

THE ORGANISATION OF CHALCID-DOMINATED PARASITOID COMMUNITIES
CENTRED UPON ENDOPHYTIC HOSTS

R.R. Askew

Department of Zoology, University of Manchester

England

The phytophagous larvae of many small endopterygote insect species complete their development inside plant tissue. Some inhabit stems or floral parts, others mine leaves and the most specialised induce hypertrophy of plant tissue to produce galls. Such endophytic species enjoy an environment largely protected from climatic extremes and one that is seldom breached by predators. Endophytes, however, are usually very vulnerable to the attack of parasitoids and they can support extremely complex parasitoid communities. These communities are self-contained in the sense that scarcely any parasitoids (or parasites as they will henceforth be termed) attack more than one group of endophytic hosts. The oak gall community is qualitatively almost totally different from the deciduous tree leaf-miner community, although both communities are part of the woodland ecosystem.

Interrelationships within an endophytic community are complex but, because activities occur within a very restricted space in which each occupant leaves some trace of its presence, it is usually not difficult to ascertain the specific rôle of each member of the community. Food webs are broad rather than long; many species may be included but since these are all more or less closely allied taxonomically they do not represent a variety of trophic levels.

It is proposed to describe two examples from Britain of endophytic communities: those in cynipid oak (*Quercus*) galls and in certain deciduous tree leaf-mines. Both, like the majority of such communities, are dominated by chalcidoid parasites. By comparing these two communities, and examining similarities and differences in their organisation, it is possible to identify some of the strategies employed by the component chalcid species.

Parasite strategies in communities centred upon a gall midge and a sawfly have been examined, respectively, by Force (1972) and Price (1973a) who conclude that development of the parasite complexes is related to plant succession with the early colonizers being highly fecund and of low competitive ability (*r*-strategists) and the late colonizers less fecund but of high competitive ability (*K*-strategists). This succession was found to apply also within a single host generation, and it is this aspect that is examined here. The present work pertains to mature woodland and the communities investigated have a much higher species diversity than those studied previously.

THE OAK GALL COMMUNITY

At least 31 species of gall-making Cynipidae are associated with oak in Britain. Most of these have two generations during a year and the galls induced by the two generations of the same species differ considerably in structure and position. The fauna known to be associated with these galls includes 15 species of inquiline cynipid and 45 species of chalcid parasite, 41 of the chalcid species being exclusively restricted to oak galls. Examination of large numbers of galls showed the community in any one type of gall to include at least some, and usually most, of the following elements (Askew 1961b).

1. gall-making cynipid feeding on gall tissue.
 2. inquiline cynipid feeding on gall tissue and usually also destroying the gall-maker.
 3. parasites of the gall-maker that are gall-specific.
 4. parasites of the gall-maker that are not gall-specific.
 5. polyphagous parasite especially of inquilines and gall-makers but sometimes of other parasites, also consuming some gall tissue (only *Eurytoma brunniventris* Ratzeburg in this category).
 6. gall-specific polyphagous parasites.
 7. polyphagous parasites associated with a variety of galls.
- } 16 species
} 28 species

No instance of host-specificity involving a host other than a gall-maker was recognised. Examples of all of the above numbered categories are found in the food web existing in galls of *Andricus curvator* Hartig (Fig. 1). This is a relatively complex food web. In other galls the pattern may be simpler, but always the same

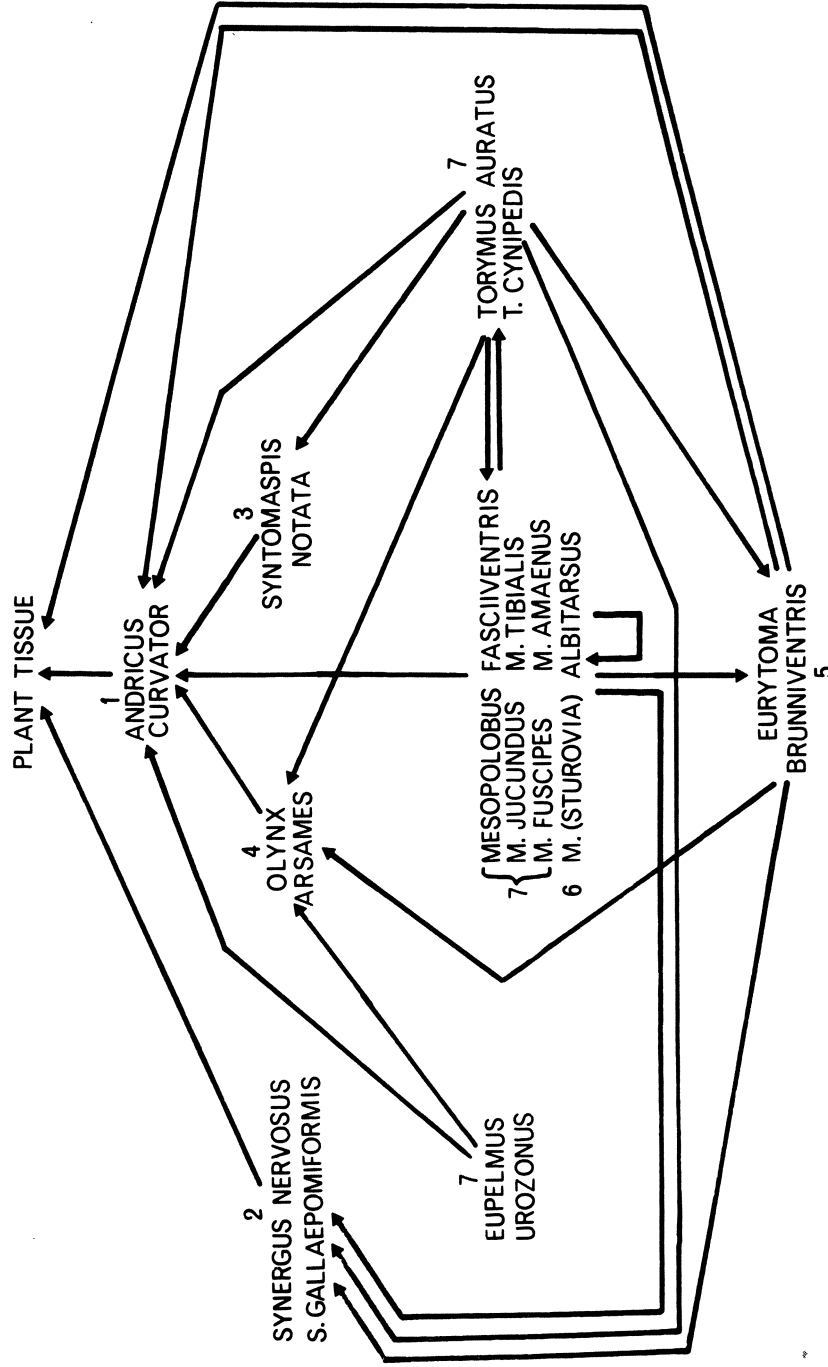


Fig. 1. Food web in galls of *Andricus curvator* Hartig. Arrows point towards the food source. Numbers refer to categories of gall inhabitants (see text).

species or their congeners occupy analogous positions in the community structure wherever they occur. Species assigned to different genera however, although taxonomically related, may occupy quite different situations (e.g. *Torymus* and *Syntomaspis*). This consistency of feeding habits within genera permits the construction of a generalised food web (Fig. 2), using data from all types of oak galls studied.

The five categories of parasites fall into two major groups; one composed of category 3 and 4 species which attack only the gall-makers and, for convenience, are all referred to as monophagous, even though those in category 4 are oligophagous, and the second of category 5, 6 and 7 species which are polyphagous. *Caenacis*, *Megastigmus* and *Tetrastichus* (also *Ormyrus* which is not included in Fig. 2) probably belong to this second group, but more data on their hosts are required.

What biological features characterise the two major groups of genera? Considering first the monophagous parasites, four families of Chalcidoidea are here represented but biological tendencies common to all, and distinguishing them from the polyphagous parasites, can be found. About half of the species are gall-specific (category 3) and the remainder (category 4) have very restricted host gall ranges, usually with a strong preference for only one or two types of gall. A striking feature of all of these species is that they make a very early attack on the gall-maker, usually achieving an initial high level of parasitism. Their flight periods are rather brief, very well synchronised with the appearance of their host galls, and they have only a single generation during a year, even though their host species may be bivoltine. Some of these features are illustrated by *Syntomaspis cyanea* (Boheman), a gall-maker parasite in galls of *Cynips divisa* Hartig (Fig. 3).

It is of interest to examine the course of parasitism in galls of the agamic generation of *Cynips divisa* through a year (Fig. 3). The galls, which are woody, globular, unilocular structures on the undersurfaces of oak leaves, first appear about the third week of June. They are very soon attacked by parasites and one of the first of these is *Syntomaspis cyanea*, the only species that restricts its attacks to the gall-making larva. *S. cyanea* is not strictly gall-specific, although its other recorded host galls all belong to the genus *Cynips*. The other parasite making an early attack on *C. divisa* galls is *Eurytoma brunniventris* which is a polyphagous species. The biologies of *S. cyanea* and *E. brunniventris* make an interesting comparison. *S. cyanea* is univoltine whilst *E. brunniventris* is multivoltine and it is mostly the second adult generation of the latter species that attacks young *C. divisa* galls. *S. cyanea* does not paralyse its host and feeds first on gall tissue, thus allowing the gall to

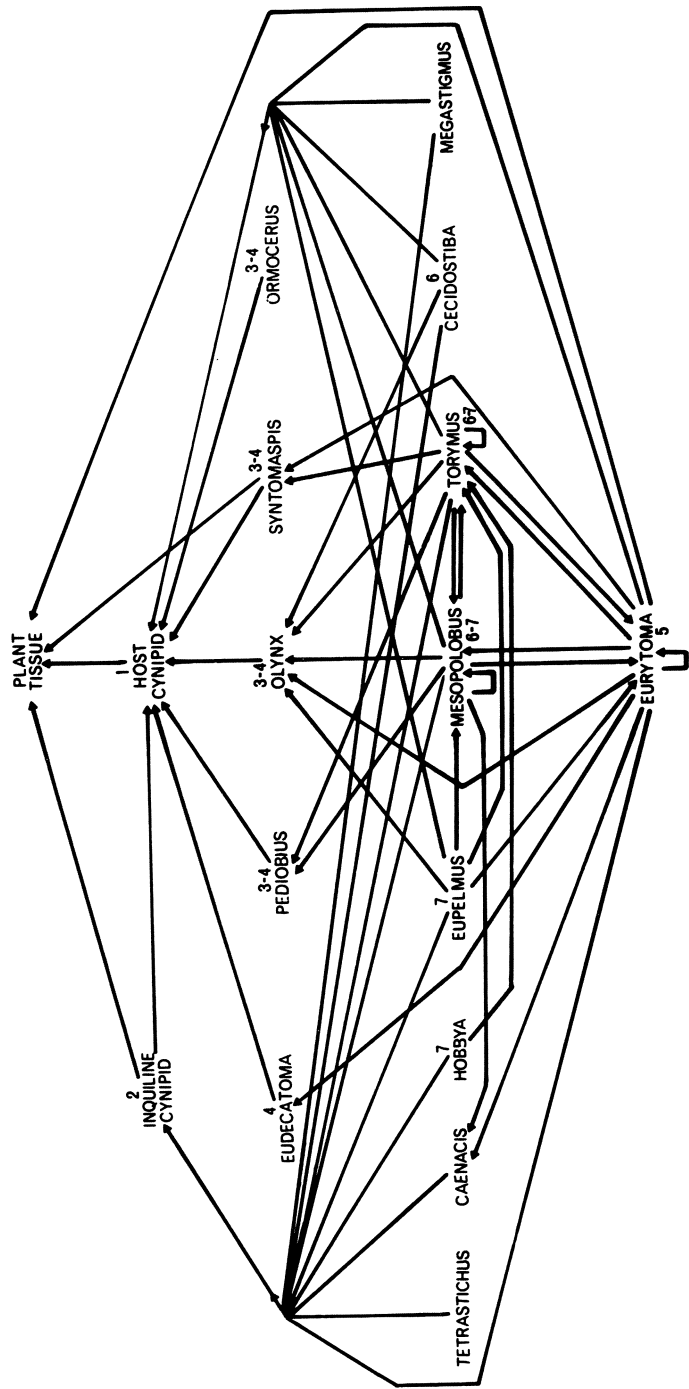


Fig. 2. Generalised diagram illustrating the interrelationships between genera of cynipid oak gall inhabitants. Arrows point towards the food source. Numbers refer to categories of gall inhabitants (see text).

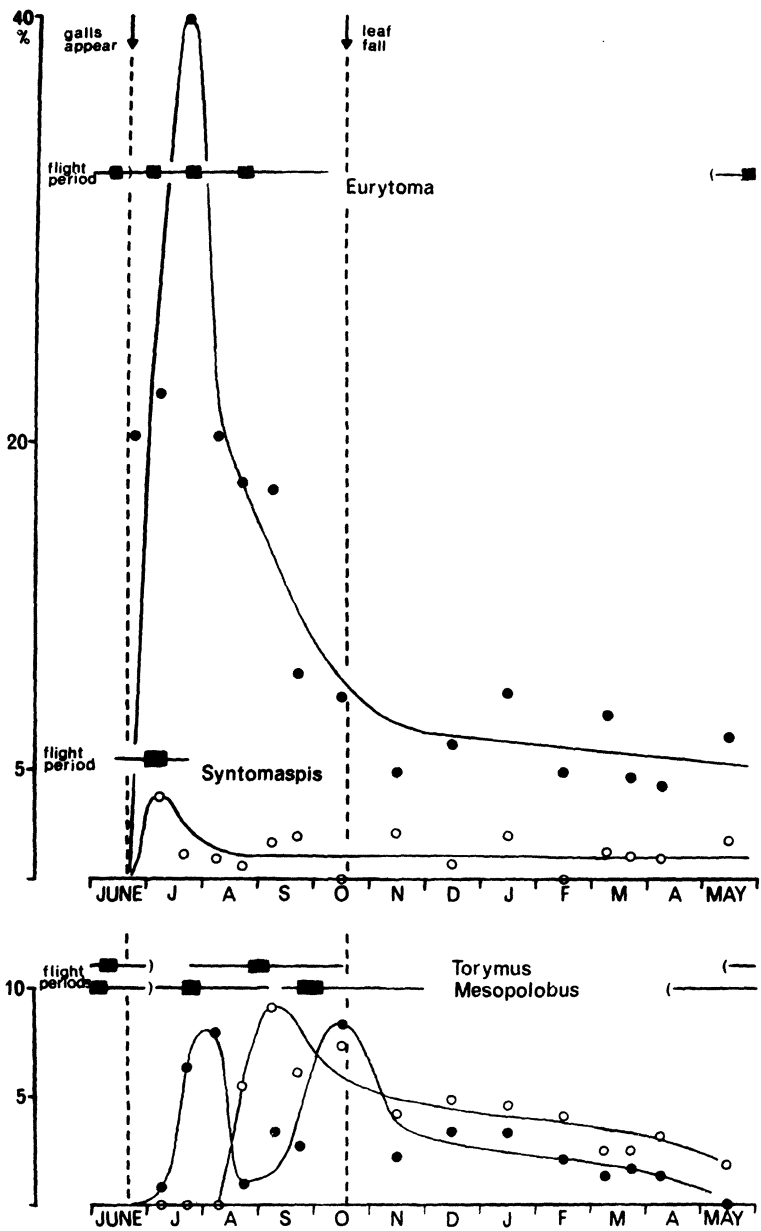


Fig. 3. Seasonal changes in percentage occurrence of the major parasites in galls of *Cynips divisa* Hartig based upon dissection of 3,281 galls collected in Wytham Wood, Berkshire, during 1958. Curves have been fitted by eye. Flight periods of the parasites are indicated by horizontal lines, the generation peaks being shown by solid rectangles.

develop fully. *E. brunniventris* usually paralyses the young *Cynips* larva which is soon eaten by the *Eurytoma* larva. This prevents further gall growth (Table 1). Since there is often insufficient food for the *E. brunniventris* larva in a young gall-maker larva, the *Eurytoma* frequently supplements its diet by also feeding on gall tissue, but this it does mostly after first consuming the gall-maker larva. *E. brunniventris* is the only polyphagous parasite known to eat gall tissue.

By allowing its host gall to develop, *S. cyanea* gains protection from attack by later parasites. It will be seen (Fig. 3) that *E. brunniventris* achieves a much greater initial parasitism of *C. divisa* than does *S. cyanea*, but that the numbers of *E. brunniventris* rapidly decline, partly as a result of the emergence of adult insects, but mostly because they are destroyed by later parasites such as *Mesopolobus* and *Torymus*. *S. cyanea* suffers to a much smaller extent from this mortality.

Olynx is another genus of monophagous parasites, the species of which, like *Syntomaspis*, do not paralyse their hosts but allow them to continue to grow and stimulate gall formation. Moreover, some species of *Olynx*, in some way unknown, alter the gall's structure so that it becomes harder and thicker-walled than normal (Askew 1961a).

In addition to benefiting from the protection of a fully-formed gall, by allowing the gall wasp larva to grow *Olynx* and *Syntomaspis* are provided with a much greater supply of animal food than would be the case if their host was paralysed by the ovipositing chalcid. In delaying destruction of their hosts, they are unusual ectoparasites. Typically, ectoparasites sting and either kill or paralyse the host at the time of oviposition. They thereby prevent the host from shedding its integument, which could be an awkward hazard to an ectoparasite, or from dislodging the ectoparasite by body movements. *Olynx* reduces the risk of dislodgement by placing its egg in the concavity of the ventral surface of its host (Askew 1961a).

By completing their development on the host stage originally attacked, typical ectoparasites do not enjoy the benefit of additional food becoming continually available to them in a host continuing to feed. Endoparasites, in contrast, seldom paralyse their host but allow it to continue feeding and growing whilst they initially consume only replaceable tissue. Perhaps the main difficulty in endoparasitism is that it necessitates overcoming the host's internal physiological defence mechanism. Endoparasitism is very rare amongst oak gall parasites but is found in *Eudecatoma* and *Pediobius*. Both of these genera are monophagous parasites and they make use of endophagy in perpetrating an early attack on their host populations.

Table 1. Sizes of *Cynips divisa* galls containing respectively, the gall-maker, *Syntomaspis cyanea* and *Eurytoma brunniventris*, showing that *S. cyanea* allows the gall to develop fully whereas parasitism by *E. brunniventris* results in a stunted gall. Data collected in Wytham Wood, Berkshire, 1958.

Contents of gall	Number measured	Mean diameter (mm)	Wall thickness of gall of mean diameter (mm)
<i>Cynips divisa</i>	7	4.7±0.15	0.9
<i>Syntomaspis</i>	14	4.7±0.13	1.0
<i>Eurytoma</i>	10	3.0±1.03	0.3

Another feature of monophagous parasites is that females tend to carry a large number of mature eggs (Table 2), an indication of high reproductive potential that in two species appears to be augmented by thelytoky, a phenomenon not associated with any of the polyphagous parasites. Males of *Olynx euedoreschus* (Walker) are exceedingly scarce; those of *Ormocerus vernalis* Walker are unknown.

Characteristics of polyphagous parasites in the oak gall community are very often complementary to those of species restricted to attacking the gall-making larvae. Most are multi-voltine (only two of the *Mesopolobus* species are univoltine), and there is a positive correlation between the number of types of gall attacked by a species and the number of generations it passes through during a year (Table 3). As well as being polyphagous within a particular gall, these species generally each attack a wide range of galls. All are ectoparasites and, with the exception of *Eupelmus urozonus* Dalman, they nearly always paralyse their hosts at the time of oviposition so that, when attacking the gall-maker, gall development is curtailed. Since their flight periods are not synchronised with particular galls, these tend to be more prolonged than are those of the monophagous parasites (although an individual's life span is not necessarily any longer), and in species with three or more generations during a year, flight periods of consecutive generations may overlap.

Females of polyphagous parasites usually carry fewer mature eggs than do those of monophagous parasites (Table 2). None of

Table 2. Egg loads of gravid chalcid parasites in cynipid oak galls and *Phyllonorycter* leaf mines. Only fully-developed or almost fully-developed eggs have been counted. All specimens were collected in the field at Abbots Moss, Cheshire, in 1974.

PARASITES IN OAK GALLS	Number gravid	Mean egg no./ gravid female	Highest egg nos.	*Mean egg length
Gall-maker parasites				
<i>Olynx skianeuros</i>	6	81.5	134,112	0.22±.01
<i>O. arses</i>	2	38.0	42,34	0.30
<i>O. gallarum</i>	2	20.0	24,16	0.15
** <i>Pediobius lysis</i>	7	40.6	60,58	0.09±.03
<i>Syntomaspis apicalis</i>	6	21.7	30,28	0.50±.03
Polyphagous parasites				
<i>Mesopolobus tibialis</i>	27	12.1	30,29	0.41±.04
<i>M. fuscipes</i>	3	9.3	14,10	0.40
<i>M. fasciventris</i>	14	9.7	18,18	0.43±.02
<i>M. jucundus</i>	4	15.3	28,12	0.50±.06
<i>Cecidostiba semifascia</i>	8	7.0	13,11	0.50±.04
<i>Eurytoma brunniventris</i>	9	10.9	20,17	0.30±.03
<i>Megastigmus dorsalis</i>	4	4.0	6,5	0.34±.04
<i>Torymus auratus</i>	22	15.6	30,24	0.47±.04
<i>T. cynipidis</i>	4	7.5	15,8	0.59±.07
PARASITES OF PHYLLOORYCTER				
Endoparasites				
** <i>Enaysma niveipes</i>	14	20.4	34,32	0.15±.02
** <i>E. latreillei</i>	12	29.1	45,42	0.15±.03
** <i>E. cilla</i>	7	33.3	54,44	0.14±.02
** <i>E. atys</i>	3	24.0	32,24	0.13
<i>Pediobius alcaeus</i>	10	10.6	18,17	0.28±.03
<i>Chrysocharis nephereus</i>	14	8.1	28,14	0.27±.03
<i>C. phryne</i>	3	7.7	12,7	0.22
<i>C. laomedon</i>	4	8.5	17,8	0.33±.03
<i>Closterocerus trifasciatus</i>	7	5.9	12,10	0.23±.03
Ectoparasites				
<i>Cirrospilus diallus</i>	17	6.6	14,10	0.40±.03
<i>C. lynceus</i>	5	6.8	15,8	0.34±.01
<i>C. vittatus</i>	3	5.0	10,4	0.24
<i>Pnigalio longulus</i>	23	7.8	23,21	0.46±.05
<i>P. soemius</i>	8	7.4	13,11	0.39±.04
<i>P. pectinicornis</i>	14	7.6	17,12	0.44±.05
<i>Sympiesis gordius</i>	2	4.5	5,4	0.40
<i>S. sericeicornis</i>	15	8.2	22,12	0.45±.05

*Excluding pedicel if present. Length in mm ± standard deviation.

**The very small eggs of these species were difficult to count and the numbers given are liable to greater inaccuracy than is the case for other species.

Table 3. The relationship between the number of generations per year and the number of types of oak gall attacked in those chalcid species whose voltinism is certainly known.

Number of generations per year	Number of chalcid species	Mean number of galls attacked per species
1	11	3.2
2	10	5.7
2-3	2	9.5
3-4	2	13.5
4-5	1	19.0

the polyphagous parasites is thelytokous, and in several the sex ratio of adults emerging from galls is male-biased. Considering all of the oak gall parasites for which adequate data are available, there appears to be a tendency for the sex ratio to become more male-biased the more types of galls are attacked (Fig. 4). Although the relationship is not close, there are significantly ($P < 0.05$) more species with less than sixty percent females amongst those attacking more than five types of galls than amongst those attacking fewer than five types of galls.

Discussion

In the description of oak gall parasites, I have attempted to show that the chalcid species adopt one of two broad strategies. In the first of these the host range is restricted to the gall-making cynipid and this is frequently accompanied by gall-specificity. This trophic restriction necessitates early attack on the gall-maker population before it is decimated by polyphagous parasites and, accordingly, we find tightly host-synchronised life cycles and adaptations to avoid possible food shortage as a result of attacking very small hosts. Because the host galls are small and soft when attacked, penetration is relatively easy and oviposition rapid. These parasites carry large numbers of eggs but often suffer considerable mortality from attack by polyphagous parasites. In some ways they may be thought of as *r*-strategists although, unlike the typical *r*-strategist parasitoid (Price 1973a),

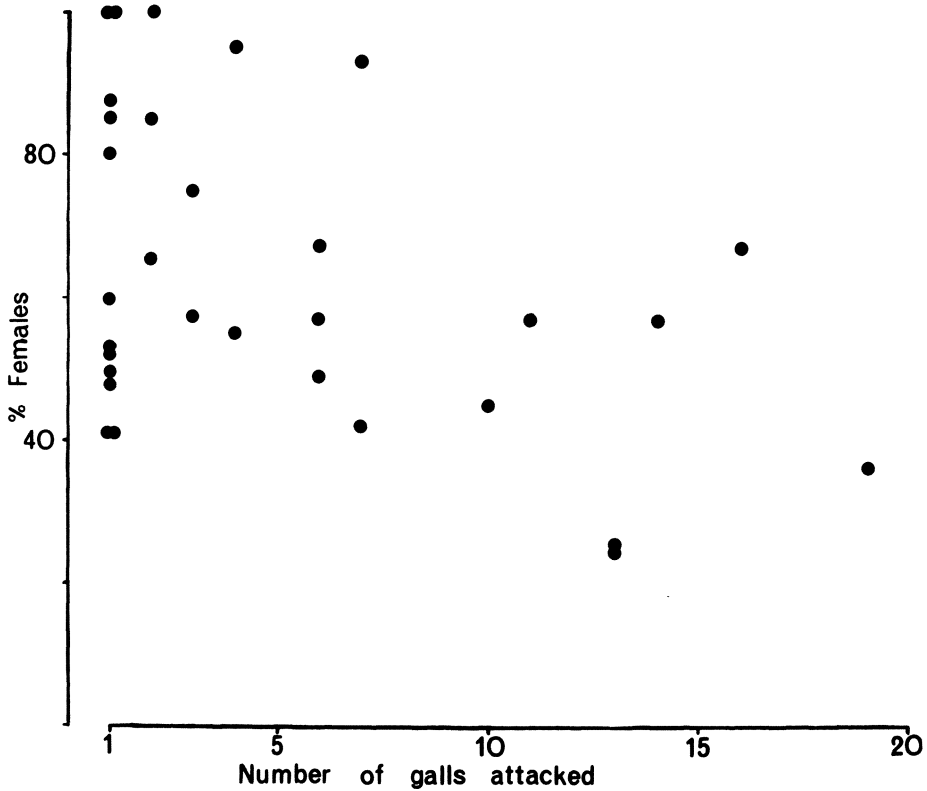


Fig. 4. Relationship between the sex ratios of emerging adults and the number of types of gall attacked for species of chalcid parasites in cynipid oak galls. Only species for which at least fifteen rearing records are available are included, and the majority of ratios are based upon much larger numbers.

they are not very dispersive, seldom being found away from the vicinity of hosts.

A quite different strategy is employed by the polyphagous parasites in oak galls. These attack hosts in galls that are usually fully-formed and therefore spend more time and energy in the deposition of each ovum than do monophagous parasites. *Eurytoma brunniventris* takes about one minute to penetrate a young gall of *Cynips divisa* but this time increases up to about 20 minutes in the case of mature galls (Askew 1961b). An ability to develop successfully on any host encountered is clearly

important. Polyphagous parasites carry fewer eggs on average than do the monophagous parasites, but this indication of lower reproductive potential is counterbalanced by their multivoltinism and by reduced mortality from hyperparasites as a result of their later attack on host galls. These polyphagous parasites have some of the attributes of *K*-strategists. It should however be noted that, because of the succession of potential hosts within a gall, a lower reproductive potential is less likely to be an adaptation to reduced host density than a response to the increased energy cost of laying each egg and the higher larval survival rate. The tendency for the sex ratio of polyphagous parasites to be less female-biased than that of monophagous parasites must also lower the reproductive potential.

A typical parasitoid *K*-strategist is characteristically prevalent in a mature ecosystem; it is a climax species. The polyphagous parasites depart from this ideal in apparently being less restricted to the environment in which their hosts are found than are the specific parasites. A collection of over six thousand chalcids from sand-dunes some considerable distance from the nearest oak tree included both sexes of five species of oak gall parasites (*Torymus auratus* (Fourcroy) and four species of *Mesopolobus*) all of which are polyphagous. Females of these species, carrying a relatively light burden of eggs, would seem more suited to dispersion than the heavily gravid females of the more host-specific gall-maker parasites. The polyphagous parasites in oak galls further depart from the ideal of a *K*-strategist in being multivoltine; paradoxically the more host-specific parasites, which are considered to be placed towards the *r* end of the *r*-*K* continuum, are univoltine.

THE LEAF-MINE COMMUNITY

Leaf-mines on deciduous trees may be formed by the larvae of certain Diptera, Coleoptera, Hymenoptera and Lepidoptera, but the chalcid parasites of these very different hosts, particularly those of the last three orders, are similar. Although many leaf-mining species may be identified by details in the form of their mines, there is no diversity of mine form comparable to the great variety of galls. The variation between mines involves little more than differences in mine outline and the track followed by the miner. All mines are essentially cavities, bordered on one or both sides by an intact layer of epidermis. Different species, however, mine different trees, and this provides a dimension to niche diversity in some ways comparable to the variety of forms exhibited by cynipid galls on oak. Qualitatively and quantitatively, the most similar leaf-miner parasite faunas are found on taxonomically allied trees (Askew and Shaw 1975); the most similar faunas in oak

galls are associated with those galls that are most alike in structure, position on the tree and season of growth (Askew 1961b).

The group of deciduous tree leaf-miners about which we have most information (Askew and Shaw 1975) is the genus *Phyllonorycter* (= *Lithocolletis*). All species of this lepidopteran genus construct very similar mines. Each of the numerous species is usually confined to a single tree genus or to allied tree genera, although several species may be found on the same tree.

The community of insects associated with *Phyllonorycter* mines on trees is, in many ways, strikingly different in structure from the oak gall community. Forty-six chalcid species were reared as parasites of *Phyllonorycter*, together with three species of Braconidae. These latter are present only at low densities and will not be considered further here. The interrelationships between chalcid genera, so far as are presently known, are indicated in Fig. 5. These are complex and, at first sight, chaotic, compared to the more structured, although equally large, oak gall community.

Endoparasites and ectoparasites are present in roughly equal numbers (21:25) in leaf-mines. The ectoparasites attack primary host larvae irrespective of whether or not they already contain endoparasites, and they thus inflict mortality on the endoparasites as well as on the leaf-miner population. Sometimes they destroy other ectoparasites, either by parasitising them directly or, more commonly, as a result of multiparasitism. Endoparasites attack predominantly the leaf-miners, but occasionally also ectoparasites, or other endoparasites usually at least after these have left their hosts' bodies. We have also recorded a few instances of endoparasites not being stung by an ovipositing ectoparasite and emerging fully fed from the primary host to leave the ectoparasite to starve. Even though there is this variety of possible interactions, hyperparasitism by endoparasites is less frequent than it is by ectoparasites. Only *Elachertus* among the ectoparasites has not so far been found as a hyperparasite, whereas of the endoparasites the several *Enaysma* species are apparently never hyperparasitic and, with the exception of *Closterocerus*, the others are only infrequently so (Table 4). This is just what would be expected. Endoparasites tend to be more restricted than ectoparasites in the hosts in which they can successfully develop because the means by which they overcome the host's defensive encapsulatory reaction do not usually operate over a wide host spectrum. *Closterocerus* is exceptional in being an endoparasite which evidently specialises to some extent as a hyperparasite (Table 4). Work at present in hand may reveal other specialisations.

Host-specificity is unusual amongst leaf-miner parasites and is developed to a high degree only in the endoparasitic genus

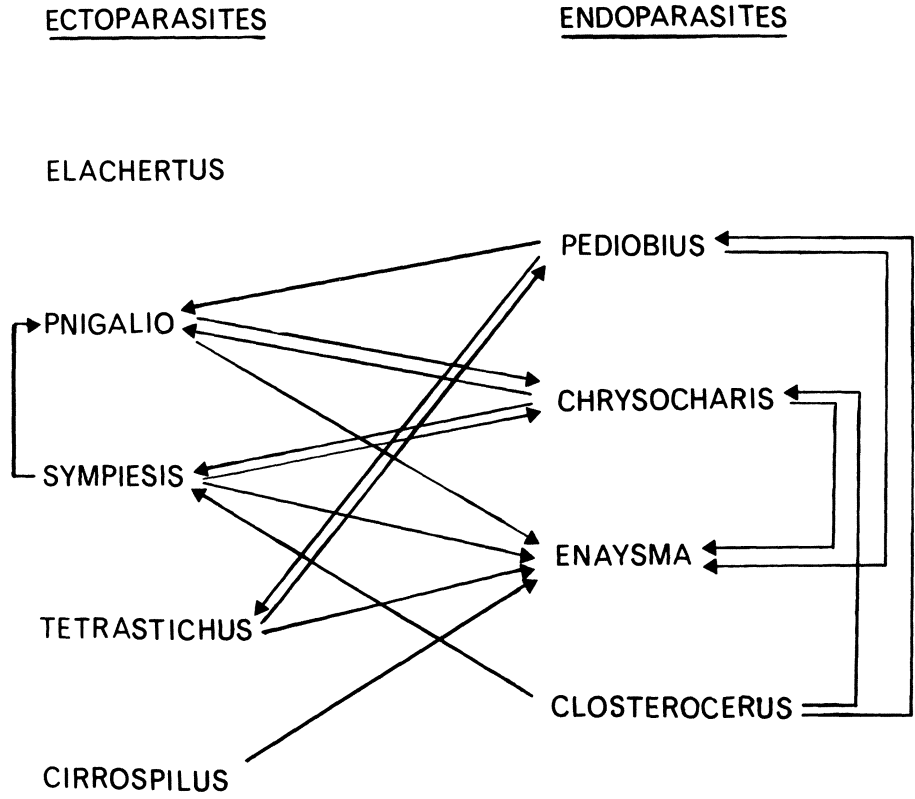


Fig. 5. Interrelationships between chalcid genera parasitic upon species of *Phyllonorycter*. Arrows point towards the food source. All genera also attack *Phyllonorycter*. Data collected in Cheshire, 1973 and from Delucchi (1958).

Table 4. Detected incidences of hyperparasitism by some *Phyllonorycter* parasites, based upon host remains in leaf-mines producing adult chalcids. Cases of hyperparasitism by ectoparasites, in which the lepidopterous primary host contains young endoparasites, would not be detected in this analysis, and the real percentage hyperparasitism by ectoparasites is certainly greater than that indicated by these data. The figures pertain to oak and birch mines collected in Cheshire, 1973.

Number developing as:			
	a)primary parasites	b)hyper- parasites	% hyper- parasitism
ECTOPARASITES			
<i>Cirrospilus diallus</i>	19	3	13.6
<i>Sympiesis sericeicornis</i>	40	4	9.1
<i>S. gordius</i>	13	0	0
<i>Phygadeuon longulus</i>	38	2	5.0
<i>P. pectinicornis</i>	48	6	11.1
<i>Tetrastichus ecus</i>	11	6	35.3
ENDOPARASITES			
<i>Pediobius alcaeus</i>	87	1	1.1
<i>Chrysocharis laomedon</i>	65	6	8.5
<i>C. nephereus</i>	34	6	15.0
<i>Enaysma latreillei</i>	21	0	0
<i>E. niveipes</i>	24	0	0
<i>Closterocerus trifasciatus</i>	12	17	58.6

Enaysma. Species of *Enaysma* probably attack only *Phyllonorycter* larvae and each species is virtually restricted to hosts mining only one or a very limited number of tree genera (Askew and Ruse 1974a). Some other endoparasites have restricted primary host ranges. Two species of *Pediobius*, *Chrysocharis gemma* (Walker) and *C. phryne* (Walker) are all associated with narrow ranges of trees; there is evidence, in fact, that *Pediobius alcaeus* (Walker) consists of two host tree-defined biological forms, one of which is thelytokous. Likewise, two tree-defined forms of *Chrysocharis nephereus* (Walker) have been recognised (Askew and Coshan 1973). Amongst the ectoparasites, a comparable situation exists only in the two sibling species *Sympiesis sericeicornis* (Nees) and *S. grahami* Erdős which, again, are predominantly associated with different trees.

As the endoparasites of *Phyllonorycter* tend to be more restricted in their host ranges than the ectoparasites, we might expect them to have some of the same biological characteristics as the specific cynipid parasites in oak galls.

Univoltinism, a feature of specific cynipid parasites, is unknown amongst *Phyllonorycter* parasites, possibly because mine form remains constant in different host generations.

The endoparasites of *Phyllonorycter*, like those of oak Cynipidae, tend to attack earlier host stages than the ectoparasites (Table 5). However, because leaf-miner development is rapid and mines at varying stages of development are present together over a long period, this does not demand that the endoparasites have an earlier flight period than the ectoparasites.

Two other features in which the endoparasites in leaf-mines show parallel adaptations to specific gall wasp parasites are egg load and sex ratio. The largest egg loads are carried by the endoparasitic *Enaysma* species (Table 2), and this can be directly related to their extremely narrow host ranges. If this is an indication that *Enaysma* are channeling their energies towards a high reproductive output, it would substantiate the proposition that they are *r*-strategists attacking an early, abundant host stage. Price (1973b) reports that ectoparasitic Ichneumonidae have fewer ovarioles per ovary than endoparasitic species.

The more host tree-restricted parasites of *Phyllonorycter* tend to have a more female-biased sex ratio (Fig. 6), and this must further contribute to their overall fecundity. *Chrysocharis phryne*, in fact, is probably thelytokous. The correlation between female bias and host range size is rather better than in the case of parasites in oak galls (Fig. 4), but this, to a large extent, is because species of the single genus *Enaysma* have a consistently small number of host trees and a high percentage of females.

Table 5. The larval instars of *Phyllonorycter* mining *Betula* attacked by endoparasites and ectoparasites, Abbots Moss, Cheshire 1974. Data obtained by examining mine contents; a *Phyllonorycter* larva containing living endoparasite eggs or first instar larvae was scored as having been originally attacked in the same instar, but larvae containing more advanced endoparasites were ignored; the figures for endoparasites thus represent the latest possible stage attacked. The presence of ectoparasites of any age was used to provide data on the instars attacked by ectoparasites.

Number of larvae attacked by:	<i>Phyllonorycter</i> larval instar attacked					Totals
	1	2	3	4	5	
Endoparasites	12	58	29	6	1	106
Ectoparasites	0	6	28	66	73	173

Discussion

Compared with galls, leaf-mines are flimsy structures. They are easily damaged and persist intact upon the trees for a comparatively short time. This probably accounts in part for the less ordered temporal sequence of parasite species in leaf-mines than in oak galls.

Leaf-miners do not modify plant tissue in the manner of gall-makers; they merely destroy it. There is no provision in leaf-mines for phytophagy by the parasites and we find no early-attacking ectoparasites in leaf-mines, supplementing their diet with plant food, like *Syntomaspis* and *Eurytoma* in oak galls. As the ectoparasites sting their hosts, they cannot rely upon host growth to supply food for their offspring, and inevitably the younger larval stages of *Phyllonorycter* are much more heavily attacked by endoparasites than by ectoparasites. Conversely, ectoparasites concentrate their attack upon older hosts. Since both endoparasites and ectoparasites are ovipositing at much the same time, this divergence in host selection must reduce, to a certain extent, the likelihood of an ectoparasite attacking a host already

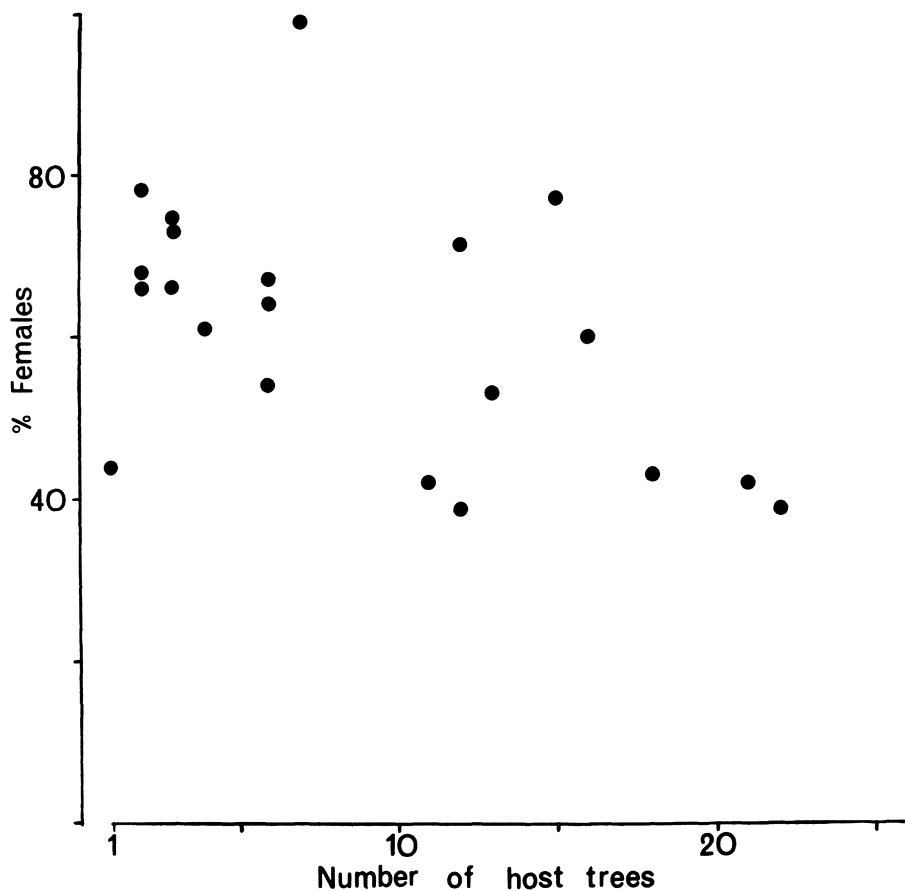


Fig. 6. Relationship between the sex ratios of emerging adults and the number of trees with which associated for species of chalcid parasites of *Phyllonorycter*. Only species for which at least fifty rearing records are available are included.

containing an endoparasite. If development of individuals in a *Phyllonorycter* population was more synchronised and the endoparasites were compelled in consequence to have a significantly earlier flight period than the ectoparasites, a greater proportion of them would presumably be later destroyed by ectoparasites, especially since the structure of a leaf-mine, unlike that of a gall, does not confer increasing protection upon its inhabitants as it matures. If the endoparasites were able to attack late larval stages of *Phyllonorycter*, they would again reduce their losses from ectoparasitic attack, but late larval stages of the host are at a

relatively low density and we have no certain evidence that this policy has been adopted by any species (although *Pediobius alcaeus* may have done so). A further factor mitigating against this strategy is that late-attacking endoparasites would be at risk from endoparasites that had previously attacked the host population since the oldest endoparasite usually survives in cases of multiendoparasitism (the converse is true in multiectoparasitism). For an endoparasite, the most likely alternative tactic to that of attacking the host at an early state of its development would seem to be that employed by *Closterocerus*. *Closterocerus* has escaped the bonds of host-specificity (theoretically, at least, difficult for an endoparasite) and become a late-attacking, polyphagous parasite.

Since host scarcity is not likely to be a serious problem for polyphagous parasites in oak galls, their smaller average egg load, compared with that of the specific parasites, is attributed to the high energy expenditure in ovipositing in mature galls (see above). In leaf-mines, however, the situation is different. Mines may be opened by insectivorous birds and there is much destruction of *Phyllonorycter* larvae by host-feeding chalcids. Thus more and more mines are without living larvae as the season progresses and, accordingly, the late-attacking polyphagous parasites carry few eggs, even though the energy cost of attacking a mature mine (excluding the cost of searching for an inhabited one) is probably no greater than that of attacking a young mine. In other words, polyphagous parasites in galls and mines are limited in the number of eggs they can successfully place in a given time but for different reasons. In galls the limitation is imposed by gall structure, in mines by host scarcity.

GENERAL DISCUSSION

Both endophytic communities described in this paper are components of mature ecosystems. Price (1973a) suggests that species in such communities may not clearly show the *r*-strategem, and this view is largely supported by the data presented here. It should be remembered, however, that nearly all of the parasites belong to a limited taxonomic group, and this no doubt places a restraint upon extreme divergence of many of their biological characteristics. It is encouraging that certain strategies are discernible and these, in most although not all features, conform in a general way to the concept of *r*- and *K*-strategies.

Parasites attacking an endophytic host in the early stages of its development find a comparatively high host density but the host individuals are small. Among such parasites we find those carrying a large number of eggs (e.g. *Olynx*, *Enaysma*), and they are either endoparasites allowing their hosts to continue their

development or, in the case of some of the oak gall parasites, they are ectoparasites also allowing continued host growth and, in a few species, supplementing their diet with gall tissue.

A major hazard confronting species attacking an endophytic host early is that of later destruction by secondary parasites. The communities become more and more complex as the season progresses and more species are included. Because the original plant-feeding host is soon decimated, and an ever-increasing proportion of live larvae in the plant cells are parasites, later parasites tend to be polyphagous, able to develop on either the primary host or its parasites. The polyphagous habit is of particular importance to oak gall parasites because time and energy spent penetrating galls in search of a selected host species would probably be considerable. We have no evidence that chalcid parasites in either leaf-miners or cynipid oak galls avoid drilling with their ovipositors into cells containing previously parasitised hosts. This apparent inability to determine the contents of a cell from the outside is perhaps one reason why no parasite in either community certainly specialises as a hyperparasite of a particular primary parasite species or even as a late-attacking primary parasite of the phytophagous host only. The only case of specialisation by parasites for a host other than the original leaf-miner or gall-maker that I am aware of is parasitisation of the inquiline cynipid *Periclistus* by *Eurytoma rosae* Nees and *Caenacis inflexa* (Ratzeburg) in rose galls of *Diplolepis rosae* (L.) (Claridge and Askew 1960, Callan 1944).

Polyphagy is generally associated with ectoparasitism, and accordingly we find that the parasites attacking older host stages usually feed in this manner. Multiparasitism must reinforce the tendency for endoparasites to attack the host early and for ectoparasites to attack it later. When larvae of two endoparasite species occur in the same host individual it is usually the older one that survives. In contrast, a younger ectoparasite normally develops at the expense of an older ectoparasite on the same primary host. Another factor that may encourage endoparasites to attack young host stages is that encapsulatory defensive reactions are probably more potent in old than in young host larvae.

The fundamental distinction between an *r*- and a *K*-strategist is reflected in their respective intrinsic rates of natural increase. These have not been ascertained for the parasites discussed in this paper, but I have used the mature egg load of gravid females caught in the field as a probable indication of reproductive potential. Those parasites attacking oak galls early often carry a large number of mature eggs. This is not so marked amongst leaf-miner parasites, only the very host-restricted

Enaysma species carrying large numbers of eggs.

An attempt has been made to present, in simplified form, the several factors that seem to be of significance for parasites attacking young and old host stages, and the strategies most frequently adopted by the parasites in response (Fig. 7). With these in mind, it is possible to speculate on the evolution of the type of community described.

It is difficult to conceive of a specific endoparasite of an endophytic host establishing itself in a community already rich in ectoparasites. Precise and perhaps complex adaptations would be required. It is much easier to envisage endoparasites becoming adapted to attacking an endophytic host before the appearance of ectoparasites in the community. However, the protected endophytic situation would, sooner or later, attract ectoparasites and competition between endoparasites and ectoparasites would ensue. Selection would then favour the adoption of more defined *r*-strategies by the endoparasites and *K*-strategies by the ectoparasites for reasons already discussed. If this generalisation is correct, an indication of the maturity of an endophytic community may perhaps be obtained by the proportion of ectoparasites in its fauna. The oak gall community includes a very high percentage of ectoparasites, far in excess of the percentage in the leaf-miner fauna, which would suggest that it is the more mature community of the two. A feature of the oak gall community consistent with this view is its taxonomic diversity, chalcids belonging to six families being represented. In contrast, the leaf-miner community is dominated by one family, the Eulophidae. The relatively few Eulophidae established in the oak gall community (*Olynx*, *Pediobius*) are taxonomically isolated there and have well-developed *r*-characteristics. It is tempting to think of them as the relic of a once more extensive eulophid element that has been decimated by the arrival of more competitive, ectoparasitic *K*-strategists. Force (1972) has postulated an increasing dominance of *K*-strategists in parasitoid communities as succession proceeds.

Arguing along these lines, a third endophytic community, that centred upon cecidomyiid galls on birch (*Betula*) leaves (Askew and Ruse 1974b), is perhaps at a relatively young evolutionary stage: endoparasites dominate its parasite fauna which includes no fewer than six species of the eulophid genus *Tetrastichus* amongst the ten chalcid species recorded.

SUMMARY

The biological strategies adopted by the parasitic chalcid components of two endophytic communities, those in cynipid oak

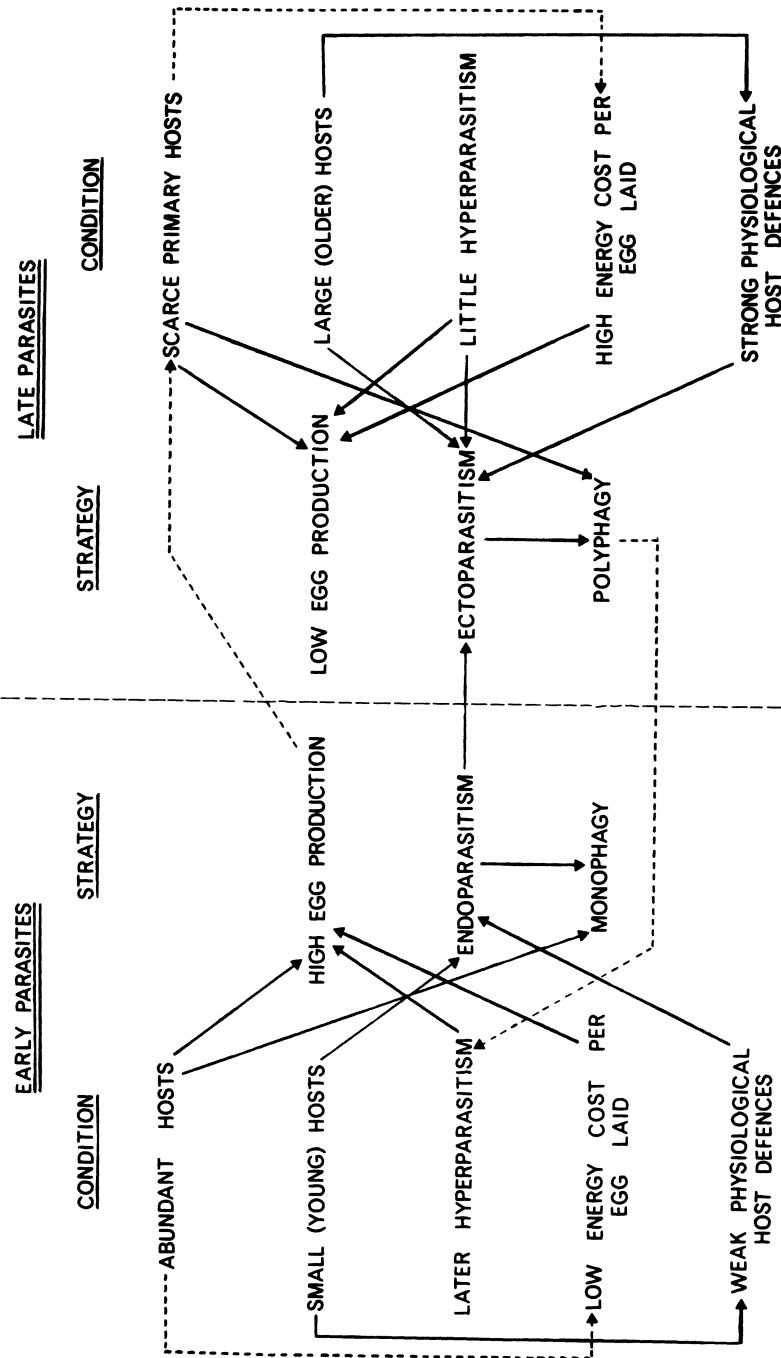


Fig. 7. Simplified scheme of basic strategies adopted in response to various conditions by chalcid parasites attacking respectively young and older host stages in endophytic communities. Most parasitoid communities examined in this paper conform to this pattern; those that do not have special adaptations.

galls and in *Phyllonorycter* leaf-mines, are described and discussed. In both communities species tending towards either end of the *r*-*K*-strategy continuum can be identified. Those thought of as *r*-strategists are characterised by being monophagous, often endoparasitic, and carrying a large egg load; those with *K*-strategist tendencies are polyphagous, ectoparasitic, and carry a smaller egg load. Biotic factors favouring the adoption of these two sets of characteristics are outlined (Fig. 7), and the possible pattern of evolution of parasite communities is discussed.

ACKNOWLEDGEMENTS

I am indebted to the Natural Environment Research Council whose grant (GR 3/864) made the time-consuming studies on the leaf-miner community possible, and to Dr. M.R. Shaw whose assistance, advice and ideas were invaluable. I am grateful also to Mr. J.G. Blower for criticism of a draft manuscript.

LITERATURE CITED

- Askew, R. R. 1961a. The biology of the British species of the genus *Olynx* Förster (Hymenoptera: Eulophidae), with a note on seasonal colour forms in the Chalcidoidea. Proc. R. Entomol. Soc. Lond., Ser. A. 36:103-112.
- Askew, R. R. 1961b. On the biology of the inhabitants of oak galls of Cynipidae (Hymenoptera) in Britain. Trans. Soc. Br. Entomol. 14:237-268.
- Askew, R. R., and P. F. Coshan. 1973. A study of *Chrysocharis nephereus* (Walker) (Hymenoptera: Eulophidae) and allied species, with observations on their biology in Northern England. J. Nat. Hist. 7:47-63.
- Askew, R. R., and J. M. Ruse. 1974a. Biology and taxonomy of species of the genus *Enayasma* Delucchi (Hym., Eulophidae, Entedontinae) with special reference to the British fauna. Trans. R. Entomol. Soc. Lond. 125:257-294.
- Askew, R. R., and J. M. Ruse. 1974b. The biology of some Cecidomyiidae (Diptera) galling the leaves of birch (*Betula*) with special reference to their chalcidoid (Hymenoptera) parasites. Trans. R. Entomol. Soc. Lond. 126:129-167.
- Askew, R. R., and M. R. Shaw. 1975. An account of the Chalcidoidea (Hymenoptera) parasitising leaf-mining insects of deciduous trees in Britain. J. Linn. Soc. In press.
- Callan, E. McC. 1944. *Habrocytus bedeguaris* Thomson and *H. periclisti* sp.n. (Hym., Pteromalidae) reared from galls of *Rhodites rosae* (L.). Proc. R. Entomol. Soc. Lond., Ser. B. 13:90-93.

- Claridge, M. F., and R. R. Askew. 1960. Sibling species in the *Eurytoma rosae* group (Hym., Eurytomidae). *Entomophaga* 5: 141-153.
- Delucchi, V. 1958. *Lithocolletis messaniella* Zeller (Lep. Gracilariidae): Analysis of some mortality factors with particular reference to its parasite complex. *Entomophaga* 3: 203-270.
- Force, D. C. 1972. *r*- and *K*-strategists in endemic host-parasitoid communities. *Bull. Entomol. Soc. Am.* 18:135-137.
- Price, P. W. 1973a. Parasitoid strategies and community organisation. *Environ. Entomol.* 2:623-626.
- Price, P. W. 1973b. Reproductive strategies in parasitoid wasps. *Amer. Natur.* 107:684-693.