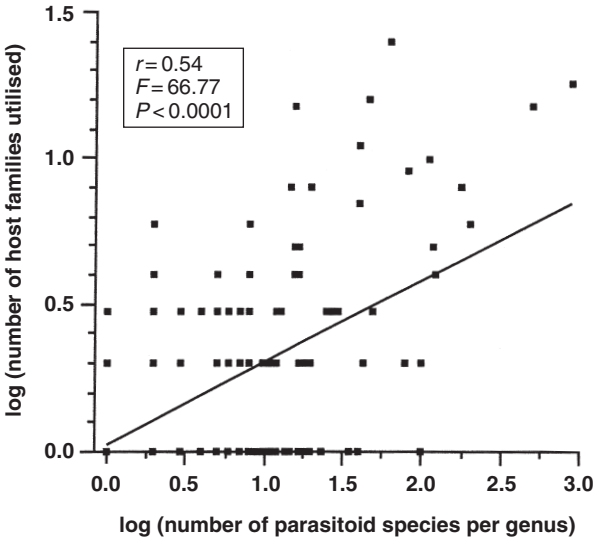

Fig. 3. Log–log plot of host family use by the number of species within a parasitoid genus. Genera with greater numbers of species tend to utilise more host families.

d.f. = 1, $\chi^2_{Wald} = 3.988$, $P < 0.05$; number of parasitoid species: Nparm = 1, d.f. = 1, $\chi^2_{Wald} = 16.267$, $P = 0.0001$).

For the braconid parasitoids in the New World, attack strategy had a significant influence on patterns of host use. Overall, koinobionts were more likely to have a narrower host range than were idiobionts. These results for the Braconidae complement previous studies that have demonstrated this dichotomy for taxonomically diverse parasitoid species reared from specific host communities (Askew & Shaw, 1986; Sato, 1990; Sheehan & Hawkins, 1991; Memmott *et al.*, 1994). Taken together, the current and previous studies suggest that attack strategy influences the host range of many parasitoids, and may be a constraining factor in the evolution of host range within parasitoid families.

Although attack strategy influences parasitoid host range, there is no question that other factors contribute to host-use patterns (e.g. Mills, 1992; Hawkins, 1994). Even within the 184 genera examined in this study, there were some koinobiont genera that utilised many host families, and some idiobiont genera that utilised only one host family. Clearly, other factors can outweigh the importance of attack strategy. The results presented here should be viewed as support for identifying another important factor determining host range rather than identifying the single major factor. The robustness of the koinobiont/idiobiont dichotomy needs to be evaluated further by additional tests of host range differences within the entire Braconidae and in other parasitoid families. The lack of host range data for many parasitoid groups, however, is a major limitation. Even for the Braconidae, data on host family use were available for only 45% of the braconid genera in the New World, and there are many species yet to be described (Wharton *et al.*, 1997). Extensive surveys and rearings of parasitoids are of paramount importance to understanding biodiversity and testing hypotheses about host-use evolution in parasitoid taxa.

Acknowledgements

I thank B. Crabb, O. Pellmyr, and especially K. Segraves for constructive discussions about specialisation and host specificity. K. Segraves, S. B. Vinson and an anonymous reviewer provided helpful suggestions for improving the manuscript. S. Merry helped with data collection and entry. This work was partially supported by NSF DEB 0075944.

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Accepted 21 April 2003