

Mortality factors affecting the leaf-mining stages of *Phyllonorycter* (Lepidoptera: Gracillariidae) on oak and birch

2. Biology of the parasite species

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Accepted for publication June 1978

Parasitic Hymenoptera attacking *Phyllonorycter* species mining leaves of oak and birch were studied at a Cheshire locality during 1974. The host developmental stages killed, and attacked, by each parasite species are analysed. Smaller species and males tend to kill earlier *Phyllonorycter* instars than do larger species and females, and certain of the endoparasites as well as the ectoparasites must discriminate between small hosts which receive haploid eggs and large hosts which receive diploid eggs. Host-feeding is very widely practised, and facultative hyperparasitism is engaged in by all except the braconids and a few specialized chalcids. The biology of a parasite species generally allows its allocation to one of three groups according to the size of host larva that it attacks, whether it is endoparasitic or ectoparasitic, whether or not the host continues to develop after parasitization, the extent of its hyperparasitic behaviour, its reproductive capacity, and the width of its host range. Different strategies, together with different specific host and habitat preferences, provide the basis for parasite complexes of high species diversity.

KEY WORDS:—leaf-miner mortality – *Phyllonorycter* parasites – oak, birch.

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INTRODUCTION

Hymenopterous parasites have a large impact upon populations of *Phyllonorycter* mining leaves of oak and birch (Askew & Shaw, 1979). The parasites, with a few exceptions, are polyphagous, most species having a wide host range

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which in some cases includes two or three host orders (Askew & Shaw, 1974; Shaw & Askew, 1976a). All parasite larvae depend for food directly or (hyperparasites) indirectly upon the leaf-miner itself. The purpose of this study is to examine the differing strategies employed by various parasite species in their exploitation of a common resource.

Populations of oak and birch *Phyllonorycter* species were studied from June to leaf-fall in 1974 at Abbots Moss in Cheshire. Mines were collected from two sites, in a wood and from trees bordering a path. Two-thirds of the birch mines were collected in the wood while two-thirds of the oak mines came from the path. The sites and treatment of these samples, which provided most of the data discussed here, are fully described elsewhere (Askew & Shaw, 1979).

Four species of *Phyllonorycter* on oak, and two on birch, were represented in the samples. The distribution of certainly identified mines of these species at the two sites is as follows:

Oak, path: 260 *quercifoliella* (Zeller), 78 *harrisella* (L.), 33 *lautella* (Zeller), 11 *messaniella* (Zeller)

Oak, wood: 166 *quercifoliella*, 30 *harrisella*, 117 *lautella*, 2 *messaniella*

Birch, path: 42 *ulmifoliella* (Hübner), 6 *cavella* (Zeller)

Birch, wood: 104 *ulmifoliella*, 15 *cavella*

All these species except *P. cavella* passed through two larval generations during the period of study. *P. cavella* is univoltine with most of its mining activity occurring during the second larval generation of the other species.

Identification of parasitized *Phyllonorycter* presents many problems since it must be based upon characters of the leaf-mine unless the *Phyllonorycter* has developed to the pupal stage. Pupae can be identified by the structure of the cremaster and the distribution of spines on the posterior segments. On oak, the structure of the cocoons of *P. quercifoliella* and *P. harrisella* differ in the first generations (Miller, 1973) and this enables prepupae to be separated, but earlier stages cannot be distinguished. *P. lautella* is often recognisable by its gregariousness and preference for mining very small oak trees and, in later instars, the characteristic feeding pattern within the mine. On birch, mines sampled during the first period of mining activity (i.e. to the end of the first week of August), and from which parasites were reared, were recorded as probably *P. ulmifoliella*, and thereafter some of the more obvious size extremes could be assigned to the smaller *P. ulmifoliella* and the larger *P. cavella*.

THE PARASITE FAUNAS

Twenty-four species of parasitic Hymenoptera were reared. These are listed (Table 1) with numbers from path and wood sites in each host 'generation' on oak and birch and, where possible, the *Phyllonorycter* host species. Figures in Table 1 are affected by the factors outlined above, and are also biased against parasite species which attack smaller mines because most small mines were opened, often preventing further development of any parasite larvae. Immature parasite stages could not usually be identified.

Fourteen of the 24 parasite species were associated with both tree species and the majority of the remainder were rare. Thus there is considerable overlap in the composition of the parasite faunas of *Phyllonorycter* on oak and birch. The percentage similarity of the faunas in the present study is 32, close to the 34%

Table 1. Numbers of parasite species reared from samples of *Phyllonorycter* mines from oak (O) and birch (B) in the two annual host 'generations' (1 and 2) collected at the path (P) and wood (W) sites, Abbots Moss 1974. Numbers from identified host species are shown: 1, *quercifoliella*; 2, *harrisella*; 3, *lautella*; 4, *messaniella*; 5, probably *ulmifoliella*; 6, probably *cavella*. For the *Achrysocharoides* species, which are partly gregarious, the numbers of host mortalities are given under 'site and generation'

Parasite species	Tree	Site and generation				Total		Host species					
		P1	W1	P2	W2	♂	♀	1	2	3	4	5	6
ICHNEUMONIDAE													
<i>Gelis</i> sp.	O	1	0	0	0	0	1	1	0	0	0	—	—
BRACONIDAE													
<i>Rhyssipolis decorator</i> (Haliday)	O	2	1	0	0	3	0	0	0	0	0	—	—
	B	0	1	0	0	1	0	—	—	—	—	1	0
<i>Colastes braconius</i> (Haliday)	O	3	6	0	0	2	7	2	1	1	0	—	—
	B	1	37	0	0	17	21	—	—	—	—	37	0
<i>Apanteles circumscriptus</i> (Nees)	O	2	1	1	5	0	9	0	0	8	0	—	—
<i>A. nanus</i> (Reinhard)	B	2	0	0	0	0	2	—	—	—	—	2	0
EULOPHIDAE (Elachertinae, Eulophinae)													
<i>Elachertus inunctus</i> (Nees)	B	0	1	0	0	1	0	—	—	—	—	1	0
<i>Cirrospilus diallus</i> (Walker)	O	64	52	4	0	61	59	29	7	3	0	—	—
	B	0	38	0	1	20	19	—	—	—	—	35	0
<i>C. lyncus</i> (Walker)	O	1	12	1	0	6	8	1	1	1	0	—	—
	B	4	5	3	0	3	9	—	—	—	—	8	0
<i>C. pictus</i> (Nees)	O	3	0	0	0	2	1	1	0	0	0	—	—
	B	1	0	0	0	1	0	—	—	—	—	0	0
<i>C. vittatus</i> (Walker)	O	65	15	10	1	44	47	0	1	1	0	—	—
	B	12	15	1	1	18	11	—	—	—	—	20	0
<i>Sympiesis xanthostoma</i> (Nees)	B	0	1	0	0	1	0	—	—	—	—	1	0
<i>S. sericeicornis</i> (Nees)	O	32	6	4	1	29	14	11	2	1	0	—	—
	B	9	6	1	1	17	0	—	—	—	—	15	0
<i>S. gordius</i> (Walker)	O	6	11	0	1	8	10	0	0	11	0	—	—
	B	6	37	0	0	26	17	—	—	—	—	40	0
<i>Pnigalio longulus</i> (Zetterstedt)	O	7	0	1	0	5	3	3	0	0	0	—	—
	B	17	70	3	2	51	41	—	—	—	—	88	1
<i>P. pectinicornis</i> (L.)	O	19	25	1	0	26	19	7	1	10	0	—	—
	B	50	16	2	3	44	27	—	—	—	—	66	2
<i>P. soemius</i> (Walker)	O	0	0	1	0	1	0	0	0	0	0	—	—
	B	26	13	0	1	23	17	—	—	—	—	37	1
EULOPHIDAE (Entedontinae)													
<i>Chrysocharis nephereus</i> (Walker)	O	28	7	1	0	16	20	13	4	0	0	—	—
	B	7	7	0	0	7	7	—	—	—	—	12	0
<i>C. laomedon</i> (Walker)	O	6	7	0	0	6	7	7	0	0	0	—	—
	B	3	45	0	0	20	28	—	—	—	—	46	0
<i>C. phryne</i> (Walker)	O	20	38	0	10	1	67	37	0	35	0	—	—
<i>Achrysocharoides latreillei</i> (Curtis)	O	43	16	24	6	51	88	2	6	0	0	—	—
<i>A. niveipes</i> (Thomson)	B	76	69	35	105	130	320	—	—	—	—	291	42
<i>Pediobius alcaeus</i> (Walker)	O	29	36	3	2	30	40	50	3	10	1	—	—
	B	2	20	0	2	5	19	—	—	—	—	22	0
<i>P. saulius</i> (Walker)	O	2	0	1	0	1	2	2	0	0	0	—	—
<i>Closterocerus trifasciatus</i> (Westwood)	O	2	3	9	9	12	11	13	0	0	0	—	—

found in earlier work (Askew & Shaw, 1974).

Comparison of the percentage representation of each species in the eight samples (Table 2) demonstrates a tendency towards greater quantitative similarity between contemporary parasite faunas at different sites than between parasite faunas of different host generations at the same site. This also accords with our earlier findings, although the two sites here discussed are adjacent.

Survival curves of *Phyllonorycter* differ in the two generations (Askew & Shaw, 1979). In the first host generations these curves are more convex because of a predominance of ectoparasites attacking later life history stages, whilst in the second generations they are more concave because of greater mortality from early attacking endoparasites and from host-feeding. Ratios of adult endoparasites (broods) to ectoparasites reared from the two generations are:

1st generations, 0.73 (oak) and 0.63 (birch) ($n = 1168$)

2nd generations, 2.84 (oak) and 7.47 (birch) ($n = 257$),

and inspection of Table 1 shows *Achrysocharoides* species to contribute most to the high proportion of endoparasites in second generation mines. Askew & Ruse (1974) have shown that *Achrysocharoides* (= *Enaysma*) of several species achieve a higher percentage parasitism on hosts of the second generation. This abundance of tree-specific *Achrysocharoides* in the second generations underlies the low percentage similarities (Table 2) between the two trees when either sample, or both, is of the second generation.

Table 2. Percentage similarities between parasites reared from the oak and birch samples at path (P) and wood (W) sites in the two host 'generations' (1 and 2) at Abbots Moss, 1974

Oak				Birch				
W1	P2	W2	P1	W1	P2	W2		
64	54	33	26	34	11	9	P1	
	34	39	29	39	14	7	W1	
		44	19	25	9	9	P2	
			10	13	4	4	W2	
				48	53	43	P1	
					34	28	W1	
						84	P2	
							W1	
							P2	
							Oak	
							Birch	

Parasite host specificity

None of the parasite species is host specific. The two *Achrysocharoides* species, however, are host plant specific and the two *Apanteles* species, *Chrysocharis phryne* and *Closterocerus trifasciatus* were associated with only one tree species in the present study. *Prigalio soemius* is only casually associated with oak and found predominantly on birch (see also Askew & Shaw, 1974).

Different *Phyllonorycter* species on the same species of host tree generally support similar parasite faunas. On oak, however, *P. lautella* was not parasitized by *Achrysocharoides latreillei*, while it was the preferred host of both *Apanteles circumscriptus* and *Chrysocharis phryne*. Data in Table 1 do not suggest that *P. lautella* was the main host of *Sympiesis gordius* on oak because most hosts of this parasite were killed at a stage (Table 3) too early for any but *P. lautella* to be positively identified.

Host stages attacked and killed by the parasites

Numbers of each *Phyllonorycter* stage killed by primary parasites are given in Table 3, the data from oak and birch being combined. Some records of *Colastes* (= *Exotheclus*) *braconius* and *Pediobius alcaeus* (tabulated as 'unsexed') are of

Table 3. The stages of development at which *Phyllonorycter* were killed by different primary parasites at Abbots Moss, 1974. Host mortalities, not individual parasite numbers, are recorded for the gregarious female *Achrysocharoides* species

Parasite species and sex	Stage at which <i>Phyllonorycter</i> is killed					
	instar 2	3	4	5	prepupa	pupa
ECTOPARASITES						
<i>Gelis</i> sp. ♀	—	—	—	—	—	1
<i>Rhyssipolis decorator</i> ♂	—	—	—	1	3	—
<i>Colastes braconius</i> ♂	—	—	2	2	15	—
♀	—	—	—	4	24	—
unsexed	—	—	3	7	38	—
<i>Elachertus inunctus</i> ♂	—	—	—	1	—	—
<i>Cirrospilus diallus</i> ♂	2	41	22	10	1	—
♀	—	—	1	34	32	5
<i>C. lynceus</i> ♂	—	9	—	—	—	—
♀	—	1	6	7	2	1
<i>C. pictus</i> ♂	—	—	1	2	—	—
♀	—	—	—	—	1	—
<i>C. vittatus</i> ♂	6	38	9	1	—	—
♀	—	11	21	14	1	—
<i>Sympiesis xanthostoma</i> ♂	—	—	—	1	—	—
<i>S. sericeicornis</i> ♂	—	6	13	18	3	2
♀	—	—	—	2	7	3
<i>S. gordius</i> ♂	—	1	20	12	1	—
♀	—	—	—	22	4	—
<i>Pnigalio longulus</i> ♂	—	1	10	37	1	—
♀	—	—	—	24	13	5
<i>P. pectinicornis</i> ♂	—	8	33	24	2	—
♀	—	—	2	27	12	3
<i>P. soemius</i> ♂	—	2	14	7	—	—
♀	—	—	6	6	1	1
ENDOPARASITES						
<i>Apanteles circumscriptus</i> ♀	—	—	—	9	—	—
<i>A. nanus</i> ♀	—	—	—	2	—	—
<i>Chrysocharis nephereus</i> ♂	—	—	3	4	3	—
♀	—	—	—	4	11	7
<i>C. laomedon</i> ♂	—	—	8	10	3	—
♀	—	—	—	15	10	7
<i>C. phryne</i> ♂	—	—	—	—	1	—
♀	—	—	1	1	2	61
<i>Achrysocharoides latreillei</i> ♂	—	—	6	35	10	—
♀	—	—	5	28	5	—
<i>A. niveipes</i> ♂	—	—	56	57	17	—
♀	—	—	5	105	45	—
<i>Pediobius alcaeus</i> ♂	—	—	—	—	1	26
♀	—	—	—	2	1	53
unsexed	—	—	—	—	—	2
<i>P. saulius</i> ♀	—	—	—	—	—	2
<i>Closterocerus trifasciatus</i> ♂	—	—	—	1	1	3
♀	—	—	—	—	—	1

parasites that had already emerged when the mines were collected, their occurrence being detected from remains in the mines.

Endoparasites do not kill their hosts until at least the tissue-feeding stage of development (fourth instar), but some ectoparasites destroy sap-feeding *Phyllonorycter* larvae of the third, or even the second, instar. None of the commoner parasite species is constant in killing its host at a particular stage, although endoparasites are more consistent than ectoparasites in this respect. The endoparasites *C. phryne* and *P. alcaeus* nearly always kill pupae inside which they pupate themselves, *C. phryne* with its head orientated towards the anterior end of the *Phyllonorycter* pupa and *P. alcaeus* (also *Pediobius saulius*) adopting the reverse position. The other parasites normally pupate free of their hosts' remains.

In those species which were reared in large numbers, it can be seen that, in nearly all, females tend to kill later developmental stages than males. This is especially marked among the ectoparasites, but it applies also to endoparasites (except *A. latreillei* and *P. alcaeus*) and is related to the size of the adult parasite. Females are generally larger than their males, and this disparity is greater in the ectoparasitic Elachertinae and Eulophinae than among the endoparasitic Entedontinae. *Achrysocharoides* is exceptional in that males may be larger than their females (Askew & Ruse, 1974), but in these species females are usually gregarious so that the biomass of a female brood generally exceeds that of a male brood.

The relationship between parasite size and host stage killed extends to congeneric parasites. *Cirrospilus vittatus* is a smaller species than *C. diallus* and tends to kill earlier host instars. Similarly, *S. gordius* is generally smaller than *Sympiesis sericeicornis* and it kills, on average, younger hosts; *Pnigalio longulus* is the largest of the three *Pnigalio* species and most of its hosts die in a late instar. *C. trifasciatus*, exceptionally, is a small species that emerges most often from *Phyllonorycter* pupae. In these, however, it is usually a hyperparasite and, although it probably oviposits only in large mines, its true host is often rather small.

The host is killed, therefore, when it is sufficiently large to provide, or have provided, its parasite with enough food for complete development. This stage of host development occurs earlier for males and for small parasite species.

Hosts of the ectoparasites do not develop after being parasitized, and therefore the host stage killed is also the stage attacked by the ovipositing parent parasite. Since females of a species emerge from larger hosts than males, the ovipositing ectoparasite must discriminate between small hosts on which it lays unfertilized male eggs and larger hosts on which fertilized female-producing eggs are laid.

In the case of endoparasites, the stage at which the host is killed is only sometimes the same stage that is attacked; typically, endoparasitized hosts continue to feed and develop after being parasitized. Numbers of *Phyllonorycter* collected at different developmental stages that eventually produced adult endoparasites are shown in Table 4. These data are strongly biased against the earlier host stages since relatively few small mines were retained for parasite rearing, but they show that some endoparasites attack even first instar *Phyllonorycter* larvae.

A. circumscriptus, *C. phryne* and *Achrysocharoides* species oviposit in small host larvae, but *C. nephereus*, *Chrysocharis laomedon* and probably *C. trifasciatus* do not attack host stages prior to the fourth instar larva. *P. alcaeus* occupies an intermediate position, sometimes attacking hosts as young as the third larval instar, but

also attacking older hosts. Rearing data (Tables 3 and 4) strongly suggest that those endoparasites (*C. nephereus*, *C. laomedon* and perhaps *C. trifasciatus*) which attack only old host larvae prevent their further development. Additional evidence for this comes from dissections of a sample of mines of the weevil *Orchestes fagi* (L.) on beech. All *O. fagi* larvae which later produced *C. nephereus* were final instar and extremely sluggish. They had conspicuous oviposition wounds, and dissection of some revealed very young endoparasite larvae. None of the hosts continued to develop before being killed by *C. nephereus*, which was the only endoparasite in the sample. Pitakpaivan (1975) records similar behaviour for *Chrysocharis gemma* (Walker) as an endoparasite of *Phyllonorycter messaniella* on *Quercus ilex*.

Table 4. Numbers of *Phyllonorycter* mines producing primary endoparasites; tabulated according to the host developmental stage estimated from the external appearance of the mines at collection, Abbots Moss, 1974

Parasite species	<i>Phyllonorycter</i> stage collected					cocoon prepupa/pupa
	larval instar					
	1	2	3	4	5	
<i>Apanteles circumscriptus</i> ♀	1	1	5	0	2	0
<i>A. nanus</i> ♀	0	0	0	0	2	0
<i>Chrysocharis nephereus</i> ♂	0	0	0	4	4	3
♀	0	0	0	0	8	17
<i>C. laomedon</i> ♂	0	0	0	9	10	2
♀	0	0	0	0	20	12
<i>C. phryne</i> ♂	0	0	0	1	0	0
♀	0	2	23	10	10	21
<i>Achrysocharoides latreillei</i> ♂	2	5	13	18	13	0
♀	0	1	12	10	13	2
<i>A. niveipes</i> ♂	1	6	32	57	34	0
♀	0	3	18	46	87	1
<i>Pediobius alcaeus</i> ♂	0	0	3	1	2	21
♀	0	0	4	2	13	37
<i>P. saulius</i> ♀	0	0	0	0	0	2
<i>Closterocerus trifasciatus</i> ♂	0	0	0	0	1	4
♀	0	0	0	0	0	1

C. nephereus, *C. laomedon*, *C. trifasciatus* and apparently also *Achrysocharoides*, like ectoparasites, distinguish between small hosts in which haploid eggs are laid and large hosts in which fertilized eggs are laid. The first three of these, by preventing host development past the stage attacked, have a fixed resource, like an ectoparasite, and this explains the disparate distribution of fertilized and unfertilized eggs. Development of hosts of *Achrysocharoides*, however, does continue after parasitization, so that there is much less restriction on the quantity of food that the endoparasitized host can supply to its parasite. Since both *Achrysocharoides* species have solitary males but usually gregarious females, it may be the stress on a small host larva of supporting several parasites that reduces the numbers of females developing in hosts attacked when young.

Hyperparasitism and multiparasitism

Recorded instances of hyperparasitism are shown in Table 5. *C. braconius* and *Achrysocharoides* species were the most frequently recorded hosts of hyperparasites,

Table 5. Recorded cases of hyperparasitism by hymenopterous parasites in *Phyllonorycter* mines at Abbots Moss, 1974

	Number behaving as:		% hyper- parasitism	Hosts of hyperparasites
	hyper- parasites	primary parasites		
ECTOPARASITES				
<i>Gelis</i> sp.	0	1		
<i>R. decorator</i>	0	4		
<i>C. braconius</i>	0	95	0	
<i>E. inunctus</i>	0	1		
<i>C. diallus</i> ♂	5	76	6	<i>C. braconius</i> (1), indet. ecto. (3), indet. (1)
♀	5	73	6	<i>C. braconius</i> (4), indet. ecto. (1)
<i>C. lynceus</i>	0	26	0	
<i>C. pictus</i>	0	4		
<i>C. vittatus</i> ♂	7	55	11	<i>C. braconius</i> (1), indet. ecto. (5), <i>C. vittatus</i> (1)
♀	9	49	16	<i>C. braconius</i> (1), <i>A. latreillei</i> (1), indet. ecto. (2), indet. endo. (3), indet. (2)
<i>S. xanthostoma</i>	0	1		
<i>S. sericeicornis</i> ♂	4	42	9	<i>C. braconius</i> (2), <i>Pnigalio</i> sp. (1), indet. (1)
♀	0	14		
<i>S. gordius</i> ♂	0	34	0	
♀	1	26	4	indet. ecto. (1)
<i>P. longulus</i> ♂	6	50	11	<i>C. braconius</i> (3), <i>A. niveipes</i> (1), indet. ecto. (1), indet. (1)
♀	2	42	5	indet. ecto. (2)
<i>P. pectinicornis</i> ♂	3	63	5	<i>A. latreillei</i> (1), indet. (2)
♀	1	45	2	indet. ecto. (1)
<i>P. soemus</i> ♂	1	23	4	indet. (1)
♀	3	14	18	<i>C. braconius</i> (1), indet. ecto. (1), indet. endo. (1)
ENDOPARASITES				
<i>A. nanus</i>	0	2		
<i>A. circumscriptus</i>	0	9		
<i>C. nephereus</i> ♂	9	14	39	<i>C. braconius</i> (2), <i>A. latreillei</i> (5), <i>C. vittatus</i> (1), indet. ecto. (1)
♀	2	25	7	indet. ecto. (1), indet. endo. (1)
<i>C. laomedon</i> ♂	5	21	19	<i>C. braconius</i> (1), indet. ecto. (3), indet. endo. (1)
♀	3	32	9	<i>A. niveipes</i> (1), indet. ecto. (1), indet. endo. (1)
<i>C. phryne</i>	0	68	0	
<i>A. latreillei</i>	0	139	0	
<i>A. niveipes</i>	0	450	0	
<i>P. alcaeus</i> ♂	8	27	23	<i>A. niveipes</i> (1), <i>A. latreillei</i> (3), indet. ecto. (2), indet. (2)
♀	4	55	7	<i>C. braconius</i> (1), <i>A. niveipes</i> (1), indet. endo. (1), indet. (1)
<i>P. saulius</i> ♂	1	0		indet. ecto. (1)
♀	0	2		
<i>C. trifasciatus</i> ♂	7	5	58	<i>A. latreillei</i> (2), <i>C. phryne</i> (1), <i>P. alcaeus</i> (1), indet. ecto. (1), indet. endo. (2)
♀	10	1	91	<i>A. latreillei</i> (1), <i>P. alcaeus</i> (1), indet. ecto. (5), indet. endo. (3)

probably only because their early stages are easy to recognise. The Ichneumonoidea did not figure as hyperparasites although *Gelis* is very frequently a hyperparasite in other situations. All of the more common ectoparasitic chalcids (except *Cirrospilus lyncus* for which data are limited) were at least occasionally recorded as hyperparasites. Among the endoparasites, *Achrysocharoides* and *C. phryne*, which attack young hosts, do not engage in hyperparasitism, but it was commonly observed in those species that attack older *Phyllonorycter*. *C. trifasciatus*, in fact, was mostly reared as a hyperparasite, and males of *P. saulius* also appear to specialise in the habit. Our few records of this latter species can be supplemented by others kindly supplied by Miss G. Bryan who reared eleven males and eight females from oak *Phyllonorycter* mines. All of the females but only three of the males developed as primary parasites. Among the hyperparasitic Entedontinae in general, except *C. trifasciatus*, males more often than females developed as hyperparasites. Perhaps surprisingly, no such sexual difference was apparent among the ectoparasitic hyperparasites (Table 5).

All of our records probably refer to pseudohyperparasitism (Shaw & Askew, 1976b). The incidence of hyperparasitism and multiparasitism is under-recorded since not all ectoparasitized hosts could be satisfactorily dissected to establish whether or not they were also endoparasitized, and not all ectoparasite larvae were examined for endoparasites.

Multiparasitism, in which more than one parasite species develops on a single host individual, was seldom successfully completed although immature stages of different parasite species were often found together. Three records of successful multiparasitism involved, in each case, an ectoparasite and an endoparasite:

- ♂ *C. nephereus* + ♀ *C. vittatus* (oak)
- ♂ *C. nephereus* + ♀ *S. sericeicornis* (oak)
- ♀ *C. phryne* + ♀ *P. pectinicornis* (oak).

HOST-FEEDING

Dead larvae of *Phyllonorycter* are often found with their dried, flattened bodies loosely adhering to the inner surfaces of their mines. No parasites are present. Such mortality is due, almost entirely, to host-feeding (predation) by adult parasitic Hymenoptera, and it has been shown (Askew & Shaw, 1979) to be a major cause of death in the first three larval instars of *Phyllonorycter*.

An investigation was undertaken in 1977 to establish which parasite species engage in host-feeding. Muslin sleeves were put on trees at Abbots Moss in April and May. Foliage enclosed by the sleeves was scrutinised for any leaf-mines already present and these, together with other invertebrates, were removed. During May adult *Phyllonorycter*, reared from mines collected in 1976, were liberated in the sleeves. Each sleeve received two or three females and two to four males of one *Phyllonorycter* species appropriate to the tree. In late May and June a number of a species of chalcid parasite, either wild caught or reared, was introduced into each sleeve (apart from two controls). The sleeves were cut down in July and mines present were examined (Table 6). Results of similar experiments in 1975 on the braconids *C. braconius* and *A. circumscriptus* are also included in Table 6.

One *Phyllonorycter* first instar larva in one of the control sleeves was scored as 'host-fed'. Since this could not have been the cause of its death, some other

factor, evidently uncommon, must have been responsible. Plant antibiosis, a reaction which kills mining larvae of *Chromatomyia syngenesiae* Hardy (Dipt., Agromyzidae) and leaves the dead animals indistinguishable from those killed by adult parasites (Hopkins, 1977), may have been the cause of death. We are confident, however, that in the great majority of cases of host-feeding recorded in the preceding paper (Askew & Shaw, 1979), the cause of death is correctly recognized.

Table 6. Results of sleeving experiments to determine which of the parasite species engage in host-feeding as adults

Tree	Parasite sp. (origin)	Date introduced	Condition of <i>Phyllonorycter</i>	<i>Phyllonorycter</i> stage					pupa	totals
				1	2	3	4	5		
<i>Phyllonorycter</i> sp.										
oak	<i>C. diallus</i> (2♀ virgin ex oak)	31.v, 2.vi	host-fed	0	0	0	0	0	0	0
	<i>quercifoliella</i>	24, 26.v	parasitized healthy	0 0	0 0	0 0	0 6	0 1	0 0	0 7
oak	<i>C. diallus</i> (2♀ wild)	9.vi	host-fed	9	2	0	0	0	0	11
	<i>quercifoliella</i>	24, 26.v	parasitized healthy	0 4	0 17	0 42	0 20	0 12	0 0	0 95
birch	<i>S. sericeicornis</i> (5♀ virgin ex oak)	28, 31.v	host-fed	15	27	8	1	0	0	51
	<i>ulmifoliella</i>	12.v	parasitized healthy	0 0	0 1	0 3	0 0	1 0	0 0	1 4
oak	<i>S. gordius</i> (2♀ wild)	9, 16.vi	host-fed	7	14	6	0	0	0	27
	<i>quercifoliella</i>	28.v	parasitized healthy	0 25	0 29	3 19	1 4	0 1	0 0	4 78
birch	<i>A. niveipes</i> (2♀ virgin ex birch)	24.v	host-fed	2	5	1	0	0	0	8
	<i>ulmifoliella</i>	16.v	parasitized healthy	0 0	1 0	3 2	3 0	0 0	0 0	7 2
birch	<i>C. nephereus</i> (3♀ wild)	9, 16.vi	host-fed	2	12	13	0	0	0	27
	<i>ulmifoliella</i>	12.v	parasitized healthy	0 0	0 0	0 0	2 1	1 4	0 2	3 7
birch	<i>C. laomedon</i> (5♀ virgin ex birch & beech)	24, 28.v	host-fed	1	0	0	0	0	0	1
	<i>ulmifoliella</i>	12.v	parasitized healthy	0 0	0 0	0 3	0 13	0 12	0 0	0 28
rowan	<i>C. phryne</i> (3♀ virgin ex rowan)	24.v	host-fed	11	12	9	0	0	0	32
	<i>sorbi</i>	16.v	parasitized healthy	2 3	5 2	4 2	0 2	0 2	0 1	11 12
birch	<i>P. alcaeus</i> (5♀ virgin ex hornbeam)	28.v	host-fed	11	5	3	0	0	0	19
	<i>ulmifoliella</i>	17.v	parasitized healthy	0 0	0 0	0 0	1 0	0 0	0 0	1 0
oak	<i>P. alcaeus</i> (5♀6♂ ex oak)	31.v	host-fed	9	5	0	0	0	0	14
	<i>harrisella</i>	26.v	parasitized healthy	0 2	0 5	0 1	0 0	0 0	0 0	0 8
oak	<i>C. braconius</i> (1♀ virgin ex beech, 1♀ wild)	30.vii, 4.viii	host-fed	1	7	10	12	3	0	33
	<i>quercifoliella</i>	14.vii	parasitized healthy	0 0	0 0	0 0	0 2	8 0	0 11	8 13
oak	<i>A. circumscriptus</i> (2♀ virgin ex beech)	30.vii	'host-fed'	2	6	0	0	0	0	8
	<i>quercifoliella</i>	9.vii	parasitized healthy	0 0	0 0	0 0	0 0	74 0	0 22	74 22
oak	no parasite (control) <i>quercifoliella</i>	26.v	'host-fed'	0	0	0	0	0	0	0
			healthy	0	0	5	11	3	0	19
oak	no parasite (control) <i>harrisella</i>	26.v	'host-fed'	1	0	0	0	0	0	1
			healthy	1	1	2	0	0	0	4

In the *A. circumscriptus* sleeve, mines scored as host-fed were few compared with the many successfully parasitized. The high level of parasitism achieved in this sleeve probably involved also considerable superparasitism, and damage resulting from oviposition rather than host-feeding is likely to have caused the low level of mortality noted.

C. diallus, *S. sericeicornis*, *S. gordius*, *Achrysocharoides niveipes*, *C. nephereus*, *C. phryne*, *P. alcaeus* and *C. braconius* all feed as adults on *Phyllonorycter* (Table 6). This list includes both endoparasites and ectoparasites, and host-feeding is probably of general occurrence amongst other parasites of *Phyllonorycter* with the exception of *Apanteles* species. It is possible also that parasitic Hymenoptera not otherwise associated with *Phyllonorycter* are responsible for some 'host-feeding'.

The purpose of host-feeding, which is practised only by females, is to obtain protein for egg production. Al Darkazly (1977) shows that female *Nasonia vitripennis* (Walker) (Hym., Pteromalidae), if deprived of hosts and fed only on sucrose, have lipid and glycogen but no protein accumulations in the fat body.

The fact that many more potential hosts in the sleeves were destroyed by host-feeding than by parasitism is some measure of its importance to parasites of *Phyllonorycter*.

BIOLOGY OF THE MAJOR PARASITE SPECIES

Some key biological characteristics of the parasite species are summarized in Table 7. Data pertain to the present study with the addition of host and host plant records from Askew & Shaw (1974) and Shaw & Askew (1976a). The species are allocated between three groups, species within a group being similar in most of the biological features compared.

The method of sampling reveals some intra-group specialisations. Within group 1, *A. circumscriptus*, *A. latreillei* and *C. phryne* were found only on oak, *A. nanus* and *A. niveipes* only on birch. *A. circumscriptus* and *C. phryne* are further limited by an apparent preference for *P. lautella*, reflecting an affinity for hosts on low-growing vegetation. Bachmaier (1965) reports *C. phryne* to be common parasite of *P. anderidae* (Fletcher) on dwarf birch (*Betula nana*), and we have found it in mines on a beech hedge, low elm scrub and honeysuckle, as well as on rowan on which tree it is not confined to the ground or shrub layer. Similarly, *A. circumscriptus* parasitises particularly *Phyllonorycter* which feed on low vegetation (Shaw & Askew, 1976a, unpublished). *A. latreillei* does not appear to parasitize *P. lautella*, all our rearings of this parasite being from mines which were, if not identifiable to another species, certainly not *P. lautella*.

Within group 2, host specializations are less apparent and no species was associated with only one of the two tree species, although *P. soemius* was nearly restricted to birch. The *Cirrospilus* species attack younger hosts than do others in the group. *C. vittatus* was most numerous at the open path site, *C. diallus* in the wood, which may be the outcome of different habitat preferences. Similarly *C. braconius*, *P. longulus* and *P. soemius* occurred more frequently on birch, the first two in the wood but *P. soemius* at the path, whilst *S. sericeicornis* apparently preferred oak at the path site. *S. gordius* was found chiefly in the wood.

In group 3, *C. trifasciatus* was found only on oak, *C. laomedon* was most numerous on birch and in the wood, and *C. nephereus* was more frequent at the path. This latter species exists in two morphological forms (Askew & Coshan,

Table 7. Summary of some biological characteristics of the regular parasites of *Phyllonorycter* on oak and birch. Data in the last two columns are from previous work (see text)

Species	Ecto- endo- parasite	Extent hyper- parasitic	Host instar attacked	Host develops after parasitism	Reproduc- tion	No. of tree genera on which attacks <i>Phyllonorycter</i>	No. of host families
GROUP 1							
<i>A. circumscriptus</i>	end.	never	early	yes	thelytokous	9	1
<i>A. nanus</i>	end.	never	early	yes	thelytokous	4	1
<i>C. phryne</i>	end.	never	early	yes	thelytokous	6	1
<i>A. latreillei</i>	end.	never	early	yes	sexual	1	1
<i>A. niveipes</i>	end.	never	early	yes	sexual	1	1
GROUP 2							
<i>C. braconius</i>	ect.	never	late	no	sexual	12	5
<i>C. diallus</i>	ect.	frequent	mid	no	sexual	13	7
<i>C. vittatus</i>	ect.	frequent	mid	no	sexual	9	6
<i>C. lyncus</i>	ect.	?	mid	no	sexual	5	2
<i>S. sericeicornis</i>	ect.	occasional	late	no	sexual	16	5
<i>S. gordius</i>	ect.	occasional	late	no	sexual	13	1
<i>P. longulus</i>	ect.	frequent	late	no	sexual	8	6
<i>P. pectinicornis</i>	ect.	occasional	late	no	sexual	13	8
<i>P. soemius</i>	ect.	frequent	late	no	sexual	5	7
GROUP 3							
<i>C. nephereus</i>	end.	frequent	late	no	sexual	11	8
<i>C. laomedon</i>	end.	frequent	late	no ?	sexual	13	4
<i>C. trifasciatus</i>	end.	usual	late	no ?	sexual	5	6
UNPLACED							
<i>P. alcaeus</i>	end.	frequent	mid	yes	sexual	11	1

1973) linked with different host trees, *C. nephereus* form *betulae* on birch and *Salix* and the typical form on other trees. No other biological differences have been discovered, and in sleeving experiments we have reared both forms through *Phyllonorycter* on the 'wrong' trees.

P. alcaeus is not placed in a group since it combines characteristics of group 1 and group 3 species.

DISCUSSION

When several fairly closely allied species of insects, such as the parasites of *Phyllonorycter*, have broadly similar modes of life, differences in the details of their ecology will be found. To understand more clearly the parts played by *Phyllonorycter* parasites in the ecology of their hosts and of each other, it is necessary first to recognise the major ecological strategies that are employed.

A preliminary attempt (Askew, 1975) at establishing a broad ecological division of the parasites of endophytic insects was based upon the stage in the hosts' life cycles at which parasite oviposition occurred. Briefly, parasites attacking early in the hosts' life cycles generally encounter an abundance of potential hosts which are small in size and have weak physiological defensive mechanisms against invasion of their bodies by endoparasites. These conditions should favour early-attacking parasites that produce many eggs, are

endoparasites and have a relatively narrow host range. Conversely, parasites attacking later in the hosts' life cycle face a relative scarcity of potential hosts which are larger and have strong defensive mechanisms, conditions favouring lower levels of egg production, ectoparasitism and polyphagy.

Achrysocharoides and *Apanteles* species, and *Chrysocharis phryne*, show the postulated adaptations of species attacking the host early. They are endoparasites with restricted host ranges. Female *Achrysocharoides* and *Apanteles* carry large numbers of small eggs and the former are often gregarious parasites of *Phyllonorycter*. The female *C. phryne* does not have a large egg load (Askew, 1975), but its reproductive potential is enhanced by thelytoky. The *Apanteles* species of this study are also thelytokous (Shaw, in prep.).

Sympiesis and *Pnigalio* conform with the characteristics typical of parasites attacking the host at a later stage of its development. They are very polyphagous, often hyperparasitic, ectoparasites and females carry relatively small egg loads (Askew, 1975). *Colastes braconius* departs from this norm only in not being hyperparasitic. *Cirrospilus* species may also be thought of in this group although they sometimes attack the host when it is still quite small; this they can do simply because they too are small and sufficient food is present in a small host for their ectoparasitic development.

A group of species that includes *Chrysocharis nephereus* and *C. laomedon* apparently attacks the host quite late in its development. They are endoparasites but polyphagous and carry small egg loads, thus combining features of the two more extreme strategies. Endoparasites are typically restricted in their host ranges by specialized adaptations required to avoid the hosts' encapsulatory defence reactions. Such adaptations are normally not effective in a wide range of host species, but the species mentioned have clearly escaped from such restriction by the expedient of quickly killing the host. Species of the ichneumonid genus *Pimpla*, which are remarkably polyphagous endoparasites of Lepidoptera pupae, also appear to kill their hosts extremely rapidly (Führer & Kilincer, 1972). Not only do *C. nephereus* and *C. laomedon* attack several host species as primary parasites, but they can also develop hyperparasitically. This latter ability is important to a parasite attacking older *Phyllonorycter* mines because at this stage there is a high level of primary parasitism and limitation to the role of primary parasite would severely reduce the number of available hosts. *Closterocerus trifasciatus* and perhaps male *Pediobius saulius* provide examples of further specialization in this direction, both most commonly behaving as hyperparasites and apparently rapidly killing their hosts. The concept of an endoparasite necessarily having a restricted host range (and therefore needing to attack young stages of an endophytic host) is clearly not universally applicable.

The parasite species can be allocated between three groups, the species in a group possessing a suite of associated characteristics (Table 7). Such grouping accommodates almost all of the regular *Phyllonorycter* parasites. *Pediobius alcaeus*, however, has biological characteristics intermediate between those of group 1 and group 3. It is moderately polyphagous, attacking a wide range of *Phyllonorycter* species but, apparently, not other genera (Askew & Shaw, 1974) unless behaving as a hyperparasite. It attacks hosts from the third instar onwards and permits their development to the pupal stage.

Evidence presented above suggests that further ecological separation of species within each group depends upon various special adaptations based upon host

plant and habitat preferences. Congeneric species tend to be segregated spatially and permutation of these preferences with the characteristics of the three major groups of parasites provides sufficient ecological niches for the minimization of interspecific competition. The *Phyllonorycter* populations thus support parasite faunas that are biologically varied and very rich in species.

ACKNOWLEDGEMENTS

We are grateful to the Natural Environment Research Council for financial support (GR/3/864), to Georgina Bryan for supplying extra data, and to Mr & Mrs Mather and Mr & Mrs Hamilton for allowing us access to private property at Abbots Moss.

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