HOST RANGES OF *ALEIODES* SPECIES (HYMENOPTERA: BRACONIDAE), AND AN EVOLUTIONARY HYPOTHESIS

Mark R. SHAW

National Museums of Scotland, Chambers Street, Edinburgh EH1 1JF, United Kingdom
(e-mail: m.shaw@nms.ac.uk)

Abstract – The host range of a parasitoid is one of its most crucial characteristics, but it needs both meaningful definition and extremely careful assessment. *Aleiodes* species are koinobiont endoparasitoids of so-called "macrolepidoptera" larvae (or in a few cases other Lepidoptera families with similar larval behaviour such as some Zygaenidae, Yponomeutidae and Pterophoridae). Because they emerge as adults from mummified host larvae, collections of reared specimens with preserved host remains can be built up for which the real host identity is unambiguous. Several distinct host range patterns can be recognised among the best known and most abundant European species. Consideration of these, including experimental evidence, suggests that under some circumstances host ranges tend to expand through the recruitment of frequently encountered new hosts, providing a basis for subsequent speciation. The hypothesis that new species arise as specialists as a consequence of this is hard to test directly, but is supported indirectly.

Key words: Braconidae, *Aleiodes*, host range, speciation

Introduction

The host range of a parasitoid species is one of its central properties, linking its evolutionary past with its present autecology. Through knowledge of the host range of parasitoids we can not only understand and predict their behaviour within current ecosystems, but also gain some understanding of the speciation processes that brought them into existence.

It is not, however, easy to define very sharply what is meant by host range. Fuller arguments are given elsewhere (Shaw 1994) for adopting a conceptual definition, that "the host range of a particular parasitoid species includes only the species of potential hosts that the parasitoid is usually able to attack successfully, following a pattern of searching behaviour enabling it to encounter them regularly". This rather loose definition is essentially practical: it was designed to address some of the problems that had inhibited the development of useful concepts of host range in the past. The definition has the following main implications:

First, it implies that some perfectly correct rearing records should be discounted if they represent only freak events – of no importance to the autecology of the parasitoid or the host, and lacking in phylogenetic significance. Accepting that such abnormal events, even if genuine, are to be discounted is the only way to ensure that erroneous records will be similarly marginalised (this can only happen, of course, if they are not reinforced regularly by the underlying error of interpretation being repeated). It is the wholly erroneous records (which are unfortunately extremely frequent in the literature, and often repeatedly copied without citation from one publication to another) that will have the most distorting effects on perceptions of host range, so finding a way to marginalise them is vitally important.

Second, it suggests that a quantitative expression of rearing data needs to be used in assessing and describing host range. Meaningful summaries can only be made on this basis (cf. Table 1).

Third, it introduces the idea that some hosts within the host range may be intrinsically more central than others that are encountered less frequently, or attacked less enthusiastically or with a less successful outcome. In addition to differentiating between genuine hosts on the grounds of suitability, there is a need to recognise phenological aspects of host range, especially in temperate climates: many parasitoids are plurivoltine yet use univoltine hosts, each available to only one generation of the parasitoid. Sometimes it happens that the parasitoid is (at least locally) entirely dependent on a single host species at one time of year but able to use a wider range of hosts at another (e.g. *Aleiodes nigricornis* Wesmael (Table 2); also the braconid *Dolichogenidea imperator* (Wilkinson), cf. Shaw & Aeshlimann 1994).

Fourth, it allows a further understanding to be developed: that a parasitoid's "realised host range" (i.e. what actually happens) may not be constant either in space or in time (unless, of course, the parasitoid is strictly monophagous). Clearly, the overlap of a parasitoid's spatial distribution with all of its potential hosts will not usually be exact, and the relative abundance of co-occurring hosts will also vary. Recognition of the realised host range at a locus in space and time is often of more practical significance – for example to population dynamicists, conservation biologists or pest control practitioners – than the potential host range of the parasitoid that may be of more interest to the evolutionary ecologist or systematist. In particular, it is regularly seen that a particular parasitoid population can be *de facto* strictly monophagous simply because only one of the species comprising its potential host range is present. An example is the braconid *Cotesia sibyllarum* (Wilkinson) which, in Britain, has only one species of *Limenitis* to use, while in many parts of Europe it has two.

Materials and Methods

Collecting the data needed to establish and understand the host ranges of parasitoids is difficult and requires great care. Dependence on literature records is completely useless for a great number of reasons that have been reviewed thoroughly by Shaw (1994)and Noyes (1994), and it is clear that more careful, quantitative and verifiable methodologies need to be developed. In a long-term study on the taxonomy and host associations of Western Palaearctic species of the genus *Aleiodes* (Braconidae: Rogadinae) I have focused on (a) my own, intensive, rearing activities aimed at sampling as wide a range of potential hosts as possible, done under careful protocols designed to minimise error (Shaw 1997): this survey needs to be as wide as possible and has been greatly supported by numerous people who give me the parasitoids they rear; (b) reared specimens in museum collections available for (my own) determination; and (c) my own experimental manipulations, particularly involving species with British populations (including mating, oviposition and rearing trials) to test the limits of host ranges as well as to resolve aggregates of cryptic species that are not easily separable morphologically.

Aleiodes species are koinobiont endoparasitoids. They attack early instar Lepidoptera larvae, almost entirely "macrolepidoptera" but including some "microlepidoptera" genera such as *Zygaena* and *Ypsolopha* and some Pterophoridae, whose suitably-sized larvae have exposed feeding habits. Only a small minority of *Aleiodes* species attack hosts feeding in semi-concealment (e.g. in seed capsules, leaf-packages, or near the soil surface), most of them using hosts that feed in more or less fully exposed situations. Nearly all species are solitary, but gregarious development is known in a few species world-wide, one of which is European.

Researching the host ranges of *Aleiodes* species has been considerably helped by the fact that pupation occurs inside the shrunken and darkened, but nevertheless often still distinctive, skin of the host larva – and these "mummies" are often present with the adult parasitoid in museum collections, allowing host determinations to be reassessed (it is surprising how very often hosts had been misidentified, even at family level!). The "mummy" is usually formed when the host is in its penultimate instar or sooner.

The names of Lepidoptera species follow Karsholt & Razowski (1996), and for brevity author's names are not given here.

Results and Discussion

The breadth of host range varies widely, both in terms of phylogenetic spread and also in the more absolute sense of the number of species seen in the (realised) host ranges of particular *Aleiodes* species, a few of which appear to be literally (i.e. universally) monophagous (e.g. *Aleiodes pallidator* (Thunberg) on *Leucoma salicis*), and some to include large numbers of host species (e.g. *A. alternator*, Table 1).

Table 1 Hosts of *Aleiodes alternator* (Nees)
(Literature records from Shenefelt, 1975. The quantitative data in the right hand column suggest that over 50% of the literature records are erroneous and – as all confirmed hosts feed on low plants – indicate a host range summarised as "low-feeding hairy caterpillars in the families Lasiocampidae, Lymantriidae and Arctiidae". While the last two families are closely related phylogenetically, Lasiocampidae is not)

Host Family	**Number of host species recorded in literature**	**Reared specimens (species)**
TORTRICIDAE	4	–
LASIOCAMPIDAE	1	164(3)
THAUMETOPOEIDAE	2	–
LYMANTRIIDAE	5	52(7)
ARCTIIDAE	4	49(12)
NOCTUIDAE	5	–
	21	**265(22)**

Overall, two major influences are evident as determinants of host range. One is host phylogeny (i.e. all hosts of a particular parasitoid may be closely related to one another) and the other is host ecology (i.e. the parasitoid may use a wider range of hosts, which are similar to one another in terms of feeding environment, behaviour, or morphology, but not all closely related to one another phylogenetically). For the present purposes I will call these two extreme types of host ranges "continuous" (e.g. Table 3) and "disjunct" (e.g. Tables 1 and 2), respectively. At a higher level it is noteworthy that some species-groups (e.g. the putative subgenera *Chelonorhogas* and *Neorhogas*) are tied to phylogenetically restricted groups of hosts while others (e.g. the putative subgenus

Aleiodes) contain apparently closely related species whose hosts – collectively – span many Lepidoptera families (Table 4). Too few host ranges of s. *Chelonorhogas* species are known for it to be possible to assess whether or not co-cladogenesis may have operated, but for s. *Aleiodes* s.str. it seems clear that the major influence on parasitoid radiation has been host ecology.

Table 2 Hosts of *Aleiodes nigricornis* Wesmael (* Lacks host remains. All hosts are Noctuidae, but *Apamea* is not phylogenetically closely related to *Orthosia*. The single record from *Mythimna* appears to be becoming marginalised and may be erroneous)

Hosts	**Reared specimens**
Overwinter	
Apamea ? crenata	4
Apamea ? monoglypha	1
Apamea ? epomidion	2
Apamea sp.	8
*Mythimna ferrago**	1
Summer	
Orthosia gothica	6
? *Orthosia gothica*	10

Another overlay that is clear is the importance of the parasitoid's searching environment. Very few *Aleiodes* species use both hosts specialised to low plants (grassland or understory) and those specialised to trees and bushes (canopy) – but with the proviso that in certain habitats (e.g. montane heaths) shrubby low plants will sometimes score as canopy. This applies equally to species having continuous (e.g. Table 3) and disjunct (e.g. Tables 1 and 2) host ranges.

Table 3 Hosts of *Aleiodes pulchripes* Wesmael and *A. rugulosus* (Nees) (All hosts are Acronictinae (Noctuidae). The two parasitoids are in the subgenus *Chelonorhogas*)

Host	***pulchripes***	***rugulosus***	**Hosts on**
Acronicta aceris	1		**Trees**
Acronicta psi	21		Trees
Acronicta tridens	4		Trees
Acronicta psi/tridens	2		Trees
Acronicta sp.	2		Trees
Acronicta auricoma		1	Low plants
Acronicta euphorbiae		2	Low plants
Acronicta menyanthidis		10	Low plants
Acronicta rumicis		3	Low plants
Acronicta sp.		3	Low plants
Simyra albovenosa		11	Low plants
Oxicesta geographica		1	Low plants

Some *Aleiodes* species are univoltine, while others are plurivoltine. Univoltine species show a strong tendency to have continuous host ranges, and the same is true of some plurivoltine species – especially (but not only) if they use plurivoltine hosts. However, a significant proportion of plurivoltine species have disjunct host ranges, often using different groups of univoltine hosts at different times of year. It is the species with disjunct host ranges that reveal the most about evolutionary processes, both of host recruitment and of parasitoid speciation.

Table 4 Biological knowledge of W. Palaearctic *Aleiodes* (Several species-groups in the subgenus *Aleiodes* contain species that are morphologically extremely close to one another, and it is in these groups particularly that speciation seems to be most active)

Subgenus	Σ Species	Biology verified (MRS)	Host families
Neorhogas	1	1	Sphingidae
Chelonorhogas	32	12	Noctuidae
Aleiodes	60+	31	14 (including Noctuidae)

The parasitoid's phenology is of course also connected to its host range. Whether univoltine or plurivoltine, different species of *Aleiodes* pass the winter as a mummy, as a small larva overwintering inside an overwintering host larva, or as an adult (Table 5). The latter behaviour is especially adopted by species attacking the larvae of arboreal Geometridae whose eggs hatch very early in spring.

Table 5 Overwintering by British *Aleiodes* species
(Only species for which understanding is good are included)

	univoltine	plurivoltine
In host larva	5	9
As mummy	10	3
As adult	3+	4+

An interesting example of realised host range varying geographically is seen in Britain in the largely plurivoltine species *Aleiodes coxalis* (Spinola) (erroneously said to be univoltine by Shaw 1994). This occurs, rather sparingly, over most of Britain and Ireland as a parasitoid of Satyridae, seeming to depend on *Coenonympha* species for a mid-summer generation but using probably a range of species including *Maniola jurtina* overwinter. In the south-east of England the hesperiid *Thymelicus lineola* occurs, often at high density, with a larva superficially similar to a satyrid and similarly feeding on Poaceae, which *A. coxalis* parasitises heavily. Through this early summer generation *A. coxalis* achieves a much higher level of abundance where *T. lineola* occurs than elsewhere in Britain. As *T. lineola* spreads northwards and westwards in Britain, the concurrent increase of the populations of *A. coxalis* having this disjunct host range is evident, but no research has been undertaken to see what deleterious effect on the satyrid hosts of *A. coxalis* this may have through the process known as "apparent competition".

There is good evidence (see discussion on especially *Aleiodes alternator* and the *Aleiodes* species using various *Orthosia* species as hosts in Shaw 1994) that hosts have been recruited to *Aleiodes* host ranges individually – i.e. that each host species in a host range has been a specific challenge to be overcome – and from experimental manipulations it is clear that some *Aleiodes* species show a willingness to oviposit into unsuitable hosts, especially if they are physically or behaviourally similar and/or phylogenetically related to suitable ones but occur only in environments in which the parasitoid does not normally search (in which case the parasitoid progeny are usually encapsulated and killed by the host's defences). If such a host, behaviourally accepted by the parasitoid, regularly appears in the parasitoid's searching environment it seems that it will eventually be recruited because of the selection pressure on the parasitoid to overcome the host's defences.

Once a parasitoid has expanded its host range, and given changing patterns of host occurrence in its searching environment, conditions that promote speciation may be expected to arise – in particular allowing specialisation, initially behavioural, on one part of the host range by parasitoid individuals that then tend to interbreed and adapt to this smaller host range (or single host) in such a way that gene flow between that population and the parent population will become sufficiently restricted for two species to result. In essence this speciation hypothesis asserts that new species arise as specialists, and it predicts that in closely related pairs of species radically different breadths of host range will sometimes be seen. (Such pairs might perhaps be thought of as either "sister species", or "parent and daughter species", depending on respectively whether or not the newly evolved species then out-competes its ancestor in respect of the initially shared part of the host range – i.e. for the "parent" to be seen as a "sister" would depend on its having been altered in some way by the speciation event. The evidence in *Aleiodes* is that competitive exclusion of this kind probably does tend to happen, although there are a few apparent species pairs in which the broader host range (? still) does cover the narrower one. Thus there is also a conceptually identifiable hypothetical process that will tend to reduce the disparity in breath of host range between "parent" and "daughter" as they move towards being "sisters").

Aleiodes are rather abnormal koinobionts in being synovigenic and having a long adult life. Nevertheless the conclusion that host ranges tend to expand by piecemeal recruitment of host species, largely through a failure of parasitoids to reject initially unsuitable hosts when they encounter them if they have enough characteristics in common with the parasitoid's actual hosts, may apply to koinobionts (though probably not to idiobionts) more generally (Shaw 1994; Shaw & Horstmann 1997). This is not to say, however, that all *Aleiodes* species (or all koinobiont parasitoids) will necessarily be on the path of expanding their host range it is equally evident that many parasitoids manage to remain as specialists, probably as a result of developing highly effective and exclusive host recognition cues.

Unfortunately the above speciation hypothesis is difficult to test at present. A robust molecular phylogeny of the *Aleiodes* species involved would be extremely helpful, and specimens are being stored in ethanol for that purpose. In the meantime one prediction is that "ancient" species that have not undergone substantial host range expansion (i.e. that have remained taxon specialists, even if using a group of closely related hosts) will have had less opportunity to speciate (i.e. they will appear to be the most morphologically isolated species, not having given rise to any very close "new" relatives). The testable prediction is not that taxon-specialists will be morphologically isolated (because the hypothesis is that new daughter species – i.e. behaviourally but not morphologically distinctive – first arise as taxon-specialists), but rather that very morphologically isolated species will be taxon-specialists. This does appear to be the case – with the single exception that *Aleiodes compressor* (Herrich-Schäffer) has aberrant morphology but regularly uses hosts in at least three and probably four families. However, this species attacks hosts entirely concealed in leaf-packages, buds etc, which it reaches with its blade-like metasoma but never contacts with other parts of itself. In other *Aleiodes* species both antennae and tarsi are employed at length in the host recognition process, and it seems that an important means to embark behaviourally on a path towards speciation through specialisation has been denied to *A. compressor*, even though it has been forced into the initial condition of host-range expansion by the same difficulty of exercising host discrimination.

Acknowledgements

A very large number of lepidopterists and others have helped me to build up pictures of host range by giving me reared parasitoids, and several have extremely kindly adopted my own research goals in their general fieldwork or hobby activities. The taxonomic end of this research on *Aleiodes* is in collaboration with Kees van Achterberg, whose role has been crucial.

References

Karsholt, O. & Razowski, J. (1996) *The Lepidoptera of Europe: A distributional checklist*. Apollo Books, Stenstrup (Denmark).

Noyes, J.S. (1994) The reliability of published host-parasitoid records: a taxonomist's view. *Norwegian Journal of Agricultural Sciences* **16**: 59-69.

Shaw, M.R. (1994) Parasitoid host ranges. pp. 111-144. *In* Hawkins, B.A. & Sheehan, W. (eds), *Parasitoid Community Ecology*. Oxford University Press, Oxford.

Shaw, M.R. (1997) *Rearing Parasitic Hymenoptera*. Amateur Entomologist's Society, Orpington, U.K.

Shaw, M.R. & Aeschlimann, J.P. (1994) Host ranges of parasitoids (Hymenoptera: Braconidae and Ichneumonidae) reared from *Epermenia chaerophyllella* (Goeze) (Lepidoptera: Epermeniidae) in Britain, with description of a new species of *Triclistus* (Ichneumonidae). *Journal of Natural History* **28**: 619-629.

Shaw, M.R. & Horstmann, K. (1997) An analysis of host range in the *Diadegma nanus* group of parasitoids in Western Europe, with a key to species (Hymenoptera: Ichneumonidae: Campopleginae). *Journal of Hymenoptera Research* **6**: 273-296.

Shenefelt, R.D. (1975) Braconidae 8. Exothecinae, Rogadinae. pp. 1115-1262. *Hymenopterorum Catalogus* (nova editio) **12.** Junk, The Hague.