THE UNIVERSITY OF HULL

STUDIES OF INSECTS ASSOCIATED WITH LOTUS CORNICULATUS L.

being a Thesis submitted for the Degree of
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by

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CONTENTS

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Summary of Thesis submitted for Ph.D. degree

by Stephen G.A. Compton

on

Studies of Insects associated with *Lotus corniculatus* L.

The major objectives of this study were to describe the insect fauna associated with *L. corniculatus* and to obtain information on the response of insects to cyanogenesis. The latter is of particular interest because some molluscs and small mammals have been shown to prefer to feed on plants which have acyanogenic leaves, and the density of these selective herbivores is considered to be one of the factors which influence the frequency of cyanogenic plants in populations of *L. corniculatus*.

During 1977 and 1978 a survey of the insects feeding on *L. corniculatus*, and their parasites, was carried out at Eppleworth Quarry, E. Yorkshire and was supplemented by samples from a number of additional sites in England, Wales and Norway. The flowers and seed pods of *L. corniculatus* were found to support a diverse insect fauna, composed of eight common phytophages and over twenty species of parasites. Competition amongst the phytophages living in the pods was investigated, and the moth *Cydia compositella* was found to displace the other species when densities were high. At Eppleworth Quarry seed predation was estimated to result in the destruction of at least 20·0% of the seeds in 1977 and 8·5% in 1978.

Laboratory feeding choice experiments showed that some grasshoppers and beetles preferentially eat acyanogenic *L. corniculatus* flowers. Greater damage to acyanogenic flowers in field populations could not be confirmed however. At Porthdafarch (Anglesey) it was found that in one area the leaves of the acyanogenic plants were more heavily chewed, but this was attributable mainly to differential feeding by molluses rather than insects. In the Jostedal Valley of Norway the *L. corniculatus* populations growing in harsh periglacial conditions were found to contain an unexpectedly high proportion of cyanogenic individuals. Possible explainations for this distribution were investigated.

The impact of insect herbivory on L. corniculatus is discussed, together with an evaluation of the role of cyanogenesis in the chemical defence of this species.

CHAPTER I

INTRODUCTION

Lotus corniculatus L. is a perennial herbaceous legume, distributed throughout much of Britain and Europe. It has also been introduced into North and South America (Seaney and Henson, 1970), where it is grown for seed and as a honey/fodder crop. Although tolerant of poor, nutrient deficient soils (unlike the related Trifolium repens L.) L. corniculatus prefers dry conditions and rarely occurs where soils are persistently damp.

Populations of this species in Western Europe are particularly interesting because they are usually polymorphic for the ability to release hydrogen cyanide (HCN) when tissues are damaged. Thus within populations some individuals are cyanogenic whereas others are not. HCN is generated by the interaction of a β - glucosidase with two cyano - glucosides, lotaustralin and linamarin (e.g. Conn, 1979). Cyanogenesis occurs in both the leaves and flower petals, (Guerin, 1929), but has not been recorded from other parts of the plant, such as the root system or the seeds, although it is known that seedlings can rapidly develop cyanogenesis after germination (Blaim, 1975).

Four phenotypes relating to cyanogenesis can be recognised. These are abbreviated as ++ (both substrates and enzyme present), + - (substrates only), - + (enzyme only), and - - (neither substrates nor enzyme present). Only + + individuals are cyanogenic.

Not all plants are consistantly cyanogenic and Ellis et al (1977 a) have shown that some plants respond to changes in temperature by altering their phenotype, a drop in temperature usually resulting in a switch to acyanogenesis. The genetics of cyanogenesis in L. corniculatus is complicated by the presence of these unstable phenotypes, and is still imperfectly understood (Ramnani, 1979). Nonetheless, it is known that the alleles determining the presence of lotaustralin, linamarin and the β - glucosidase are dominant. It has also been established that cyanogenesis is inherited independently by the leaves and flowers, and at one site near Birmingham Jones and Crawford (1977) found that all 16 possible phenotypic combinations occurred together, although in ratios which suggested that a significant disequilibrium was present. L. corniculatus is also polymorphic for the character of petal keel colour, with brown-red keels being dominant over yellow ones (Hart and Wilsie, 1959). Using cultivated material, Bubar and Miri (1965) suggested that at least one locus might be involved in the control of both leaf cyanogenesis and keel colour, resulting in an excess of cyanogenic dark keeled and acyanogenic light keeled plants. Breeding experiments carried out by Ramnani (1979) have failed to confirm this relationship, however, and Jones and Crawford (1977) found no relevant correlations in the field populations they examined.

Jones (1977) has mapped the proportions of leaf cyanogenic plants in European populations of L. corniculatus and has shown that there is a general decline in the cyanogenic morph from the south west to the north east. In Britain most populations were found to be predominantly cyanogenic, but with more acyanogenic plants occurring in the south and west. Similiar studies of the keel colour distribution showed the presence of a cline in Britain, with significant regressions of the proportion of dark keeled plants with increasing latitude (Jones and Crawford, 1977) and from west to east (Abbott, 1981). Parallel results were not obtained on the mainland of Europe however, where no latitudinal cline was observed.

Cyanogenesis occurs in a wide variety of plant species (e.g. Siegler, 1975) and an increasing number are known to be polymorphic for this character

(Fikenscher and Hegnauer, 1977). It can be argued that in species monomorphic for cyanogenesis this character consistently provides a selective advantage, either directly or indirectly whereas in polymorphic species, on the other hand, there are situations where cyanogenesis is neutral or even disadvantageous. Selection will favour cyanogenic morphs only when the metabolic costs of maintaining the ability for cyanogenesis are outweighed by the benefits that cyanogenesis provides. The ability of some individuals to vary their expression of cyanogenesis perhaps represents a flexible response to annual cyclic changes in the relative advantage of possessing a particular phenotype.

Three factors have been nominated as possible mechanisms for the maintenance of cyanogenic polymorphism in L. corniculatus - temperature, droughting and differential feeding by animals. The influence of temperature is known to be important in T. repens, which is also polymorphic for cyanogenesis. Daday has shown convincingly that in European populations of this species the frequency of the cyanogenic form is correlated both with mean January temperature (1954 a) and with altitude (1954 b). Cyanogenic plants were found to be at a disadvantage at low winter temperatures, possibly because frost damage causes poisoning by their own HCN (Jones, 1972 a). Daday (1965) was able to show that at higher temperatures it was the possession of the glucoside that was advantageous, as plants containing only glucoside and those with both glucoside and enzyme had the greater reproductive success. He concluded that under these conditions it was some other character, linked to the production of the cyanoglucoside, that was important, and not cyanogenesis per se.

The relationship between temperature and cyanogenesis is clearly different in L. corniculatus, as the proportions of the cyanogenic morph are not known to vary with altitude (Keymer, 1978), nor do they correspond with European mean January temperatures (Jones, 1977). After finding no differential response to cold stress, Ellis et al (1977a) concluded that there was no convincing evidence for cold temperature being a selective agent in this species. Jones (1970) has provided a possible explanation for the observed differences in the response to temperature in T. repens and L. corniculatus, suggesting that in T. repens the genes concerned with this response are genetically linked to the glucosidic genes, whereas in L. corniculatus they are not.

A differential response to drought stress was observed by Foulds and Grime (1972), who compared the proportions of cyanogenic L. corniculatus growing in drought - prone and normal areas of Derbyshire, and found that significantly fewer cyanogenic plants were present in drought prone areas. Jones (1973) confirmed this relationship, but found that it did not occur when the size of drought prone areas was very small (less than 4 m^2).

Cyanogenesis has often been considered to have a defensive function in plants. This was first demonstrated experimentally when Jones (1962) showed that some mollusc species preferred to eat acyanogenic or weakly cyanogenic L. corniculatus in feeding trials. Crawford - Sidebotham (1972) and Angseesing and Angseesing (1973) have subsequently confirmed the existance of differential feeding by a number of mollusc species, using both L. corniculatus and T. repens, but observations of significant differential feeding by molluscs in natural populations (e.g. Jones, 1966 and Whitman, 1973) have been rather less conclusive. Ellis et al (1977 b) have nonetheless found good circumstantial evidence that selective eating by molluscs was at least partly responsible for the distribution of cyanogenic plants on the south west coast of Holy Island, Anglesey.

Bracken, Pteridium aquilinum (L.), is also polymorphic for cyanogenesis. Cooper-Driver and Swain (1976) have suggested that both sheep and deer prefer to eat acyanogenic fronds of this species, yet sheep are not selective when feeding on T. repens (Corkill, 1952). Possibly this reflects differences in the concentrations of cyanide found in these plant species. Microtus agrestis L. (the field vole) is another species which will select acyanogenic plants (Jones 1966), although in feeding trials with L. corniculatus differential feeding was observed to occur only when the animals were provided with an adequate alternative food supply. *Oryctolagus cuniculus* (rabbits) were suggested as a possible selective agent in the maintenance of a cline in *L. corniculatus* cyanogenesis in the Netherlands (Jones, 1972 b), but this was later found to be unlikely (Jones, 1976) and Keymer (1978) has since shown that this species is probably not a selective grazer of *L. corniculatus*.

Studies of the relationship between insects and cyanogenesis in field populations of *T. repens* have failed to find any tendency for acyanogenic plants to suffer increased damage (Miller *et al*, 1975, Knight *et al*, 1978, Dritschilo *et al*, 1979). Lane (1962) has shown that females of *Polyommatus icarus* Rott. do not distinguish acyanogenic *L. corniculatus* when deciding on oviposition sites, and the larvae of *Zygaena* species are also non-selective when examined in feeding trials (Jones, 1966). Perhaps these experiments reflect the adaptations of insects specialised for feeding on cyanogenic plants rather than the absence of a protective role for cyanide in Legumes.

Cyanogenesis can be categorised as a qualitative, toxic defense, typical of plant species "unapparent" in the sense of Feeny (1976), yet the ability to detoxify small quantities of cyanide is widespread amongst both plants and animals (Jones, 1981). The presence of the cyanide de-toxifying enzyme rhodanese has been confirmed in a variety of species, including the *Lotus* feeding *Polyommatus icarus* and *Hypera plantaginis* (Degeer) (Parsons and Rothchild, 1964), and a second system, involving detoxification via β-cyanoalanine production, has been suggested for *Sitophilus granarius* (L.) (Bond, 1961).

Some of the species which feed on cyanogenic plants are known to use the presence of cyanide to their own advantage. *Epilachna varivestis* Mulshant, for example, uses cyanogenic glucosides as feeding stimulants (Nayer and Fraenkel, 1963). The aposematic Lepidoptera of the genus *Zygaena* are even more specialised and apparently synthesise their own cyano-glucosides (Jones *et al*, 1962). The cyanide is used as a defense against predators and perhaps also against their parasites. It is intriguing that the cyanoglucosides synthesised de novo by *Z. filipendulae* are exactly the same as the ones found in *L. corniculatus* (a preferred food plant), that is linamarin and lotaustr

(Davis and Nahrstedt, 1979).

The concentrations of cyanoglucosides in bracken show a spring maximum that is followed by a decline which continues throughout the summer. A corresponding increase occurs in the number of insect species colonising the plant (Lawton, 1976). Although this may represent the response of the insect community to a change in the defensive armoury of the plant, Lawton had argued that a more likely explanation is that as the plant develops its architecture becomes more complex, thus providing more niches to colonise.

Acridoids have been used by several workers to study the response of insects to cyanogenesis, and Cooper-Driver and Swain (1976) have demonstrated that at least one species of Locust, *Schistocerca gregaria* F. will differentially avoid eating cyanogenic bracken fronds. Cyanogenesis has also been shown to be a major source of resistance to *Locusta migratoria* (L.) in young *Sorghum bicolor* (L.) (Woodhead and Bernays, 1978) and against *Zonocerus variegatus* (L.) in *Manihot esculenta* Crantz. (Bernays *et al*, 1977), although this has not prevented *Zonocerus* from becoming a pest of this crop (Page *et al*, 1980).

Possession of the cyanoglucoside alone can act as a deterrant (Nayer and Fraenkel, 1963) but in general it is the release of HCN while tissues are being damaged which is believed to provide the major deterrant effect (Woodhead and Bernays, 1977).

Fisk (1980) has concluded that it is unlikely that cyanogenesis influences the palatability of *S. bicolor* to the planthopper *Peregrinus maidis* (Ashmead) because phloem-feeding species will come into contact with relatively little cyanide during probing. Results perhaps contrary to this view were obtained by Dritschilo *et al* (1979), however, who found that acyanogenic stands of *T. repens* were preferentially colonised by the Aphid *Aphis craccivora* Koch.

Harris (1972) and Cavers (1973) have reviewed the effects of phytophagous insects on their food-plants and have shown that limited damage is not necessarily harmful and can occasionally even be beneficial. Thus the observation of preferential feeding on particular phenotypes of a polymorphic plant species does not necessarily imply that a corresponding selective pressure would be exerted under natural conditions. Soybeans (Glycine max, L), for example, compensate for the removal of up to 22% of their seed pods by increasing the weight of the surviving seeds and by reducing the rate of natural pod abortion (Smith and Bass, 1972). While this example demonstrates that the effect of damage to reproductive structures can be difficult to analyse, the seed mortality caused by herbivores (seed predation) can nonetheless have an important influence on the degree of reproductive success in plants (Janzen, 1969). Many of the toxic substances found in seeds are likely to have a defensive function (e.g. Janzen, 1971) and the relationship between seeds and their adapted predators is now seen as a prime example of 'co-evolution' (Center and Johnson, 1974).

Whittaker (1979) noted that it is rare for invertebrate herbivores to destroy the plants on which they are feeding and has stressed that the major result of grazing is to reduce the competitive ability of the plant. Root competition in particular is likely to be affected, because defoliation is known to result in a reduction of the root/shoot ratio (e.g. Weiss, 1976). Crawford-Sidebotham (1972) and Jones (1972 a) have argued that differential feeding on acyanogenic L. corniculatus would only be of significance to mature plants when the herbivore load was extremely heavy, whereas even slight grazing would reduce the fitness of seedlings. Furthermore, Schreiber (1967) and Laskey and Wakefield (1978) have demonstrated the pronounced effects of competition by other species during the establishment of L. corniculatus seedlings.

The results of simulated grazing experiments on seed production in L. corniculatus have shown that particular phenotypes can respond differently to defoliation (Keymer and Ellis, 1978). Plants containing the cyanogenic glucoside were found to produce significantly more pods under control conditions, but lost this advantage after clipping.

The relationship between L. corniculatus and insects has been recognised for many years, as is demonstrated by the large number of species bearing the specific name of '<u>loti</u>' or with '<u>loti</u>' as a synomym. On the other hand there have been few studies focusing on the insect fauna of <u>L. corniculatus</u> itself and even these have been carried out mainly in North America and in Eastern Europe, where this plant is grown commercially. Collation of records on <u>L. corniculatus</u>-feeding insects must therefore rely mainly on host-plant lists produced for particular insect taxa.

Tables 1.1 and 1.2 are lists of the phytophagous insects recorded on <u>L. corniculatus</u>. Most of these species were specifically stated as feeding on this plant species, but this was not stated explicitly in some cases. For convenience I have included in Table 1.1 only those species given by "A check list of British insects" (second edition) as occurring in Britain, while Table 1.2 contains the remaining 'alien' species. Table 1.3 provides the authors and dates of the publications consulted. A total of over 130 British species are present, representing eight insect orders with the Lepidoptera providing almost half of the species recorded.

Neunzig and Gyrisco (1955) and Guppy (1958) have provided annotated lists of the insect communities present on <u>L. corniculatus</u> in the U.S.A., and those species found to be destructive have been included here. Similiar surveys on cultivated material in Romania and Yugoslavia by Perju and Cantoreanu (1973), Perju (1974), and Balarin (1975) show that <u>L. corniculatus</u> (as with some other forage legumes) supports a particularly rich Hemiptera community, with 74 Heteroptera and 17 Homoptera, Auchenorrhyncha being recorded, some of which are knownto be of economic importance (MacCollan, 1967, Neunzig and Gyrisco, 1958). The Hemiptera host records in tables 1.1.and 1.2 include only the most abundant of the many species listed as occurring on <u>L. corniculatus</u> by these European workers.

The analysis of the relationship between insect faunas and tree abundance carried out by Southwood (1961) has stimulated a general interest in the

Table 1.1 Phytophagous insects recorded as occurring on Lotus corniculatus
1. British species (literature search completed in 1981).

		Reference Sources[1]
	Collembola	
1	Sminthurus viridis (L.)	43
	Heteroptera	
1	Berytinus signoreti (Fieber)	50
2	Plagiognathus chrysanthemi (Wolff)	3,21,22,45
3	Lygus pratensis (L.)	3
4	Lygus rugulipennis Poppins	46
5	Calocoris norvegicus (Gmelin)	3
6	Calocoris roseomaculatus (Degeer)	50,62
7	Adelphocoris lineolatus (Goeze)	3,4,6,21,31
8	Adelphocoris seticornis (F.)	3,32,46
9	Notostira elongata (Geoffroy)	46
	Homoptera	
1	Philaenus spumarius (L.)	21,41
2	Cicadella viridis (L.)	41
3	Scleroracus corniculus (Marshall)	41
4	Macrosteles laevis Ribault	41
5	Empoasca pteridis (Dahlbom)	41
6	Therioaphis trifolii (Monell)	57
7	Aphis craccivora Koch.	13
8	Aphis loti Kaltenbach	56
9	Aphis lotiradicis Stroyan	56
10	Acyrthosiphon loti (Theobald)	9
11	Acyrthosiphon pisum (Harris)	9,21
12	Planchonia arabidis (Signoret)	13
	Thysanoptera	
1	Aeolothrips tenuicornis Bagnall	60
2	Sericothrips abnormis (Karny)	42
3	Odontothrips loti (Haliday)	6,13,37,38,40
4	Kakothrips pisivorus (Westwood)	12
5	Thrips atratus Haliday	60
6	Thrips physapus L.	60
7	Thrips vulgatissimus Haliday	60
	Lepidoptera	
1	Trifurcula cryptella (Stainton)	18,23
2	Trifurcula eurema (Tutt)	18,23
3	Zygaena purpuralis (Brunnich)	48
4	Zygaena loti (Den. and Sch.)	49
5	Zygaena viciae (Den. and Sch.)	48,49
6	Zygaena filipendulae (L.)	40,49
7	Zygaena trifolii (Esper)	48,49,58
8	Zygaena lonicerae (Scheven)	48,49,58
9	Leucoptera lotella (Stainton)	11,18,33
10	Phyllonorycter insignitella (Zeller)	24
11	Phyllonorycter nigrescentella (Logan)	24
12	Bembecia scopigera (Scopoli)	19,48,49
13	Coleophora discordella Zeller	8,18,33
14	Xystophora pulveratella (Herr-Sch.)	18
15	Aproaerema anthyllidella (Hubner)	24
16	Syncopacma larseniella (Gozmany)	18
17	Syncopacma sangiella (Stainton)	18,33

Table 1.1 (Continued)

18	Syncopacma taeniolella (Zeller)		18,33
19	Syncopacma cinctella (Clerck)		18,33
20	Scythris picaepennis (Haworth)		18,33
21	Scythris siccella (Zeller)		18,33
22	Cydia succedana (Den. and Sch.)		10,18,20,33
23	Cydia compositella (F.)		10,40
24	Olethreutes lacunana (Den. and Sch.)		6
25	Aphelia viburnana (Den. and Sch.)		10
26	Clepsis senecionana (Hubner)		10
27	Paraclepsis cinctana (Den. and Sch.)		10,18,33
28	Philedone gerningana (Den. and Sch.)		10
29	Cnephasia communana (Herr. - Sch.)		10
30	Cnephasia stephensiana (Doubleday)		24
31	Cnephasia interjectana (Haworth)		24
32	Cnephasia pasiuana (Hubner)	Pers. Ob.	
33	Cnephasia incertana (Treitschke)		10
34	Dolicharthria punctalis (Den. and Sch.)		7,18,33
35	Endotricha flammealis (Den. and Sch.)		33
36	Oncocera semirubella (Scopoli)		7,18,33
37	Pima boisduvaliella (Guanee)		7,18
38	Erynnis tages (L.)		25,48,54
39	Leptidea sinapis (L.)		25,48,54
40	Colias hyale (L.)		1,33,54
41	Colias croceus (Geoffroy)		1,33,54
42	Callophrys rubi (L.)		1,54
43	Everes argiades (Pallas)		1,54
44	Plebejus argus (L.)		25
45	Polyommatus icarus (Rottemburg)		25,48,54
46	Lysandra coridon (Poda)		25,48
47	Lasiocampa trifolii (Den. and Sch.)		1
48	Scopula emutaria (Hubner)		48,49
49	Idaea ochrata (Scopoli)		48
50	Scotopteryx bipunctaria (Den. and Sch.)		1,49
51	Selidosema brunnearia (Villers)		48
52	Cleora cinctaria (Den. and Sch.)		1
53	Aspitates gilvaria (Den. and Sch.)		1
54	Aspitates ochrearia (Rossi)		1
55	Eilema caniola (Hubner)		1,48
56	Eilema complana (L.)		48
57	Nola aerugula (Hubner)		1,48
58	Egira conspicillaris (L.)		1,48
59	Euclidia glyphica (L.)		1,49
60	Plathypena scabra (F.)		36
61	Monochroa quaestionella (Herr.-Sch.)		33
	Coleoptera		
1	Brachypterolus pulicarius (L.)		36
2	Meligethes aeneus (F.)		40
3	Meligethes erythropus (Marsham)		17
4	Subcoccinella 24-punctata (L.)		40
5	Bruchus loti Paykull		15,59
6	Bruchidius cisti (F.)		59
7	Apion ebeninum Kirby		28,59
8	Apion loti Kirby		6,34,40,47
9	Apion subulatum Kirby		26,47,59
10	Nanophyes gracilis Redtenbacher		59
11	Otiorhynchus ligustici (L.)		36
12	Trachyphloeus aristatus (Gyllenhal)		59

Table 1.1 (Continued)

13	Trachyphloeus asperatus Boheman		59
14	Phyllobius viridiaeris (Laicharting)	Pers. Ob.	
15	Phyllobius roboretanus Gredler	Pers. Ob.	
16	Sitona lineatus (L.)		26
17	Sitona puncticollis Stephens		47
18	Sitona sulcifrons (Thunberg)		47
19	Sitona waterhousei Walton		26,28,29,59
20	Hypera arator (L.)		59
21	Hypera meles (F.)		26,47
22	Hypera nigrirostris (F.)		15
23	Hypera plantaginis (Degeer)		39
24	Hypera postica (Gyllenhal)		6,27,47
25	Hypera suspiciosa (Herbst)		28,59
26	Hypera venusta (F.)		15,26,47,59
27	Pachytychius haematocephalus (Gyllenhal)		26,59
28	Tychius flavicollis Stephens		15,26,28,47,59
29	Tychius junceus (Reich)		15,59
30	Tychius pusillus Germar		2
31	Miarus plantarum (Germar)		29,59
	Diptera		
1	Dasineura loti (Kieffer)		5,13
2	Jaapiella loticola (Rubsaamen)		5,13
3	Asphondylia melanopus kieffer		5,13
4	Contarinia barbichei (kieffer)		5,13
5	Contarinia loti (Degeer)		5,13,53
6	Melanagromyza cunctans (Meigen)		51,52
7	Liriomyza congesta (Becker)		24
8	Phytomyza horticola Goureau		24
	Hymenoptera		
1	Tenthredo acerrima Benson		61
2	Tenthredo arcuata Forster		30
3	Eurytoma platyptera (Walker)		14,35,40,55

[1] Authors given in Table 1.3

Table 1.2 Phytophagous Insects recorded as occurring on Lotus corniculatus
Non-British species

		Reference Sources [1]
	Orthoptera	
1	Melanoplus femur-rubrum (Degeer)	21,36
2	Melanoplus bivittatus (Say)	21,36
3	Melanoplus differentialis (Thos.)	36
4	Acheta assimilis (F.)	36
5	Nemobius fasciatus (Degeer)	36
	Heteroptera	
1	Plagiognathus politus Uhler	45
2	Lygus lineolaris (P. de B.)	21,31,36,44,45
3	Adelphocoris rapidus (Say)	21,31 36
4	Euschistus variolaris (P. de B.)	36
	Homoptera	
1	Empoasca fabae (Harr.)	21
2	Asterolecanium fimbriatum (Fonsc.)	13
	Thysanoptera	
1	Taeniothrips meridionalis Priesner	43
2	Frankliniella tritici (Fitch)	35
	Lepidoptera	
1	Apterona helicinella (Herr-Schaff)	24
2	Apterona crenulella Brd.	24
3	Coleophora crocinella Tgstr.	24
4	Stigmella ridiculosa Wlsgh.	24
5	Archips rosaceana (Harr.)	36
6	Sparganothis sulphurana (F.)	36
7	Tortrix pallorana (Robn.)	36
8	Tortrix velutinana (Walker)	36
	Coleoptera	
1	Meligethes seminulum Lec.	16
2	Phytodecta fornicata Bruggm.	40

[1] Authors given in table 1.3

Table 1.3

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38 Obrtel R. 1965
39 Parsons J. & Rothschild M. 1964
40 Perju T. 1974
41 Perju T. & Cantoreanu M. 1973
42 Pitkin B.R. 1976
43 Popov T. 1976
44 Ridgeway R.L. & Gyrisco G.G. 1960
45 Ridgeway R.L. & Gyrisco G.G. 1961
46 Ruszkowski A. 1968
47 Scherf H. 1964
48 Scorer A.G. 1913
49 South R. 1961
50 Southwood T.R.E. & Leston D. 1959
51 Spencer K.A. 1972
52 Spencer K.A. 1976
53 Stelter H. 1958
54 Stokoe W.J. 1948
55 Strong F.E. 1962
56 Stroyan H.L.G. 1972
57 Stroyan H.L.G. 1977
58 Tremewan W.G. 1965
59 Walsh G.B. & Dibb J.R. 1975
60 Ward L.K. 1973
61 Waterhouse F.L. & Sanderson R. 1958
62 Woodroffe G.E. 1955

factors determining the size and composition of the phytophagous insect faunas associated with plants. In general this has taken the form of comparative studies, using faunal lists prepared by extracting information from a number of standard tests. Most have concentrated on the British fauna because plant distribution and insect-host relationships are well documented here. While such extracted information can only be as comprehensive as its source material allows, Lawton and Schroder (1977) and Lawton et al (1981) have argued that any resultant inaccuracy will only increase the variance of the data, without introducing any systematic errors.

Geographical range has proved to be the major determinant of insect numbers, with more widespread species of plants accumulating larger faunas (Strong, 1974, 1979, Lawton and Schroder, 1977). Growth form - tree, shrub or herb (Strong and Levin, 1979) and degree of taxonomic isolation (Connor et al, 1980) are also influential, but to a lesser degree.

The size of the L. corniculatus faunal list presented in tables 1.1 and 1.2 is far greater than those included in most of these comparative studies of herbaceous species, presumably because of the difference in scope of the literature on which they are based. Lawton (1976), for example, records no herbaceous plants with more than 70 associated phytophagous insects - slightly over half the total given here for L. corniculatus. Evidence that the L. corniculatus fauna may be not unusually large is provided by the results of Pimental and Wheeler (e.g. 1973), whose summary of the Arthropod fauna on Alfalfa (Medicago sativa L.) contains 189 phytophagous insects (including nectivores) after 'casual' species are eliminated.

Lawton (1976) has shown that the composition of the insect community on bracken differs significantly from that found on a selection of other herbaceous plants. Using Lawton's data it is possible to compare the species recorded on L. corniculatus in a similiar way (table 1.4). The resultsof this comparison indicate that the fauna of L. corniculatus is also significantly different from the average and suggests that it may include both an unusually high

Table 1.4 A comparison of the recorded herbivore communities of *L. corniculatus* and a selection of other herbaceous plants. Minor groups (for example Collembola) have been omitted.

Order	Total Records (Data of Lawton,1976)	*Lotus* Records[1] 'Observed'	*Lotus* Records[1] 'Expected'
Coleoptera	146	31	20.0
Diptera	162	8	22.2
Heteroptera	44	9	6.0
Homoptera	152	12	20.8
Hymenoptera	43	3	5.9
Lepidoptera	359	61	49.1
	906	124	124.0

$X^2\,[5] = 14.24,\ P < 0.05$

---

[1] extracted from Table 1.1

proportion of Coleoptera species and a relative scarcity of Diptera.

One disadvantage with comparative assesments of this type is that the degree of host plant specificity of the animals is not taken into account. Monophagous insects restricted to a single species or genus are thus given equal status with polyphagous insects that occur on a wide variety of food plants and feed only casually on the plant under consideration. Host records based only on the capture of adult insects can also be misleading, because the adults of many species are considerably more polyphagous than their larvae (e.g. Ward, 1973). Bruchus loti Paykull adults can be seen feeding on a variety of legumes, including Lotus spp. but in Northern England this species breeds commonly only in Lathyrus pratensis L. Similarly, Phyllobius spp. adults will feed on the flower petals of L. corniculatus, but breeding apparently occurs elsewhere.

Published accounts on the biology of some of the species listed in table 1.1 would suggest that their association with L. corniculatus is, at most, infrequent. Notostira elongata (Geoffroy) for example, is regarded by Kullenberg (1946) as a grass feeding species, and Johnson (1965) has concluded that Apion subulatum Kirby breeds only rarely, if ever, on L. corniculatus. While these conflicting reports partly reflect observational inaccuracies, they also illustrate the limitations of faunal comparisons based on records that have not been critically assessed. In some cases there are advantages, therefore, in considering only those species that genuinely depend on a particular food plant.

In Table 1.5 the insects recorded on L. corniculatus have been placed, wherever possible, into one of three feeding categories, (sensu Slansky, 1976) These are :-

1. Monophagous species which normally eat only L. corniculatus or, in addition, other species of Lotus.
2. Oligophagous species that are recorded from a number of Leguminosae, including L. corniculatus.
3. Polyphagous species that occur on plants from several different families.

Table 1.5 A summary of the food relationships of insects recorded from *L. corniculatus*. Definitions of feeding categories are recorded in the text.

Order	Monophagous Species	Oligophagous Species	Polyphagous Species	Information not available
Coleoptera	7	13	7	4
Collembola	0	0	1	0
Diptera	6	1	1	0
Heteroptera	0	3	6	0
Homoptera	2	4	5	1
Hymenoptera	2	1	0	0
Lepidoptera	6	32	22	1
Thysanoptera	1	2	5	0
Totals	24	56	47	6

Approximately equal numbers of polyphagous and oligophagous insects are found to occur on L. corniculatus, but monophagous species are in a distinct minority. The Diptera show a clear exception to this trend however, mainly due to a predominance of species from the Cecidomyiidae, a family noted for its extreme host specificity.

After flower-feeding species are discounted, comparison of table 1.5 with a similar summary of the bracken fauna (Lawton, 1976) leads to the view that these two species support approximately the same number of 'specialist' insects, a conclusion which provides support for the assertions of Lawton, and of Auerbach and Hendrix (1980), that ferns are not under-utilized by phytophagous insects.

Why then does L. corniculatus, in comparison with bracken, have such an excess of species in the 'generalist' categories? The major component of the fauna consists of insects which will feed on several species of Leguminosae - a large family containing more species in Britain than the combined total of all ferns. Lawton and Schroder (1977) have used the 'number of species per plant genus' as a measure of isolation in their study of the relationship between the taxonomic isolation of herbaceous plants and the size of their insect fauna. Perhaps re-analysis using 'species per plant family' (as in Connor et al, 1980) would show that isolation at this level is also important.

A large polyphagous fauna may also result partly from the diversity of the botanical environment in which the plant grows. At Wharram Quarry in North Yorkshire, where L. corniculatus is perhaps the most abundant plant, as many as 15 other species can be found within half a metre of an individual L. corniculatus plant (Beesley and Compton, unpublished). This high diversity provides many opportunities for 'accidental' transfer of generalist phytophages from one plant to another. In contrast, bracken tends to form dense stands that contain few other plant species and will provide fewer opportunities for chance colonisation by insects.

The size of the insect assemblage that is associated with L. corniculatus suggests that insects may represent a major influence on the genetic structure of populations of this plant. Before genecological studies of this relationship can be attempted, however, it is necessary to clarify the identity, numbers and trophic relationships of the insects concerned. It is this rationale which prompted the initiation of this study.

The research presented in this thesis is concerned both with the insect communities associated with L. corniculatus and also with how these insects react to known variation in the host plant. The specific topics that were investigated were:-

1. The identities, life-histories and inter-relationships of the species which inhabit the leaf mines and reproductive structures of the plant.
2. The degree of pre-dispersal seed predation and the factors which influence it, and
3. The relationships between plant phenotype and the insect communities.

CHAPTER II

MATERIALS, METHODS AND LOCALITIES

Introduction

The insects that occur in the flowers and pods of L. corniculatus have been investigated at a number of localities in Britain, and also in Norway. These investigations consist of a detailed census carried out during 1977 and 1978 at Eppleworth Quarry in East Yorkshire and, for comparison, a number of supplementary samples taken at other sites.

Eppleworth Quarry is situated approximately two miles west of Cottingham and consists of a large pit (approximately six hectares) cut into flinty chalk in the valley at the base of Skidby Hill. It has been disused for many years and was known in the past as Eppleworth Limekilns (Wright and Wright, 1942). National Grid co-ordinates are TA 023327.

L. corniculatus is common throughout the quarry and at the time this study was initiated it was particularly abundant on the slopes facing east. A relatively homogeneous section of this area, consisting of a gently sloping bank approximately 35 metres long, was chosen for intensive sampling. L. corniculatus was the dominant plant on the lower part of the bank, and over the lowest five metres grew in an almost continuous mat.

During 1978 however, the quarry began to be used extensively by motorcycle enthusiasts who inevitably began to cause widespread damage to the plants.

Disturbance has subsequently increased and L. corniculatus is now declining at the site.

L. corniculatus can propagate vegetatively and form extensive clones. It is important therefore to space sampling points at minimum intervals if it is required that the same clone should only rarely be encountered twice. Jones (1963) has determined that a one metre spacing is adequate for this purpose and has discussed the statistical implications of this sampling method (1977). Southwood (1978) has noted the problems associated with the sampling of whole insect faunas. Precise sampling regimes that are suitable for a single species (such as that described by Guppy and Harcourt, 1977 on Alfalfa for example) cannot be modified for whole faunal studies because different species vary both in their density and pattern of dispersion.

At Eppleworth samples were collected at weekly or fortnightly intervals during the period when flowers or pods were available. In 1977 a sampling unit consisted of all flowers and pods contained within a 929 cm^2 (1 $ft.^2$) solid sided quadrat. Flowers were removed first in order to prevent any disturbed insects from escaping. Pods were picked and then stored together, whereas flower umbels were kept individually in plastic containers. In 1978 this proceedure was modified slightly, with the sample unit being reduced to 250 cm^2 and with all the remaining plant tissue also being removed, in order to record the levels of bud damage that were present.

Sampling points were chosen at random using co-ordinates determined by pairs of pseudo random numbers that were obtained from random number tables or generated by a Hewlett-Packard HP97 calculator. These co-ordinates were paced out and the nearest L. corniculatus plant was chosen. Usually three replicates were obtained on each sampling date, with no attempt being made to prevent different clones of the same plant from being sampled. Details of dates and sample sizes are given in tables 3.1 and 3.2.

Localities in Britain where collections of L. corniculatus have been made are listed in table 2.1. Individual umbels were collected at one metre plus intervals when populations were sufficiently large, but at smaller sites it was necessary to collect material as and where available.

One of these smaller sites, at Bulkington in Warwickshire, was sampled intensively. The site consists of the steep easterly facing side of a section of cutting that forms part of the main Leicester to Rugby railway line. The vegetation is dominated by Gorse (*Ulex europaeus* L.) and rough grasses, but because of disturbance and fires (probably caused by sparks from the railway) there are also areas of regeneration where shorter herbs, including *L. corniculatus*, are present. During the five years from 1975 to 1980 the main colony of *L. corniculatus* has been more or less eliminated by encroaching grasses. A new colony has appeared nearby however, on an area damaged by fire in 1976.

Specimens of seed predators and their parasites have also been obtained from a small "seed bank" maintained by Professor D.A. Jones of the Hull University Unit of Genetics. This collection consists of seeds of *L. corniculatus* and other species of *Lotus*, some of which have been provided by European botanical institutions, but mainly collected by Professor Jones himself.

Recording and Analysis

Flowers were usually stored in a frozen condition as this prevented deterioration and made dealing with the more active insects much easier. Flowers were dissected under a binocular microscope and their contents recorded. The colour of the keel petals was also scored as being either dark or light, depending on the presence or absence of any brown pigment, and the petals were then tested for cyanogenesis.

Plants were scored for cyanogenesis using the sodium picrate test of Guignard (1906) as modified by Jones (1966). Briefly, filter paper soaked in sodium picrate solution was suspended above the plant material to which had been added two drops of toluene in order to disrupt the cells. After 48 hours at room temperature (24 for leaf tissue) the petals were scored as positive for cyanogenesis if the picrate paper had turned from yellow to red. With the

Table 2.1 U.K. Collecting sites for L. corniculatus flowers and seed pods.

Locality	National Grid Reference	Dates	Description
Aldbrough, E. Yorks.	TA 257398	6.11.77	Roadside Verge
Bentley, E. Yorks.	TA 021349	5. 7.78	Roadside Verge
Bulkington, Warwicks.	SP 379873	Various	Railway Cutting
Burdale Qu., N. Yorks.	SE 871626	Various	Chalk Quarry
Cauldon Lowe, Staffs.[1]	SK 083486	Various	Quarry
Chapel Farm, Warwicks.	SO 946806	23. 8.77	Roadside Verge
Church Bay, Anglesey	SH 300892	Various	Sea Cliffs
Cottingham, E. Yorks.	TA 020257	5. 7.78	Roadside Verge
Cottingham Gardens, E. Yorks	TA 054327	5. 9.77	Experimental Plot
Crowle Moors, N. Lincs.	SE 751159	30. 7.78	Railway Embankment
Eppleworth Qu., E. Yorks.	TA 023327	Various	Chalk Quarry
Flamborough, N. Yorks.	TA 254704	28. 6.78	Sea Cliffs
Hutton Cranswick, E. Yorks.	TA 032532	11. 9.79	Roadside Verge
Newbury, Berks.[1]	SP 502718	24. 7.81	Pasture
North Cave, E. Yorks.	SE 918328	5. 7.78	Chalk Quarry
Porthdafarch, Anglesey.	SH 233799	11. 6.79	Sea Cliffs
Porthmelgan, S. Wales.[2]	SM 728280	15. 8.80	Earth Cliff
Spurn Point, E. Yorks.	-	23. 6.77	Sandy Peninsula
Wawensmoor, Warwicks.	SP 129639	23. 8.77	Roadside Verge
Wharram Qu., N. Yorks.	SE 859653	Various	Chalk Quarry
Windmill Hill, W. Midlands[1]	SO 970778	13. 7.78	Rough Grassland
Wolvey, Warwicks.	SP 406865	23. 8.77	Roadside Verge

[1] Collected by D.A. Jones

[2] Collected by R.S. Key

exception of certain Norwegian populations, no attempt was made to differentiate between the three different acyanogenic phenotypes or to quantify the strength of the cyanogenic response.

Immature insects obtained from the flowers and pods were stored in 70% ethanol or kept in plastic petri dishes for rearing. These were lined with filter paper and periodically moistened to maintain a suitable humidity. Whenever necessary, growth of moulds was inhibited by using a weak solution of 'Nipagin' (Methyl Ester of Hydroxy Benzoic Acid) rather than pure water. Those species which pupate in the soil were also provided with a layer of sand in the bottom of their petri dish. Any specimens which entered diapause were kept through the winter months in an unheated insectary on the roof of a university building.

Insects were identified using published keys and descriptions, with measurements being made using a calibrated eyepiece graticule. Authorities on the taxonomy of the various groups were then consulted in order to confirm (or correct) the identifications. Details of those people who kindly provided taxonomic assistance are included in the acknowledgements. In several cases it was not possible to identify insects to species either because of taxonomic problems in particular genera or because no adults had been reared successfully.

Galls and Leaf Mines

Galled flowers and leaf mines were sometimes obtained during routine sampling at Eppleworth Quarry and elsewhere. These occurred at low densities however and in order to obtain sufficient numbers it was necessary to carry out systematic searches of L. corniculatus in areas away from the main study sites. After collection, both galls and mines were initially maintained in petri dishes in order to allow their occupants to mature, and were then dissected.

Further details of experimental and analytical procedures are provided in relevant chapters.

CHAPTER III

INSECTS ASSOCIATED WITH THE FLOWERS AND FLOWERS BUDS OF L. CORNICULATUS

The insects feeding on the reproductive structures of L. corniculatus were investigated at Eppleworth Quarry during 1977 and 1978, and supplementary information was obtained from a number of other sites. These studies were concentrated on the biology of those phytophagous insects and their parasites that develop inside the flowers and seed pods and the effects that they had on the reproductive success of the plant. During the second flowering season a survey of flower bud mortality was also undertaken, in order to find whether feeding by insects was important during the earliest stages of flower development.

The sampling programmes at Eppleworth are described below and this is followed by a summary of the flowering phenology of L. corniculatus. Flower bud mortality is then analysed and the importance of feeding by insects is discussed. The response of colonising insects to the keel colour polymorphism is also assessed and finally a description is provided of the biology of the insects associated with the flowers of L. corniculatus.

THE SAMPLING PROGRAMMES

Samples were taken at regular intervals throughout each season, with the sampling unit consisting of all the flowers and pods present within a randomly placed quadrat. Tables 3.1 and 3.2 record the dates when samples were collected, together with the numbers of flowers and pods that each contained. Usually three samples were taken during each visit, but this was reduced to two in October 1977, when few suitable plants were available, and increased to seven in June 1978 in order to allow more flowers to be included.

In 1978 the quadrat size was reduced from 929 cm^2 to 250 cm^2 and all the included vegetation was removed, in addition to the flowers and pods. This change in quadrat size may have had the effect of changing the apparent density of the reproductive structures. Between July and September 1977 the mean density of seed pods was recorded as 1094.3 per m^2, compared with 1584.0 per m^2 during the same period of 1978 ($t_{[49]} = 1.627$, $0.2 > P > 0.1$).

The flower buds in the vegetation samples were separated on the basis of colour into two age groups, 'green' and 'orange'. Green buds were usually sessile, with peduncle elongation beginning early in the orange phase. Each bud was then recorded as either healthy or dead/dying. Buds were scored as 'young flowers' when the petals projected beyond the sepals. Anther condition was used to monitor the stages of flower development as this was considered likely to correspond with the phases of insect colonisation. Red and early yellow flowers had immature 'closed' anthers which 'opened' during the pollination phase and became exhausted ('empty') during senescence.

Leaves and flowers were scored for cyanogenesis throughout 1977 but this was discontinued because it became apparent that the population was effectively monomorphic for both cyanoglucoside and β-glucosidase production. No acyanogenic flowers were recorded and only one individual had acyanogenic leaves. The colour of the keel petals was recorded throughout both seasons.

A second sampling programme was conducted during 1978 in another section of Eppleworth Quarry, about 30 metres from the main sampling area. One flower

Table 3.1 Eppleworth Quarry - Sampling dates and quadrat contents, 1977

Date	Sample	Umbels	Flowers	Pods
19.7.77	1.1	44	13	89
	2	87	35	139
	3	52	19	81
26.7.77	2.1	85	12	133
	2	50	11	69
	3	60	2	100
31.7.77	3.1	97	9	199
	2	47	0	108
	3	77	17	90
10.8.77	4.1	65	0	116
	2	69	0	127
	3	60	0	113
14.8.77	5.1	26	0	50
	2	58	0	98
	3	93	0	191
26.8.77	6.1	103	0	177
	2	23	0	30
	3	13	0	20
31.8.77	7.1	13	0	20
	2	97	0	172
	3	85	0	147
6.9.77	8.1	34	0	65
	2	84	0	154
	3	13	0	21
11.9.77	9.1	70	0	120
	2	24	0	41
	3	51	0	75
9.10.77	10.1	35	0	39
	2	38	0	51
27.10.77	11.1	13	0	16
	2	30	0	37
Totals		1696	118	2888

Table 3.2 Eppleworth Quarry - Sampling Dates and quadrat contents, 1978

Date	Sample	Umbels	Flowers	Pods
23.6.78	1.1	13	39	0
	.2	41	124	0
	.3	9	24	0
	.4	2	5	0
	.5	7	15	0
	.6	20	55	0
	.7	2	5	0
12.7.78	2.1	24	14	19
	.2	34	39	37
	.3	59	46	91
27.7.78	3.1	10	1	11
	.2	24	28	22
	.3	30	30	46
15.8.78	4.1	11	0	19
	.2	9	0	16
	.3	2	6	0
23.8.78	5.1	30	0	48
	.2	9	0	11
	.3	33	0	70
30.8.78	6.1	6	0	7
	.2	23	0	51
	.3	31	0	51
5.9.78	7.1	22	0	34
	.2	33	0	52
	.3	74	3	126
12.9.78	8.1	21	0	25
	.2	37	0	64
	.3	8	0	11
18.9.78	9.1	38	0	66
	.2	6	0	9
	.3	15	0	24
Totals		683	434	910

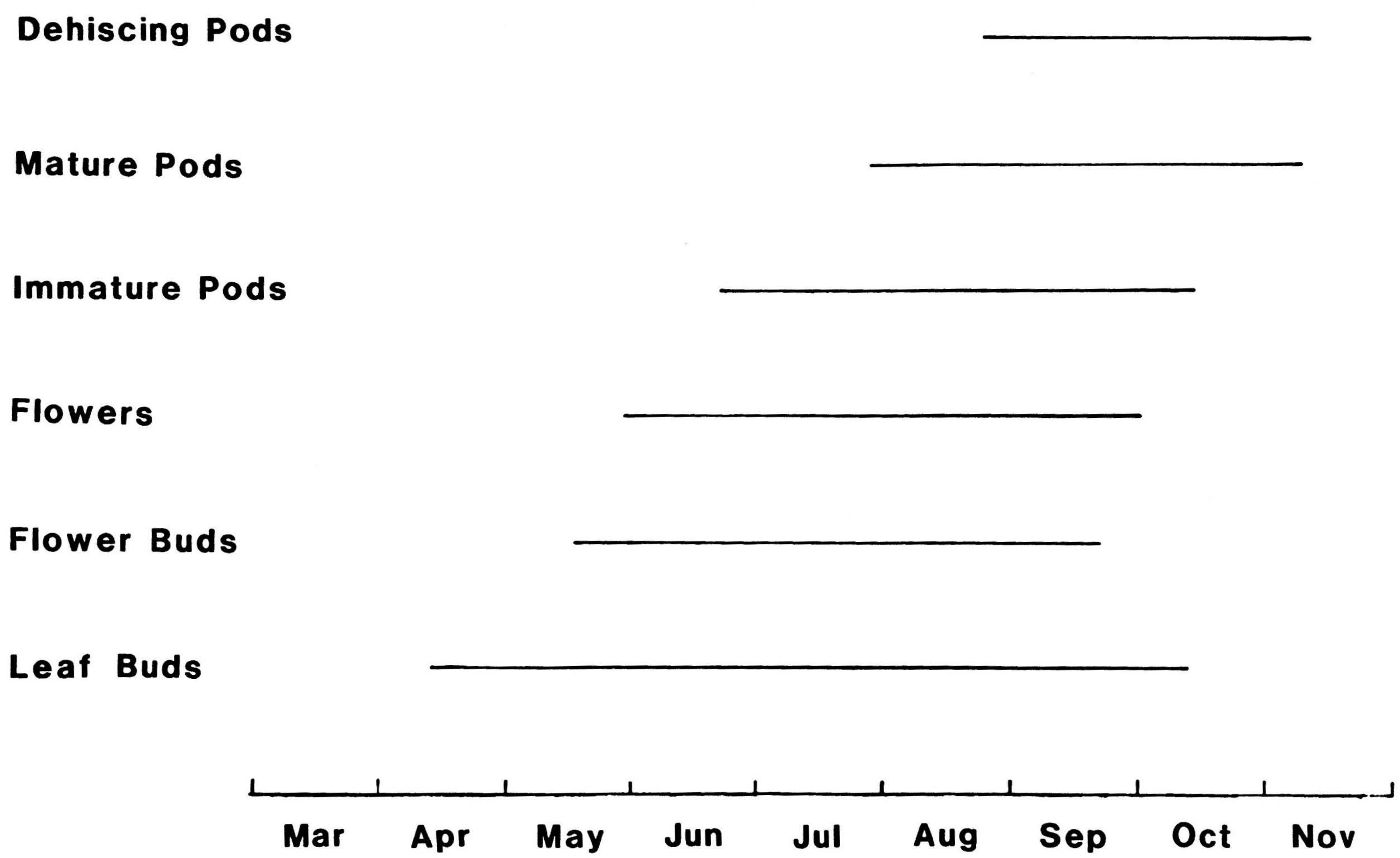
umbel was removed from each plant, with a limitation that no two umbels were removed within one metre of each other. This allowed the maximum number of plants to be sampled, while reducing the chance of scoring one clone more than once. The umbels that were collected were later scored for keel colour, damage and any insect inhabitants.

The Phenology of L. corniculatus at Eppleworth Quarry

In the spring of 1978 new vegetative growth did not begin before early April and was not extensive until mid-May. Subsequent development was rapid however, with the first flowers appearing at the end of May and the peak flowering period following shortly after. This extended throughout June and July, with scattered flower production continuing through until September. Species of Bombus were observed pollinating the flowers, and Apis mellifera L. is known to be another pollinating agent (Bader and Anderson, 1962, De Grandi and Collison, 1980).

Seed pod enlargement began during flower senescence and continued until the seeds began to reach maturity and the pod walls darkened from green to brown. In 1978 pods first appeared during late June and continued to be produced until October. The first mature pods were found in late July, and no dehiscence was noted until almost a month later. A proportion of the pods produced late in the season failed to dehisce before their peduncles rotted and these pods fell, intact, into the litter at the base of the plant. The damp conditions there made dehiscence unlikely, and resulted in some seeds germinating while still inside their pods.

L. corniculatus development during 1978 is summarised in figure 3.1. Although bud production was not monitored during 1977, the onset and duration of the flowering periods were broadly similar in the two years (tables 3.3 and 3.4). Exceptional weather conditions can alter considerably this pattern, however, as for example during the hot summer of 1976, when a survey at Bulkington on July 9 showed that no flowers remained and pod production was already well advanced.



Dehiscing Pods
Mature Pods
Immature Pods
Flowers
Flower Buds
Leaf Buds
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov

FIGURE 3.1

The development of L. corniculatus at Eppleworth Quarry in 1978.

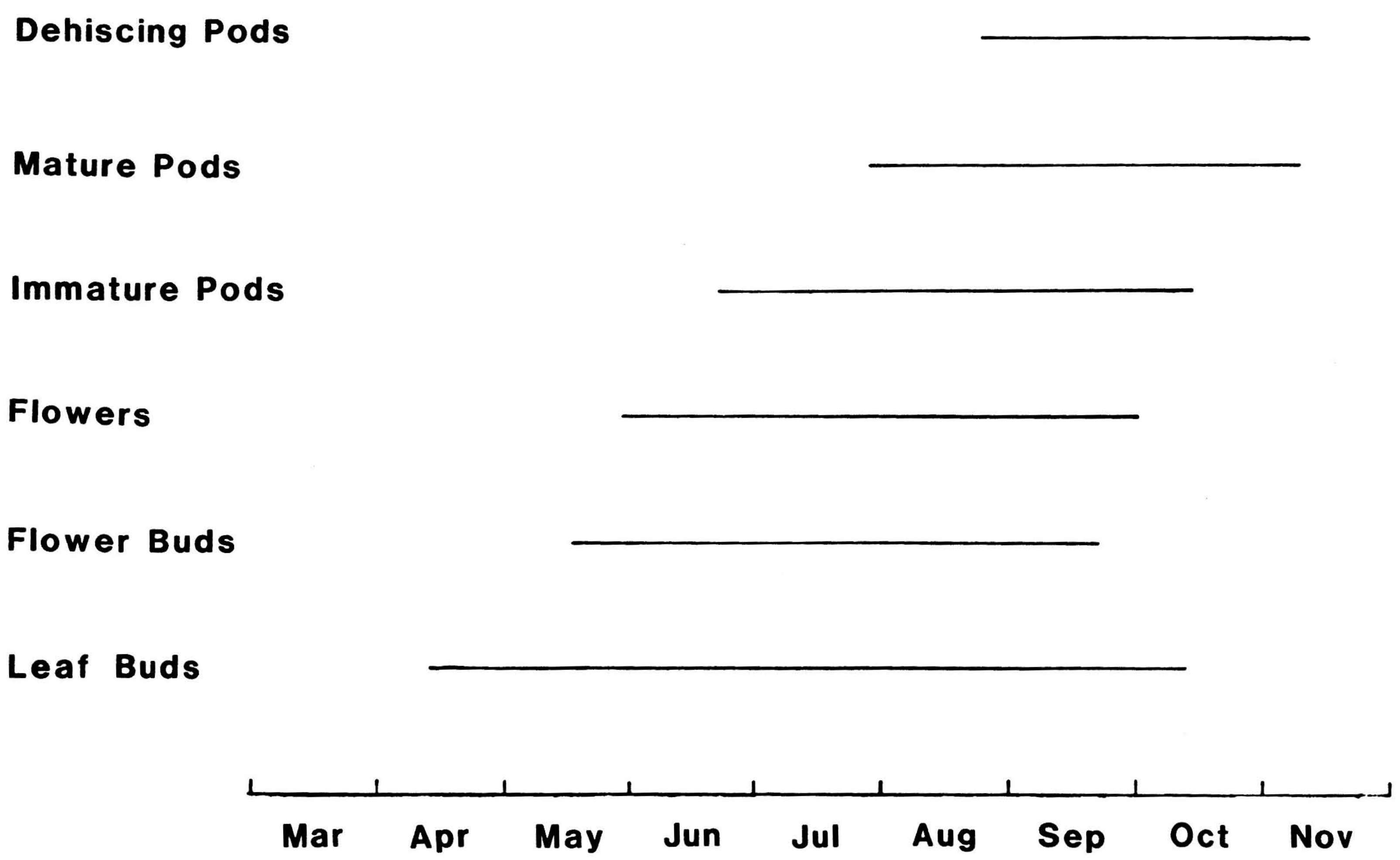

Dehiscing Pods
Mature Pods
Immature Pods
Flowers
Flower Buds
Leaf Buds
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov

Table 3.3 Development of L. corniculatus reproductive structures during 1977. (Healthy umbels only) Sampling dates are provided in table 3.1.

Sample	Anthers Closed	Anthers Open	Anthers Empty	Pods Entire	Pods Dehisced
1.1	4	5	4	89	-
1.2	-	12	19	131	-
1.3	2	13	4	74	-
2.1	-	4	6	102	-
2.2	-	4	-	53	-
2.3	2	-	9	70	-
3.1	-	-	-	196	-
3.2	-	-	5	96	-
3.3	-	6	-	84	-
4.1	-	-	-	115	-
4.2	-	-	-	118	-
4.3	-	-	-	105	-
5.1	-	-	-	46	-
5.2	-	-	-	93	-
5.3	-	-	-	183	-
6.1	-	-	-	172	-
6.2	-	-	-	29	-
6.3	-	-	-	19	-
7.1	-	-	-	20	-
7.2	-	-	-	157	-
7.3	-	-	-	141	-
8.1	-	-	-	64	-
8.2	-	-	-	148	6
8.3	-	-	-	20	1
9.1	-	-	-	111	9
9.2	-	-	-	38	3
9.3	-	-	-	60	15
10.1	-	-	-	30	9
10.2	-	-	-	47	4
11.1	-	-	-	15	1
11.2	-	-	-	36	1
Annual Totals	8	44	47	2662	49

Table 3.4. Development of <u>L. corniculatus</u> reproductive structures during 1978. (Healthy umbels only) Sampling dates are provided in table 3.2.

Sample	Anthers Closed	Anthers Open	Anthers Empty	Pods Immature	Pods Mature	Pods Dehisced
1.1	-	24	7	-	-	-
1.2	26	78	11	-	-	-
1.3	8	11	-	-	-	-
1.4	2	3	-	-	-	-
1.5	3	8	3	-	-	-
1.6	22	30	-	-	-	-
1.7	-	-	3	-	-	-
2.1	-	8	6	18	-	-
2.2	-	28	5	36	-	-
2.3	3	20	17	85	-	-
3.1	2	-	1	11	-	-
3.2	-	14	2	21	-	-
3.3	11	17	1	38	-	-
4.1	-	-	-	4	10	-
4.2	-	-	-	5	7	-
4.3	-	4	2	-	-	-
5.1	-	-	-	1	36	2
5.2	-	-	-	-	10	-
5.3	-	-	-	32	35	-
6.1	-	-	-	-	6	-
6.2	-	-	-	8	37	-
6.3	-	-	-	3	38	2
7.1	-	-	-	-	29	1
7.2	-	-	-	2	36	7
7.3	1	2	-	9	90	9
8.1	-	-	-	-	7	11
8.2	-	-	-	-	45	5
8.3	-	-	-	2	6	1
9.1	-	-	-	-	51	1
9.2	-	-	-	-	4	3
9.3	-	-	-	4	12	-
Annual Totals	85	255	67	279	459	42

Flower Bud Development at Eppleworth Quarry

Results

Flower bud mortality was assessed from quadrat samples taken during five weeks of 1978. The dates and contents of the fifteen quadrats and the condition of the buds that were found, are given in table 3.5 and tables 3.6 and 3.7. Figure 3.2 summarises these results.

In 1978 the main flowering season for L.corniculatus was effectively over by the end of July, with only nine flowers appearing in samples taken later in the season. This does not appear to have resulted from a reduction in the numbers of flower primordia being produced, as the number of green bud umbels collected did not differ significantly between the five sampling dates (Analysis of variance, V.R. [4 and 10] = 0.64, $P > 0.05$).

The success of the green stage buds that were produced did decline rapidly, however, and after late July unhealthy buds were consistently forming over 75% of the total. This resulted mainly from a greater increase in the proportion of totally unhealthy umbels, which rose from 46.4% in July to 81% over August and September.

The numbers of older (orange stage) buds rapidly declined through the season, with the numbers of both bud umbels and individual florets showing highly significant regressions with time (V.R. [1 and 13] =18.34, $P < 0.001$, and 16.73, $P < 0.01$, respectively). This had the effect of steadily increasing the proportion of green umbels in the samples, from around 30% in early July to over 90% by the end of the season.

Within the rapidly declining numbers of orange buds the proportion which were damaged or unhealthy fluctuated considerably. Very few orange buds were collected later in the season, but those which were present did not appear to contain fewer healthy buds than those produced earlier (table 3.7). The rapid decline in the density of orange

Table 3.5 Flower buds collected in quadrat samples at Eppleworth Quarry during 1978

Date	Sample	Green Stage		Orange Stage	
		Umbels	Buds	Umbels	Buds
12.7.78	2.1	17	40	46	121
	2.2	47	211	128	504
	2.3	33	138	71	254
27.7.78	3.1	18	78	20	72
	3.2	43	114	32	85
	3.3	94	374	44	283
15.8.78	4.1	56	182	1	2
	4.2	38	125	14	38
	4.3	64	218	7	54
30.8.78	6.1	21	80	0	0
	6.2	21	78	1	5
	6.3	50	152	4	16
18.9.78	9.1	50	145	6	16
	9.2	25	74	2	7
	9.3	69	268	3	11
Totals		646	2277	379	1468

Table 3.6 The condition of flower buds of L. corniculatus during 1978. Stage 1, green buds.

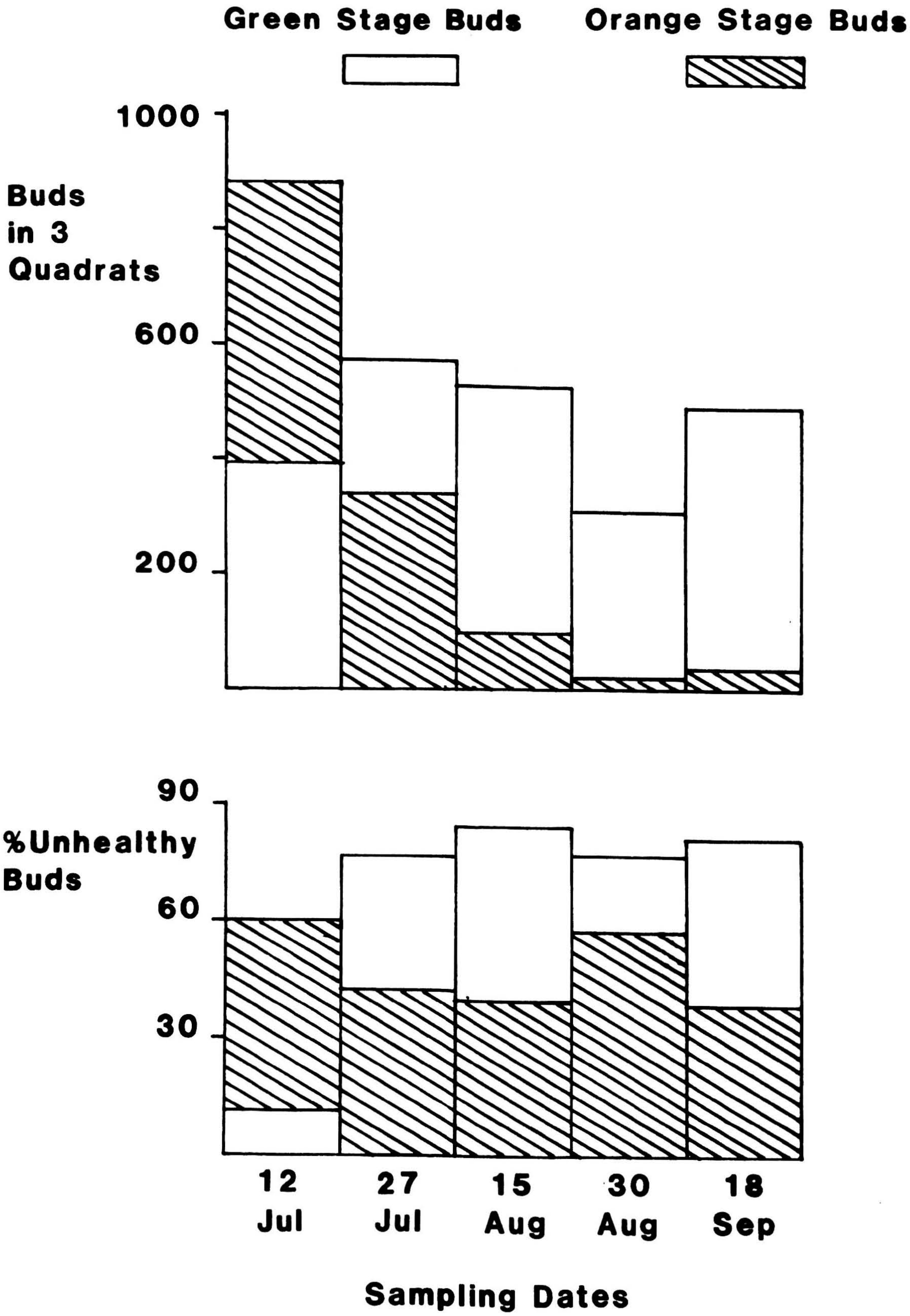
Sample	n (umbels)	Healthy buds	Unhealthy buds	Percentage unhealthy buds	Percentage totally unhealthy umbels
2.1	17	22	18	45.0	35.3
2.2	47	191	20	9.5	8.5
2.3	33	132	6	4.3	3.0
3.1	18	25	53	67.9	55.6
3.2	43	30	84	73.7	67.4
3.3	94	80	294	78.6	72.3
4.1	56	22	160	87.9	89.3
4.2	38	10	115	92.0	92.1
4.3	64	54	164	75.2	73.4
6.1	21	18	62	77.5	80.9
6.2	21	0	78	100.0	100.0
6.3	50	56	96	63.2	68.0
9.1	50	43	102	70.3	70.0
9.2	25	6	68	91.9	92.0
9.3	69	42	226	84.3	82.6
Annual Totals	646	733	1546	67.8	68.0

Table 3.7 The condition of flower buds of *L. corniculatus* during 1978.
Stage 2, orange buds.

Sample	n (umbels)	Healthy buds	Unhealthy buds	Percentage unhealthy buds	Percentage totally unhealthy umbels
2.1	46	78	43	35.5	43.5
2.2	128	216	288	57.1	52.3
2.3	71	56	196	77.8	66.2
3.1	20	19	53	73.6	60.0
3.2	32	34	51	60.0	53.1
3.3	44	142	41	22.4	0
4.1	1	2	0	0	0
4.2	14	24	14	36.8	21.4
4.3	17	31	23	42.6	29.4
6.1	0	0	0	0	0
6.2	1	0	5	100.0	100.0
6.3	4	9	7	43.7	50.0
9.1	6	9	7	43.7	16.7
9.2	2	5	2	28.6	0
9.3	3	7	4	36.4	0
Annual Totals	373	726	618	46.0	46.9

FIGURE 3.2

Densities of *L. corniculatus* flower buds in 1978 quadrat samples and the proportions of buds which were found to be unhealthy


Green Stage Buds
Orange Stage Buds
1000
Buds
in 3
Quadrats
600
200
90
%Unhealthy
Buds
60
30
12
Jul
27
Jul
15
Aug
30
Aug
18
Sep
Sampling Dates

buds was therefore mainly attributable to the rise in green phase mortality.

An estimate of overall bud mortality can be obtained by assuming an initial average of five primordia on each umbel and deducting from this expected value the numbers of healthy buds which still remained (table 3.8). Values of 77.3% green phase and 67.4% orange phase mortality are produced, but these will necessarily be underestimates because it is not possible to account for all the whole umbels which die and fall. Most green phase bud loss occurred through the death of entire umbels and the loss of individual buds was relatively unimportant (table 3.9a). A different pattern of mortality was found during the orange phase (table 3.9b) where loss of individual buds was more important and a far smaller proportion of the umbels was totally unhealthy.

Discussion

The low viability of green buds throughout much of the summer is likely to be mainly attributable to a high level of spontaneous umbel abortion, rather than to be the result of damage by animals. Joffe (1958) studied the development of L. corniculatus flowers under experimentally controlled photoperiods and found that sixteen hours of daylight were required for maximum flower production. Although the plants would continue to produce considerable numbers of flower primordia at suboptimal day-lengths, an increasing proportion would abort as the photoperiods were reduced. Other factors can also alter the levels of bud abortion, including temperature, nutrient levels, disease, insects and artificial defoliation (Seaney and Henson, 1970, Winch and Macdonald, 1961).

A bud mite (Acarina, Eriophyidae) may also have contributed to the high levels of abortion during the green phase. The identity of the species involved was not confirmed, but Eriophyses euaspis Nalepa is the only Eriophyid recorded from L. corniculatus by Buhr (1964) and Farkas (1965). The mite was widely distributed at Eppleworth Quarry and galled leaves and stems were numerous. Galled plants had a characteristic appearance, with swollen, often red marked, leaves and short inter-node lengths. No galled flowers were found

Table 3.8a Estimated Mortality of <u>L. corniculatus</u> flower buds 1. Green bud stage.

Sample	n (Umbels)	'Expected' buds	Observed buds	Estimated Mortality (%)
2.1	17	85	22	74.1
2.2	47	235	191	18.7
2.3	33	165	132	20.0
3.1	18	90	25	72.2
3.2	43	215	30	86.0
3.3	94	470	80	83.0
4.1	56	280	22	92.1
4.2	38	190	10	94.7
4.3	64	320	54	83.1
6.1	21	105	18	82.9
6.2	21	105	0	100.0
6.3	50	250	56	77.6
9.1	50	250	43	82.8
9.2	25	125	6	95.2
9.3	69	345	42	87.8
Annual Totals	646	3230	733	77.3

Table 3.8b Estimated Mortality of <u>L. corniculatus</u> flower buds 2. Orange bud stage

Sample	n (Umbels)	'Expected' buds	Observed buds	Estimated Mortality (%)
2.1	46	230	78	66.1
2.2	128	640	216	66.2
2.3	71	350	56	84.0
3.1	20	100	19	81.0
3.2	32	160	34	78.7
3.3	44	220	142	35.4
4.1	1	5	2	60.0
4.2	14	70	24	65.7
4.3	17	85	31	63.5
6.1	0	-	-	-
6.2	1	5	0	100.0
6.3	4	20	9	55.0
9.1	6	30	9	70.0
9.2	2	10	5	50.0
9.3	3	15	7	53.3
Annual Totals	389	1940	632	67.4

Table 3.9a Frequencies of healthy buds in umbels of *L. corniculatus*.
Stage 1, green buds.

Sample	Healthy buds per umbel						
	0	1	2	3	4	5	6
2.1	6	5	3	1	2	0	0
2.2	4	0	1	4	14	23	1
2.3	1	1	3	5	7	14	2
3.1	10	2	1	2	1	1	1
3.2	29	4	4	6	0	0	0
3.3	68	6	8	2	1	6	3
4.1	50	0	2	1	1	1	1
4.2	35	1	0	0	1	1	0
4.3	48	2	3	1	7	3	0
6.1	17	0	0	0	2	2	0
6.2	21	0	0	0	0	0	0
6.3	34	2	2	3	4	5	0
9.1	35	3	0	8	4	0	0
9.2	23	1	0	0	0	1	0
9.3	58	0	0	4	5	2	0
Totals	439	27	27	37	47	59	8

Table 3.9b Frequencies of healthy buds in umbels of *L. corniculatus*.
Stage 2, orange buds.

Sample	Healthy buds per umbel						
	0	1	2	3	4	5	6
2.1	20	4	5	6	9	2	0
2.2	67	8	9	9	13	21	1
2.3	47	8	4	4	3	4	1
3.1	12	3	2	1	1	1	0
3.2	17	3	7	3	2	0	0
3.3	0	7	10	9	5	10	3
4.1	0	0	1	0	0	0	0
4.2	3	5	2	1	3	0	0
4.3	5	2	4	3	3	0	0
6.1	0	0	0	0	0	0	0
6.2	1	0	0	0	0	0	0
6.3	2	0	0	0	1	1	0
9.1	1	2	2	1	0	0	0
9.2	0	2	0	0	1	0	0
9.3	0	1	1	0	1	0	0
Totals	175	45	47	37	42	39	5

and umbel development appeared to be inhibited at an early stage. An assessment of the importance of this species was not attempted, but the related *Eriophyses medicaginis* Keifer is known to have a significant effect on the growth of *Medicago* (Ridland and Halleran, 1979).

Photoperiod related abortion was unlikely to have been the main cause of orange phase bud loss because abortion is usually completed during the early stages of bud growth (Joffe, 1958). Feeding by insects was more apparent, however, with most of the observed damage being the result of 'blasting' by bugs. In smaller umbels this caused the death of the whole cluster of buds, whereas feeding on more mature umbels often resulted only in the loss of the individual buds that were damaged. Damaged buds had a pale, dry appearance, with characteristic circular feeding holes. In addition to the feeding activity of Hemiptera there was also some damage caused by insects which normally developed in the flowers and pods. Those responsible were larvae of *Odontothrips loti*, *Contarinia loti*, *Cydia compositella* and *Hypera plantaginis*.

Four species of Hemiptera were found to be particularly common on *L. corniculatus* at Eppleworth Quarry. Of these, *Philaenus spumarius* is a xylem feeder and *Stenocranus minutus* (Fabr.) is specificly associated with the grass *Dactylis glomerata* L. (May, 1975). The remaining two species, *Calocoris norvegicus* and *Plagiognathus chrysanthemi*, are bud feeders and both are recorded as economic pests of *L. corniculatus* (Balarin, 1975 and Guppy, 1963).

C. norvegicus is a polyphagous species (Woodroffe, 1955) recorded from a variety of host plants, including *Urtica dioica* and *Rumex obtusifolius* L. (Davies, 1973 and Smith, 1977). It feeds on both buds and stems, and can occur in sufficient numbers for flowering to be totally inhibited (Steer, 1929). *P. chrysanthemi* is also polyphagous (Kullenberg, 1946) and has been introduced into North America, where it is a pest of *L. corniculatus* and alfalfa (Wheeler, 1974). This was the most abundant Heteroptera species on *L. corniculatus* at Eppleworth Quarry. Nymphs were found throughout the early summer and into

August, with the adults present from late July and persisting until September.

Guppy (1963) estimated that in some cultivated stands of L. corniculatus only 20% of the flower buds successfully developed into flowers, and that P. chrysanthemi was the major cause of this low success rate. In the native population at Eppleworth Quarry losses were almost as high, but they cannot be attributed to one particular causal agent.

The importance to the plant of bud losses is particularly difficult to judge. Inherently high abortion rates are apparently typical for L. corniculatus throughout much of its flowering period and extraneous debudding could therefore be compensated for by reducing the levels of such abortions, in addition to responding with increased bud production. Damage is also likely to be more significant if it affects mature buds, because the plant has committed more resources into their production. Debudding may also have additional indirect effects, for example by increasing the root: shoot ratio (Craille and Heichel, 1981). Large bug populations can nonetheless have a dramatic effect on the success of sexual reproduction in L. corniculatus. This was shown conclusively by the studies of MacCollan (1958) and Ridgeway and Gyrisco (1961) who found that treatment with insecticides could increase the weight of seed yields by up to 100%.

Differential abortion rates or flower damage associated with phenotypic differences may be of importance and the next section considers one example of this type of situation. Ultimately it is the differential production of progeny capable of reproduction that is important, and the later in the 'cycle' that selection acts the more effective it will be.

Keel Colour Polymorphism and Colonisation of Flowers by Insects.

Flowers were only present regularly in the quadrat samples during the early part of each season, although sporadic flowering did continue until well into September. Few of the flowers at Eppleworth showed any signs of injury (tables 3.10 and 3.11) and only a low density of insects was recorded (tables 3.12 and 3.13). Flowers scored as unhealthy appeared to be undamaged but were

Table 3.10 The condition of *L. corniculatus* flowers collected during 1977.

Sample	Extensively Damaged	Unhealthy	Petals/Calyx Damaged	Pollen Sacs Damaged	Galled by Contarinia loti	Total Flowers
1.1	0	0	0	0	0	13
1.2	0	2	0	3	1	35
1.3	0	0	0	0	0	19
2.1	1	0	0	1	0	12
2.2	0	0	0	1	0	11
2.3	0	0	0	0	0	2
3.1	0	0	0	0	0	9
3.3	3	0	2	2	0	17
Totals	4	2	2	7	1	118
Percentage	3.4	1.7	1.7	5.9	0.8	

Table 3.11 The condition of *L. corniculatus* flowers collected during 1978

Sample	Extensively Damaged	Unhealthy	Petals/Calyx Damaged	Pollen Sacs Damaged	Galled by *Contarinia loti*	Total Flowers
1.1	3	1	3	5	0	39
1.2	7	0	4	4	0	124
1.3	2	0	3	3	0	24
1.4	0	0	0	0	0	5
1.5	0	0	1	0	0	15
1.6	0	0	1	2	0	55
1.7	0	1	0	1	0	5
2.1	0	0	0	0	0	14
2.2	1	0	3	1	0	39
2.3	2	0	1	5	3	46
3.1	0	0	0	0	0	1
3.2	0	0	2	6	0	28
3.3	0	0	1	0	0	30
4.3	0	0	0	0	0	6
7.3	0	0	0	0	0	3
Totals	15	2	19	27	3	434
Percentage	3.5	0.5	4.4	6.2	0.7	

Table 3.12 Insect inhabitants of *L. corniculatus* flowers collected at Eppleworth Quarry 1977.

Sample	Flowers Present	*Apion loti*		*Meligethes erythropus*	*Hypera plantaginis*	Thysanoptera spp.		*Cydia compositella*
		E	L	L	L	L	A	L
1.1	13	1	2	0	0	10	0	0
1.2	35	3	4	1	0	29	0	0
1.3	19	1	5	1	0	22	0	0
2.1	12	0	2	0	1	5	0	1
2.2	11	0	6	0	0	2	0	0
2.3	2	0	1	0	0	0	0	0
3.1	9	0	1	0	0	0	0	0
3.3	17	1	0	0	0	6	0	1
Totals	118	6	21	2	1	74	0	2

E. Eggs
L. Larvae
A. Adults

Table 3.13 Insect inhabitants of <u>L. corniculatus</u> flowers collected at Eppleworth Quarry 1978.

Sample	Flowers Present	*Apion loti*		*Meligethes erythropus*	*Hypera plantaginis*	*Thysanoptera* spp.	
		E	L	L	L	L	A
1.1	39	19	7	1	2	0	0
1.2	124	24	30	2	0	0	0
1.3	24	2	4	0	1	0	0
1.4	5	5	1	0	0	1	0
1.5	15	1	5	0	0	0	0
1.6	55	5	6	0	0	0	0
1.7	5	0	1	0	0	0	0
2.1	14	0	0	0	0	6	0
2.2	39	0	1	1	1	2	1
2.3	46	2	13	6	0	11	0
3.1	1	0	0	0	0	0	0
3.2	28	3	1	0	0	10	0
3.3	30	0	0	0	0	2	1
4.3	6	0	0	0	0	0	0
7.3	3	0	0	0	0	3	0
Totals	434	61	69	10	4	35	2

E. Eggs L. Larvae A. Adults

showing signs of premature senescence and were unlikely to set seed successfully. A mean of 2.0 flowers per umbel was recorded during 1977 and 2.7 flowers per umbel in 1978. During both seasons the mean number of pods per umbel was 1.8, representing a loss of 10% of the flowers during the first year and 33% during the second.

The proportion of dark keeled flower umbels in the quadrat samples was 71.2% in 1977 and 61.2% in 1978. The second area of the quarry, where sampling was of one umbel at metre plus intervals, had an average of 48.3% dark keeled plants. (table 3.14). The numbers of dark keeled umbels remained fairly constant through the season, but there was a noticeable decline in the light keeled individuals. It remains to be established whether this reflects a genuine difference in the flowering patterns of the two morphs, but it is interesting that Jones and Crawford (1977) obtained increasing proportions of dark keeled plants from successive seed samples taken during one season at a site in the West Midlands.

The technique of sampling single umbels at intervals is not suitable for comparing the numbers of flowers on each umbel because the eye of the collector tends to select the more prominent flower groups, which contain the most flowers. In the quadrat samples (table 3.15 and 3.16) the dark keeled plants supported a greater number of flowers per umbel during both seasons (tables 3.15 and 3.16), but the frequencies were not significantly different (X^2 [2] = 3.87 in 1977, X^2 [3] = 4.29 in 1978, $P > 0.05$). A similar, but more extensive sampling programme conducted at Wharram Quarry in 1980 also failed to detect any differences in the numbers of flowers per umbel produced by the keel colour morphs (Beesley and Compton, unpublished).

Which *L. corniculatus* flowers will be colonised by insect larvae is determined mainly or wholly by adult females when they choose their oviposition sites. Analysis of the distribution of several insect species within *L. corniculatus* flowers suggests that their choice is not influenced by the colour of the keel petals (table 3.17). Possible exceptions were at Eppleworth, where

Table 3.14 L. corniculatus keel colour frequences in a section of Eppleworth Quarry during 1978. Umbels were sampled at metre plus intervals.

Sampling Dates	Dark Keel n(umbels)	Dark Keel Flowers per umbel	Light Keel n(umbels)	Light Keel Flowers per umbel	% Dark Keels (umbels)
20.7.78	15	2.5	30	3.2	33.3
27.7.78	14	2.0	12	2.9	53.8
15.8.78	19	2.4	18	2.2	51.4
30.8.78	16	2.7	15	2.2	51.6
4.9.78	9	2.1	9	2.4	50.0
19.9.78	11	2.5	6	2.5	64.7
Totals	84	2.39	90	2.67	48.3

Table 3.15 Comparison of flower-numbers per umbel on dark and light keeled plants. 1977.

Sample	Dark Keel		Light Keel	
	n(umbels)	Flowers per umbel	n(umbels)	Flowers per umbel
1.1	3	4.0	1	1.0
1.2	15	2.3	-	-
1.3	9	1.8	2	1.5
2.1	-	-	8	1.5
2.2	-	-	5	2.2
2.3	-	-	1	2.0
3.1	3	3.0	-	-
3.3	12	1.4	-	-
Totals	42	2.1	17	1.7

Table 3.16 Comparison of flower numbers per umbel on dark and light keeled plants 1978.

Sample	Dark Keel		Light Keel	
	n(umbels)	Flowers per umbel	n(umbels)	Flowers per umbel
1.1	12	3.2	-	-
1.2	41	3.0	-	-
1.3	7	2.3	-	-
1.4	-	-	2	2.5
1.5	5	2.2	2	2.0
1.6	7	2.7	11	3.0
1.7	1	4.0	-	-
2.1	-	-	8	1.75
2.2	-	-	16	2.4
2.3	17	2.7	-	-
3.2	-	-	11	2.4
3.3	3	2.3	6	3.1
4.3	-	-	2	3.0
7.3	-	-	1	3.0
Totals	93	2.85	59	2.54

Table 3.17 Comparisons of insect frequencies in dark and pale keeled *L. corniculatus* flowers. Sampling methods are described in Chapter 2.

Locality Code	Date	Sampling Method	Species	Dark Keels Colonised	Dark Keels Not Colonised	Pale Keels Colonised	Pale Keels Not Colonised	$\chi^2[1]$	P
A	1977	Quadrats	A. loti (larvae)	8	79	6	23	2.7	-
A	1978	Quadrats	A. loti (eggs)	38	216	6	139	11.0	<0.001
A	1978	Quadrats	A. loti (larvae)	55	203	6	139	21.3	<0.001
B	26.6.77	As Available	A. loti (eggs + larvae)	41	41	17	27	1.5	-
C	5.7.78	Metre Plus	A. loti (eggs + larvae)	24	171	8	79	0.6	-
D	23.6.77	Metre Plus	H. plantaginis (larvae)	73	39	37	28	1.2	-
C	5.7.78	Metre Plus	H. plantaginis (larvae)	24	171	14	73	0.7	-
C	5.7.78	Metre Plus	M. erythropus (larvae)	26	169	17	70	1.8	-
A	1977	Quadrats	Thrips (larvae)[1]	31	56	9	20	0.2	-
A	1978	Quadrats	Thrips (larvae)	10	248	17	128	9.1	<0.01
A	1978	Metre Plus	Thrips (larvae)	45	39	51	39	0.2	-
C	5.7.78	Metre Plus	Thrips (larvae)	35	160	14	73	0.1	-
C	5.7.78	Metre Plus	Thrips (adults)	51	144	15	72	2.7	-

Localities

A	Eppleworth Quarry
B	Bulkington
C	Cottingham
D	Spurn Point

[1] *Odontothrips loti* and *Aeolothrips tenuicornis* combined

in 1978 dark keeled flowers contained many more Apion loti eggs and larvae and thrip larvae but these are clearly not typical of these species in general.

The Insect Community in and on the Flowers of L. corniculatus

'Extensively damaged' flowers at Eppleworth had large sections of petals and pods removed, probably as the result of grazing by molluscs, mammalian herbivores (voles and rabbits were present in the quarry) or larger chewing insects such as grasshoppers. Species of Orthoptera were recorded as pests of L. corniculatus by Neunzig and Gyrisco (1955) and Guppy (1958), but this mainly graminivorous group find L. corniculatus leaves distasteful (Bernays and Chapman, 1977). Cyanogenesis may be partly responsible (Bernays and Chapman, 1975) but the acyanogenic L. uliginosus is also disliked (Blank et al, 1980).

Acridids eat L. corniculatus flowers much more readily than leaves, however, and feeding experiments suggest that at least two species prefer to eat acyanogenic flowers. Feeding trials were conducted in rectangular seed trays (15.5 x 21.5 cms.) with transparent lids. The floor of each tray was covered with sand, on which were placed eight L. corniculatus umbels bearing one (Series A) or two flowers (Series B). In order to keep the flowers in a fresh condition, the peduncles were inserted into narrow water filled tubes, the tops of which were sealed with 'Blu-Tack'. Flowers were obtained from stock plants that had originally been collected at Porthdafarch, Anglesey and were growing at the University Botanic Gardens. Four cyanogenic clones (A - D) and four acyanogenic clones (E - H) were used in each trial, with phenotypes arranged alternately in two rows of four (for example as AEBF : GCHD, with A facing G etc.). Flowers were placed approximately 3 cms. apart from their nearest neighbours, and had their keel petals resting on the sand.

Adults of Omocestus viridulus (L.) and Myrmeleotettix maculatus (Thunberg) were collected on 18 and 25 August 1981 at Wharram Quarry. No food was provided overnight and six specimens of each species were introduced into separate test trays the following morning. The insects were removed approximately 24 hours later.

The five petals of each flower (the standard, two wings and two keel petals) were examined individually and each was recorded as being either undamaged or damaged. Two categories of damaged petals were recognised, consisting of those which had less than one quarter of their surface area removed and those which had sustained more extensive damage. Petals in the first damage category were considered to result from 'investigation' and subsequent rejection of the plant tissue.

The frequencies of undamaged and damaged petals of the two phenotypes in each trial are given in table 3.18. The standard was consistently the most heavily damaged petal on each flower, irrespective of phenotype, presumably because of its vertical orientation (Bernays and Chapman,1970). Between phenotype comparisons indicate a tendency for more of the acyanogenic petals to be damaged, although this difference was only significant on two occasions. Comparisons of the frequencies of investigated and heavily damaged petals again suggest that the acyanogenic phenotype was preferred.

Similar choice experiments were carried out using leafy stems of <u>L.corniculatus</u> in the place of flower umbels (table 3.19). Both species of Grasshopper were found to be very reluctant to feed on the leaves and in order to obtain reasonable levels of damage it was necessary to maintain the insects on the plants for periods of between three and five days. Leaf damage was scored on a presence or absence basis and the ratios of damaged to undamaged leaves were compared for each phenotype. No clear preference for acyanogenic leaves was detected, although one significant X^2 value was obtained.

Problems were sometimes encountered because of animals chewing the leaf stems at their bases and causing them to wilt. Similar 'felling' behaviour has been described in feeding experiments with molluscs (Dirzo and Harper, 1980),and was thought to be a response to an unpalatable food plant. 'Felling' may be of value to herbivores when they are required

Table 3.18 The feeding preferences of adult *Orthopterans* given a choice between Cyanogenic and Acyanogenic *L.corniculatus* flowers.

a *Omocestus viridulus*

trial	*L.corniculatus* phenotype	Undamaged petals	'Investigated' petals with <0.25 removed	Extensively damaged petals
1	++	22	17	1
	-	9	9	22

X^2 [1] Damaged : Undamaged petals = 8.90, $P < 0.01$

X^2 [1] Investigated : Extensively damaged petals = 19.56, $P < 0.001$

trial	*L.corniculatus* phenotype	Undamaged petals	'Investigated' petals with <0.25 removed	Extensively damaged petals
2	++	9	10	1
	-	7	7	6

X^2 [1] Damaged : Undamaged petals = 0.42, $P > 0.05$

X^2 [1] Investigated : Extensively damaged petals = 3.96, $P < 0.05$

b *Myrmeleotettix maculatus*

trial	*L.corniculatus* phenotype	Undamaged petals	'Investigated' petals with <0.25 removed	Extensively damaged petals
1	++	21	17	2
	-	11	11	18

X^2 [1] Damaged : Undamaged petals = 5.21, $P < 0.05$

X^2 [1] Investigated : Extensively damaged petals = 12·54, $P < 0.001$

trial	*L.corniculatus* phenotype	Undamaged petals	'Investigated' petals with <0.25 removed	Extensively damaged petals
2	++	5	13	2
	-	5	9	6

X^2 [1] Damaged : Undamaged petals = 0.0, $P > 0.05$

X^2 [1] Investigated : Extensively damaged petals = 2.73, $P > 0.05$

Table 3.19 The feeding preferences of two species of Orthoptera when given a choice between Cyanogenic and Acyanogenic *L. corniculatus* leaves.

		Cyanogenic Leaflets		Acyanogenic Leaflets		$\chi^2[1]$
Species	Expt.	Damaged	Undamaged	Damaged	Undamaged	
Omocestus viridulus	a	52	63	64	56	1.55
	b	44	71	30	70	1.62
	c	64	71	69	56	1.58
Myrmeleotettix maculatus	a	41	99	58	72	6.82 ($P<0.01$)
	b	52	78	55	85	0.014

to survive for short periods on food plants which would normally be rejected. Bernays (1977), for example, has shown that nymphs of Zonocerus variegatus (L.) preferentially eat wilted cassava leaves, and that this is probably due to a reduced rate of HCN release in wilted plants. 'Felling' behaviour could therefore result in a decline in the effectiveness of plant defences, making them marginally more palatable.

Bernays and Chapman (1970) concluded that Chorthippus parallelus (Zetterstedt) rarely ate plants other than grasses because of chemical inhibition, rather than any physical deterance. Acyanogenic L. corniculatus leaves appear to be as highly distasteful to grasshoppers as cyanogenic ones, which suggests that cyanogenesis is at most a minor component of the overall feeding inhibition. By comparison L. corniculatus flowers are readily eaten, presumably because some other deterant chemicals are absent - perhaps Tannic Acids, Phenylethylamine or Alkaloids, all of which have been isolated from L. corniculatus (Bernays and Chapman, 1975).

Before Acridids begin to feed they perform a sequence of behaviour which involves palpation of the food surface, biting but not ingesting, nibbling small quantities of food and finally continuous feeding (Bernays and Chapman, 1970). If the food plant proves to be unsuitable at any stage, then the insect stops and moves elsewhere. An experiment similar to that devised by Bernays and Chapman, (1970) was carried out in order to determine at which stage in the above feeding sequence M. maculatus rejected the cyanogenic flowers of L. corniculatus. Adults collected from Wharram Quarry were starved for between three and five hours before being introduced (singly) into a glass tube approximately 7.5 cm. long and with a 2.5 cm. diameter. The response of the grasshopper to a single cyanogenic or acyanogenic flower was then observed, together with the stage at which feeding was terminated. Insects were removed after five minutes if no response had occurred and in order to avoid any conditioning each grasshopper was used only once.

Feeding commenced on 75% of the acyanogenic flowers, but on only 10% of the cyanogenic (table 3.20). Flower surfaces were inspected by the antennae and palps before the first bite, and the insects did not give any indication of aversion to cyanogenic flowers at that stage. Inhibition clearly occurred later, during nibbling, as most specimens moved off the cyanogenic flowers at that point, sometimes after jolting backwards or shaking their heads.

These results demonstrate that cyanogenesis can cause a significant reduction in the amount of *L. corniculatus* flower tissue consumed by Acridids. The relevance of this protection for natural populations is uncertain, however, because the degree of flower feeding by grasshoppers is generally considered to be limited. Nonetheless, the exclusively cyanogenic flowers at Eppleworth may have conferred some protection against generalist herbivores.

Petal damage at Eppleworth resulted mainly from the feeding activities of the larvae of *Hypera plantaginis* and *Cydia compositella*. At other sites the adults of *Phyllobius roboretanus* and *P. viridiaeris* were also found feeding on the flowers of *L. corniculatus* (table 3.21) and feeding choice experiments have shown that both species will preferentially select acyanogenic flowers. These experiments were carried out on a similar basis to those with grasshoppers, except that a plastic petri dish was used as a test chamber. Three umbels of each phenotype were spaced equally around the periphery of the dish, with their peduncles (enclosed in water-filled tubes) projecting out through holes made in the dish wall. Three flowers per umbel were used with *P. roboretanus* and two flowers per umbel with *P. viridiaeris*. Beetles were starved overnight and maintained on the flowers for approximately 24 hours.

Both *Phyllobius* spp. consistently ate more of the acyanogenic petals (table 3.22), although the amounts were not always significantly higher. At Bulkington during late May 1979, these species were found in considerable numbers on the flowers of *L. corniculatus* and any acyanogenic flowers can be expected to have suffered disproportionately. Witter and Fields (1977) recorded 22 host species for adults of *P. oblongus* L., and *P. roboretanus* appears to be equally polyphagous. A collection of this species at Hessle Quarry, E. Yorks.

Table 3.20 The responses of adult *Myrmeleotettix maculatus* during five minute periods with flowers of *L. corniculatus*.

	No. tested	No response	Palpating	Biting	Nibbling	Feeding
Cyanogenic flowers	20	4	2	1	11	2
Acyanogenic flowers	20	4	0	1	0	15

Table 3.21 Records of *Phyllobius* spp. (Coleoptera, Curculionidae) feeding on flowers of *L. corniculatus*.

Species	Locality	Dates
P. roboretanus	Bulkington	29 May 1979
	Hessle Quarry	7 July 1981
	Wharram Quarry	27 June 1978
		18 June 1981
P. viridiaeris	Bulkington	29 May 1979
	Hessle Quarry	July 1979
	Ulley, N. Lincs.	15 June 1980
	Windmill Hill	13 July 1978
		June 1979

Table 3.22 The feeding preferences of Phyllobius (Col., Curculionidae) given a choice between cyanogenic and acyanogenic L.corniculatus petals.

a P. roboretanus

trial	L. corniculatus phenotype	Undamaged petals	'Investigated' petals with <0.25 removed	Extensively damaged petals
1	++	38	16	6
	-	4	11	15
	$X^2[2] = 5.01$, $P > 0.05$			
2	++	33	5	7
	-	25	10	10
	$X^2[2] = 3.30$, $P > 0.05$			
3	++	39	6	0
	-	26	8	11
	$X^2[2] = 13.89$, $P < 0.001$			
totals	++	110	27	13
	-	85	29	36
	$X^2[2] = 14.07$, $P < 0.001$			
	Heterogeneity $X^2[4] = 8.13$, $P > 0.05$			

b P.viridiaeris

trial	L.corniculus phenotype	Undamaged petals	'Investigated' petals with <0.25 removed	Extensively damaged petals
1	++	14	10	6
	-	12	1	17
	$X^2[2] = 12.78$, $P < 0.01$			
2	++	16	9	5
	-	12	9	9
	$X^2[2] = 1.71$, $P > 0.05$			
totals	++	30	19	11
	-	24	10	26
	$X^2[2] = 9.54$, $P < 0.01$			
	Heterogeneity $X^2[2] = 4.49$, $P > 0.05$			

(Grid Reference TA 020 257) found adults feeding on the flowers of *Rosa* Sp., *L. corniculatus* and a *Ranunculus* Sp.

Cnephasia is another genus of flower feeding species that was found on *L. corniculatus* at some sites, but not at Eppleworth Quarry. *Cnephasia* larvae are leaf miners for a short period (Chambon and Genestier, 1980) but soon begin feeding in a canopy of flowers and leaves spun together with silk (Emmet, 1980). Three *C. longana* larvae were collected from separate *L. corniculatus* flowers at Spurn Point on 23.6.77. By early July these had pupated inside a group of dead leaves and adults emerged between eight and ten days later. A larva of a second species, *C. pasiuana*, was present inside *L. corniculatus* flowers collected at North Newbald (E. Yorks.) on 6 July 1981 by D.A. Jones. The adult had appeared by mid July. *Cnephasia* species are highly polyphagous (e.g. Bradley *et al*, 1973) and five species have now been recorded as feeding on *L. corniculatus* (table 1.1).

Cydia compositella was the only member of the Lepidoptera encountered frequently in the flowers of *L. corniculatus*. This is mainly a seed eating species (Chapter four) but some larvae developed in the flowers (or even the flower buds), where they fed indiscriminantly on the stamens, corolla and immature seed pods. Olaife and Akingbohunghe (1981) have noted a similar flexibility in the feeding habits of *C. ptychora* (Meyrick).

The larvae of *H. plantaginis* were regularly encountered in the flowers of *L. corniculatus*, yet this species has not generally been regarded as a host plant (exceptions are Anderson, 1948 and Parsons and Rothschild, 1964). Walsh and Dibb (1975) and Scherf (1964) list *H. plantaginis* as being associated with *Plantago*, *Anthyllis* and *L. uliginosus*. An *H. plantaginis* cocoon was collected from a *Plantago* leaf at Bulkington, but as larvae were found to be on *L. corniculatus* nearby, this was probably only a casual record. The *Anthyllis* association was confirmed by Anderson (1948) and larvae of *H. plantaginis* were present in both *L. corniculatus* and *L. uliginosus* flowers collected by D.A. Jones at Windmill Hill, Warwickshire on 10 July, 1978.

The feeding activity of H. plantaginis larvae produced characteristic damage in the flowers of L. corniculatus. The areas of the petals alongside the seed pod were usually eaten first, together with the distal section of the pod. In heavily chewed flowers the petals were visibly ragged and the pod could be entirely destroyed apart from a short stump projecting from the calyx.

Young larvae are brownish yellow with a prominent prothoracic shield, but later they develop a bright green colouration with a pale yellow mid-dorsal stripe. Larvae were present in L. corniculatus flowers soon after the flowering season had commenced (table 3.23), but were not found after mid July. Suction sampling carried out at Wharram Quarry (figure 3.3) shows that the larval period is not terminated because of a shortage of potential feeding sites as these were available well into August.

Pupation occurs inside a cocoon that is produced in an L. corniculatus flower or on nearby vegetation. The cocoon is yellowish-green initially but gradually darkens to a dull brown. Larvae collected on L. corniculatus produced adults from early July until mid August. One very late pupal cocoon was collected at Eppleworth Quarry on 30 August. This may have represented an individual from a partial second brood, although clearly H. plantaginis is primarily univoltine. H. nigrirostris has been found to have a similar partial second generation each year (Detwiler, 1923).

Emerging adults enter a period of voracious feeding which lasts for several days and usually commences with the walls of their cocoon. Flower petals are the preferred food item, but at least in the laboratory some L. corniculatus leaves are also eaten. Similar post-emergence periods of intense feeding activity have been reported for H. rumicis (L.) and H. postica by Chamberlain (1933) and Bland (1971). Adults reared in August were successfully overwintered in an outdoor insectary and, like some well known species of Coccinellidae, were found to cluster together under the available cover.

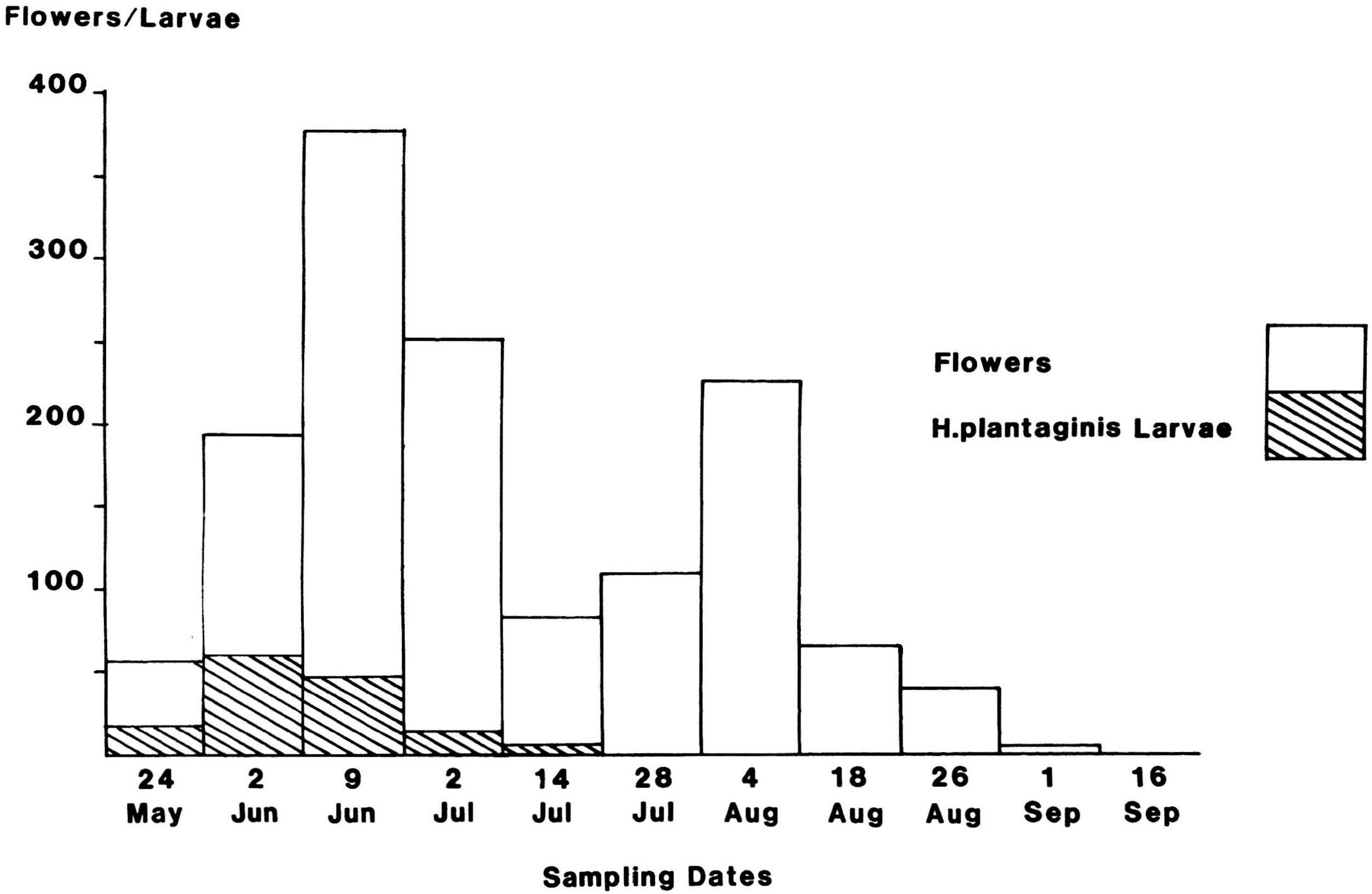
A total of seven Hypera species are recorded in the literature as

Table 3.23 Hypera plantaginis collected on flowers of L. corniculatus.

Locality	Dates Larvae	 Pupae	 Adults
Porthdafarch	11.6.79	-	-
Eppleworth Quarry	23.6.78	-	-
Spurn Point	26.6.77	-	-
South Cave	-	26.6.78	-
North Cave	5.7.77	-	-
Cottingham	5.7.78	5.7.78	-
Spurn Point	9.7.78	-	-
Bulkington	-	10.7.77	-
Windmill Hill, Warwicks	10.7.78	-	-
Eppleworth Quarry	12.7.78	12.7.78	-
Hardargerfjord, Norway	12.7.79	-	-
Flamborough	-	16.7.78	-
Eppleworth Quarry	-	-	27.7.78
Eppleworth Quarry	-	-	15.8.78
Eppleworth Quarry	-	30.8.78	-

FIGURE 3.3

Hypera plantaginis larvae collected in D-Vac suction samples at Wharram Quarry during 1980, and the numbers of L. corniculatus flowers in the suctioned areas. 14 or 15 samples, each of 0.05 m^2, were collected on each sampling date.


Flowers/Larvae
400
300
200
100
Flowers
H.plantaginis Larvae
24 May
2 Jun
9 Jun
2 Jul
14 Jul
28 Jul
4 Aug
18 Aug
26 Aug
1 Sep
16 Sep
Sampling Dates

occurring on *L. corniculatus* (table 1.1), but *H. plantaginis* was the only species found at over ten British localities where collections were made. One possible exception was at Eppleworth Quarry, where a cocoon of *H. nigrirostris* was collected on *L. corniculatus* leaves on 12 July 1978. This is a well know *Trifolium* feeding species (Makkula and Tinnila, 1956) and Guppy (1958) failed to detect it on *L. corniculatus* when it was numerous nearby on three species of clover. The cocoon found at Eppleworth may have been produced by a larva that had fed elsewhere and moved on to *L. corniculatus* to pupate. No larvae agreeing with the description of *H. nigrirostris* (Anderson, 1948) were found on *L. corniculatus*, although adults were collected on this plant at Eppleworth Quarry (27.7.78) and Cornelian Bay, Scarborough (5.7.80).

The Ichneumonoid genus *Bathyplectes* was found to contain the most important parasites of *H. plantaginis*. Parasitised beetle larvae were apparently healthy and active until pupation (*Bathyplectes* larvae are endoparasitic). Examination of their pupal cases however, revealed a second cocoon rather than a healthy larva or pupa. The *Bathyplectes* cocoon is a purplish brown ovoid with a raised white equatorial stripe (figured by Cross and Simpson, 1972).

Two or more species of *Bathyplectes* were reared from *H. plantaginis*, but their identities have not been established (table 3.24). Females of species A and B were most easily separated on the basis of ovipositor and antennal characters. Both *Bathyplectes* at Eppleworth Quarry overwintered inside their cocoons and are probably univoltine like their host. The *Bathyplectes* from Flamborough emerged within one month of collection however, suggesting that these males may represent a third species.

There is an extensive literature on the biology of *B. anura* (Thomson) and *B. curculionis* (Thomson) because they are parasites of *H. postica*, an important alfalfa pest in the U.S.A. *B. curculionis* is known to be a parasite of *H. plantaginis* (Horstmann, 1974) but this species has not been recorded from Britain (Fitton *et al*, 1978).

Bathyplectes cocoons collected at Eppleworth and Bulkington exhibited

Table 3.24 Contents of the cocoons of Bathyplectes spp., parasitic on Hypera plantaginis

Locality	Collection Date	Contents	Sex	Emergence Date
Flamborough	4.7.78	Bathyplectes Sp.	3 Males	24.7.78
Eppleworth Qu.	7.7.78	Bathyplectes Sp. A	Female	18.4.79
Eppleworth Qu.	12.7.78	Bathyplectes Sp. B	Female	3.5.79
Eppleworth Qu.	15.8.78	Bathyplectes Sp.	Male	12.4.79
Eppleworth Qu.	27.7.78	Gelis Sp. A	Female	-.8.78
Eppleworth Qu.	15.8.78	Gelis Sp. A	Female	23.8.78
Bulkington	10.7.77	Sceptrothelys grandiclava	1 Male 5 Females	25.7.77
Eppleworth Qu.	6.9.77	Sceptrothelys grandiclava	-	-

an interesting jumping behaviour which has been described previously with B. anura, but does not occur with B. curculionis. When placed in direct sunlight the parasite cocoon can react by jumping distances of up to several centimetres. The significance of this behaviour has been investigated by Day (1970) who showed that, when compared with B. curculionis cocoons, significantly fewer B. anura cocoons were parasitised by the polyphagous Dibrachys cavus (Walker). Successful avoidance was repeated even after the cocoons were prevented from jumping, which indicates that larval movements inside the cocoon were as important as the jumping ability per se. Askew (1971) suggested that the jumping action may be used to force an exit from the surrounding Hypera cocoon in order to avoid searching parasites, in particular Sceptrothelys grandiclava (Walker). The larval movements that cause the cocoon to jump have a different effect when the cocoon is still retained within that of its host. Under these conditions they result in the Bathyplectes cocoon rotating rapidly. This should help to reduce the success of hyperparasites when they find Bathyplectes in this exposed position, because insertion of their ovipositor through the cocoon wall will be made much more difficult.

S. grandiclava was recorded as a parasite of H. plantaginis via a Bathyplectes sp. by Askew (1970) and as a parasite of H. postica via B. curculionis by Pike and Burhardt, (1974). In the U.S.A. S. grandiclava can have three or more generations each year and a generation time of only 20 days (Simpson et al, 1979). Bathyplectes cocoons with S. grandiclava inside were collected at Bulkington and Eppleworth Quarry (table 3.24) and contained six and four larvae respectively. Those from Eppleworth successfully overwintered as larvae, but quickly dehydrated after their host cocoon was opened for inspection, while the Bulkington specimens produced adults shortly after being collected. This species is therefore likely to be at least bivoltine in the U.K. Graham (1969) gives the flight period as between June and August, and this can now be extended by the record of one female collected by sweeping on L. corniculatus at Eppleworth Quarry on 12 September 1978.

The six Bulkington specimens of S. grandiclava emerged via a common exit hole positioned at one of the poles of the cocoon. One female was placed with a healthy (bouncing) Bathyplectes cocoon in a petri dish. The bouncing stopped immediately after successful penetration of the cocoon, showing that the female of this species paralyses its host. The jumping action of the Bathyplectes failed to dislodge the female, as did rolling the cocoon around the bottom of the dish. When the cocoon was examined the following spring it contained three healthy S. grandiclava larvae.

A species of Gelis was also reared as a secondary parasite of Bathyplectes (table 3.24). Adult females emerged late in the summer, suggesting that they may overwinter as adults. Gelis species are also major parasites of B. curculionis in the U.S.A., where over 20% of the Bathyplectes can be destroyed (Caldwell and Wilson, 1975). A second Gelis species was reared from an H. plantaginis cocoon as a direct parasite of the beetle (Eppleworth Quarry, cocoon collected 30.8.78, female Gelis emerged 10.9.78). This species differed from those reared as hyperparasites by having a relatively shorter thorax, paler colouration and in the proportions of the antennal segments. Gelis species have been recorded previously as direct parasites of Hypera species (ex H. postica, Horn, 1976).

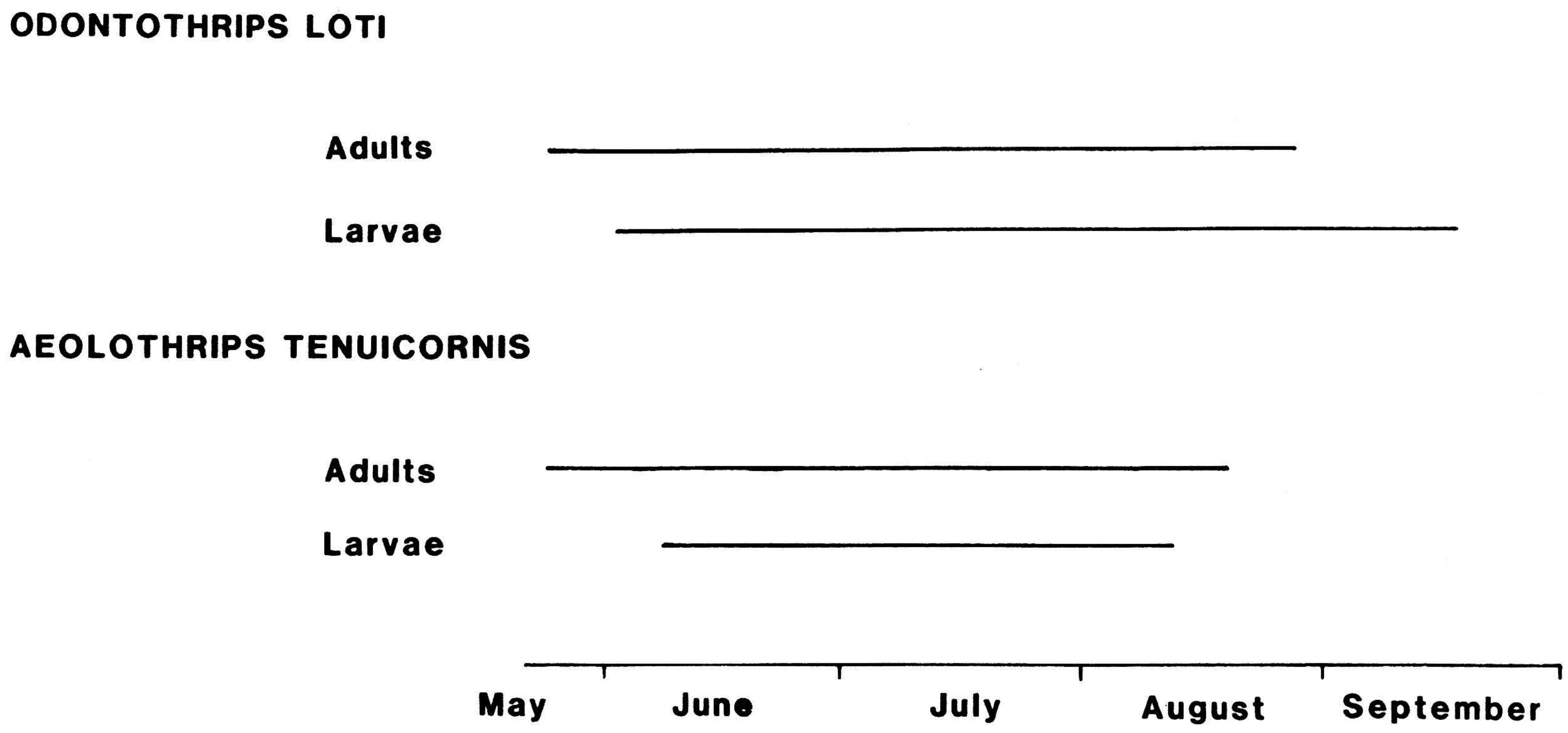
At Eppleworth Quarry the adults and larvae of Odontothrips loti and Aeolothrips tenuicornis were found in L. corniculatus flowers throughout the flowering period, from late May to September. In 1980 an extensive survey at Wharram Quarry confirmed the long flight periods of these species (figure 3.4).

O. loti has been recorded from the flowers of a number of legume genera, including Medicago (Banita, 1976), and is widely distributed in Southern and Western Europe (Pitkin, 1972). This species was present in L. corniculatus flowers from the Jostedalen, Norway (August, 1979) which extends its known distribution into Scandinavia.

Both active stages of O. loti are regarded as economic pests in Czechoslovakia, where leaf curling, floral abortion and reduced seed output are

FIGURE 3.4

Odontothrips loti and Aeolothrips tenuicornis on L. corniculatus at Wharram Quarry during 1980. Larvae were obtained mainly by hand searching of flowers, adults by suction sampling.


ODONTOTHRIPS LOTI
Adults
Larvae
AEOLOTHRIPS TENUICORNIS
Adults
Larvae
May
June
July
August
September

attributed to their feeding activities (Obrtel, 1965). In Britain the highest densities of O. loti were found at Bulkington, where up to nine larvae were recorded from one flower. First instar larvae are pale and virtually transparent, while second instar larvae develop a bright orange colouration. At these high densities their feeding results in the surface of the young pods developing a silvered appearance, similar to that developed in Ulex and Cytisus flowers after injury by other Odontothrips species (Morison, 1928).

Many O. loti larvae had bright green gut contents, showing that chlorophyll containing tissues are a major item in their diet. This view received support from the results of a survey of Contarinia loti flower galls carried out in Leirdalen, Norway. O. loti was unusually numerous in these flowers, with a maximum of 14 larvae found in one gall. As galled flowers produce almost no pollen this demonstrates that pollen cannot be required by the thrip larvae. Chi square analysis of the distribution of thrip larvae within L. corniculatus flowers at Eppleworth showed that during 1977 the pollen producing phase of anther development was nonetheless preferred (table 3.25). χ^2 [1] for flowers at the 'open' or 'empty' stages, with or without thrip larvae = 10.7 ($P < 0.01$) and 0.64 ($P > 0.05$) for 1977 and 1978. Immature 'closed', flowers were the least favoured stage during both seasons.

O. loti larvae eventually vacate the flowers and pupate in underground cells (Obrtel, 1963). Mature larvae were present on L. corniculatus from early July to September, suggesting that two or more generations may be achieved each year. Adults have been found in turf samples collected during the winter (Ward, 1967), but Pitkin (1972) has suggested that O. loti may normally overwinter as a larva.

A. tenuicornis is a more polyphagous species than O. loti, and Ward (1973) collected its larvae from the flowers of 23 plant species. At Eppleworth and Wharram Quarries adult A. tenuicornis were only numerous on L. corniculatus during the early part of each season and, from late June onwards, only an occasional specimen was recorded. Ward (1973) observed that adults feed on

Table 3.25 The numbers of thrip larvae in L. corniculatus flowers at different stages of development. Eppleworth Quarry, 1977 and 1978.

Year	Anther Condition	Total Flowers	Total Thrip larvae	Flowers with Thrip L.	Flowers without Thrip L.
	Closed	9	0	0	9
1977	Open	47	56	26	21
	Empty	55	16	13	42

$\chi^2[2]$ (flowers with or without thrip L.) = 16.5, $P < 0.001$

Year	Anther Condition	Total Flowers	Total Thrip larvae	Flowers with Thrip L.	Flowers without Thrip L.
	Closed	85	1	1	84
1978	Open	255	23	19	236
	Empty	67	7	7	60

$\chi^2[2]$ (flowers with or without thrip L.) = 5.9, $P > 0.05$

L. = larvae

pollen and suggested that the larvae may be predators on small arthropods, including other thrips. On *L. corniculatus* the *A. tenuicornis* larvae were never as numerous as those of *O. loti*, and were more dispersed, rarely occurring twice in one flower. They were sometimes found together with *O. loti* larvae, but no clear association was observed. No pupae were found in the flowers and pupation probably occurs in the soil.

The larvae of *Ceranisus* species develop as endoparasites in the larvae of thrips (Boucek and Askew, 1968). In England *C. pacuvius* (Walker) adults were often found in *L. corniculatus* flowers collected during the early summer (table 3.26), but were not recorded later than mid July. The flight period appears to extend to rather later in the year in Norway, however, with adults recorded through until August. Kutter (1937) reared *C. pacuvius* from *Kakothrips robustus* Uzel and gave a detailed description of the immature stages. The parasites pupated inside the pre-pupa of the thrips, and showed few signs of parasitism before this point. In the laboratory the adults of both sexes of *C. pacuvius* are agoraphobic, searching deep into *L. corniculatus* flowers or whatever other dark, narrow spaces are available. Attempted oviposition into second instar larvae was observed, but no parasites were reared.

C. menes (Walker) was the only *Ceranisus* found in *L. corniculatus* flowers at Eppleworth, but generally this species was encountered much less frequently than *C. pacuvius*. This may be because *C. pacuvius* has a flight period which corresponds more closely to the peak flowering season of *L. corniculatus*. The development of *C. menes* has been described by Buhl (1936), and Sakimura (1937) who showed that in Japan four generations were produced each year. *C. menes* has a wide range of hosts (Boucek and Askew, 1958), one of which may be associated with thistles because very large numbers of *C. menes* were collected from these plants at Thixendale, N. Yorks. in July 1980.

Adults and larvae of the pollen beetle *Meligethes erythropus* were regular members of the insect community inside *L. corniculatus* flowers, but never occurred in large numbers. The eggs of this species are white elongate ovoids,

Table 3.26 Records of Adult *Ceranisus menes* and *Ceranisus pacuvius*.

	Ceranisus menes			*Ceranisus pacuvius*			
	Numbers	Date	Location	Numbers		Date	Location
	F			F	M		
May	1	-.4.81	Skipwith Common, Yorks		2	21.4.81	Kenfig Burrow, S. Wales
June	1	22.6.78	Eppleworth Quarry	1	6	2.6.80	Wharram Quarry[1]
				41	29	9.6.80	Wharram Quarry[1]
				8	2	13.6.78	Wharram Quarry[1]
					2	20.6.79	Hessle Quarry
				6	1	26.6.77	Bulkington[1]
				4	3	26.6.78	South Cave
					6	27.6.78	Wharram Quarry[1]
				12	2	31.6.77	Bulkington[1]
July	5	2.7.78	Eppleworth Quarry		2	10.7.77	Bulkington[1]
	1	12.7.78	Eppleworth Quarry[1]	1	3	12.7.79	Hardangerfjord, Norway[1]
	1	14.7.77	Eppleworth Quarry[1]		1	19.7.79	Gaupne, Norway[1]
	30	26.7.80	Thixendale, N. Yorks		1	22.7.79	Stordalen, Norway
	1	30.7.80	Crowle, S. Humber.	13	3	24.7.79	Leirdal, Norway[1]
August	2	2.8.80	Brumby Common, Lincs.	1		4.8.79	Leirdal, Norway[1]
	1	11.8.79	Vigdalen, Norway				

[1] Collected from flowers of *L. corniculatus*

with parallel ribs running along the major axes. They were found between the petals of *L. corniculatus*, or in the pollen mass at the apex of the keel, on dates in June, July and August. No eggs were found in the flower buds, which is the preferred site for *M. aeneus* (Williams and Free, 1978). Larvae were present throughout the same period as the eggs, and were usually found inside the keel petals, where they were feeding on pollen. A characteristic pure white frass was produced and in older flowers this provided a useful indication of past *M. erythropus* activity. The major dorsal markings of mature *M. erythropus* larvae are pairs of sub-lateral ovals, which extend the whole length of the trunk. Smaller, more irregular, mid-dorsal spots are also present, and these become more conspicuous towards the end of the abdomen.

Prior to pupation the larvae leave the flowers and enter the soil. Larvae collected in June and July produced adults in approximately three weeks. Adults were collected from *L. corniculatus* flowers at Eppleworth Quarry between May and July and suction sampling at Wharram Quarry during 1980 showed that the flight period also includes August. *M. aeneus* overwinters as an adult (Fritzsche, 1957) and the early appearance of adult *M. erythropus* in the spring suggests that this may also be the case with this species.

M. erythropus is the only member of the genus associated primarily with *L. corniculatus* (Easton, 1955), but more generalist species have also been recorded from this plant. *M. erichsoni* Brisout will develop on *Lotus* spp. if its regular host, *Hippocrepis comosa* L. is not available (Easton, 1955), and Perju (1974) has also recorded *M. aeneus* from *L. corniculatus*. On rare occasions the larvae of an unindentified second species of *Meligethes* were collected in *L. corniculatus* flowers (Spurn Point, 23.6.77 and Cob Hill, E. Yorks., 7.7.81). These larvae were darker, with conspicuously long thoracic and abdominal setae, and do not fit the description of *M. aeneus* (Scherney, 1953).

The potential damage caused by *Meligethes* species has received particular attention with *M. aeneus*, which can occur in large numbers on the flowers of

Rape and other Crucifers. Fritzsche (1957) found that adults caused considerable damage to the flower buds, but that larval feeding was unimportant, whereas Williams and Free (1978) concluded that no economic damage was caused by the activities of either adults or larvae. Kelm (1976) even considered that *M. picipes* Sturm was beneficial to *Vicia faba*, because it improved pollination.

It is unlikely that *M. erythropus* larvae were detrimental to *L. corniculatus* because a maximum of two larvae were present in any one flower and Williams and Free (1978) found that densities of even ten *Meligethes* larvae per flower did not cause noticeable damage to Rape. A parasite of *M. erythropus* was only observed once, when an endoparasitic Hymenoptera larva emerged from a host larva collected at Eppleworth Quarry on 23.6.78. Unfortunately it died shortly after and could not be identified.

Walsh and Dibb (1975) record *Bruchus loti* as being associated with *L. corniculatus* and this was confirmed when adults of this species were found feeding on the pollen in *L. corniculatus* flowers (Bulkington 26.6.77, 20.5.78 and Hessle Quarry 18.7.78). A search at Bulkington showed that *B. loti* was also feeding in the flowers of *Ulex europaeus* L. and *Trifolium* spp. *B. loti* larvae do not develop on *L. corniculatus* and although other Bruchids have been associated with *Lotus* species (*Acanthoscelides aureolus* and *A. fraterculus*, in Johnson, 1970 and see Southgate, 1979) there are few records of any British members of this family breeding on *L. corniculatus*.

The major host plant of *B. loti* appears to be *Lathyrus pratensis* L. (for example records in de Luca, 1965, and Graham, 1969) and visits to Bulkington and Hessle Quarry revealed as many as 89 *B. loti* eggs on one vetchling pod. The eggs were mainly concentrated around the edges of the pod valves, with some scattered across the face. Larvae tunnelled through the bottom of the egg and through the pod wall before entering a seed. A single adult only emerged from each seed, in August or September. An overwintering adult was found sheltering in an old *Biorrhiza pallida* (Olivier) gall collected at Bulkington on 4 March 1978.

Aphids were generally scarce on *L. corniculatus* (see also Jones, 1966) and only an occasional green nymph appeared in the flower samples at Eppleworth and elsewhere. The largest numbers were recorded in a 5 July 1978 collection at a roadside north of Cottingham, where 46 nymphs were collected from fewer than 300 flowers and one flower-contained five nymphs. During June and July 1980 two species of Aphid were found on the *L. corniculatus* grown at the University Botanic Gardens, Cottingham, and these reached very high densities, with several plants supporting hundreds of individuals. A larger, green species, *Acyrthosiphon loti*, was found mainly on the flowers, while the black *Aphis* (*Pergandeida*) *loti* developed on the young shoots and immature seed pods. Both Aphids are virtually specific to *Lotus* species (R.L. Blackman, Pers. Comm.). The colonies of both were almost eliminated when Syrphid larvae appeared on the plants.

Contarinia loti is a cecidomyiid gall midge that develops inside the flowers of *L. corniculatus* and produces a distinctive bright red gall. The stamens and developing pod become distorted and swollen, with seed and pollen production usually prevented. *C. loti* is also frequently recorded as producing galls in the buds and young leaves of *L. corniculatus*, and to form similar bud and flower galls on several species of *Vicia* (Buhr, 1965 and Neacsu, 1980). Problems arise with the identification of bud galling Cecidomyiids on *L. corniculatus* because *Contarinia barbichei* and *Dasyneura loti* form similar galls (Barnes, 1946), and no morphological characters are available for the separation of most *Contarinia* species (K. Harris, Pers. Comm.).

The identity of the species responsible for '*C. loti*' galls on *Vicia* spp. is also a problem, because similar galls are known to be caused by related species (Barnes, 1946). Galling most commonly involves the flowers of *L. corniculatus*, but a different preference is shown on *Vicia*, where galling of the buds is more frequent (Darlington, 1968 and Pers. Obs.). Stelter (1958) has shown that *C. loti* and *C. craccae* Kieffer are distinct species, but whether the latter is responsible from all the *Vicia* records remains to be established.

A number of galled *L. corniculatus* flowers were collected at Eppleworth Quarry during July and August 1977 and between June and September, 1978. The galls were kept inside petri dishes and any larvae that emerged were placed in sand filled tubes. *C. loti* larvae were found to be yellowish white in colour and, after strongly arching their bodies, were capable of jumping several centimetres. The larvae burrowed eagerly into the sand, and formed cocoons around themselves. No adults were reared the first season however, as the larvae all failed to survive the winter. Efforts in 1978 were more successful and a 12 July gall collection produced a total of nine *Contarinia* adults less than one month later. They emerged between 17 and 22 days after entering the sand, thereby confirming Stelter's (1958) observation that this species can be bivoltine.

A collection of galled flowers at Leirdal, S.W. Norway, on 4 August contained 80 galled flowers on 36 umbels, and a total of 251 larvae. This represented an average of 4.6 *C. loti* larvae per gall, and the maximum was 17. At Eppleworth an average of only 1.7 galled flowers per umbel was recorded, and the maximum number of larvae in one gall was only six.

The galled flowers at Leirdal were found to be particularly favoured by *Odontothrips loti*, with up to 14 larvae present in one gall. *Cydia compositella* larvae were also recorded from galled flowers, at Eppleworth (15.8.78) and Bulkington (21.8.77), but *Apion loti* was consistantly absent.

No parasites were reared from any flowers galled by *C. loti* in England, but there were three species in the 4 August collection at Leirdal. Single Ichneumonoid larvae were found browsing on apparently paralysed *Contarinia* larvae in six of the galls, but unfortunately none were successfully reared. A hairy ectoparasitic Chalcidoid larva was also present, but again this failed to reach maturity. This larva resembled that of *Torymus* (*Lioterphus*) *nitidulus* (Walker) which Hodges (1969) reared from *Oligotrophus betulae* (Winnertz), another Cecidomyiid, and may have been the very closely related *T. fuscicornis* (Walker) as an adult of that species was collected in an *L. corniculatus* flower at Leirdal, just eleven days earlier.

During September and October 1979 adults of Gastrancistrus glabellus (Nees), (four females, three males), emerged from the sand filled tubes provided for the C. loti larvae. The biology of this parasite appears similar to that of Gastrancistrus hamillus Walker, which Askew and Ruse (1974) reared from the Cecidomyiid Massalongia betulifolia Harris. They are both endoparasites and their hosts were active and apparently healthy before they entered the ground, which suggests that most of the parasites development is delayed until later. The known flight period of G. glabellus extends from June to August (Graham, 1969 and table 3.27) suggesting that perhaps the emergence of the reared adults in September and October may have been premature, due to the larvae being maintained indoors. C. loti may prove to be one of the major host species for G. glabellus because L. corniculatus was growing at all the sites listed in table 3.27 and an additional female was found inside an L. corniculatus flower collected by D.A. Jones (Wolla Bank, S. Humberside, 7.7.81). No previous host records have been published (Boucek, 1977).

Leaf/bud galls on L. corniculatus were collected at Eppleworth Quarry between July and September, 1978. These are much less conspicuous than flower galls (which may partly explain their apparent scarcity) and consist of a group of fattened, distorted leaves that curl around and shelter the damaged growing point. Leaf galls were only found at high densities on one occasion (Spurn Point, June 1980), where a suspicious lack of any flower galls suggested that another Cecidomyiid, and not C.loti, may have been responsible.

No parasites were reared from leaf galls on L. corniculatus but a female Spintherus dubius (Nees) emerged from ?C. loti galls on a Vicia sp. (Eppleworth Quarry, July 1978) and a male Mesopolobus sp. emerged from similar Vicia galls collected at Bulkington the same month. S. dubius is a common parasite of Apion spp. in Trifolium flowers (Boucek, 1970) and this record of a Dipteron host appears to be atypical for this species.

Gijswijt (1976) recorded Omphale salicis Haliday as a parasite of C. loti

Table 3.27 Records of adult Gastrancistrus glabellus (Nees) collected by sweep netting.

Locality	Date(s)	Numbers
Eppleworth Quarry	5.7.78	1 Female
	13.8.78	2 Males
Norway, Faberg	22.7.79	2 Females, 1 Male
Norway, Gaupne	19.7.79	2 Females
Norway, Kaupanger	27.7.79	1 Female
Norway, Vigdal	11.8.79	1 Male

on Vicia. The galls were collected in July and adult parasites appeared in July of the following year. Evidence for a relationship between O. salicis and C. loti on L. corniculatus is provided by records of several specimens collected on this plant in the Jostedalen and one female found inside an L. corniculatus flower at Eppleworth Quarry on 31.8.77.

This chapter has described the biology of the insects that live and feed inside the flowers of L. corniculatus, with a particular emphasis being placed on the likely consequences of their feeding activities on the reproductive output of the plant. The response of insects to known variation in the plant has also been assessd, and it has been concluded that petal cyanogenesis can deter some generalist herbivores from feeding on the flowers of L. corniculatus. Keel colour phenotype does not appear to influence the colonisation of flowers by insects, and the significance of this polymorphism remains something of a mystery.

CHAPTER IV

THE INSECTS THAT FEED INSIDE THE SEED PODS OF L. CORNICULATUS

The insects which develop inside the seed pods of L. corniculatus form an essentially self-contained community of phytophages, parasites and decomposers. The relative simplicity of such phytophagous assemblages makes them ideal for studies of many of the basic concepts of community ecology, including competition and coexistence, predator-prey interactions and food web architecture. Sequential sampling of L. corniculatus pods at Eppleworth Quarry and elsewhere has provided basic information on the composition, trophic relationships and dynamics of this particular community. In this chapter the biology and interactions of the phytophagous insects are discussed and this if followed in chapter five by a description of the higher trophic levels in the community.

The Eppleworth Quarry collection dates and the numbers of pods obtained in the samples were given in tables 3.1 and 3.2. Approximately 3.5% of the 1977 pods and 10% of the 1978 pods had either dehisced or had become detached from their peduncles, and were found at the base of the plant or in the litter beneath (tables 4.1 and 4.2). The seed pods in these two categories have not been included in the analyses in this and the following chapter. The higher proportion of detached pods in 1978 probably reflects the more efficient sorting that was possible in that year because of the removal of all vegetation found in the quadrats.

The insects feeding in the seed pods of *L. corniculatus* were also investigated at 21 other localities in the U.K., Norway and Denmark, and seed samples from Austria, France, Holland and Hungary were also examined. A summary of the phytophagous species that were present is given in table 4.3. Several of the species recorded in the literature from *L. corniculatus* seed pods were not detected, including *Cydia succedana*, whose main host appears to be *Ulex* (Emmet, 1980). Only three species were routinely encountered in the collections, *Cydia compositella*, *Eurytoma platyptera* and *Apion loti*. All were widely distributed, and *Apion loti* was present at every native *L. corniculatus* population that was examined.

A fourth phytophagous species was encountered only rarely in *L. corniculatus* pods. At Eppleworth Quarry six unidentified Cecidomyiid larvae were found in separate pods on dates in August and September 1977 and in September 1978, and a further specimen was collected at Bulkington in August 1977. The larvae were rounded, but mobile, and had a deep red colouration. Three of the specimens successfully overwintered as larvae inside flimsy pupal chambers formed inside plant debris, but none produced adults.

The description of the larvae agrees with that of *Clinodiplosis leguminicola* Milne (Milne, 1960) which, together with over thirty other taxa, is now synonymised under *C. cilicrus* Kieffer (Skuhrava, 1973). This species is known from a wide variety of locations, including galls on *Betula* spp., cultivated pea pods and *Trifolium* flowers (Roskam, 1979), and related species have been described from pods of Sweet Pea (*Lathyrus odoratus* L.), *Ulex* sp. and *Sarothamnus scoparius* L. (Barnes, 1948 and Parnell, 1963).

Table 4.1 The condition of L. corniculatus seed pods collected during 1977 at Eppleworth Quarry. Sampling dates are given in table 3.1.

Sample	Dehisced and Detached	Externally Damaged	Unhealthy	Total
1.1	0	0	0	89
1.2	0	0	0	139
1.3	2	0	5	81
2.1	7	9	15	133
2.2	6	8	2	69
2.3	9	16	5	100
3.1	0	2	1	199
3.2	0	5	7	108
3.3	0	6	0	90
4.1	0	1	0	116
4.2	0	8	1	127
4.3	0	5	3	113
5.1	0	4	0	50
5.2	0	3	2	98
5.3	0	0	8	191
6.1	9	0	5	177
6.2	0	0	1	30
6.3	0	0	1	20
7.1	0	0	0	20
7.2	12	0	3	172
7.3	4	0	2	147
8.1	0	0	1	65
8.2	6	0	0	154
8.3	1	0	0	21
9.1	9	0	0	120
9.2	3	0	0	41
9.3	15	0	0	75
10.1	9	0	0	39
10.2	4	0	0	51
11.1	1	0	0	16
11.2	1	0	0	37
Totals	98	67	62	2888

Table 4.2 The condition of <u>L. corniculatus</u> seed pods collected during 1978 at Eppleworth Quarry. Sampling dates are given in table 3.2.

Sample	Dehisced and Detached	Externally Damaged	Unhealthy	Total
2.1	0	1	0	19
2.2	0	1	0	37
2.3	2	4	0	91
3.1	0	0	0	11
3.2	1	0	0	22
3.3	0	0	8	46
4.1	3	0	2	19
4.2	1	2	1	16
4.3	-	-	-	-
5.1	3	5	3	48
5.2	1	0	0	11
5.3	1	1	1	70
6.1	0	0	1	7
6.2	2	0	4	51
6.3	2	2	6	51
7.1	4	1	0	34
7.2	10	4	0	52
7.3	14	8	5	126
8.1	14	3	1	25
8.2	11	3	7	64
8.3	1	2	0	11
9.1	10	2	3	66
9.2	4	1	0	9
9.3	7	0	1	24
Totals	91	40	43	910

Table 4.3 Phytophagous Insects recorded from seed pods of L. corniculatus. Map references are provided in Chapter 2.

Locality	Cydia compositella	Eurytoma platyptera	Apion loti	?Clinodiplosis sp.
Aldbrough			+	
Bulkington	+	+	+	+
Burdale Qu.		+	+	
Cauldon Lowe	+	+	+	
Chapel Farm		+	+	
Church Bay		+	+	
Cottingham	+		+	
Cottingham Gdns.		+		
Crowle Moor		+	+	
Eppleworth Qu.	+	+	+	+
Hutton Cranswick			+	
Newbury		+	+	
Porthdafarch	+	+	+	
Porthmelgan			+	
Spurn Point	+	+	+	
Wawensmoor		+	+	
Wharram Qu.	+	+	+	
Wolvey		+	+	
Denmark, Sundstrup		+	+	
Norway, Fossen		+	+	
Norway, Gaupne		+	+	
Norway, Oslo		+	+	
Austria, Lind		+		
France, Col de la Forclaz		+	+	
France, Sal de Bisanne		+	+	
Holland, Callantsoog		+		
Hungary, Budapest		+		

The larvae found on L. corniculatus were present in old mature pods, some of which were unhealthy and had an inner lining of mycelia. It appears likely that the larvae were feeding on the decaying pod walls and any associated mould because there was no evidence of any harm being caused to any other insects and the hard mature seeds that were present would represent an unlikely food source. C. sarothamni Kieffer is believed to have similar feeding habits inside the seed pods of Broom (Parnell, 1963).

Galls caused by a second species of Cecidomyiid were observed on only one occasion, at the University Botanic Gardens, Cottingham, on 6 August 1982. The bases of two of the four seed pods on an L. corniculatus umbel were grossly swollen to about twice their usual diameter, while the remaining sections of the pods were rather narrower than normal, indicating that gall formation has impeded the development of the pods as a whole.

Examination of one of the galls showed that it was unilocular and contained a single Cecidomyiid larva. The larva was larger, and more rounded, than the larvae of Contarinia loti, and was bright orange in colour.

A. melanopus is the only gall midge that Barnes (1946) recorded from the seed pods of L. corniculatus. The galls of this species are described as 'pea-shaped swellings' on the pods, a description which could be applied to the galls collected at Cottingham, but would be rather inappropriate. The larvae of A. melanopus are described as yellow, not orange, and this also suggests that two different species may be involved.

A search of the many other L. corniculatus pods at the Botanic Gardens failed to produce any further examples of galls other than those of C. loti. L. corniculatus pod-galls are clearly very uncommon, at least in Northern England, and perhaps they are caused by an oligophagous species that only occasionally utilises L. corniculatus as a host plant.

Cydia compositella

Cydia compositella is regarded as mainly a Trifolium feeding species in the U.K., but elsewhere in Europe this species has been recorded from Medicago sativa and L. corniculatus (Bradley et al, 1979, Graaf Bentinck and Diakanoff, 1968, Perju, 1974). When feeding on Trifolium, C. compositella has two generations each year, with larvae of the first generation developing inside the stems, and those of the second in spun terminal leaves or flowerheads (Emmet, 1980).

At Eppleworth Quarry, larvae of C. compositella were found in L. corniculatus flowers and seed pods from July through until September (tables 3.12 and 4.4). The larvae of both generations fed on the reproductive organs, and no stem boring was observed. The stamens, petals and young pod were damaged by larvae feeding in the flowers. Young larvae entered more mature pods through a small hole, which was often chewed at the base of the pod, from beneath the cover provided by the surrounding calyx. Once inside, feeding commenced on the young green seeds and their surrounding pith, and the whole pod was eventually hollowed out in many cases. Damaged pods contained a conglomerate of seed remnants, silk and frass, which often spilled out through the entrance hole. This was widened as the larva increased in size, and if the hole was situated at the basal end of the pod, it was continued directly through the calyx. Normally only a single larva developed inside each pod, and on the only occasion when two were present (at Bulkington in 1976) this involved immature specimens that were feeding at opposite ends of the pod. It appears that many larvae feed in more than one pod during their development, as damaged pods considerably outnumbered the larvae that were collected. Similar movement from pod to pod has been seen when C. succedana feeds on Ulex (Bradley et al, 1979).

No eggs were found on either the pods or flowers of L. corniculatus, which suggests that C. compositella oviposits on the leaves as it is known to do when feeding on Trifolium (Emmet, 1980). Young C. compositella larvae have a dull yellowish colour, but during maturation they

Table 4.4 Cydia compositella in seed pods of L. corniculatus at Eppleworth Quarry.

a 1977

Sampling Date	Cydia compositella larvae Healthy	Dead	Parasitised	Damaged	Seed Pods Total No.	% Damaged
19 July	3	0	0	3	307	1.0
26 July	3	0	0	14	280	5.0
31 July	9	0	0	19	397	4.8
10 August	12	0	0	25	356	7.0
14 August	2	1	0	14	339	4.1
26 August	7	1	3	26	218	11.9
31 August	8	1	3	29	323	9.0
6 September	0	0	3	7	233	3.0
11 September	1	0	0	9	209	4.3
9 October	0	0	0	3	77	3.9
27 October	0	0	0	0	51	0
1977 Totals	45	3	9	149	2790	5.3

b 1978

Sampling Date	Healthy	Dead	Parasitised	Damaged	Seed Pods Total No.	% Damaged
12 July	0	0	0	0	145	0
27 July	0	0	0	0	78	0
15 August	1	0	1	3	31	9.7
23 August	2	0	0	4	124	3.2
30 August	0	0	1	2	105	1.9
5 September	0	0	0	2	184	1.1
12 September	0	1	0	2	76	2.6
18 September	0	0	0	1	78	1.3
1978 Totals	3	1	2	14	821	1.7

become a deep red. This (presumably) warning colouration may help to provide protection during the vulnerable period when the larvae leave the pods and descend into the ground litter to pupate. Overwintering larvae lose this bright colouration and during diapause return to a dull yellow.

Larvae feeding on *L. corniculatus* in June and July quickly pupated after forming their cocoons and produced adults in July and August. This species flies during the day and adults were collected on *L. corniculatus* at Flamborough (3.7.78) and Eppleworth (26.7.77, 31.7.77 and 10.8.77). Larvae of the second generation continued to develop inside *L. corniculatus* pods until September. They overwintered inside their cocoons and, after pupation, produced adults the following June. One larva was atypical because after being collected from a *Trifolium pratense* flower head in July it produced an adult on 10 September of the same year. Presumably this was an individual of a second brood which responded to laboratory conditions by failing to enter diapause.

C. compositella is considered to be more common in the south of England than the north (Bradley *et al*, 1979). The rearing results from *L. corniculatus* also suggest that this species has a southerly preferance, as *C. compositella* was apparently absent from the Jostedal Valley in Norway, but was abundant in the Midlands of England, where at Bulkington up to 25% of the seed pods showed signs of damage during the exceptionally warm and sunny summer of 1976 (table 4.5).

Eurytoma platyptera

The phytophagous Eurytomid feeding in the seeds of *L. corniculatus* has been known by a variety of names since its original discovery. For many years the 'seed chalcids' developing in a variety of legume species were all called *Bruchophagus gibbus*, but in 1950 Kolobova recognised that the forms on *Medicago*, *Trifolium* and *Lotus* were three separate species, and in 1956 Fedoseeva described the new species from *L. corniculatus* as *B. kolobovae*. This separation was confirmed by Perju (1960) and Strong (1962) and finally Graham (1970)

Table 4.5 *Cydia compositella* in seed pods of *L. corniculatus* at Bulkington in 1975 and 1976.

a 1975

Sampling Date	*C. compositella* larvae	Parasite larvae		Seed Pods	
			Damaged	Total	% Damaged
15 July	4	0	4	41	9.8
22 July	2	0	3	18	16.7
30 July	1	0	1	18	5.5
6 August	0	0	0	28	0
13 August	1	0	2	38	5.3
19 August	1	1	3	39	7.7
25 August	2	1	7	45	15.6
31 August	1	0	1	31	3.2
11 September	1	0	2	42	4.8
17 September	0	1	5	58	8.6
23 September	3	0	13	60	21.7
3 October	0	0	1	65	1.5
1975 Totals	16	3	42	483	8.7

b 1976

9 July	3	0	4	55	7.3
17 July	2	0	3	57	5.3
2 August	4	2	14	125	11.2
8 August	3	3	28	145	19.3
16 August	3	2	23	161	14.3
24 August	0	4	24	113	21.2
30 August	0	1	14	56	25.0
1976 Totals	15	12	110	712	15.4

synonymised *B. kolobovae* with the older name of *B. platypterus*. Meanwhile, *Bruchophagus* is now considered as a sub-genus of *Eurytoma* (Boucek, 1954 and Fitton *et al*, 1978) and hence the current name of this species is *Eurytoma platyptera*.

E. platyptera is widely distributed in England (table 4.3) but was rarely found at high densities. At Eppleworth it was found in *L. corniculatus* seeds throughout the 1977 sampling period (table 4.6) but was almost absent in 1978, when only one larva was collected.

Mayr (1878) considered that *E. platyptera* was a parasite of *Apion loti*, but Crevecoeur (1946) established that it was phytophagous, with each larva developing inside a single *L. corniculatus* seed. Tests of host plant acceptability carried out by Neunzig and Gyrisco (1958) and Batiste (1967) have shown that *L. corniculatus* and *L. uliginosus* are acceptable host plants, with seeds of other *Lotus* species being less readily selected. Batiste (1967) also reported a second, undescribed, species of *Bruchophagus* which develops inside the seeds of the North American *L. purshianus* Benth. and Johnson (1970) has recorded *Bruchophagus* spp. from a wide range of legume species, including *L. crassifolius* Benth. and *L. purshianus*. Collections of *L. uliginosus* seeds from Porthmelgan and the Derwent Valley of North Yorkshire have failed to confirm that this plant is utilised by natural populations of *E. platyptera*.

Species closely related to *E. platyptera* are important pests of *Trifolium* and *Medicago* in the U.S.A. E. *platyptera* has therefore been studied intensively because of worries that it might pose similar problems for growers of *L. corniculatus*. Batiste (1967) showed that in the U.S.A. (where *E. platyptera* was probably introduced with seed of *L. corniculatus*) there are three or four annual generations, with larvae as the overwintering stage. In England, *E. platyptera* appears to be normally bivoltine, as larvae feeding in July and early August were found to produce adults within two or three weeks, whereas larvae collected any later did not pupate until the following spring.

Table 4.6 *Eurytoma platyptera* in seed pods of *L. corniculatus* at Eppleworth Quarry (1977).

Sample	*E. platyptera* larvae	Seed Pods collected	No. of suitable seeds	% of seeds damaged
1.1	0	89	497	0
1.2	2	139	591	0.0034
1.3	0	79	287	0
2.1	0	126	314	0
2.2	0	63	265	0
2.3	0	91	384	0
3.1	0	199	1159	0
3.2	0	108	297	0
3.3	0	90	146	0
4.1	10	116	388	0
4.2	4	127	308	0.0130
4.3	0	113	324	0
5.1	10	50	172	0.0581
5.2	1	98	157	0.0064
5.3	1	191	443	0.0023
6.1	15	168	375	0.0400
6.2	1	30	28	0.0357
6.3	0	20	35	0
7.1	12	20	105	0.1143
7.2	2	160	617	0.0032
7.3	8	143	501	0.0160
8.1	1	65	277	0.0036
8.2	0	148	675	0
8.3	0	20	85	0
9.1	21	111	359	0.0585
9.2	0	38	114	0
9.3	0	60	351	0
10.1	7	30	119	0.0588
10.2	9	47	177	0.0508
11.1	0	15	49	0
11.2	2	36	99	0.0202
Totals	106	2790	9698	0.0109

Larvae overwintered in the laboratory were found to emerge as early as March, but those kept outdoors did not produce adults until July.

Ovipositing females drill holes through the walls of the seed pod and the seed, laying a single egg on the surface of a cotyledon, immediately beneath the testa. Using artificially pollinated flowers, Batiste established that seeds ten to twelve days after pollination were at the stage preferred for oviposition. This is several days after the first A. loti and C. compositella begin feeding. The larva passes through five instars (Batiste, 1967) and usually consumes the entire contents of the seed. Mature seeds that contain E. platyptera larvae can usually be distinguished from healthy seeds by their slightly larger size, reduced levels of dark spotting and softer walls. Seeds containing overwintering larvae also typically develop a thin layer of surface mould.

Adults emerge by chewing an exit hole through the testa and, if necessary, through the walls of the seed pod. 201 adults of the overwintering generation were reared (table 4.7), with females forming 65.7% of the total. Batiste recorded a similar excess of females, but attributed this to increased male mortality under artificially dry rearing conditions. The succeptibility of E. platyptera to dehydration proved to be a problem with the Eppleworth samples, because it was necessary to open the seeds in order to record their contents and larvae exposed in this way suffered high mortality rates. It appears unlikely that males suffer disproportionatly, however, as subsequent dissection of the seeds collected at other sites showed that deaths were infrequent and could not account for the higher proportion of females that were reared.

Adult females of E. platyptera were collected on L. corniculatus during June (Wharram Quarry, 10.6.80), July (Spurn Point, 22.7.80) and August (Scunthorpe, 30.8.79). Records of male E. platyptera collected by sweeping have not been included because they are more difficult to distinguish from

Table 4.7 Reared adults of the overwintering generation of <u>Eurytoma platyptera</u>

Source	Dates	Males	Females	% Female
Eppleworth Quarry	1977-8	15	23	60.5
Bulkington	1977-8	14	8	36.4
Wolvey	1977-8	21	66	75.9
Cottingham Gardens	1977-8	19	35	64.8
Totals		69	132	65.7

those of closely related species.

Apion loti

Apion loti was the most numerous inhabitant of L. corniculatus seed pods in all the natural populations that were examined. Other species of Apion have also been described as associated with L. corniculatus (A. ebininum Kirby by Joy, 1932 and A. subulatum Kirby by Scherf, 1964), but these probably represent misidentifications or, at most, atypical host records. Weevils of the genera Miccotrogus and Tychius have also been reared from seed pods of L. corniculatus (Perju, 1974, and quoted by Morris, 1967) but none were found during this study.

The species of Apion are strongly host specific and Dieckmann (1973, 1977) has established that the records of A. loti developing on L. uliginosus refer to a second, closely related species, A. sicardi Desbrochers. Morris (1975) showed that A. sicardi was present in the south of England and tabulated its differences from A. loti. Examination of L. uliginosus flowers and seed pods from Windmill Hill and the Derwent Valley failed to detect this species, but a survey of L. uliginosus populations in S. Wales, carried out at my request, showed that A. sicardi is widespread in South Wales (Key, 1981). A third member of this species group, A. fallens Desbrochers, is a southern European species which has not been recorded from the U.K. It is a halophytic species, and L. tenuis (which in Britain has a mainly coastal distribution) has been suggested as a possible host plant (Dieckmann, 1977). There are also records of A. loti developing on L. tenuis (Scherf, 1964), although this has not been confirmed in the U.K. (Morris, 1975), and on Tetragonolobus maritimus L. (Scherf, 1964).

Overwintering A. loti adults have been collected in turf samples from ungrazed Down grassland (Freeman, 1965). They appear on L. corniculatus during May (Eppleworth Quarry 9.5.78, 17.5.78 and 30.5.78, Bulkington 29.5.77, and Wharram Quarry 12.5.80), often well before the first flowers are produced.

Two females that were collected on 9 May were found to be sexually immature and to have been recently feeding on chlorophyllous tissues. Feeding by adults occurred on the stems and peduncles of *L. corniculatus* and consisted of boring short holes into these tissues or, in confinement, chewing at the broken ends of peduncles.

Mating pairs were first observed on *L. corniculatus* during late May and oviposition commenced as soon as flowers appeared. Females bore a hole with their mandibles through the calyx and petals and into the immature seed pod. A single egg is then laid at the bottom of the hole. Because of the small size of the pod at this stage, the eggs are often partly or wholly exposed at the pod surface and eggs are also sometimes mistakenly placed between the petals or amongst the stamens. The tissue at the base of the pod, connecting it to the peduncle, is also a common oviposition site during the flower stage. Eggs laid in these 'accidental' locations presumably hatch successfully, but they never produced mature larvae. Brown oviposition scars are produced on the surface of the sepals and because the petals are often still expanding, neat oval holes are sometimes visible on the petals, reflecting their earlier position behind the sepals at the time when oviposition took place.

Oviposition continues after the petals have fallen, but ceases when the seeds begin to harden. Eggs in maturing pods are generally laid from the dorsal surface, again producing an oval brown scar. These often considerably outnumbered the *A. loti* present in the pods, suggesting either a large degree of selectivity by ovipositing females or the extensive use of pod tissues for adult feeding. Ovipositing females stand parallel to the long axis of the pod, gnawing a hole through the pod wall. The rostrum is then pushed deep into the pod and the head is moved from side to side, presumably widening the hole and perhaps also investigating the pod's interior. The antennae are drawn backwards along the sides of the rostrum during this period. This takes eight to ten minutes and is followed by the female quickly removing her rostrum, turning through 180° and laying her egg. The surface of the hole is generally sealed with a drop of clear liquid, in a manner similar to that described by Noe - Nygaard in *A. striatum* Kirby (1978). Eggs were usually found in the pith between the seeds, but some were laid on the surface of seeds. Eggs were also sometimes positioned partially or wholly in the pod walls and these usually caused slight galling of the wall tissue, as described by Buhr (1965). Whether this harmed the eggs is unclear, but Van Emden and Way (1973) have shown that about half of the eggs laid by *Phytomyza rufipes* Mg. in *Brassica napus* L. were suffocated by the growth of similar 'callus' tissue.

The eggs are initially pale yellow, but darken to a yellow brown, with the larval head capsule becoming visible prior to emergence. Measurements of eight *A. loti* eggs collected at Bulkington gave an average length of 322 µm and width of 246, values slightly smaller than those obtained by Williams (1966). At Eppleworth, both eggs and young larvae were found in even the most immature flowers and by the end of the flowering stage a majority of the eggs had already hatched (table 4.8). Densities of eggs and larvae were consistantly higher in pods than flowers (table 4.9) reflecting the additional space available as the pods expand and the long period that pods remain suitable for oviposition.

In flowers, the young larvae commence feeding on the seeds/ovules, but in more mature pods the area of pith surrounding the larva is usually consumed first, before any seeds are damaged. Larvae normally feed by enlarging the cavity in which they are developing. Feeding from inside a seed was only observed when small larvae had failed to complete their development before the seeds had hardened. These larvae were unable to penetrate the seed walls and were forced to restrict themselves to the relatively softer cotyledons of seeds that they had already penetrated.

Van Emden (1938) has provided a key for the identification of many *Apion* larvae, including *A. loti*. *Apion* larvae have three larval instars (Williams

Table 4.8 The numbers of Apion loti eggs and larvae in L. corniculatus flowers at different stages of development. Eppleworth Quarry, 1977 and 1978.

Year	Anther Condition	Total Flowers	A. loti Eggs	A. loti larvae	A. loti total	Mean Apion per flower
	Closed	9	1	1	2	0.22
1977	Open	47	4	4	8	0.17
	Empty	55	1	13	14	0.25
	Closed	85	7	2	9	0.11
1978	Open	255	43	47	90	0.35
	Empty	67	8	13	21	0.31

Table 4.9 The proportion of <u>Apion loti</u> eggs and larvae in flowers and seed pods of <u>L. corniculatus</u>. Eppleworth Quarry, 1977 and 1978. Only apparently healthy eggs/larvae are included.

Sample	No. of flowers	No. of pods	% as flowers	% <u>A. loti</u> eggs in flowers	% <u>A. loti</u> larvae in flowers
a 1977					
1.1	13	89	12.7	2.5	7.4
1.2	35	139	20.1	18.2	2.5
1.3	19	79	19.4	3.8	5.8
2.1	12	126	8.7	0	0.9
2.2	11	63	14.9	0	12.8
2.3	2	91	2.2	0	1.6
3.1	9	199	4.3	0	1.1
3.2	0	108	0	0	0
3.3	17	90	15.9	6.2	0
Totals	118	984	10.7	4.1	2.6
b 1978					
2.1	14	19	42.4	0	0
2.2	39	37	51.3	0	12.5
2.3	46	89	34.1	8.0	41.9
3.1	1	11	8.3	0	0
3.2	28	21	57.1	25.0	8.3
3.3	30	46	39.5	0	0
Totals	425	223	65.6	59.8	48.1

1968, Parnell 1962) and mature larvae enter a short pre-pupal phase prior to pupation. At Eppleworth Quarry the first pupae were present during late July in 1977 and mid August in 1978 (tables 4.10 and 4.11 and figures 4.1 and 4.2). Pupal cells similar to those of A. fuscirostre (Fabr.) and A. ulicis (Forster) in the pods of broom and gorse (Parnell, 1962) are not produced.

Adults emerge by chewing exit holes through the pod walls. Williams (1966) concluded that it was not possible to estimate reliably the numbers of adult A. loti that are produced because several adults can emerge from one exit hole and because the exit holes produced by parasites are indistinguishable. It appears, however, that each A. loti adult normally produces its own exit hole, immediately above its pupation site, and up to eight holes were recorded from one pod. Careful searching for ectoparasite exuviae was sufficient to eliminate the second complication and it has therefore been assumed that each exit hole represents the emergence of one adult A. loti.

At Eppleworth Quarry the first adult A. loti emerged in mid-August and they continued to appear for another month after this (figures 4.1 and 4.2). There was little overlap between recently emerged adults and egg production, suggesting that only one generation was produced each year. Oviposition at Eppleworth was roughly concurrent with the flowering period of L. corniculatus and hence with the production of suitable immature seed pods (figures 4.3 and 4.4). In Yorkshire, during 1980, there was an early spring followed by a generally cold and wet summer. At Wharram Quarry this resulted in an unusually long flowering season for L. corniculatus that extended from May until September (table 4.12 and figure 4.5) and provided many suitable pods for any second A. loti generation in the late summer. Pod production was poor during the first flowering peak in July, but was more successful in August. Oviposition by A. loti continued throughout the flowering period, but again showed a gradual decline after a spring peak, with no indication of a second generation being produced.

Table 4.10 Apion loti in the flowers and seed pods of L. corniculatus, Eppleworth Quarry, 1977. Apparently healthy individuals only (larvae containing endoparasites are included).

Sample	Eggs	Larvae	Pupae	Adults	Exit Holes	Total
1.1	40	27				67
1.2	11	80				91
1.3	26	69				95
2.1	6	106	1			113
2.2	5	47				52
2.3	6	63				69
3.1	4	94	1			99
3.2	7	114				121
3.3	16	66	1			83
4.1		98	11			109
4.2	1	88	2			91
4.3	4	128	9			141
5.1		18	2			20
5.2		75	14		1	90
5.3		106	21	3		130
6.1	1	45	18	5	10	79
6.2	1	16	4	2	3	26
6.3		6	2		3	11
7.1	1	20			3	24
7.2	3	46	39	4	18	110
7.3	1	42	19	10	27	99
8.1		3	10	1	5	19
8.2		2	15	10	26	53
8.3			3	1	8	12
9.1			2	14	32	48
9.2				3	20	23
9.3			2	10	19	31
10.1					20	20
10.2				2	13	15
11.1					7	7
11.2					22	22
Totals	133	1359	176	65	237	1970

Table 4.11 Apion loti in the flowers and seed pods of L. corniculatus, Eppleworth Quarry, 1978. Only healthy individuals and larvae containing endoparasites are included.

Sample	Eggs	Larvae	Pupae	Adults	Exit Holes	Total
1.1	19	7				26
1.2	24	30				54
1.3	2	4				6
1.4	5	1				6
1.5	1	5				6
1.6	5	6				11
1.7		1				1
2.1	2	6				8
2.2	5	8				13
2.3	25	31				56
3.1	2	13				15
3.2	12	12				24
3.3		29				29
4.1	2	2				4
4.2		1		1	5	7
4.3						0
5.1		1	5		7	13
5.2		2			2	4
5.3		1	2			3
6.1			1		1	2
6.2		3	2			5
6.3		4	3	2	6	15
7.1			1	3	1	5
7.2				1	5	6
7.3		4	5		2	11
8.1			1			1
8.2					8	8
8.3					1	1
9.1					7	7
9.2						0
9.3			2	2	5	9
Totals	104	171	22	9	50	356

FIGURE 4.1

Densities of <u>Apion loti</u> in flowers and pods of <u>L. corniculatus</u> at Eppleworth Quarry, 1977.

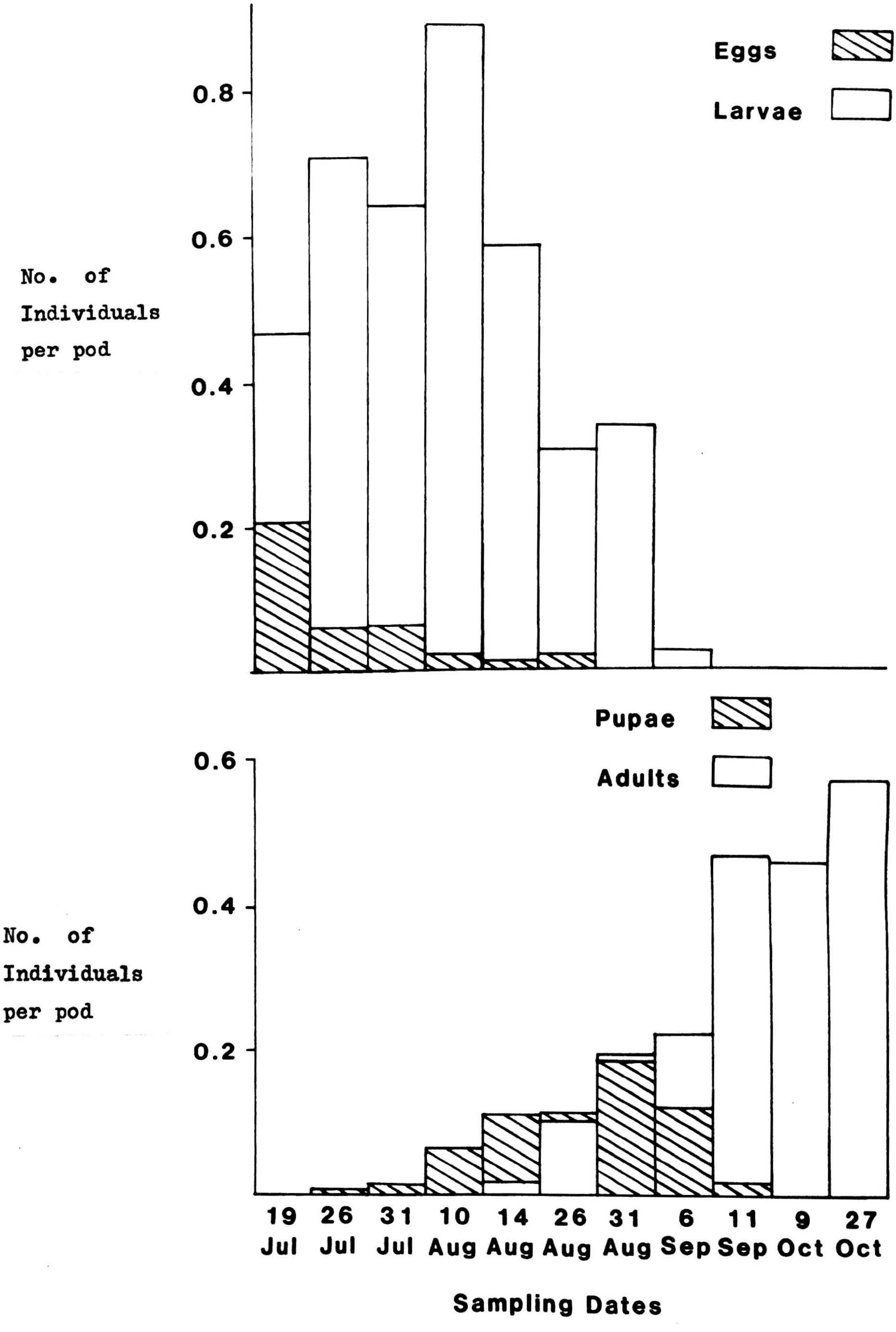

Eggs ▨
Larvae ☐
0.8
0.6
0.4
0.2
No. of Individuals per pod
Pupae ▨
Adults ☐
0.6
0.4
0.2
No. of Individuals per pod
19 Jul
26 Jul
31 Jul
10 Aug
14 Aug
26 Aug
31 Aug
6 Sep
11 Sep
9 Oct
27 Oct
Sampling Dates

FIGURE 4.2

Densities of Apion loti in flowers and pods of L. corniculatus at Eppleworth Quarry, 1978.

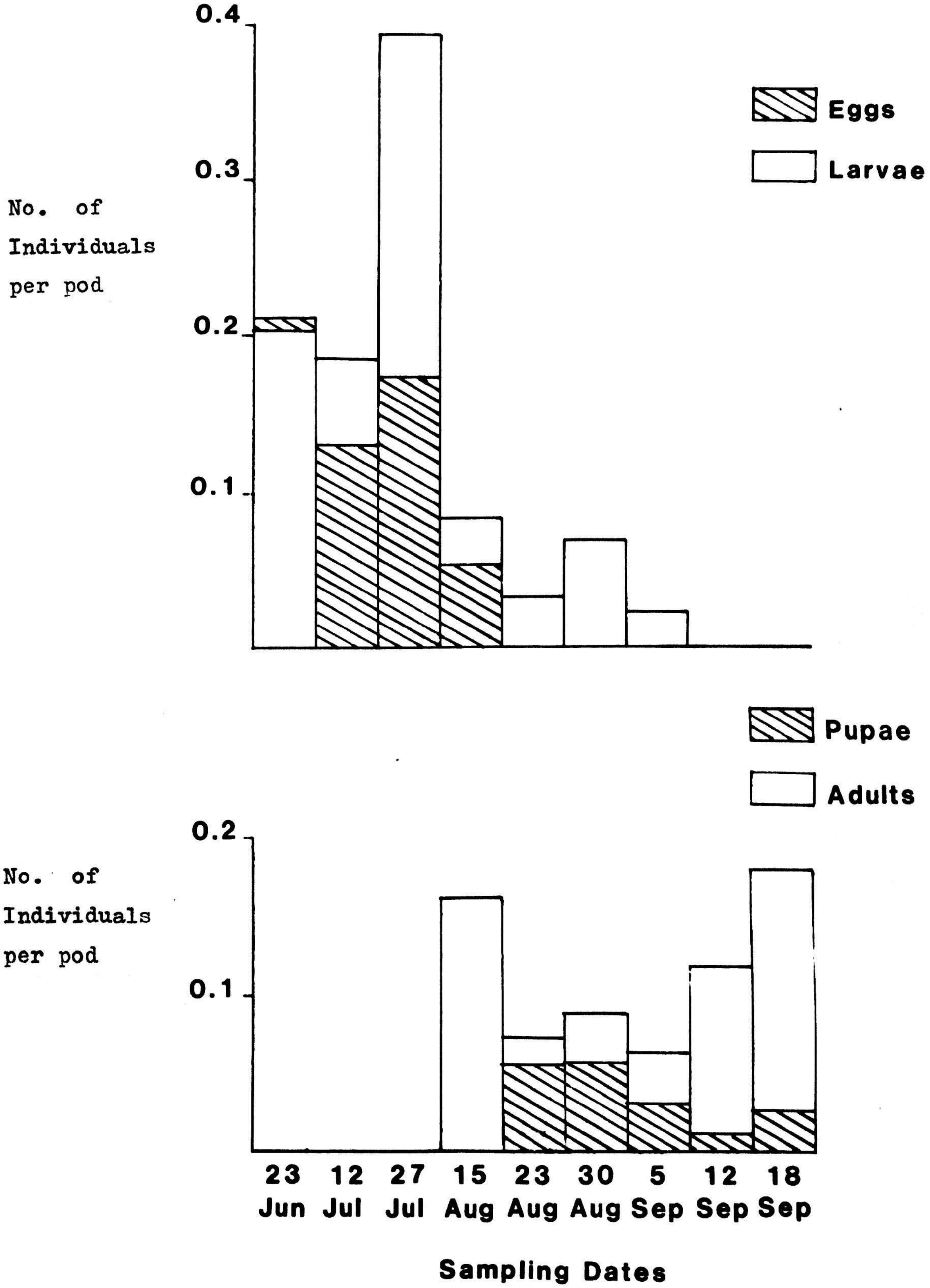

0.4
0.3
0.2
0.1
No. of Individuals per pod
Eggs
Larvae
Pupae
Adults
0.2
0.1
No. of Individuals per pod
23 Jun
12 Jul
27 Jul
15 Aug
23 Aug
30 Aug
5 Sep
12 Sep
18 Sep
Sampling Dates

FIGURE 4.3

L. corniculatus flower and seed pod production and the numbers of *Apion loti* eggs and larvae that they contained. Eppleworth Quarry, 1977. Weeks 10 and 11 are based on just two quadrat samples and only apparently healthy *A. loti* are included throughout.

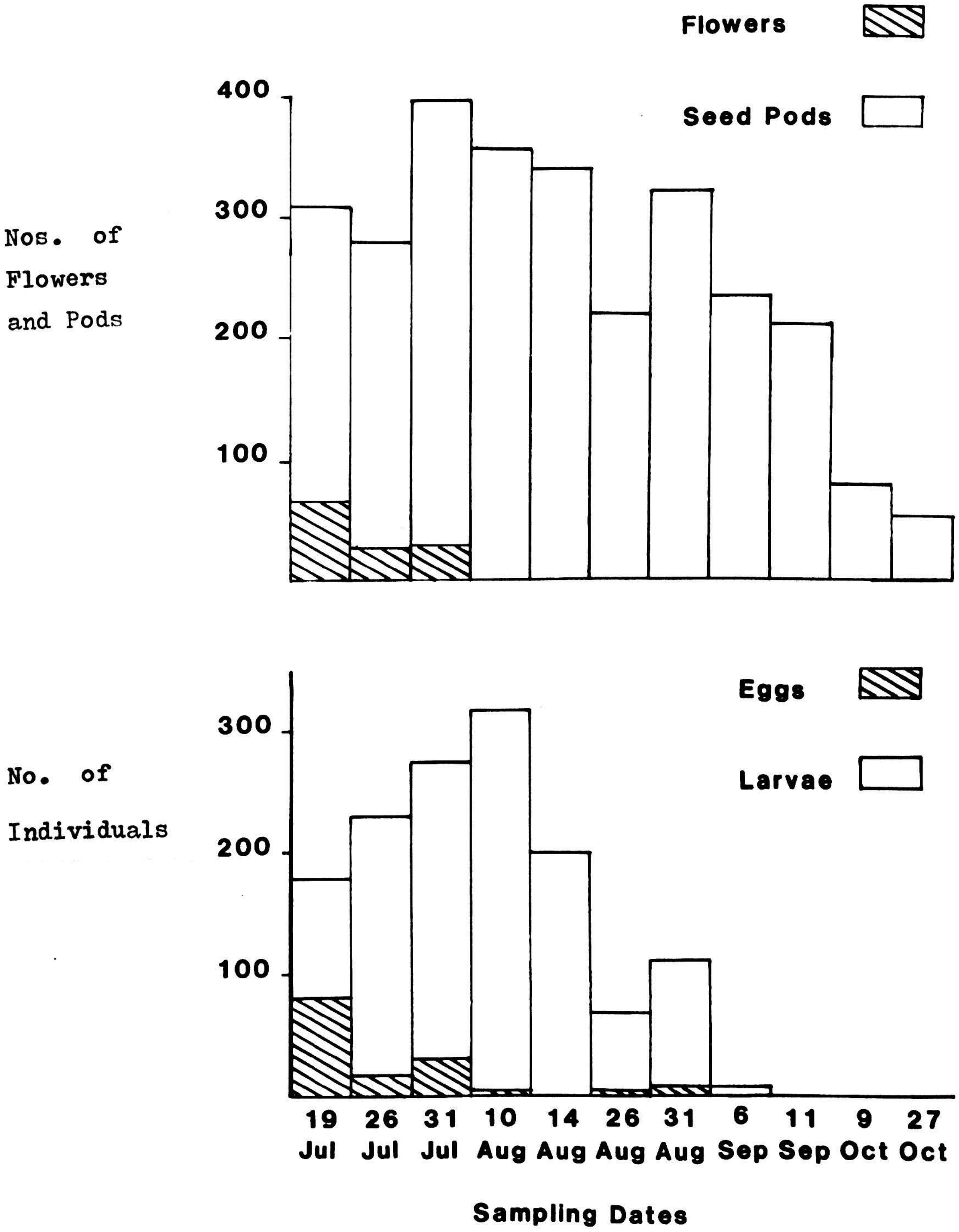

Flowers ▨
Seed Pods ☐
Nos. of Flowers and Pods
400
300
200
100
Eggs ▨
Larvae ☐
No. of Individuals
300
200
100
19 Jul
26 Jul
31 Jul
10 Aug
14 Aug
26 Aug
31 Aug
6 Sep
11 Sep
9 Oct
27 Oct
Sampling Dates

FIGURE 4.4

L. corniculatus flower and seed pod production and the numbers of Apion loti eggs and larvae that they contained. Eppleworth Quarry, 1978. Week 1 includes seven quadrat samples. Only apparently healthy A. loti are included.

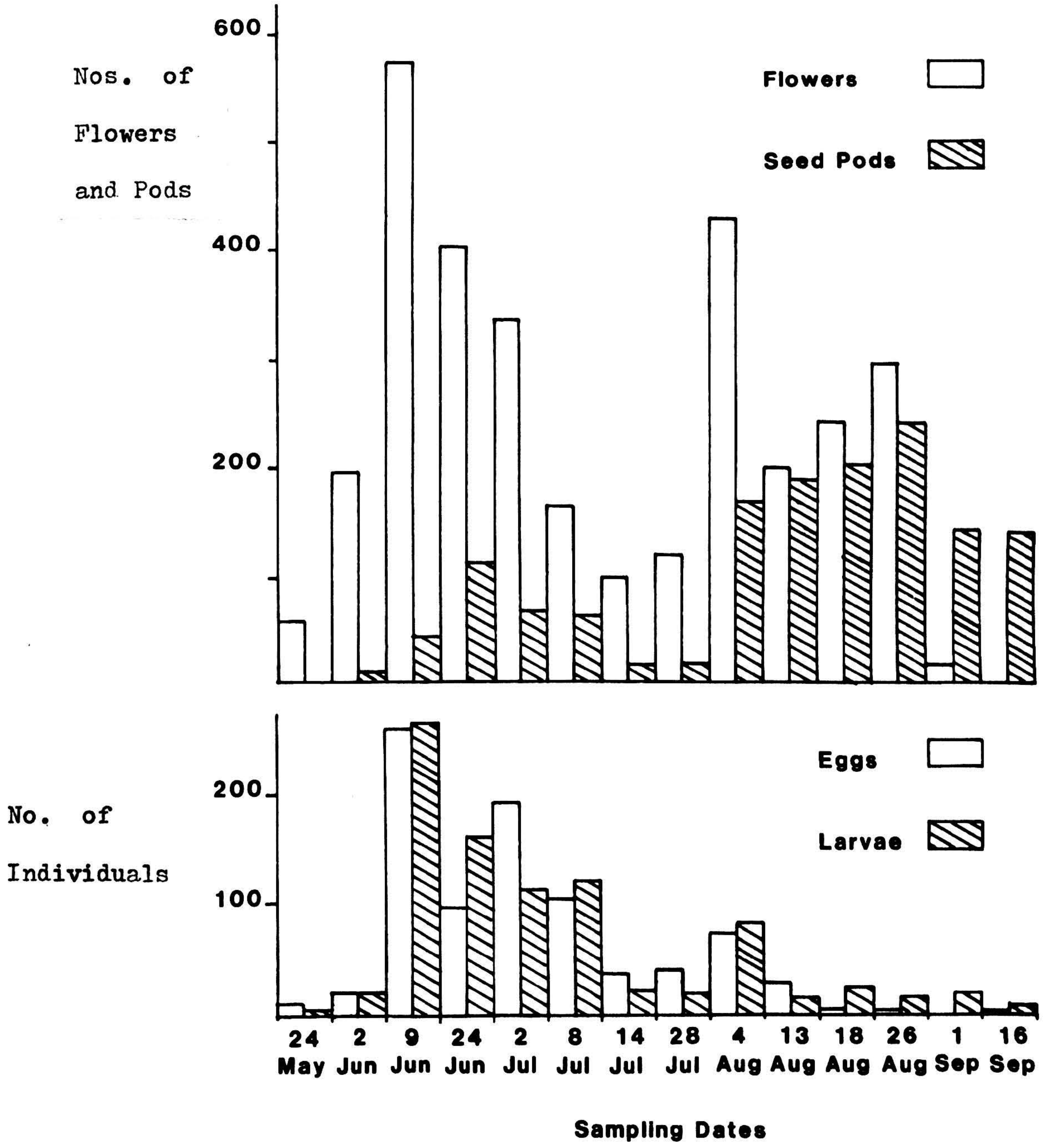

250
200
150
100
50
Nos. of Flowers and Pods
Flowers ▨
Seed Pods ☐
100
50
No. of Individuals
Eggs ▨
Larvae ☐
23 Jun
12 Jul
27 Jul
15 Aug
23 Aug
30 Aug
5 Sep
12 Sep
18 Sep
Sampling Dates

Table 4.12 *Apion loti* in the flowers and seed pods of *L. corniculatus* at Wharram Quarry, 1980. Samples of 14 or 15 quadrats, each of 0.05 m^2, were obtained on the sampling dates.

Date	Flowers	Seed Pods	Total Flowers and pods	*A. loti* eggs	*A. loti* larvae	Mean *Apion* per pod	% *A. loti* as eggs
24 May	55	0	55	7	1	0.14	87.5
2 June	189	5	194	17	17	0.17	50.0
9 June	570	39	609	256	259	0.85	49.7
24 June	397	108	505	97	157	0.50	38.2
2 July	331	67	398	187	115	0.76	61.9
8 July	162	60	222	102	119	0.99	46.2
14 July	93	13	106	36	21	0.54	63.2
28 July	115	15	130	43	20	0.48	68.2
4 Aug	424	165	589	73	82	0.26	47.1
13 Aug	220	185	405	28	16	0.11	63.6
18 Aug	241	199	440	6	25	0.07	19.3
26 Aug	240	292	532	2	16	0.03	11.1
1 Sept	16	140	156	0	21	0.13	0.0
16 Sept	0	139	139	2	6	0.06	25.0
Totals	3053	1337	4390	866	875	0.40	49.7

FIGURE 4.5

L. corniculatus seed pod and flower production and colonisation by Apion loti. Wharram Quarry 1980.


Nos. of Flowers and Pods
600
400
200
Flowers
Seed Pods
No. of Individuals
200
100
Eggs
Larvae
24 May
2 Jun
9 Jun
24 Jun
2 Jul
8 Jul
14 Jul
28 Jul
4 Aug
13 Aug
18 Aug
26 Aug
1 Sep
16 Sep
Sampling Dates

Figures 4.4 and 4.5 illustrate annual variation in the pattern of flowering in L.corniculatus, with one flowering peak in 1978 and two in 1980. Clearly, monophagous species like A. loti must be flexible in order to adapt to these annual variations in the phenology of their host plant. The development of A. loti during five summers from 1975 to 1980 is summarised in figure 4.6. The warm early spring of 1980 resulted in early flowering, and hence eggs and larvae being produced in May, a full month earlier than at Eppleworth two years earlier. The unusually hot summer of 1976 also had pronounced effects, with adults present by mid July, again a month earlier than that recorded during other years.

Competition for Food Inside the Seed Pods of L. corniculatus.

Introduction

Insects developing inside L. corniculatus seed pods are in a microhabitat which contains only a limited quantity of suitable food and has a carrying capacity which is determined by the size, number and quality of the seeds that are present. Most U.K. populations of L. corniculatus have two or three species of phytophagous insects feeding in their pods (table 4.3) and two species (A. loti and E. platyptera) are particularly vulnerable to food shortage because they must complete their development within the confines of a single pod.

The Intensity of Competition

Average densities of insects inside L. corniculatus pods at Eppleworth Quarry were 1.09 in 1977 and 0.41 in 1978 (tables 4.13 and 4.14). These values are obtained by combining the totals for the phytophagous species with those of their parasites. This gives a more relevant measure than if phytophagous insects alone are considered, because each host feeds more or less normally until it is killed and eventually produces only one parasite (Chapter Five). A. loti was numerically the dominant species during both seasons at Eppleworth, and it was also the most numerous species in all the other natural populations of L. corniculatus that were investigated.

FIGURE 4.6

Annual variation in the development of Apion loti in flowers and seed pods of L. corniculatus. Vertical bars indicate the periods when records were obtained.

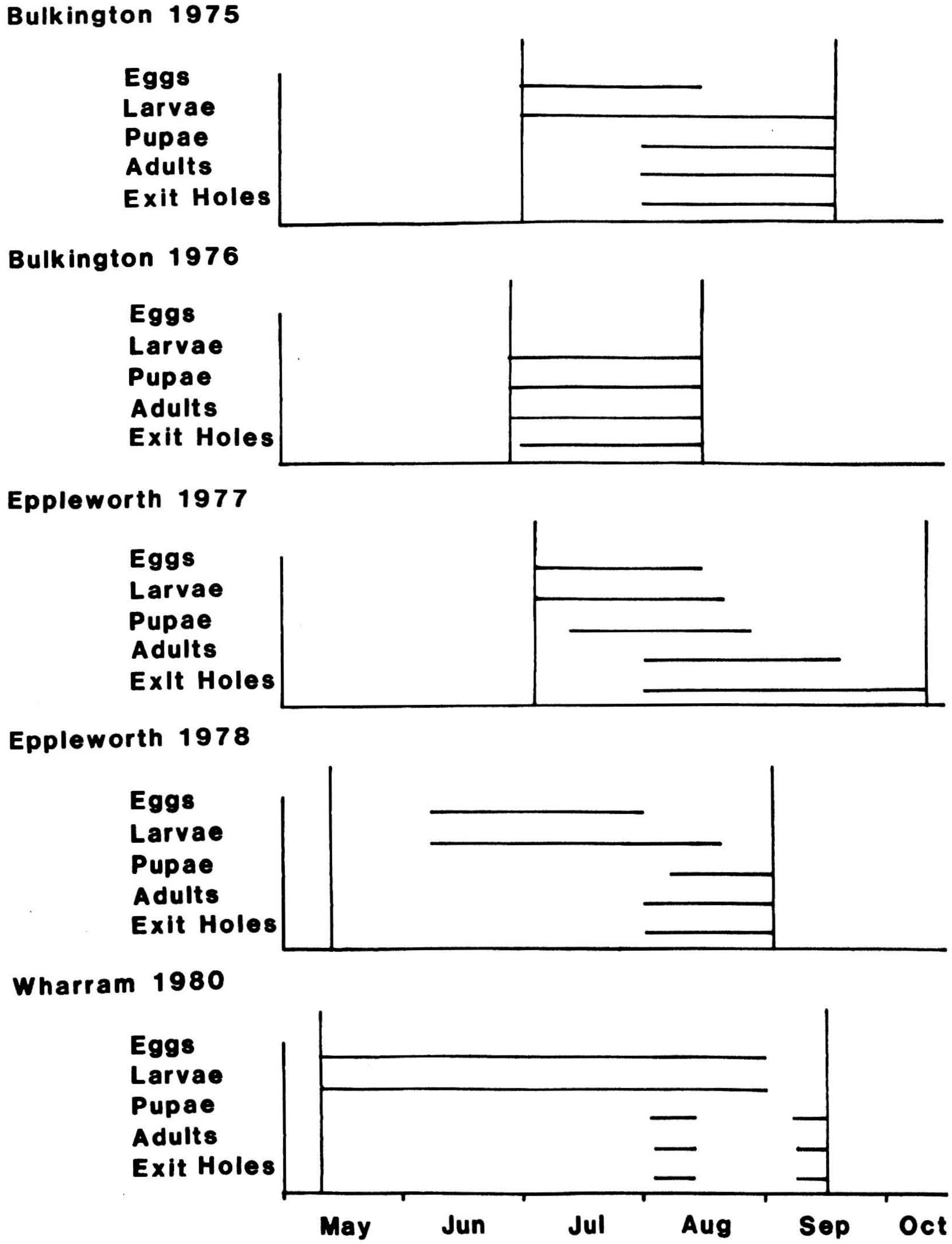

Bulkington 1975
Eggs
Larvae
Pupae
Adults
Exit Holes
Bulkington 1976
Eggs
Larvae
Pupae
Adults
Exit Holes
Eppleworth 1977
Eggs
Larvae
Pupae
Adults
Exit Holes
Eppleworth 1978
Eggs
Larvae
Pupae
Adults
Exit Holes
Wharram 1980
Eggs
Larvae
Pupae
Adults
Exit Holes
May
Jun
Jul
Aug
Sep
Oct

Table 4.13 Densities of phytophagous insects in seed pods of *L. corniculatus* at Eppleworth Quarry, 1977. Note that values include specimens destroyed and replaced by their parasites.

Sample	No. of Pods	*E. platyptera*	*C. compositella*	*A. loti*	Total density per pod
1.1	89	0	0	72	0.81
1.2	139	2	0	94	0.69
1.3	79	0	3	98	1.28
2.1	126	0	3	168	1.36
2.2	63	0	3	50	0.84
2.3	91	0	8	78	0.94
3.1	199	0	3	115	0.59
3.2	108	0	3	137	1.30
3.3	90	0	13	90	1.14
4.1	116	10	2	141	1.32
4.2	127	4	11	129	1.13
4.3	113	0	12	169	1.60
5.1	50	10	0	39	0.98
5.2	98	1	5	127	1.34
5.3	191	1	9	191	1.05
6.1	168	15	16	146	1.05
6.2	30	1	7	36	1.47
6.3	20	0	0	19	0.95
7.1	20	12	0	31	2.15
7.2	160	2	9	164	1.09
7.3	143	8	17	164	1.32
8.1	65	1	1	30	0.49
8.2	148	0	4	110	0.77
8.3	20	0	1	17	0.90
9.1	111	21	6	99	1.13
9.2	38	0	0	44	1.16
9.3	60	0	3	48	0.85
10.1	30	7	0	26	1.10
10.2	47	9	3	24	0.77
11.1	15	0	0	14	0.27
11.2	36	2	0	33	0.97

Table 4.14 Densities of phytophagous insects in seed pods of *L. corniculatus* at Eppleworth Quarry, 1978. Note that values include specimens destroyed and replaced by their parasites.

Sample	No. of Pods	*E. platyptera*	*C. compositella*	*A. loti*	Total density per pod
2.1	19	0	0	8	0.42
2.2	37	0	0	14	0.38
2.3	89	0	0	44	0.49
3.1	11	0	0	15	1.36
3.2	21	0	0	23	1.09
3.3	46	0	0	32	0.70
4.1	16	0	0	8	0.50
4.2	15	0	3	11	0.93
5.1	45	0	0	19	0.42
5.2	10	0	0	7	0.70
5.3	69	0	4	3	0.10
6.1	7	0	0	2	0.29
6.2	49	0	0	16	0.33
6.3	49	0	1	20	0.43
7.1	30	1	0	8	0.30
7.2	42	0	0	10	0.24
7.3	112	0	2	21	0.21
8.1	11	0	1	2	0.27
8.2	55	0	0	24	0.44
8.3	10	0	1	3	0.40
9.1	56	0	1	16	0.30
9.2	5	0	0	0	0.00
9.3	17	0	0	17	1.00

Approximately half of the inhabited pods at Eppleworth contained only a single insect, but some pods had large numbers of individuals (figures 4.7 and 4.8) with a maximum of nine being recorded in 1977 and six in 1978. The majority of insect larvae were therefore liable to be sharing pods with others, and potentially faced competition for the available resources.

Mortalities apparently resulting from starvation were occasionally observed within the seed pods. Deaths involving *A. loti* resulted from larvae failing to complete development before the seeds hardened or being in small pods where no suitable seeds were present. Mortalities attributable to competition for food were observed when an *A. loti* larva had a larger larva on each side and these two had eaten all the available food, or when a larva became isolated because of the feeding activities of *C. compositella* or (in flowers) *Hypera plantaginis*. Young *E. platyptera* larvae were particularly vulnerable and usually died if the seeds that they inhabited were damaged by either of the other species. No larvae were observed killing or eating other larvae and any mortalities resulting from interactions between the species are assumed to have been caused indirectly.

Rathke (1976) found that competition was generally unimportant to a guild of stem feeding insects in North America and concluded that a lack of competitive organisation may be widespread amongst insect communities. Varley *et al* (1973) similarly believed that the insect larvae feeding on young Oak leaves did not suffer from extensive competition and attributed this to the effects of parasites which maintained population levels below the thresholds required for competition to occur. Different results were obtained by Zwoelfer (1979) who carried out a detailed study of the competitive interactions between larvae inhabiting the seed heads of various species of Compositae. He described a competitive hierarchy within the seed heads, with Lepidoptera larvae having the highest 'intrinsic' superiority and other species reducing the effects of direct competition by a variety of evasion strategies. A similar hierarchy

FIGURE 4.7

The numbers of insects supported by individual *L. corniculatus* seed pods and the abundance of *Apion loti*, *Eurytoma platyptera* and *Cydia compositella* in relation to the total numbers that each pod contained. Eppleworth Quarry, 1977. Note that parasites are included within the totals of their respective host species.

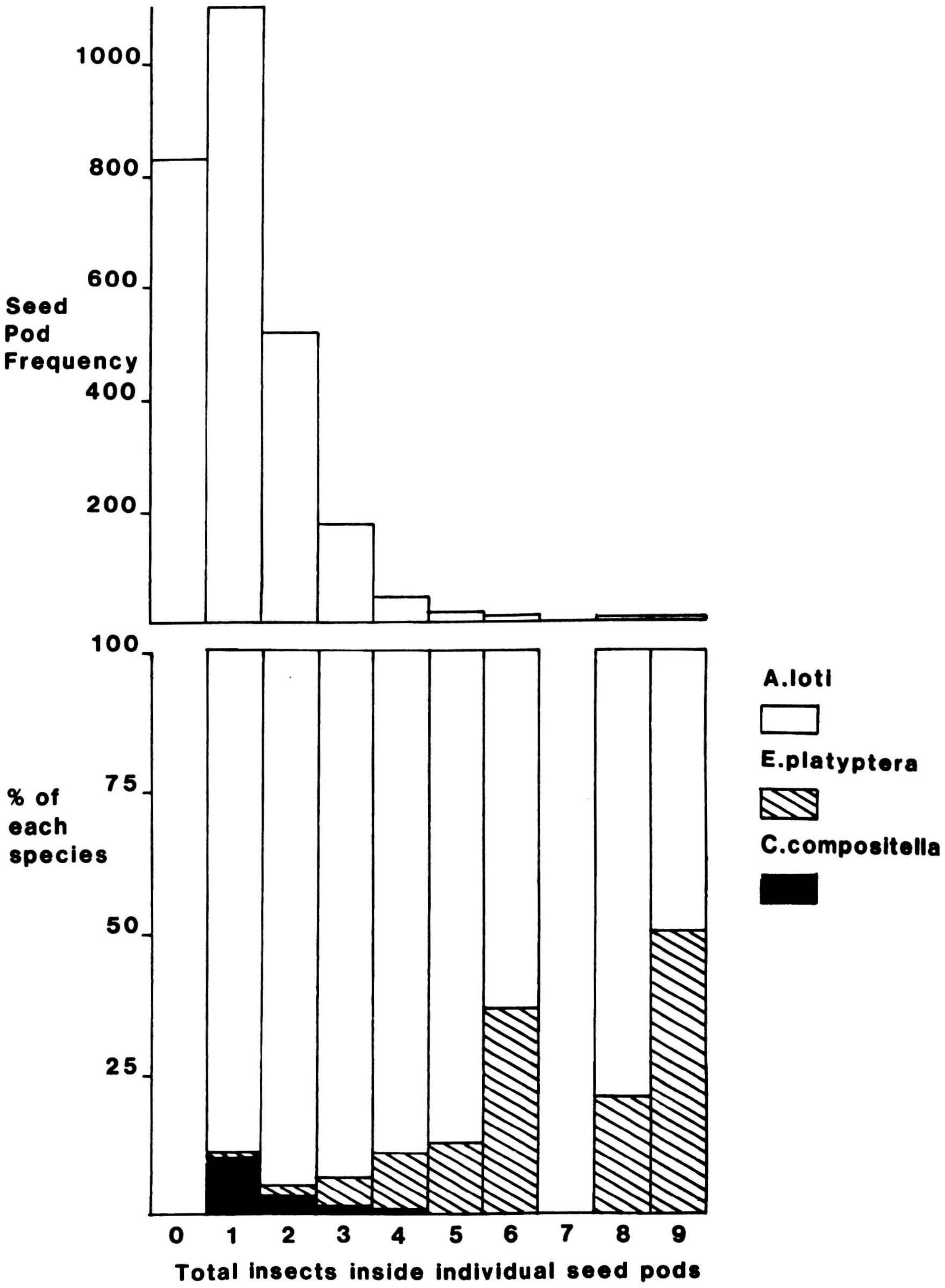
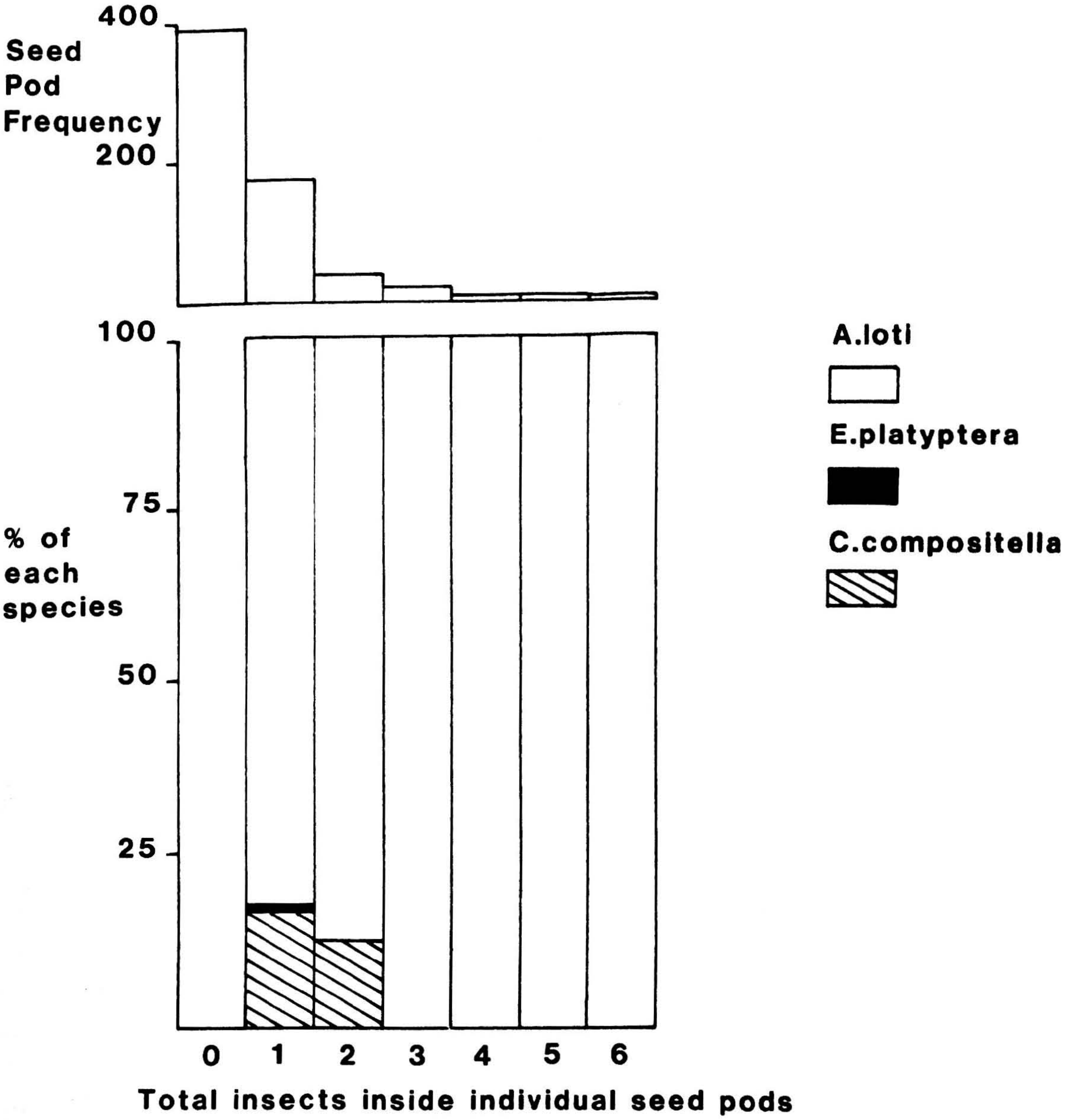

1000
800
600
Seed Pod Frequency
400
200
100
75
% of each species
50
25
0
1
2
3
4
5
6
7
8
9
Total insects inside individual seed pods
A.loti
E.platyptera
C.compositella

FIGURE 4.8

The numbers of insects supported by individual *L. corniculatus* seed pods and the abundance of *Apion loti*, *Eurytoma platyptera* and *Cydia compositella* in relation to the total numbers that each pod contained. Eppleworth Quarry, 1978. Note that parasites are included within the totals of their respective host species.


400
Seed Pod Frequency
200
100
75
% of each species
50
25
0
1
2
3
4
5
6
Total insects inside individual seed pods
A.loti
E.platyptera
C.compositella

in competitive ability is present inside the seed pods of L. corniculatus, where again it is a Lepidopteran, C. compositella, which is the intrinsically superior species. The high competitive ability of C. compositella results from its large size and mobility; this species having the option of moving on to other pods if its food supply becomes exhausted. E. platyptera is the weakest competitor because it relies on the resources provided by a single seed and it usually dies if other species also feed on that seed.

Feeding by insects removed a considerable proportion of the total seed output of L. corniculatus at Eppleworth Quarry (Chapter Six). Each E. platyptera larva destroys a single seed, but the damage caused by the other species is more variable and harder to assess, because the number of damaged seeds cannot be counted reliably. Feeding by each A. loti larva removed an average of approximately two seeds, while each C. compositella destroyed at least three or four (table 4.15). Competition for food was likely to be most intense in pods where no healthy seeds remained and here C. compositella had a marked effect, destroying all the viable seeds in over 75% of the pods where it was present (table 4.16).

Direct observations of mortality levels provide the most convenient index of competitive interactions. These only indicate the most extreme consequences, however, and more subtle effects, such as a reduction in adult size or survival, may be of equal importance. Few dead C. compositella and E. platyptera were recorded at Eppleworth (table 4.17) and numbers were insufficient for any quantitative assessments to be made. The proportions of dead A. loti were 16.1% in 1977 and 11.0% in 1978, with most of the deaths occurring during the larval stage (tables 4.18 and 4.19). Deaths of pupae and adults often involved small specimens and these may also have resulted from inadequate nutrition during the larval period. Not all larval deaths can be attributed to a lack of suitable food, however, and parasites, perhaps through accidents during oviposition, may have been important contributory factors. Mortalities

Table 4.15 The relationship between the presence of phytophagous insects and the numbers of healthy seeds in *L. corniculatus* seed pods at Eppleworth Quarry. Note that only seed pods capable of supporting insects have been included in the analysis.

		Pods containing Insects			Pods with no Insects		
Species	Year	No.	Insect Density per pod	Healthy seeds per pod	No.	Healthy seeds per pod	Reduction in seed numbers per pod
C. compositella	1977	142	1.0	0.56	2528	3.81	3.25
C. compositella	1978	13	1.0	1.08	626	4.79	3.71
A. loti	1977	1715	1.56	1.56	955	4.44	2.88
A. loti	1978	230	1.4	2.35	409	6.05	3.70

Table 4.16 The effects of the presence of insects on the numbers of <u>L. corniculatus</u> seed pods containing no healthy seeds. Eppleworth Quarry, 1977 and 1978.

		Insects Present			Insects Absent		
Species	Year	Total pods	Pods with no healthy seeds	%	Total pods	Pods with no healthy seeds	%
<u>Apion loti</u>	1977	1715	380	22.2	1075	212	19.7
<u>Apion loti</u>	1978	230	110	47.8	591	192	32.5
<u>Cydia compositella</u>	1977	142	109	76.8	2648	483	18.2
<u>Cydia compositella</u>	1978	13	11	84.6	808	291	36.0
Total Animals	1977	1845	472	25.6	945	120	12.7
Total Animals	1978	242	120	49.6	579	182	31.4

Table 4.17 Dead larvae collected in *L. corniculatus* seed pods at Eppleworth Quarry.

	1977			1978		
	Dead Larvae	Healthy Larvae	Percentage Mortality	Dead Larvae	Healthy Larvae	Percentage Mortality
Cydia compositella	3	45	6.25	1	3	25.0
Eurytoma platyptera	7	99	6.6	0	1	0.0

Table 4.18 Dead *Apion loti* collected in the flowers and seed pods of *L. corniculatus* at Eppleworth Quarry during 1977

Sample	Eggs	Larvae	Pupae	Adults	% of Total
1.1	1	7	-	-	10.7
1.2	1	9	-	-	9.9
1.3	-	7	-	-	6.9
2.1	-	15	-	-	11.7
2.2	-	4	-	-	7.1
2.3	-	10	-	-	12.7
3.1	-	17	-	-	14.7
3.2	-	16	-	-	11.7
3.3	-	8	-	-	8.8
4.1	-	30	-	-	21.6
4.2	-	37	-	-	28.9
4.3	1	24	-	-	15.1
5.1	-	14	-	-	41.2
5.2	-	22	-	-	19.6
5.3	-	43	-	-	24.9
6.1	-	16	3	-	19.4
6.2	-	6	-	-	18.7
6.3	-	5	-	-	31.2
7.1	-	2	1	-	11.1
7.2	-	11	1	1	10.6
7.3	-	15	3	-	15.4
8.1	-	3	-	-	13.6
8.2	-	10	8	-	25.3
8.3	-	-	-	-	0.0
9.1	-	7	1	2	17.2
9.2	-	1	-	2	11.5
9.3	-	4	1	1	16.2
10.1	1	1	1	1	16.7
10.2	-	1	-	1	11.8
11.1	-	-	-	-	0.0
11.2	-	-	1	2	12.0
Total	4	345	20	10	
% of Total (Apion)	2.9	20.2	10.2	3.2	16.1

Table 4.19 Dead *Apion loti* collected in the flowers and seed pods of *L. corniculatus* at Eppleworth Quarry during 1978.

Sample	Eggs	Larvae	Pupae	Adults	% Total Apion
1.1	1	-	-	-	3.7
1.2	3	1	-	-	6.9
1.3	-	-	-	-	0.0
1.4	-	-	-	-	0.0
1.5	-	-	-	-	0.0
1.6	-	-	-	-	0.0
1.7	-	-	-	-	0.0
2.1	-	-	-	-	0.0
2.2	-	2	-	-	13.3
2.3	-	3	-	-	5.1
3.1	-	-	-	-	0.0
3.2	-	3	-	-	11.1
3.3	-	3	-	-	9.4
4.1	-	-	-	-	0.0
4.2	-	1	1	-	22.2
4.3	-	-	-	-	0.0
5.1	-	3	-	-	18.7
5.2	-	2	1	-	42.9
5.3	-	-	-	-	0.0
6.1	-	-	-	-	0.0
6.2	-	3	-	-	37.5
6.3	-	2	-	-	11.8
7.1	-	1	-	-	16.7
7.2	-	1	-	-	14.3
7.3	-	4	-	-	26.7
8.1	-	-	-	-	0.0
8.2	-	4	1	-	38.5
8.3	-	-	-	-	0.0
9.1	-	2	-	-	22.2
9.2	-	-	-	-	0.0
9.3	-	2	-	-	18.2
Total	4	37	3	0	
% Total (Apion)	3.7	17.8	12.0	0	11.0

can also result from unusually severe weather conditions, as was observed in the Jostedal Valley during 1979, when very heavy rainfall drowned almost all the pod inhabitants.

Inside L. corniculatus pods the proportion of dead A. loti was inversely correlated with the numbers of viable seeds that were present, indicating that more mortalities occurred when few seeds were present (Pearson Correlation Coefficients =-0.0902, $P < 0.001$ and-0.0608, $P < 0.05$ for 1977 and 1978, n = 2790 and 821). The proportion of dead A. loti did not increase with the density of that species, however, (tables 4.20a and b) and in 1977 far fewer dead individuals ($P < 0.001$) were found in pods containing a large number of individuals. This is unlikely to reflect genuinely improved survival at higher densities and suggests that the feeding activities of other larvae may lead to the disappearance of dead specimens. The presence of C. compositella also caused a reduction in the proportion of dead A. loti recorded (not statistically significant, table 4.20c) and it must be concluded that the numbers of dead A. loti do not provide a satisfactory method for assessing mortalities in this species.

Zwoelfer (1979) used the ratio of eggs to pupae of Rhinocyllus conicus Froel. as a means of comparing the success of that species in the presence or absence of a superior competitor. Comparison of the ratio of eggs and larvae to pupae and adults of A. loti indicates that at high densities there is a significantly lower success rate, (tables 4.21a and b). However, the presence of C. compositella did not influence the proportion of A. loti reaching the pupal stage (table 4.21c).

Contingency tables provide a convenient method for detecting whether the distributions of two species occur independently within a given habitat (Southwood, 1978). The Fisher Exact Test is normally used in place of the Chi Square Test in situations (for example table 4.22c) where one or more cells contain values of zero. Recent studies by Yarnold and Larntz (discussed

Table 4.20 Dead *Apion loti* in relation to *Apion loti* density and the presence of *Cydia compositella*. Eppleworth Quarry 1977 and 1978

a 1977 Dead *A. loti* and *A. loti* density

	Total *A. loti* per pod		
	1	2	>2
Healthy	851	828	629
Dead	177	138	58
% Dead	17.2	14.3	8.4

x^2 [2] = 26.6, $P < 0.001$

b 1978 Dead *A. loti* and *A. loti* density

	Total *A. loti* per pod		
	1	2	>2
Healthy	151	64	74
Dead	19	12	8
% Dead	11.2	15.8	9.8

x^2 [2] = 1.54, $P > 0.05$

c 1977 Dead *A. loti* and *C. compositella*

		C. compositella	
		absent	present
Dead	absent	2324	131
A. loti	present	334	11
% pods with dead *A. loti*		12.6	7.7

x^2 [1] = 2.57, $P > 0.05$

Table 4.21 The ratio of *Apion loti* eggs and larvae to pupae and adults in relation to *A. loti* density and the presence of *Cydia compositella*. Eppleworth Quarry, 1977 and 1978.

a 1977 — *A. loti* density

	Total *A. loti* per pod				
	1	2	3	>3	
Eggs and Larvae	692	439	293	176	X^2 [3] = 49.9, P < 0.001
Pupae and Adults	309	317	117	44	
% achieving pupal stage	30.9	41.9	28.5	20.0	

b 1978 — *A. loti* density

	Total *A. loti* per pod				
	1	2	3	>3	
Eggs and Larvae	93	43	21	27	
Pupae and Adults	75	33	24	5	X^2 [3] = 11.9, P < 0.01
% achieving pupal stage	44.6	43.4	53.3	15.6	

c 1977 — The presence of *C. compositella*

	C. compositella absent	*C. compositella* present	
Eggs and Larvae	1805	29	
Pupae and Adults	836	11	X^2 [1] = 0.315, P > 0.05
% achieving pupal stage	31.6	27.5	

Table 4.22 The frequencies of coexistance amongst phytophagous insects in the seed pods of *L. corniculatus*. Eppleworth Quarry, 1977 and 1978.

a *A. loti* and *C. compositella*, 1977

		A. loti		
		absent	present	
	absent	846	1682	
C. compositella	present	109	33	$X^2 [1] = 109.7, P < 0.001$

b *A. loti* and *C. compositella*, 1978

		A. loti		
		absent	present	
	absent	398	228	
C. compositella	present	11	2	$X^2 [1] = 2.45, P > 0.05$

c *C. compositella* and *E. platyptera*, 1977

		C. compositella		
		absent	present	
	absent	2649	142	
E. platyptera	present	59	0	$X^2 [1] = 3.39, P > 0.05$ Note A

d A. loti and E. platyptera, 1977

		A. loti		
		absent	present	
	absent	934	1677	
E. platyptera	present	21	38	$X^2 [1] = 0.0008, P > 0.05$

Note A - See text for comments on the validity of the Chi Square statistic in contingency tables where one or more cells have a value of zero.

by Wells and King, 1980) have concluded, however, that adequate criteria for the Chi Square Test exist in contingency tables where all expected values are greater than 1.33. As this is the case in tables 4.22c 4.23c etc. the Chi Square Test has been retained throughout this thesis. Tables 4.22a and 4.22b show that at Eppleworth Quarry there was significant disassociation between A.loti and C.compositella in 1977, but not in 1978, when the densities of both species were considerably lower. No disassociations between other species pairs were obtained during 1977 (tables 4.22 c-d) or 1978, when combinations were too infrequent for worthwhile analyses. Similar analyses of data obtained at Bulkington in 1975, when E.platyptera and C.compositella were more numerous, show that both A.loti and E.platyptera were significantly displaced by the presence of C.compositella (table 4.23). The mean density of A.loti was lower in pods shared with C.compositella in both 1977 and 1978 (table 4.24). Pods containing neither insects nor any healthy seeds were excluded from the X^2 calculations because these were considered to have been unsuitable for the insects and as such their inclusion would have biased the calculations by increasing the apparent aggregation of the species.

Parasites are a major source of mortalities in the A.loti populations at Eppleworth and elsewhere (Chapter five) and, as with competitive interactions, their importance may vary according to the per pod density of A.loti. In order to compare the overall success of A.loti at different densities it is therefore necessary to make an assessment which incorporates the effects of both these factors. Table 4.25 (a1 and b1) summarises the components of the A.loti populations at Eppleworth Quarry in 1977 and 1978. The parasites category includes both parasitised A.loti and those which had been killed and replaced by their parasites. An estimate of the 'success' of A.loti at different densities is achieved by comparing the proportion which had successfully reached the pupal or adult stages with the remaining categories (table 4.25, a2 and b2). Dead A.loti were not included in either group because, as noted previously, it appears that dead individuals are 'lost' at high densities and hence their inclusion would bias the estimates. Chi square analysis suggests that the overall success of *A.loti* varied according to density in 1977, but not in 1978. Note that table 4.21 includes fewer *A.loti* than table 4.25. This is because the former does not include those parasitised *A.loti* where the stage at which death occurred could not be established.

Most insects display an aggregated pattern of distribution, with the degree of aggregation often varying according to density (Southwood, 1978). Figures 4.9 and 4.10 illustrate the distribution of the three major phytophages inside the seed pods of *L.corniculatus*. Comparison of these with a Poisson series of the same mean provides a method for detecting whether they are distributed at random within the seed pods. For *E.platyptera* in 1977 a $\chi^2[1]$ of 47.44 is obtained, $P < 0.001$, indicating a significantly aggregated distribution. Only small numbers of *C.compositella* were detected and despite being observed exclusively at a density of one insect per pod the distribution of this species was not significantly regular in either 1977 or 1978 ($\chi^2[1] = 0.598$ and 0.027, $P > 0.05$). *A.loti* did not have an aggregated distribution in 1977 ($\chi^2[4] = 2.25$, $P > 0.05$) but did have at the lower densities recorded in 1978 ($\chi^2[2] = 16.58$, $P < 0.001$). Southwood (1978) quotes examples of both insect populations which become more aggregated at higher densities and of others which become more regular. At Bulkington in 1975 both density and aggregation (as measured by the variance/mean ratio) of *A.loti* were particularly high, but this collection is not necessarily comparable with those at Eppleworth because the sampling was not carried out at random and pods containing high densities of insects may have been selected inadvertently.

The application of Taylor's power law provides an index of

Table 4.23 The frequencies of coexistance amongst phytophagous species in the seed pods of *L. corniculatus*. Bulkington, 1975

a

		A. loti		
		absent	present	
	absent	160	274	
C. compositella	present	42	7	X^2 [1] = 43.2, $P < 0.001$

b

		A. loti		
		absent	present	
	absent	306	254	
E. platyptera	present	25	27	X^2 [1] = 0.83, $P > 0.05$

c

		E. platyptera		
		absent	present	
	absent	382	52	
C. compositella	present	49	0	X^2 [1] = 6.58, $P < 0.05$ Note A

Note A - See text for comment on the validity of the Chi Square statistic in contingency tables where one or more cells have a value of zero.

Table 4.24 A comparison of the mean density per pod of *Apion loti* in the presence or absence of *Cydia compositella*. Eppleworth Quarry 1977 and 1978. Note that pods unsuitable for insects have been discounted from the analysis.

a 1977

	C.compositella present	*C.compositella* absent
No. of Pods	148	2528
Mean *A.loti*/pod	0.270	1.045
Variance estimate	0.307	1.030

d [147 and 2527] = 15.562, $P < 0.001$

b 1978

	C.compositella present	*C.compositella* absent
No. of Pods	14	625
Mean *A.loti*/pod	0.143	0.514
Variance estimate	0.132	0.705

d [13 and 624] = 3.611, $P < 0.01$

The d statistic was calculated as in R.E.Parker (1973), Introductory Statistics for Biology, published by Edward Arnold.

aggregation ('b') which is independent of the mean and which is considered to be generally constant for each species (Southwood, 1978). Values of b of less than one indicate a tendency for a regular distribution, while values greater than one indicate an increasingly clumped distribution. With *A.loti* (including dead specimens and parasites) the values of b were 1.17 in 1977 and 1.08 in 1978, and these do not differ significantly (t [49] = 0.0998). Comparisons of the aggregation of *A.loti* at different stages in its life history during 1977 also indicate that it did not alter significantly (eggs, b =1.19; larvae, b = 1.10; pupae , b = 1.00; adults plus exit holes, b = 0.90 -t [24] for the extreme values = 0.153, $P > 0.05$). Note that within each stage samples were discounted if less than 3 individuals were found. Insufficient numbers of *A.loti* prevent a similiar analysis of the 1978 data.

Conclusions on the intensity of competition in *L.corniculatus* seed pods can be summarised as follows:

1. Many seed pods contain examples of more than one species.
2. Insects consume a considerable proportion of the seeds that are available in the pods that they inhabit.
3. The numbers of dead *A.loti* do not provide a good measure of competitive interactions involving this species.
4. There is some evidence of intraspecific competition amongst *A. loti* larvae when more than three individuals share a pod.
5. A hierarchy of intrinsic superiority is present, with *C.compositella* as the best competitor and *E.platyptera* as the worst.
6. The presence of *C.compositella* appears to displace *A.loti* and *E.platyptera* in years when combined densities are high.
7. Although physical contact between *A.loti* and *E.platyptera* generally results in the death of *E.platyptera*, the number of contacts was insufficient for competitive displacement to be detected.

Zwoelfer (1979) has described several adaptations which serve to reduce the number of interspecific contacts in the seed heads of Compositae

Table 4.25 The relationship between the density of *A.loti* inside *L.corniculatus* seed pods and the proportion of healthy pupae and adults that were recorded. Wharram Quarry 1977 and 1978.

a1 1977. The categories of *A.loti* recorded in relation to density.

Density of *A.loti* per pod[1]

		1	2	3	4+
A.loti Categories	Eggs + Larvae	541	507	259	165
	Pupae + Adults	157	174	114	33
	Dead *A.loti*	177	138	43	15
	Parasites	153	147	46	12

a2 1977. The proportion of healthy pupae and adults present.

Density of *A.loti* per pod[1]

	1	2	3	4+
Pupae + Adults	157	174	114	33
Remainder [2]	694	654	305	177
%	18.4	21.0	27.2	15.7

$X^2\ [3] = 16.66,\ P < 0.001$

b1 1978. The categories of *A.loti* recorded in relation to density.

Density of *A.loti* per pod[1]

		1	2	3	4+
A.loti Categories	Eggs + Larvae	73	29	18	25
	Pupae + Adults	43	24	11	3
	Dead *A.loti*	19	12	6	1
	Parasites	33	11	10	2

b2 1978. The proportion of healthy pupae and adults present.

Density of *A.loti* per pod[1]

	1	2	3	4+
Pupae + Adults	43	24	11	3
Remainder [2]	106	40	28	27
%	28.9	37.5	28.2	10.0

$X^2\ [3] = 7.55,\ P > 0.05$

[1] Includes dead specimens and those replaced by parasites.

[2] Dead *A.loti* are not included, see page 126.

FIGURE 4.9

The numbers of Eurytoma platyptera and Cydia compositella in seed pods of L. corniculatus. Individuals destroyed by parasites are included.

E. platyptera

Bulkington, 1975 Pods with Zero individuals = 433, $\bar{x} = 0.259$, $S^2/\bar{x} = 3.30$
Eppleworth, 1977 Pods with Zero individuals = 2731, $\bar{x} = 0.038$, $S^2/\bar{x} = 2.89$

C. compositella

Bulkington, 1975 Pods with Zero individuals = 391, $\bar{x} = 0.046$,
Eppleworth, 1977 Pods with Zero individuals = 2648, $\bar{x} = 0.051$,
Eppleworth, 1978 Pods with Zero individuals = 808, $\bar{x} = 0.016$,

Dispersion parameters are not appropriate for C. compositella because this species occurred only at a density of one individual per pod.

The hatched areas represent additional L.corniculatus pods where C.compositella damage was recorded.

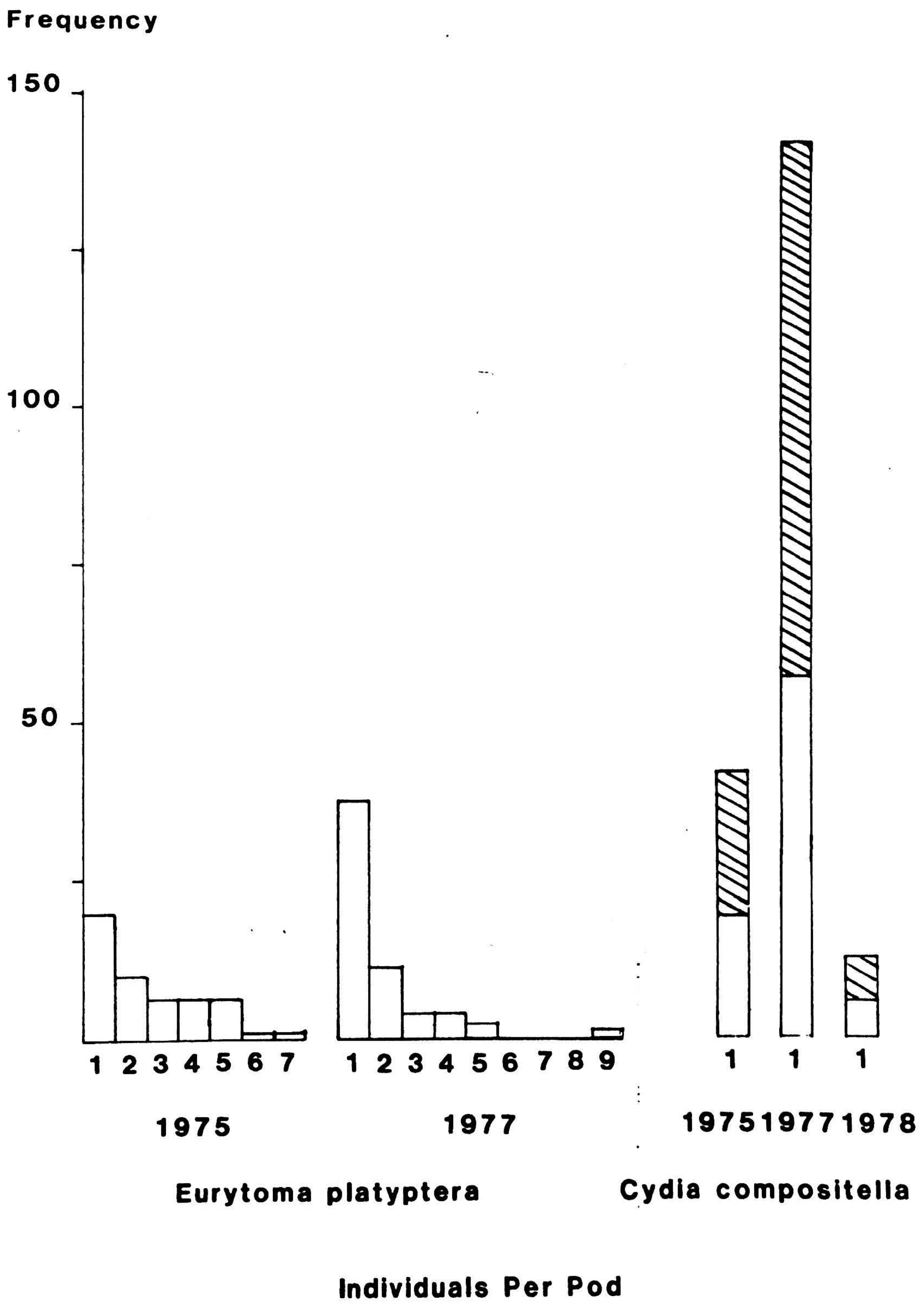

Frequency
150
100
50
1 2 3 4 5 6 7
1975
1 2 3 4 5 6 7 8 9
1977
Eurytoma platyptera
1
1975
1
1977
1
1978
Cydia compositella
Individuals Per Pod

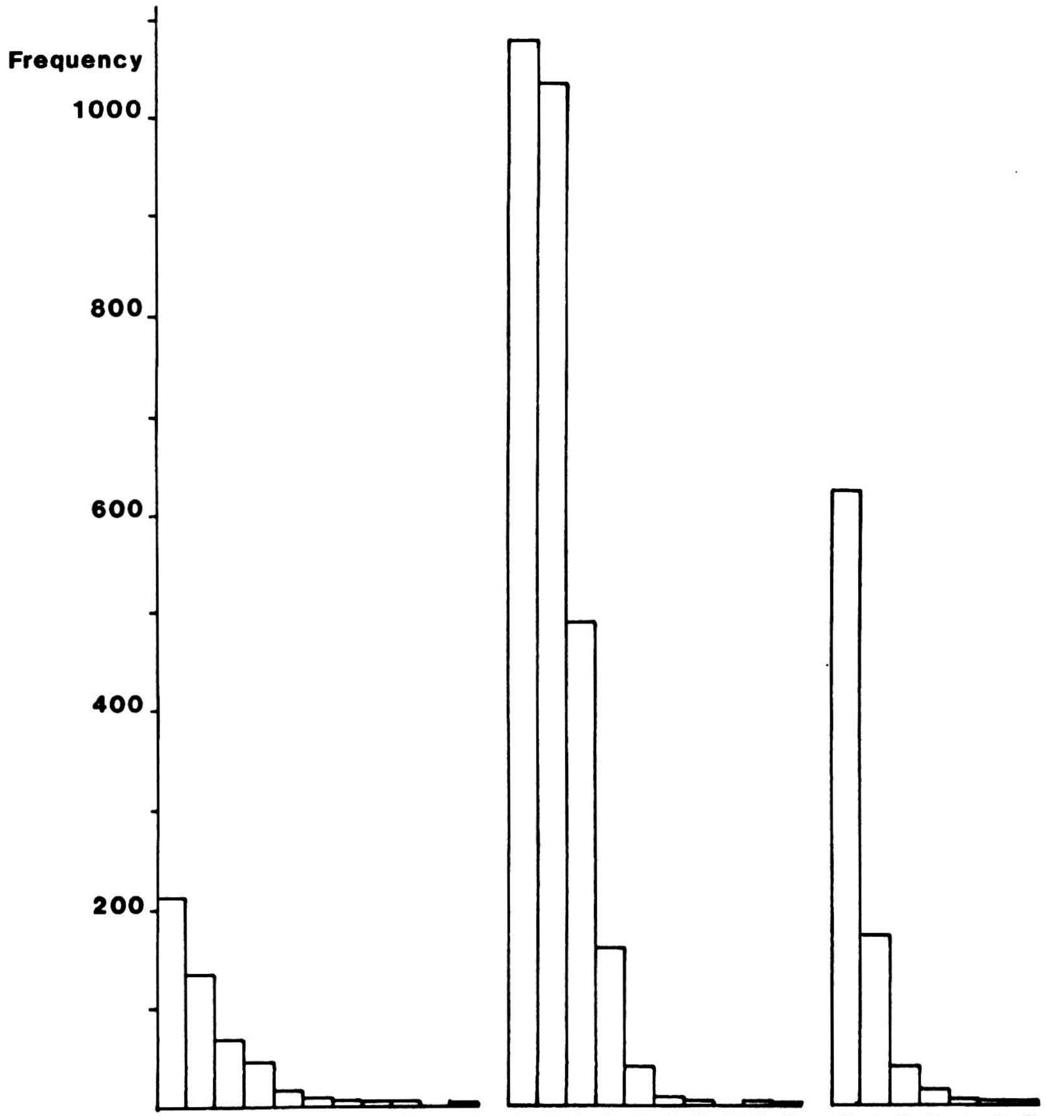
FIGURE 4.10

The numbers of Apion loti present in seed pods of L. corniculatus. Individuals destroyed by parasites are included.

1975 $\bar{x} = 1.141$, $s^2/\bar{x} = 1.97$

1977 $\bar{x} = 0.961$, $s^2/\bar{x} = 1.06$

1978 $\bar{x} = 0.393$, $s^2/\bar{x} = 1.49$


Frequency
1000
800
600
400
200
0 1 2 3 4 5 6 7 8 9 10
0 1 2 3 4 5 6 7 8 9
0 1 2 3 4 5 6
Bulkington 1975
Eppleworth 1977
Eppleworth 1978
Densities of A.loti in individual pods

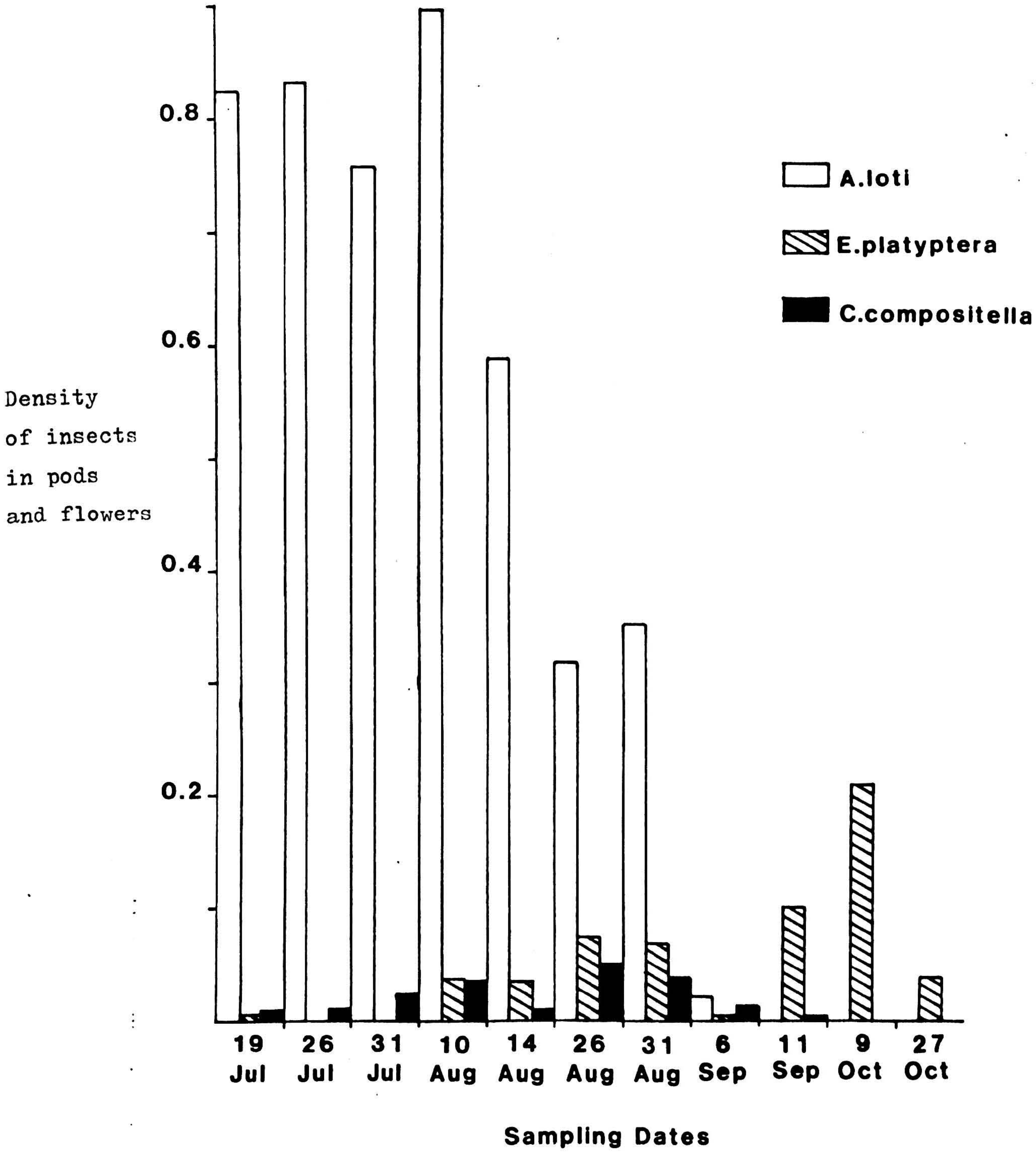
and which allow intrinsically inferior species to coexist with their more aggressive neighbours. Selection of food plants which are at different stages of development is one possible avoidance mechanism. The seeds in L. corniculatus pods are only suitable from the time that the ovules are formed until seed hardening occurrs and there may not be sufficient time for any temporal separation because this is roughly equal to the period required for insect development to be completed. The first arrivals are at an advantage in a 'scramble' competition situation and selection for early entry into the pods might be expected if competition is important. E. platyptera must rely on the resources inside one seed, however, and this prevents it from commencing feeding before a critical seed size is reached. This species is therefore restricted to older pods and this contributes to its competitive weakness.

Phytophagous insects can also reduce competition by colonising the same host species at different times of the year. Figure 4.11 illustrates the densities of eggs and larvae in L. corniculatus pods during the 1977 season. The maximum density of each species peaks at different times, but overlap is present throughout almost the whole period. The highest numbers of E. platyptera were present at the end of the season, when feeding by other species was minimal, but this is due to the larval overwintering strategy of this species and by September most E. platyptera had also ceased feeding. A. loti is unable to take full advantage of flowering during the second half of the season because of its univoltine breeding system and this could provide the second generation of E. platyptera with an advantage. Breeding late in the season is often relatively insignificant in Britain, where the summers are relatively short, but in warmer climates such as those in central Europe the reproductive potential of E. platyptera may be greatly increased.

Larinus sturnus Scholl. females select relatively small Carduus seed heads for oviposition, and this reduces the level of larval competition because most other species prefer larger seed heads (Zwoelfer, 1979). Erdelyi et al

FIGURE 4.11

The combined densities of eggs and larvae of the phytophagous species feeding in the flowers and seed pods of L. corniculatus. Eppleworth Quarry, 1977.


A.loti
E.platyptera
C.compositella
Density of insects in pods and flowers
0.8
0.6
0.4
0.2
19 Jul
26 Jul
31 Jul
10 Aug
14 Aug
26 Aug
31 Aug
6 Sep
11 Sep
9 Oct
27 Oct
Sampling Dates

(1979) have also shown that *Eurytoma roddi*, the Alfalfa Seed Chalcid, may have no preference for pods containing more than four seeds, whereas the competing *Tychius flavus* Beck. **prefers larger pods.** It is difficult to assess whether *C. compositella* and *A. loti* select pods on the basis of their seed content because their feeding activity destroys too many seeds and this results in both species having a strong negative correlation with healthy seed number. Selection on the basis of seed number is easier to investigate with *E. platyptera* and, unlike *E. roddi*, this species clearly prefers pods which contain a large number of seeds (table 4.26).

One strategy adopted by inferior competitors is to lay small numbers of eggs in as many host plants as possible. By 'spreading the risk ' these species increase their chances of finding some feeding sites where all the competing species are absent. This tactic does not appear to be employed in *L. corniculatus* pods, where *E. platyptera* (the least able competitor) has the most aggregated distribution (figure 4.9).

During 1977 a number of additional quadrat samples were taken on a relatatively flat area of short turf approximately 20 metres away from the main sampling area at Eppleworth Quarry. The *L. corniculatus* pods collected from this 'low growth habitat' contained smaller numbers of *A. loti* than the nearby main sampling area, but had a much higher density of *E. platyptera* (table 4.27). *A. loti* numbers are greatly reduced when *L. corniculatus* is grazed by large mammals (Morris, 1967). *A. loti* mortality levels were significantly higher in the low growth area than at the main sampling site, (ratio of healthy to dead *A. loti* = 184:57, compared with 2302:379 giving a $\chi^2_{[1]}$ of 15.8, $P < 0.001$). This is attributable to the increased levels of trampling and grazing by rabbits on the flat low growth area. The relative success of *E. platyptera* and *A. loti* can therefore vary according to the environment in which the host plant is growing and this apparent difference in habitat preferences may be one way by which *E. platyptera* can reduce the levels of competition with *A. loti*.

Table 4.26 The number of L. corniculatus seed pods colonised by Eurytoma platyptera in relation to seed content. Eppleworth Quarry, 1977.

Seed Content	Number of pods	Pods inhabited by E. platyptera	%
1	367	4	1.1
2	355	7	2.0
3	317	5	1.6
4	284	7	2.5
5	236	6	2.5
6-9	486	20	4.1
9+	153	10	6.5

Table 4.27 *Apion loti* and *Eurytoma platyptera* in seed pods of *L. corniculatus*. Eppleworth Quarry, 1977, 'low growth habitat'. Note that values include individuals represented by their parasites.

Sampling Dates	Sample	No. of seed pods	No. of seeds	*E. platyptera* total	*E. platyptera* per pod	*E. platyptera* percentage dead	*A. loti* total	*A. loti* per pod	*A. loti* Percentage dead
26.8.77	1	39	79	3	0.077	33.3	23	0.820	26.1
	2	66	183	41	0.621	9.8	42	0.636	35.7
	3	26	64	7	0.269	0	16	0.615	12.5
	4	57	126	11	0.193	0	21	0.368	33.3
	5	42	90	22	0.524	0	13	0.309	30.8
6.9.77	1	59	176	37	0.627	8.1	22	0.373	13.6
	2	41	75	39	0.951	2.6	27	0.658	14.8
	3	24	35	1	0.042	0	6	0.250	16.7
	4	74	210	15	0.203	13.3	31	0.419	29.0
	5	83	266	30	0.361	16.7	40	0.482	15.0
Totals		511	1304	206	0.403	7.8	241	0.472	23.6

E. platyptera may intrinsically prefer to colonise *L. corniculatus* growing in short turf, or the plants may just have been more suitable because their flowering period was more conveniently synchronised with its oviposition period.

E. platyptera oviposits into seeds that are at a relatively late stage of development. This is a disadvantage in terms of direct competition between its larvae and those of the other spesies, but it does provide the option of avoiding pods which already contain potential competitors. The total absence of *E. platyptera* from pods containing *C. compositella* may have been an example of this, but pods containing *A. loti* did not appear to be avoided (table 4.28). If pods containing more than ten healthy seeds are discounted, significantly fewer pods containing *A. loti* were colonised at the main site however (table 4.29a and Paired $t_{[2]} = 8.0$, $P < 0.05$). This was not repeated in the low growth area (table 4.29b) and further observations will be required before it can be established whether avoidance does in fact occur.

The competitive displacement that has been demonstrated inside *L. corniculatus* seed pods does not appear to have resulted in the development of well defined evasive strategies amongst the less able competitors. *E. platyptera* may prefer plants growing in open situations and may show active avoidance of pods containing potential competitors, but these are likely to have only a marginal influence on the number of interspecific contacts that take place.

The fecundities of the three species have not been established, but preliminary studies and extrapolation from related species would suggest that there will be little difference between their egg laying capacities (Batiste, 1967, Bradley *et al* 1973, Markkula and Myllymaki, 1957). *E. platyptera* may benefit from overwintering inside the protective covering of the seed testa, but this does not appear to provide protection from parasitic Hymenoptera and mortalities due to parasitism were again roughly similar amongst the three phytophagous species (Chapter five).

C. compositella is the best competitor inside *L. corniculatus* pods, yet

Table 4.28 The frequencies of coexistance of Eurytoma platyptera and Apion loti in seed pods of L. corniculatus. Eppleworth Quarry, 1977. Note that pods containing no seeds suitable for E. platyptera have not been included.

a

Main Sampling Area

		E. platyptera	
		absent	**present**
	absent	842	21
A. loti	**present**	1297	38

X^2 [1] = 0.34, P > 0.05

b

Low Growth Habitat

		E. platyptera	
		absent	**present**
	absent	196	59
A. loti	**present**	153	34

X^2 [1] = 1.59, P > 0.05

Table 4.29 The frequencies of <u>L. corniculatus</u> pods containing <u>Eurytoma platyptera</u> in the presence or absence of <u>Apion loti</u>. Eppleworth Quarry, 1977.

a Main Sampling Area

		Seeds Present			
		1-2	3-5	6-10	>10
<u>A. loti</u>	absent	0.028	0.039	0.062	0.18
	present	0.016	0.027	0.054	0.32

b Low Growth Habitat

		Seeds Present			
		1-2	3-5	6-10	> 10
<u>A. loti</u>	absent	0.22	0.26	0.31	0.33
	present	0.19	0.42	0.29	0

E. platyptera occurs in almost equal numbers and A. loti is numerically the most successful species. Competitive ability cannot therefore be the major factor determining the relative success of these species. One contributory factor may be that the larger size of C. compositella larvae, which helps to give them a competitive advantage, also makes them more vulnerable once they leave the seed pods. C. compositella eggs are also more likely to suffer extensive predation because they are laid in exposed positions and are liable to predation from mites and Heteropterans (Glen, 1977).

CHAPTER V

THE PARASITES OF L. CORNICULATUS SEED HERBIVORES

Investigations of the insects feeding inside the seed pods of *L. corniculatus* revealed that the three common phytophagous species support a diverse complex of parasites and hyperparasites (following Askew, 1971, the term 'parasite' has been used in preference to 'parasitoid'). Seed pods from a large number of sites in Great Britain and Norway were examined and this has allowed assessments of the relative importance of each parasite in terms of its geographical distribution and abundance. Rearing records were supplemented with information on the flight periods of many of the species. Adult insects were collected by sweep netting and with a 'D-Vac' suction sampling machine. Information on the design and effectiveness of the 'D-Vac' has been provided by Dietrick (1961) and Stevens and Steinhauer (1973).

The larvae of *Lestodiplosis* sp. and *Macroneura vesicularis* (Ratz.) are known to be capable of acting as active predators and destroying a whole series of hosts (Barnes, 1928, Morris, 1938), but this form of behaviour was not observed while these species were feeding inside *L. corniculatus* pods. Gregarious development was also absent, and each host individual provided sufficient resources for the successful development of only one parasite.

The parasites reared from the seed pods can be separated into five groups on the basis of their choice of hosts, frequency of occurrence and published host records (table 5.1). Group one consists of the species reared only from *C. compositella*. Unlike the other groups (which are dominated by members of the Chalcidoidea) it is composed mainly of species from the families Braconidae and Ichneumonidae. *C. compositella* is considerably larger than the other phytophagous species feeding in *L. corniculatus* pods and this presumably makes it more vulnerable to attack by Ichneumonoids, which in general require larger hosts than chalcids. Endo - and ectoparasites of *C. compositella* were collected, but the small number of records prevents any conclusions on the structure of the parasite complex of this species.

The second group of parasites consists of two species associated with *Eurytoma platyptera*, the larvae of which are enclosed inside the seeds of *L. corniculatus*. The endoparasitic *Tetrastichus endemus* was the most numerous parasite and on rare occasions it was found developing on alternative hosts, whereas the ectoparasite *Pteromalus* sp. C. was restricted entirely to *E. platyptera*. *T. endemus* probably has a wide range of host species (M.W.R. Graham, Pers. Comm.), but in *L. corniculatus* pods it does not act as a polyphage and the examples of development on other hosts demonstrates that its virtual restriction to *E. platyptera* is facultative and not determined by physiological limitations.

The parasites restricted to *Apion loti* form the largest group and this reflects the abundance of this host species. The endoparasite *Entedon diotimus* and the ectoparasite *Trichomalus rufinus* are the only ubiquitous parasites, however, and the other parasites, even in combination, are relatively

Table 5.1 The host relationships and abundance of parasites reared from L. corniculatus seed pods

Group	Parasite species	Major host species	No. of hosts recorded	No. of sites recorded	Approximate no. of individuals recorded
1	Scambus brevicornis	C. compositella	1	1	4
	Scambus eucosmidarum	C. compositella	1	1	3
	Diadegma sp.	C. compositella	1	1	1
	Clinocentrus sp.	C. compositella	1	1	1
	Euderus albitarsis	C. compositella	1	1	1
2	Tetrastichus endemus	E. platyptera	3	9	150+
	Pteromalus sp. C.	E. platyptera	1	8	45
3	Entedon diotimus	A. loti	1	14	2000+
	Trichomalus rufinus	A. loti	1	12	500+
	Trichomalus campestris	A. loti	1	2	14
	Trichomalus helvipes	A. loti	1	1	3
	Necremnus tidius	A. loti	1	1	2
	Triaspis sp.	A. loti	1	4	50
	Bracon sp.	A. loti	1	1	10
4	Macroneura vesicularis	A. loti	4	6	20
	Pteromalus sequester	E. platyptera	2	4	20
	Pteromalus chrysos	C. compositella	4	1	8
	Pteromalus semotus	A. loti	2	1	76
	Lestodiplosis sp.	A. loti	2	4	10
5	Pteromalus sp. A	-	2	1	2
	Mesopolobus ? diffinis	-	2	2	2
	Homoporus sp.	E. platyptera	1	1	2
	Callitula pyrrhogaster	E. platyptera	1	1	1

unimportant. Published accounts of their biology suggest that these infrequent parasites of *A. loti* also develop on a number of other *Apion* species and their presence in *L. corniculatus* pods reflects an overlap with closely related hosts feeding on other plants.

Macroneura vesicularis was the most widespread of the polyphagous parasites developing inside *L. corniculatus* pods, but always occurred at low densities. *Pteromalus semotus* was numerically the most abundant of the known polyphages, but was reared almost entirely from *A. loti*. This virtual restriction to one host reflects a scarcity of alternatives at Wharram Quarry - the only site where *P. semotus* was recorded. *Pteromalus sequester* attacked almost equal numbers of *A. loti* and *E. platyptera*, which perhaps indicates a preference for the latter as *E. platyptera* was much less numerous than *A. loti*. *P. sequester* may have a relatively restricted host range, as it appears to specialise on hosts feeding inside legume pods.

The final group of parasites contains 'accidental' species which occurred only rarely in *L. corniculatus* pods and whose published host ranges (where known) suggest that they are normally associated with hosts that are not closely related to those utilised in the seed pods. *Homoporus* species and *Callitula pyrrhogaster* generally develop as parasites of insects feeding in grass stems, and *Mesopolobus diffinis* is known as a parasite of Dipterons. The identity and host preferences of *Pteromalus* sp. A could not be established, but for convenience and because of its scarcity, it has also been included in this group.

The life-histories of the parasites reared from *L. corniculatus* seed pods.

A Species reared as parasites of *Cydia compositella*

Scambus brevicornis (Gravenhorst) (Hym., Ichneumonidae)

Three female and one male *S. brevicornis* were reared as ectoparasites of *C. compositella* from *L. corniculatus* pods collected at Epplewerth Quarry in August and September 1977. Adults emerged in the Spring of 1978 after overwintering as larvae inside their cocoons. Randall (1982) and others have reared *S. brevicornis* from *Coleophora alticolella* Zeller, and Aeschlimann (1974) reared small numbers of both *S.eucosmidarum* and *S. brevicornis* from one host species, the Lepidopteran *Anchinia laureolella* Herrich - Schaffer.

Scambus eucosmidarum (Perkins) (Hym., Ichneumonidae)

A female of *S. eucosmidarum* was reared from *L. corniculatus* pods collected at Bulkington in 1975. It developed as an ectoparasite of a *C. compositella* larva and, after overwintering as a larva, pupated and emerged in April 1976. A male *Scambus*, perhaps of the same species, was reared from a *C. compositella* larva collected at Bulkington on 16.8.76. This sample also contained a *Scambus* cocoon from which a secondary parasite, *Pteromalus chrysos*, subsequently emerged. *Scambus* species are known to prefer Lepitoptera larvae and pupae that develop in concealed situations (Askew, 1971).

Diadegma sp. (Hym., Ichneumonidae)

Diadegma species are solitary endoparasites that usually develop inside Lepidoptera larvae feeding in semi-concealed situations (Shaw and Askew, 1976). Only one example of this genus was obtained, with a single female emerging from a *C. compositella* larva collected in *L. corniculatus* pods at Eppleworth Quarry on 26.6.77.

Clinocentrus sp. (Hym., Braconidae)

A *Clinocentrus* sp. male was reared from a *C. compositella* larva collected at Eppleworth Quarry on 30.8.77. The species of *Clinocentrus* are endoparasites and pupate inside the larval skin of their hosts, which become dry and hard (Shaw and Askew, 1976). The *C. compositella* larva was already in this condition when it was collected, and examination in March 1978 showed that a yellow parasite larva had overwintered. The adult male appeared shortly after, in April 1978, and escaped by chewing an irregular exit hole at one end of its host. Lacatusu et al (1978) have previously reared Clinocentrus cunctator Haliday from seed pods of L. corniculatus, but the host species was not established.

Euderus albitarsis (Zetterstedt) (Hym., Eulophidae)

A male Euderus albitarsis emerged on 30.8.78 from an L. corniculatus pod collected at Eppleworth Quarry on 20.7.78. Examination of the pod revealed that the host had been a small larva of C. compositella which had been destroyed before it had reached its maximum size. E. albitarsis is a relatively polyphageous species and has been reared from Scolytid beetles, Cephid sawflies and various Lepidoptera (Bouček and Askew, 1968).

B Species associated mainly with Eurytoma platyptera

Tetrastichus endemus (Walker) (Hym., Eulophidae)

T. endemus was the most numerous and widespread parasite of E. platyptera (table 5.2) and was often reared in larger numbers than its host. The identity of this species was only recently clarified (Bouček and Graham, 1979) and published records are restricted to those of Nikolskaja (1934) who reared small numbers from Eurytoma roddi on Medicago and Parnell (1964) and Randall (1982) who reared T. endemus as a hyperparasite of the pupae of Pteromalus sequester Walker and Elachertus olivaceus (Thomson). T. endemus was also reared as a secondary parasite in L. corniculatus pods (table 5.3) and M.W.R. Graham (Pers. Comm.) believes that T. endemus is a relatively polyphageous species.

T. endemus may be synonymous with T. bruchophagi Graham, but the type specimen will need to be compared before this can be confirmed. (M.W.R. Graham, Pers. Comm.). Specimens of T. bruchophagi were obtained from the U.S. National Museum (three females ex seeds of Foeniculum vulgare Miller, Gardena, California and one female collected in a wheat field at Lehi, Utah) and are very similar to specimens of T. endemus reared from E. platyptera, differing mainly in some colour characters.

Table 5.2 The distribution of parasites reared from seed pods of L. corniculatus. Species are arranged in order of abundance of individuals.

Species	Sites																				Totals
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
Entedon dietimus	+	+	+	+	+			+	+		+	+			+	+		+	+	+	14
Trichomalus rufinus	+	+	+	+	+				+		+		+		+			+	+	+	12
Tetrastichus endemus	+	+	+		+		+			+	+			+			+				9
Triaspis sp.			+	+	+			+													4
Pteromalus semotus			+																		1
Pteromalus sp. C.	+	+			+	+					+				+			+	+		8
Pteromalus sequester		+			+	+								+							4
Macroneura vesicularis	+	+	+			+					+			+							6
Trichomalus campestris		+	+																		2
Bracon sp.		+																			1
Lestodiplosis sp.	+	+	+	+																	4
Pteromalus chryses		+																			1
Scambus brevicornis	+																				1
Trichomalus helvipes			+																		1
Scambus eucosmidarum		+																			1
Necremnus tidius			+																		1
Homoporus sp.		+																			1
Pteromalus sp. A		+																			1
Mesopolobus diffinis		+	+																		2
Callitula pyrrhogaster	+																				1
Euderus albitarsis	+																				1
Diadegma sp.	+																				1
Clinocentrus sp.	+																				1

Key to Sites

1 Eppleworth Quarry, E. Yorks.
2 Bulkington, Warwicks.
3 Wharram Quarry, N. Yorks.
4 Hutton Cranswick, E. Yorks.
5 Caulden Lowe, Staffs.
6 Cottingham Gardens, E. Yorks.
7 Chapel Farm, Warwicks.
8 Crowle Waste, N. Lincs.
9 Newbury, Berks.
10 Wavensmoor, Warwicks.
11 Wolvey, Warwicks.
12 Burdale Quarry, N. Yorks.
13 Porthmelgan, Pembs.
14 Spurn Point, E. Yorks.
15 Porth Ruffydd, Anglesey

16 France - Col de la Forclaz
17 Holland - Callantsoog
18 Norway - Fossen
19 Norway - Gaupne
20 Norway - Oslo

Table 5.3 Tetrastichus endemus reared from hosts other than Eurytoma platyptera in seed pods of L. corniculatus.

Locality	Collection Date	Host Species and stage	T. endemus sex
Bulkington, Warwicks	2.8.76	T. rufimus pupa	male
	2.8.76	E. diotimus pupa	female
	8.8.76	E. diotimus larva	female
	24.8.76	not known	female
	24.8.76	E. diotimus pupa	male
	24.8.76	E. diotimus pupa	female

T. bruchophagi is widespread in North America (Butler *et al*, 1968) and has also been recorded from Russia (Nikolskaja, 1932), Belgium (Crevecoeur, 1946), Hungary (Erdos, 1956), Austria (Domenichini, 1965a) and Argentina (Burks, 1943). In the U.S.A. the important host species are the three *Eurytoma* (*Bruchophagus*) species associated with *Medicago*, *Trifolium* and *Lotus* and there is also a record of secondary parasitism of *Hypera postica* via *Bathyplectes curculionis*. European records of *T. bruchophagi* also cite *E. platyptera* and *E. roddi* as the host species (Domenichini, 1965b, Nikolskaja, 1932).

The life histories of *T. endemus* and *T. bruchophagi* also appear to be very similar. *T. endemus* larvae were reared as endoparasites of *E. platyptera* larvae, *T. rufinus* pupae and both larvae and pupae of *E. diotimus*. The *E. diotimus* larva which acted as host developed a hard and stiff cuticle, through which an exit hole was chewed. Inside the seeds of *L. corniculatus* the *T. endemus* larvae also exited from their host larvae before pupation, but did not induce the conspicuous hard cuticle.

In *L. corniculatus* seed pods there are two generations each year corresponding to the generations of its principal host, whereas Randall (1982) reared only one annual generation from the seeds of *Juncus squarrosus* L. Mature larvae form the overwintering stage and in the laboratory produce adults between March and June. Adults of the summer generation emerge between August and October.

Urbahns (1917), Butler *et al* (1968) and Batiste (1967) have described the biology of *T. bruchophagi*, and their observations closely agree with those described here for *T. endemus*. The orginal account by Urbahns does however differ in some respects from the findings of the later workers, as he found that *T. bruchophagi* was usually an ectoparasite, with only a small proportion of the larvae developing as facultative endoparasites. A possible explanation is that the host larvae may have been damaged as they were being removed from the seeds. In the case of *A. loti* any damage often results in *E. diotimus* larvae being expelled through the body wall, and this gives the impression that the larvae are feeding as ectoparasites.

Female *T. endemus* considerably outnumber the males, and during the course of this study only eight of the latter were obtained. No males were recorded from several sites and reproduction in *T. endemus* must be principally parthenogenetic. There is some evidence that a higher proportion of male *T. endemus* were produced from the atypical hosts than from *E. platyptera*. At Bulkington six *T. endemus* adults were reared from hosts other than *E. platyptera*, two of which were males. Five further males were reared from *E. platyptera*, compared with approximately 120 females. The χ^2 [1] (with Yates' Correction) for these figures is 9.74, and is significant at the 1% level, but must be regarded with caution because of the very small numbers of males that were reared. Flanders (1965) has discussed several other examples of parasite sex ratios varying with host species.

T. bruchophagi has been reared from *E. platyptera* feeding in both *L. corniculatus* and *L. tenuis* and from other *Eurytoma* species developing in *Trifolium* and *Medicago* spp. (Neunzig and Gyrisco, 1959 and Batiste, 1967). Seed samples obtained from Hungary have shown that *T. endemus* will also attack *E. platyptera* in *L. tenuis* seeds (two females and one male collected in a seed sample at Kunpeszer, Hungary, 1972 by O. Borsos) but collections of *Trifolium* at Epplewerth and Bulkington failed to extend its known host range to *E. gibba*.

Pteromalus sp. C (Hym., Pteromalidae)

Pteromalus sp. C was reared as a parasite of *E. platyptera* from six localities in the U.K. and two in Norway (table 5.2). Despite its widespread distribution this species is apparently undescribed (Z. Bouček and M.W.R. Graham, Pers. Comms.) and specimens have been deposited with Dr. Graham at the University Museum, Oxford.

In *L. corniculatus* pods *Ptermalus* sp. C was only recorded from *E. platyptera*, and developed as an ectoparasite from eggs laid on the surface of its host.

At Fossen, in Norway, up to seven eggs were found on one host larva. Pteromalus sp. C overwinters as a larva inside the seeds of L. corniculatus and it appears to be univoltine as no adults were produced from current year seeds. This species could be a candidate for biological control useage, if management practices change and E. platyptera becomes a pest of economic importance in the U.S.A. To assist with the identification of Pteromalus sp. C an informal description is provided below:

Female

> Length approximately 1.7mm. Head and body metallic green. Femora, mid and hind tibiae fuscous, paler near the joints. Gaster short, about as long as the thorax. Clypeus striate, shallowly emarginate anteriorly. Funicle stout, widening distally, with all segments, except sometimes the first, transverse. Pronotal collar not margined anteriorly. Line of hairs on underside of costal cell complete. Basal vein hairy, with the basal cell having a few hairs distally. Marginal vein short, about as long as the postmarginal and 1.2 x length of the stigmal vein. Median area of propodeum strongly reticulate, with a large reticulate nucha.

Male

> Similar to female, with legs paler, having only the femora fuscous. Antennae more elongate, proximal funicle segments distinctly longer than broad, distal segments subquadrate.

C Parasites associated with Apion loti

Entedon diotimus (Hym., Eulophidae)

Entedon diotimus is the commonest species of its genus in the U.K. (Graham, 1963) and was the most widespread and numerous of the parasites reared from A. loti (table 5.2).

Several Apion species have been recorded as hosts for Entedon species (for example Fisher, 1970). Graham (1971) stated that E. diotimus had been reared from seed pods of L. corniculatus and a Trifolium species, and Bouček (1977) suggested that the propable hosts were Apion species feeding on these plants. Several other host records for E. diotimus were listed by Bouček and Askew (1968) as 'doubtful' and Graham (1971) has suggested that some of these records may refer to E. heyeri (Ratz.). Morris (1967) mentioned an 'endoparasitic Pteromalid' reared from A. loti and this may also have been E. diotimus as no other endoparasitic chalcidoids were reared from A. loti during this study.

An Entedon sp. was reared from A. loti by Williams (1969) who also described aspects of its biology. This account probably refers to E. diotimus, but enquiries at the British Museum (Natural History), Oxford University Museum and Imperial College, London have failed to trace any material reared by Williams, and this opinion cannot be confirmed. Williams also reared the Entedon sp. from Apion species developing on Rumex stems, but two species may have been involved because the insects reared from the two plants had slightly different life-histories. Rumex stems collected at Bulkington (18.4.79) were found to contain Entedon pupae, but these proved to be E. rumicis Graham.

Entedon loti Erdos, which was collected in association with L. corniculatus, is very similar to E. diotimus and Bouček and Graham (1979) have suggested that it may be only a form of the latter. Erdos (1951) also collected Entedon fufius Walker (as E. montanus Erdos) from an area that contained large quantities of L. corniculatus and suggested that an Apion sp. on L. corniculatus might be the host. E. fufius was present at Gaupne in Norway (one female collected 19.7.79), but no specimens were reared from the A. loti larvae collected at that site.

E. diotimus females were found searching L. corniculatus flowers at Bulkington (26.6.77) and at Leirdal in Norway (24.7.79). Another E. diotimus female was observed standing at one end of a seed pod, while a female A. loti was ovipositing into the same pod (Eppleworth Quarry, 12.7.78). After laying its egg the beetle disturbed the parasite, which flew off without examining the oviposition site.

Beaver (1966) and Fisher (1970) have described three Entedon species that oviposit into the eggs of their Coleopteran hosts, while Abedin and Quayam (1971) found that the young larvae of an unidentified Entedon species actively burrowed into the body cavities of their hosts. Just hatched A. loti larvae already contained E. diotimus larvae, showing that they are attacked at either the egg or very early larval stages. No E. diotimus eggs or larvae were seen on the surface of the host, suggesting that they are probably placed internally. Repeated searches were made in A. loti eggs and larvae, but unfortunately no eggs of E. diotimus were found.

Three distinct larval stages were detected, and their morphology was found to correspond closely to the three larval instars of E. ergias Walker described by Beaver (1966). First instar larvae of E. diotimus have twelve apparent body segments and a prominent head. There is also a prominent plate on the surface of the last segment which bears several long spines and there are several rows of short spines projecting backwards from some of the intersegmental areas. Second and third instar larvae are similar to each other in general appearance, having a smooth cuticle and thirteen body segments. Second instar larvae are nonetheless easily distinguished by the lack of sclerotisation of the mandibles.

A. loti larvae were divided by eye into three size classes on the basis of the size of their head capsules. The contents of the larvae were examined and the instars of any E. diotimus larvae were recorded (table 5.4a). First instar larvae were found in all three sizes of A. loti larvae, whereas the second and third parasite instars were effectively restricted to the most mature hosts. The larvae continue to grow during all three instars (table 5.4b), but development is slow during the first instar. Beaver (1966) found that E. ergias larvae have a similar pattern of development. The strategy of E. diotimus is clearly to cause as little damage as possible to the host before it has reached a size that is sufficient to support the mature larva. The moult into a second instar larva, and the phase of rapid growth that follows, occur at about the time of the hosts moult into a third instar. The reason for entering the host at an early stage may be because it is necessary in order to avoid encapsulation and competition with ectoparasites. Early entry is a feature of most endoparasitic insects (Askew, 1975).

The mandibular sclerotisation of the three instars of E. diotimus reflects

Table 5.4a The larval instars of *Endedon diotimus* inside *Apion loti* larvae of different ages. *Apion loti* were collected at Eppleworth Quarry between 14 August and 6 September 1977.

E. diotimus larval instar	Estimated *A. loti* larval instar			Totals
	1	2	3	
1	21	20	15	56
2	0	7	56	63
3	0	4	143	147

Table 5.4b Lengths of *Entedon diotimus* larvae obtained from *Apion loti* larvae collected at Eppleworth Quarry between 14 August and 6 September 1977. Lengths were measured after lowering a cover-slip onto the parasite larvae. All lengths are in mm.

E. diotimus larval instar	number of measurements	Mean bodylength ± 1 S.D.	Maximum Length	Minimum Length
1	26	0.56 ± 0.19	0.96	0.26
2	17	1.13 ± 0.21	1.59	0.85
3	28	1.86 ± 0.35	2.60	1.23

the changing needs of the parasite during its development. First instar larvae require their mandibles for breaking their egg membrane and probably for use in aggressive encounters with other *E. diotimus* larvae. Two or even three larvae were occasionally recorded inside one host, but no more than one second instar larva was ever recorded, and there were no records of two parasites successfully developing on one host. Elimination of supernumeries may have been through direct fighting, but physiological suppression may also have been involved (Fisher, 1970).

Second instar larvae feed on the softer tissues of their hosts and have weakly sclerotised mandibles, whereas those of final instar larvae are once more strongly sclerotised. These are needed during the final instar because the larva destroys the internal organs of the host, and it must also rupture the cuticle of *A. loti* in order to emerge prior to pupation.

Parasitised *A. loti* larvae appear to feed normally and do not shew outward signs of the presence of *E. diotimus* until shortly before the parasite larva emerges. During these later stages the body contents of the host are rapidly consumed and eventually only the head capsule and cuticle remain. After emerging from its host the larva produces a bright orange meconium and enters a short pre-pupal phase. The pre-pupa assumes the general shape of the pupa and is white in colour. The nervous tissue in the head is bright red and the brain, a pair of commissures, and a large cephalic ganglion are prominently displayed.

The pupa of *E. diotimus* is similar to those of other members of the genus and has a strong, hard, blue-black integument. *E. diotimus* is almost entirely univoltine and these pupae form the overwintering stage. When the *L. corniculatus* pods dehisce the pupae are ejected and fall to the ground. They remain on the surface, where some will become covered by leaf litter etc., and can be obtained by suction sampling followed by hand sorting.

On two occasions *E. diotimus* larvae failed to destroy the host larva before it began to pupate. Both parasites successfully emerged from the *A. loti* pupae but formed pupae which were visibly deformed and did not survive.

One adult male *E. diotimus* emerged in 1977 from a pupa collected in a current year *L. corniculatus* pod, and collections in 1978 again produced one example (a female) of *E. diotimus* failing to enter diapause. Both adults have some structural features which are atypical for *E. diotimus*. The male has a strongly arched thorax and a scutellum with a partial transverse groove that is asymmetrical and uneven. The female is unusually dark, with the areoles of the mesoscutum and scutellum relatively broader and shallower than in typical specimens. There is again a transverse depression across the scutellum, and the antennae are unusually short and broad, with the first funicle segment quadrate and shorter than the second.

Overwintering *E. diotimus* pupae require a period of cold conditioning before diapause is terminated. Pupae kept outdoors during the winter produce adults from the following April, but no adults are produced if the pupae are kept in the laboratory through the same period. These pupae often remain healthy and can produce adults after 18 months in diapause if they are exposed to cold during their second winter. The success rate is nonetheless considerably lower after an extra years delay.

Adult *E. diotimus* were collected between May and September (table 5.5 and 5.6). Males are most abundant in June, with females reaching their peak numbers a month later. The earlier appearance of the males is a feature of many species of Chalcidoid Hymenoptera (Askew, 1968). Females formed approximately 60% of the adults that were collected, but reared material contained equal proportions of the two sexes (table 5.7a) and this difference may reflect a longer life span in the adult females.

Trichomalus rufinus (Walker) (Hym., Pteromalidae)

T. rufinus was the most numerous of the ectoparasitic species reared from *A. loti*, and occurred at all the sites where extensive sampling took place (table 5.2).

Table 5.5 Records of adult *Entedon diotimus* collected in the U.K. by sweeping or with a suction sampler.

Locality	Date	Numbers Female	 Male
Brumby Common, Lincs.	2.8.80	3	0
Bulkington, Warwicks.	26.6.77	0	1
	21.7.80	1	5
Crowle Waste, Lincs.	31.7.78	0	1
	2.8.80	1	0
Eppleworth Quarry, E. Yorks.	14.7.77	1	0
	22.6.78	5	3
	7.7.78	2	1
	27.7.78	1	0
Flamborough, N. Yorks.	5.7.78	5	3
Goulceby, N. Lincs. [1]	27.7.80	1	0
Hessle Quarry, E. Yorks.	14.5.79	0	1
	20.6.79	2	1
	10.5.82	1	0
Hose, Leics.	2.7.79	2	0
	10.6.80	1	2
Langdale End, N. Yorks.	14.7.78	1	0
Llangenith Burrows, Gower.	8.6.80	2	1
North Newbold, E. Yorks.	6.6.79	1	1
Scarborough, N. Yorks.	5.7.80	6	1
Silpho Quarry, N. Yorks.	15.7.78	2	3
	16.7.78	1	0
University Campus, Hull	18.6.79	0	1
Wharram Quarry, N. Yorks.	2.6.80	0	4
	9.6.80	9	14
	2.7.80	6	0
	8.7.80	1	0
	14.7.80	3	0
	28.7.80	3	0
	4.8.80	3	0
	18.8.80	2	0
	26.8.80	1	0
	1.9.80	1	0
Totals		68	43

[1] Collected by R.S. Key

Table 5.6a Summary of records of adult <u>Entedon diotimus</u> collected in the U.K. by sweeping or with a suction sampler.

Month	*Entedon diotimus* Female	*Entedon diotimus* Male
May	1	1
June	20	28
July	36	14
August	10	0
September	1	0
Totals	68	43

Table 5.6b Records of adult <u>Entedon diotimus</u> collected by sweeping. Records from outside the U.K.

Locality	Date	Numbers Female	Numbers Male
France (Pyrenees)[1]			
Commun St. Lary Seulan	11.8.80	0	1
Vallee d'Aure	21.7.80	1	0
	25.7.80	3	0
Norway (Jestedalen)			
Fossen	24.7.79	1	0
Gaupne	16.7.79	2	1
	19.7.79	3	3
	6.7.81	1	0
Leirdal	4.8.79	1	0

[1] Collected by M.J. Cripps

Table 5.7a The sex ratios of adult Entedon dietimus emerging from pupae in Spring, 1977. Immature stages were reared as parasites of Apion loti in L. corniculatus pods collected at Bulkington, Warwicks.

Collection Date	Adults Female	 Male	Failed to Emerge
9.7.76	7	4	5
8.8.76	22	19	6
16.8.76	24	31	2
24.8.76	14	18	1
30.8.76	6	2	3
Totals	73	74	17

Table 5.7b The sex ratios of adult Trichomalus rufinus reared as parasites of Apion loti in seed pods of L. corniculatus.

Locality	Numbers Female	 Male
United Kingdom		
Bulkington	18	9
Caulden Lowe [1]	45	31
Eppleworth Quarry	17	6
Hutton Cranswick	2	5
Perthmelgan[2]	24	5
Norway		
Fossen (Jostedalen)	22	22
Oslo	6	0
Totals	134	78

[1] Collected by D.A. Jones and T.J. Crawford

[2] Collected by R.S. Key

Adult parasites attributable to both *T. rufimus* and *T. inops* (Walker) were reared from *A. loti*, but difficulties arose in separating many of the specimens. In Graham's (1969) key to the species of *Trichomalus*, *T. rufimus* and *T. inops* are separated on the basis of the colour of their fore- coxae. Specimens with fore-coxae yellow/testaceous or infuscate at the extreme base are placed as *inops* while those with at least the outer coxal face entirely metallic green are placed as *rufimus*. While attempting to separate reared series of these two species it became apparent that no discrete division of fore-coxal colouration was present. A complete spectrum from entirely yellow to entirely green often occurred in specimens reared from the same site. Table 5.8 summarizes the observed variation at five sites where *Trichomalus* was abundant.

Being unable to find any other characters on which to separate these species I consulted Dr. M.W.R. Graham, who confirmed that they were separated on the basis of colour alone. As this appeared unreliable and in the absence of other morphological differences, I believed that there were no grounds for maintaining this division. As both names were published in the same paper (Walker, 1835) I proposed *rufimus* as the valid name and that *inops* should be regarded as a junior synonym (Compton, 1981).

T. rufimus was first reared as a parasite of *A. loti* by Richards (1935) and this relationship has also been reported by Bouček (1977) and by Williams (1969) who also described the life-history and larval morphogy of *T. rufimus*. Richards (1935) also reared *T. rufimus* from *A. sicardi* in seed pods of *L. uliginosis*, and this host record was confirmed by the emergence of two female *T. rufimus* from *L. uliginosus* pods collected at Goodwick, Pembrokeshire.

The larvae of *T. rufimus* develop as ectoparasites on the mature larvae and pupae of *A. loti*. They hatch from eggs that are laid into the general lumen of the seed pods or, more rarely, from eggs that are present on the surface of their hosts. Ovipositing females do not appear to paralyse potential

Table 5.8 Colour variation in _Trichomalus rufinus_ adults reared from _Apion loti_

Locality	Sex	Colour of Fore-coxa Entirely yellow	Intermediate	Outer aspect entirely green	n
Bulkington	Female	4	4	18	26
	Male	1	0	9	10
Cauldon Lowe[1]	Female	1	8	36	45
	Male	0	5	26	31
Eppleworth Quarry	Female	0	3	14	17
	Male	0	2	4	6
Porthmelgan[2]	Female	0	0	24	24
	Male	0	0	5	5
Fossen (Norway)	Female	2	13	7	22
	Male	3	6	13	22
Totals		11	41	156	208

[1] Collected by D.A. Jones and T. Crawford

[2] Collected by R.S. Key

hosts and the young parasite larvae usually have both to find, and to subdue, their victims. A. loti larvae that are attacked by T. rufimus quickly cease feeding and often develop a blotchy 'bruised' appearance. Dmoch and Rutkowska - Ostrowska (1978) showed that female Trichomalus perfectus (Walker) are stimulated to oviposit into rape seed pods by the presence of frass produced by third instar larvae of Ceutherrhynchus assimilis (Paykull) and a similar trigger pattern may be operating with T. rufimus.

At Epplewerth Quarry T. rufimus larvae first appeared in L. corniculatus pods during July and August (tables 5.18 and 5.19). After feeding was completed these early larvae quickly pupated and the first adults were produced in August. Williams (1969) recorded that pupation in T. rufimus lasted 4 - 5 weeks, but in the present study it was found that pupae kept in an unheated room could produce adults after as few as five days and usually took less than ten. The whole life cycle can proceed very rapidly and one T. rufimus egg collected at Bulkington on 13.8.75 hatched the next day and had produced an adult only fourteen days later.

Most of the larvae produced late in the season enter diapause and do not pupate until the following Spring. Adults are an alternative overwintering stage, however, and can be produced as late as October. In the laboratory overwintered larvae produced adults during May and June. Most adults were collected in the field during July and August, but records from the west coast of Britain indicate that T. rufimus can be active as early as April (table 5.9). Graham (1969) collected examples of this species during May and between September and November. Considerably more female than male T. rufimus were reared from A. loti (table 5.7b) and this high female:male ratio was also present amongst the specimens collected as adults.

Trichomalus campestris (Walker) (Hym., Pteromalidae)

A total of 14 T. campestris adults (12 females, 2 males) were reared as parasites of A. loti from L. corniculatus pods collected at Wharram Quarry

Table 5.9 Records of adult <u>Trichomalus rufinus</u> collected by sweep netting or with a suction sampler

Locality	Date	Numbers	
		Female	Male
United Kingdom			
Aberffraw, Anglesey	9.6.79	1	0
Barrow Haven, Lincs.	[1] 10.8.80	0	1
Bulkington, Warwicks.	21.8.77	1	0
Crowle, N. Lincs.	25.8.80	1	0
Eppleworth Quarry, E. Yorks.	13.8.78	0	1
Flamborough, N. Yorks.	5.7.78	1	0
Llangennith Burrows, Gower.	23.4.81	1	0
Spurn Point, E. Yorks.	9.7.78	0	1
Wharram Quarry, N. Yorks.	28.7.80	1	0
	4.8.80	0	1
	9.8.80	0	1
	26.8.80	1	1
	1.9.80	0	1
France			
Vallee d'Aure, Pyrenees	[2] 22.8.80	1	0
Norway (Jostedalen)			
Faberg	22.7.79	2	0
Fossen	24.7.79	2	0
Gaupne	16.7.79	1	0
	19.7.79	2	0
	24.7.79	1	0
	4.8.79	1	0
Nigard	6.8.79	1	0
Totals		18	7

[1] Collected by R.S. Key

[2] Collected by M.J. Cripps

between 30 July and 28 August 1981. An additional specimen, possibly of this species, was reared from *A. loti* collected at Bulkington on 21.8.77. Most *T. campestris* have a dark discal cloud on their fore-wings (Graham, 1969), but this was absent in all the examples reared from *A. loti*. Previously recorded hosts for this common species are *A. loti* and an *Apion* sp. in *Trifolium* inflorescenses (Bouček, 1977), *A. arrogans* (Melamed-Madjar, 1970), an *Apion* sp. in *Rumex* stems (Askew, 1970) and a *Ceuthorynchus* sp. in seed heads of *Thlaspi arvense* L. (Bouček, 1970).

Adult females are an overwintering stage for *T. campestris* and these are active as early as April (table 5.10). Specimens collected at Wolvey were sheltering on *Chamaecyparis lawsoniana* Murr. in company with females of *T. helvipes*, a species which also overwinters in the adult stage (Graham, 1969).

Trichomalus helvipes (Walker) (Hym., Pteromalidae)

T. helvipes was the least abundant of the *Trichomalus* species found to parasitise *A. loti*. Larvae were present in seed pods collected at Wharram Quarry on 30.7.81 and 11.8.81 and three adult females had appeared by late August. Previous host records for this species are of *Brachyonyx pineti* Paykull and ? *Apion* sp. developing in seed heads of *Trifolium* (Graham, 1969).

Necremnus tidius (Walker) (Hym., Eulophidae)

Two female *Necremnus tidius* were reared as parasites of *A. loti* in *L. corniculatus* seed pods collected at Wharram Quarry on 30.7.81 and 11.8.81. The previously recorded hosts for this species are beetles of the families Chrysomelidae and Curculionidae (Bouček, 1977) and it has been reared from *Apion arrogans* Wenck. in Israel (Melamed-Madjar, 1970).

Triaspis sp. (Hym., Braconidae)

Triaspis sp. was reared as a parasite of *A. loti* at four localities, but not from either Bulkington or Eppleworth (table 5.11). At least seven *Apion* species have been recorded as hosts of *Triaspis* spp. (Bertran and Jourdheuil,

Table 5.10 Adult *Trichomalus campestris* collected by sweeping or with a suction sampler

Location	Date	Numbers Female	 Male
United Kingdom			
Barrow Haven, Lincs.[1]	10.8.80	1	-
Bridestones, N. Yorks.	20.8.78	-	1
Bulkington, Warwicks.	27.4.77	13	-
	15.5.77	2	-
Gibralter Point, Lincs.	15.9.79	2	-
Rhosneigr, Anglesey	10.6.79	1	-
Wharram Quarry, Yorks.	1.9.80	1	-
Wolvey, Warwicks.	20.4.79	-	-
Denmark			
Nymindegab, Jutland	22.8.79	-	1
France			
Valle d'Aure, Pyrenees[2]	22.8.80	-	1
Totals		20	3

[1] Collected by R.S. Key

[2] Collected by M.J. Cripps

Table 5.11 *Triaspis* sp. reared from *Apion loti* in seed pods of *L. corniculatus*.

Locality	Collection Date	Numbers	
		Female	Male
Caulden Lowe, Staffs.[1]	19.10.72	20+	20+
Crowle Waste, N. Lincs.	30.7.78	-	1
Hutton Cranswick, E. Yorks.	19.9.79	6	4
Wharram Quarry, N. Yorks.	11.8.81	2	1
	28.8.81	3	3

[1] Collected by D.A. Jones and T.J. Crawford

1973, Easton, 1946, Lacatusu *et al*, 1978, Legowski, 1955, and Melamed - Madjar, 1970) and the immature stages of representatives of this genus have been described by Obrtel (1960) and Parnell (1964). *Triaspis* eggs are laid into the eggs of their host and Turnbull and Chant (1961) have suggested that *T. thoracicus* (Curtis) may require hosts which bury their eggs beneath the surface of plant tissues. The larvae develop as endoparasites and after destroying their hosts they produce a characteristic loose cocoon. Specimens reared from *A. loti* quickly pupated and produced adults between August and October. Parnell (1964) found that *T. ? obscurellus* (Nees) adults also emerged late in the season, but believed it unlikely that they overwintered as adults and suggested that they may attack some other species which has an overwintering egg stage.

Examples of a second *Triaspis* species (distinguished by its longer ovipositor) were reared form *Trifolium* seed heads collected at Bulkington (22.7.78) and Epplewerth (4.9.78).

Bracon sp. (Hym., Braconidae)

A total of ten elongate cocoons were found in association with the remnants of *A. loti* larvae in *L. corniculatus* pods collected at Bulkington on 21.8.77. Larvae overwintered inside the cocoons and in 1978 five *Bracon* sp. males successfully emerged. An *A. loti* ectoparasite collected at Epplewerth on 6.9.77 produced a similar cocoon, but it died before pupating and its identity cannot be confirmed. *Bracon* species are known mainly as parasites of Lepidoptera (for example Shaw and Askew, 1976b), but another *Bracon* male was reared from *Rumex* stems inhabited by *Apion* species (Cocoon collected at Bulkington 18.4.79, producing an adult by 3.5.79) and Lacatusu *et al* (1978) have reared *Bracon variator* (Nees) from *Apion* spp. developing on *Trifolium repens*.

D Polyphagous parasites

Macroneura vesicularis (Retz.) (Hym., Eupelmidae)

Most published accounts prior to Graham (1969b) refer to this species as Eupelmella vesicularis (Retz.). M. vesicularis is an extremely polyphagous parasite and has been recorded from a wide variety of insect hosts (Gahan, 1933, Muesbeck et al, 1951). More recent host records include Scolytus pygmaeus (Fabr.) under Ulmus bark (Michalski, 1973) and a Tetramesa sp. in galls on Phragmites australis Car. (Bouček, 1970). In addition to specimens reared from L. corniculatus pods, M. vesicularis was reared as a parasite of an Apion sp. in Lathyrus pratensis seed pods (collected Hutton Cranswick 11.9.79 and Hessle Quarry, 23.7.78) and from galls of Aulacidea hieracii (Bouche) on Hieracium sp. (Spurn Point, 28.8.79).

Male M. vesicularis are fully winged, but females are brachypterous. Females can reproduce parthenogenetically and considerably outnumber males in European populations. In North America, where this species is probably introduced (Bouček, 1977), reproduction is entirely by parthenogenesis and no males have been recorded.

In the United States Neunzig and Gyrisco (1959) recorded M. vesicularis as a parasite of Eurytoma platyptera, and in the U.K. Williams (1969) reared it as a hyperparasite of Apion loti via Trichomalus rufinus and an Entedon sp. These records have been confirmed and M. vesicularis has also been reared as a primary parasite of A. loti (table 5.12). Adult insects were collected from May to August, with both sexes represented throughout this period (table 5.13). Most of the larvae collected in late summer entered diapause and did not pupate until the following Spring. Some individuals pupated quickly however and adults continued to be produced as late as October.

M. vesicularis was recorded from L. corniculatus pods at most of the sites where samples were taken (table 5.2). Densities were always very low, however, and this appears to be typical of M. vesicularis, as similar results were obtained by Sorenson (1934), Abu and Ellis (1975) and others.

Table 5.12 Host records of Macroneura vesicularis inside seed pods of L. corniculatus.

Host Species	Host Stage	M. vesicularis sex Female	Male	Unknown
Apion loti	larva	3	-	1
Apion loti	pupa	3	-	-
Entedon diotimus	larva	2	1	-
Entedon diotimus	pupa	2	1	-
Trichomalus rufinus	larva	1	-	-
Eurytoma platyptera	larva/pupa	10	-	-
		21	2	1

Table 5.13 Records of adult Macroneura vesicularis collected by sweeping

Locality	Date	Numbers Female	Male
United Kingdom			
Aberffraw, Anglesey	9.6.79	-	1
Askham Bog, Yorks.	23.8.80	1	-
Bulkington, Warwicks.	24.7.80	-	1
Crowle Waste, Lincs.	27.5.78	1	-
	30.7.78	1	-
Eppleworth Quarry, E. Yorks.	22.6.78	1	1
Flamborough, N. Yorks.	4.7.78	8	-
Scunthorpe, Lincs.	11.8.78	-	1
Stone Creek, E. Yorks.	7.6.80	-	1
Wharram Quarry, N. Yorks.	12.5.80	1	-
	29.7.80	1	-
	9.8.80	1	1
Denmark			
Esbjerg	23.8.79	2	-
Rold Forest	17.8.79	2	-
	18.8.79	-	1
Ulbjerg	19.8.79	1	1
	20.8.79	1	-
United States of America			
Dinosaur State Park, Conn.	3.5.80	7	-

Pteromalus sequester Walker (Hym., Pteromalidae)

P. sequester was reared from L. corniculatus pods at a number of localities (table 5.2), but was apparently absent from Eppleworth Quarry. E. platyptera was found to be the preferred host, with A. loti the only other host species recorded (table 5.14a). Three specimens probably conspecific with H. sequester were also reared from a sample of Lotus tenuis seed sent from Kunpeszer in Hungary, but the host was not established.

Parnell (1964) reared P. sequester as a parasite of three Coleoptera species in the seed pods of gorse and broom and has described the immature stages and like-history of this species. He found that P. sequester had two generations each year on gorse, but only one on broom. One generation each year may also be typical of this species when it is developing on L. corniculatus, as no adults were reared before late August, which gave little time for the production of a second generation.

Adult P. sequester are present throughout the summer period (table 5.15a) and most specimens were collected from gorse bushes. Parnell (1964) found that Ulex was the most important host plant for P. sequester and this was also the case at Bulkington, where large numbers were reared as parasites of Apion ulicis larvae and pupae (pods collected 22.7.78 and 5.8.78 produced 26 females and 26 males). P. sequester was also reared from Bruchidius ater in broom pods (one male produced from pods collected on 28.8.78 from a quarry north of Stoney Stanton, Leics.) and from seed heads of a Trifolium sp. (Bulkington, collected 22.7.78, one female).

The P. sequester species group also contains P. cionobius (Erdos) P. act inopterae (Hedqvist) and P. medicaginis (Gahan), (Graham 1969, Hedqvist, 1977). P. actinopterae has only recently been described (Hedqvist, 1977) and the only confirmed records of P. cionobius are from Hungary (Graham, 1969) although specimens from Andorra agree very well with the description (three females, two males collected at St. Julia on 27 and 30 August 1980 by M.J. Cripps).

Table 5.14 *Pteromalus* spp. reared from seed pods of *L. corniculatus*.

a *Pteromalus sequester*

Locality	Collection Date	Host Species	Numbers Female	 Male
Botanic Gardens, Cottingham	1977	E. platyptera	1	-
Bulkington, Warwicks.	25.8.75	A. loti	2	-
	31.8.75	E. platyptera	1	-
	2.8.76	A. loti	1	-
	16.8.76	E. platyptera	5	-
Caulden Lowe, Staffs[1]	19.10.72	-	1	-
Spurn Point, E. Yorks.	-.7.81	E. platyptera	17	-

b *Pteromalus chrysos*

Locality	Collection Date	Host Species	Numbers Female	 Male
Bulkington, Warwicks.	-.7.76	C. compositella	-	2
	-.8.76	C. compositella	1	2
	-.8.76	Scambus eucosmidarum	-	1
	-.8.76	Entedon diotimus	-	1
	-.8.76	E. platyptera	-	1

c *Pteromalus semotus*

Locality	Collection Date	Host Species	Numbers Female	 Male
Wharram Quarry, N. Yorks.	26.10.79	C. compositella	1	-
	11.4.80[2]	-	-	1
	11-28.8.81	A. loti	30+	30+

[1] Collected by D.A. Jones and T.J. Crawford

[2] Inside a 1979 pod which had failed to dehisce

Table 5.15 Adult *Pteromalus* spp. collected by Sweeping

a *Pteromalus sequester*

Location	Date	Numbers Female	Male
Brumby Common, Lincs.	13.8.78	1	-
	2.8.80	5	2
Bulkington, Warwicks.	20.5.78	1	-
	2.6.78	2	-
	2.7.78	1	-
Goodwick Reedswamp, Pembs.[1]	20.9.80	3	-

b *Pteromalus chryses*

Location	Date	Numbers Female	Male
Eppleworth Quarry, E. Yorks.	1.6.78	-	1
	13.8.78	1	-
New Galloway, Scotland [2]	23.8.78	1	-
Scarborough, N. Yorks.	21.10.79	1	-

[1] Collected by R.S. Key

[2] Collected by D.C. Compton

P. medicaginis is a parasite of *Bruchophagus* species, including *E. (Bruchophagus) platyptera* (Urbahns, 1916) and was first described from the U.S.A. Nikolskaja (1932) recorded *P. medicaginis* from Russia and commented that it was one of three European parasites of *Bruchophagus* spp. that may have been introduced, with their hosts, into the U.S.A. The presence of *P. medicaginis* in Europe has not been confirmed and Graham (1969) has suggested that *P. medicaginis* may be identical with one of the better known European species in the *sequester* group. *P. sequester* is a strong candidate for any synonymy because it has a similar host range to *P. medicaginis*.

Specimens of *P. medicaginis* that had been determined by Gahan were obtained from the U.S. National Museum and these have been compared with reared specimens of *P. sequester*. The two species appear to be very similar, but the sculpturing of the propodeum is distinctly stronger in the specimens of *P. medicaginis*. In this respect *P. medicaginis* more closely resembles *Pteromalus* sp. B, which was reared from *L. corniculatus* pods collected in France and may also be synonymous with *P. sequester*. A study of the type material and a more extensive appraisal of the range of variation will be necessary before the synonymy of this group can be clarified.

Pteromalus sp. B (Hym., Pteromalidae)

A single female *Pteromalus* sp. was obtained from a *L. corniculatus* seed sample collected at Col de la Forclaz, Lac d'Annecy, Haute Savoie, France by D.A. Jones. The host species was not established, but both *A. loti* and *E. platyptera* were also present. *Pteromalus* sp. B is a member of the *sequester* group, the species of which have the anterior margin of their clypeus deeply incised (Graham, 1969) and is characterised by the form of the propodeum, which is unusually short, and by the presence of a number of hairs along the basal vein of the forewing. It may be synonymous with *P. sequester*.

Pteromalus chrysos Walker (Hym., Pteromalidae)

P. chrysos is a polyphagous species with a list of host species that consists mainly of Lepidoptera and their parasites (Bouček, 1977) but also includes the phytophagous chalcid *Megastigmus spermatrophus* Wachtl (Lessman, 1974). *L. corniculatus* pods collected at Bulkington in 1976 produced eight *P. chrysos* adults which as larvae had developed as ectoparasites of four different host species (table 5.14b). Adults were collected by sweeping at several other sites and these included one female found on *L. corniculatus* at Eppleworth Quarry (table 5.15b).

Pteromalus semotus Walker (Hym., Pteromalidae)

P. semotus is a common species that is known mainly as a primary and secondary parasite of Lepidoptera. Recent host records include those of Kolaib *et al*, 1980, Pyornila and Pyornila, 1979, Raske, 1979 and Shaw, 1981. Gradwell (in Graham, 1969) reared *P. semotus* from *Apion pomonae* (F.) in vetch pods and *A. loti* was the most important host in *L. corniculatus* pods, with only one individual reared from an alternative host (*C. compositella*). *P. semotus* was only found in *L. corniculatus* pods at Wharram Quarry (table 5.14c), where in 1981 it was one of the most abundant of the ectoparasites reared from *A. loti*. Specimens collected in August 1981 produced adults within a few days, but those collected in previous years showed that this species can also overwinter as a larva. *P. semotus* was also reared from an *Apion* sp. in pods of *Lathyrus pratensis* collected at Hutton Cranswick on 11.9.79. Large numbers of *Bruchus loti* were also present in the pods, but none of them were attacked.

Lestodiplosis sp. (Diptera, Cecidomyiidae)

Active Diptera larvae were occasionally found inside mature seed pods of *L. corniculatus*. These were identified as a species of *Lestodiplosis* using the key of Roskam (1979), but as no adults were reared their identity has not been confirmed. The larvae are more elongate than those of ? *Clindiplosis* sp. (the only other species of Dipteron found in *L. corniculatus* pods) and are a bright red with orange and white lateral blotches. Features characteristic of *Lestodiplosis* larvae were the pairs of pseudopeds and the absence of a sternal spatula.

Lestodiplosis larvae have also been recorded from the seed heads of *Trifolium* and *Centaurea* (Nijveldt, 1963 and Otter, 1938), *Sarothamnus* seed pods (Parnell, 1963) and *Betula* catkins (Hodges, 1969). The larvae are predatious, with most host records referring to other cecidomyiids (Barnes, 1928).

In *L. corniculatus* pods *Lestodiplosis* sp. larvae were present mainly in the late summer and autumn and were seen feeding on the larvae and pupae of *A. loti* and on the pupae of *E. dictimus* (table 5.16). Parnell (1964) has also recorded *Lestodiplosis* larvae attacking larvae of the parasite *Mesopolobus mediterraneus* (Mayr), a rare example of tertiary parasitism. The preference shown for mature pods may be because *Lestodiplosis* can only gain entry after *A. loti* exit holes are available. Feeding behaviour appeared to be similar to that described by Nijveldt (1963), with the larvae piercing the surface of their prey and then sucking out their body contents. Although capable of attacking a series of hosts it appeared that each parasite could develop from only one. Mature *Lestodiplosis* larvae overwintered successfully, but no adults were produced.

E 'Accidental' species

Pteromalus sp. A (Hym., Pteromalidae)

Two males of this species emerged during November 1975 and May 1976 from *L. corniculatus* pods collected at Bulkington in 1975. Their larvae developed as ectoparasites of an *E. platyptera* larva and an *A. loti* pupa. The identification of isolated *Pteromalus* males is often very difficult, but these can distinguished from the other *Pteromalus* males reared from *L. corniculatus* by their elongate antennae (all segments longer than broad), lightly reticulate propodeum, complete costal hair line and hairy basal vein.

Table 5.16 Records of Lestodiplosis larvae (Cecidomyiidae) feeding in seed pods of L. corniculatus.

Location	Date	Host	Host Stage
Bulkington	21.8.77	-	-
Epplewerth Quarry	19.7.77	-	-
	14.8.77	Apion loti	Larva
	26.8.77	Apion loti	Larva
	26.8.77 (2)	Apion loti	Pupa
	26.8.77	Entedon diotimus	Pupa
	31.8.77	Apion loti	Pupa
	6.9.77	Apion loti	Pupa
	27.10.77	-	
Hutton Cranswick	11.9.79	Entedon diotimus	Pupa
Wharram Quarry	26.10.79	-	-
	30.9.80	Apion loti	Pupa

Mesopolobus ? diffinis (Hym., Pteromalidae)

Two female specimens of *Mesopolobus ? diffinis* were reared from *L. corniculatus* seed pods. The first was reared from *E. platyptera* collected at Bulkington on 8.8.76 and the second was reared from an *A. loti* larva collected at Wharram Quarry on 11.8.81. Both adults emerged during late August. The females in this group of *Mesopolobus* are difficult to identify and some species remain to be described (R.R. Askew, Pers. Comm.). *M. diffinis* is known mainly as a parasite of Cecidomyiids (Askew, 1970, Redfern, 1975) although a Lepidopteran host has also been recorded (Bouček, 1977). Three examples of the distinctive male of *M. diffinis* were collected during suction sampling at Wharram Quarry on 28.7.81, 4.8.81 and 26.8.81 and an additional male was collected by sweeping at Gibralter Point, Lincs. on 15.9.79.

M. bruchophagi was described by Gahan (1917) from the United States and was recorded as a parasite of *Eurytoma roddi* in Russia by Nikolskaja (1952). Neunzig and Gyrisco (1959) established that *E. platyptera* was an alternative host and Peck (1963) has listed a total of five *Eurytoma* (*Bruchophagus*) species as hosts. *M. bruchophagi* was recorded from Europe by Nikolskaja (1932) but specimens have not been compared with other European species (for example in von Rosen, 1958 and Graham, 1969) and the status of this species in Europe has not been clarified.

Homoporus sp. (Hym., Pteromalidae)

L. corniculatus seed samples collected at Bulkington in 1977 produced two males of a *Homoporus* sp. in April of the following year. Males of this genus are often difficult to identify with certainty and some U.K. species have not yet been described. No *Homoporus* have been reared from *E. platyptera* before and the more usual hosts are a variety of insects developing inside grass stems and Cynipidae in galls on herbaceous plants (Graham, 1969).

Callitula pyrrhogaster Walker (Hym., Pteromalidae)

A single male *Callitula pyrrhogaster* was reared from an *L. corniculatus* seed collected at Eppleworth Quarry on 14.7.77. where it had presumably developed as a parasite of *Eurytoma platyptera*. The insect was found in a pod which had been produced the previous year but had failed to dehisce. No other examples of this species were found in association with *L. corniculatus* and the recorded hosts are small Diptera in grass stems (Bouček, 1977). Brachypterous *C. pyrrhogaster* adults were collected at a number of localities, including several where *L. corniculatus* was sampled (table 5.17) and *E. platyptera* is clearly an exceptional host for this species.

The parasites of *Apion loti* at Eppleworth Quarry and the relationship between host density and frequency of parasitism.

At Eppleworth the *A. loti* parasite complex was relatively simple and consisted of only one endoparasite (*Entedon diotimus*) and three ectoparasites (*Trichomalus rufinus*, *Macroneura vesicularis* and a *Lestodiplosis* sp.). During the two year sampling period only five specimens of *M. vesicularis* and six of *Lestodiplosis* sp. were reared from *A. loti*, and these polyphageous species therefore constituted a negligable mortality factor for the *A. loti* population.

T. rufinus was the most frequent ectoparasite of *A. loti*, but nontheless individuals were reared from only 1.79% of the *A. loti* in 1977 and 4.95% in 1978. Larvae of *T. rufinus* developed as parasites of both the larvae and pupae of *A. loti* (tables 5.18 and 5.19) and several of the former will have been feeding on hosts which already contained larvae of the endoparasite *E. diotimus*. *E. diotimus* was the most numerous parasite of *A. loti* at Eppleworth Quarry, and attacked an estimated 37.3% of the host population in 1977 and 32.0% in 1978 (tables 5.20 and 5.21).

The relationship between parasitism and host density is of particular interest because it can influence the stability of host-parasite interactions. The aggregation of parasites in areas of high host density ('non-random searching') improves the stability of many host-parasite models (Hassell and May, 1974) and has been demonstrated in a number of laboratory studies (for

Table 5.17 Records of adult *Callitula pyrrhogaster* collected by sweeping and with a suction sampler.

Location	Date	Numbers Female	Male
Askham Bog, Yorks.	23.8.80	4	-
Bulkington, Warwicks.	15.8.78	-	1
Goodwick Reedswamp, Pembs.[1]	20.9.80	1	-
Gundale, N. Yorks.	18.10.81	1	-
Porthdafarch, Anglesey	17.5.81	1	-
Raincliff Wood, Scarborough	16.9.78	1	-
Wharram Quarry, N. Yorks.	2.6.80	1	-
	2.7.80	1	2
	14.7.80	-	2
	28.7.80	-	1
	18.8.80	2	1
	26.8.80	1	-
	1.9.80	-	1

[1] Collected by R.S. Key

Table 5.18 *Trichomalus rufinus* in seed pods of *L. corniculatus* collected at Eppleworth Quarry in 1977

Sample	*T. rufinus* larvae on *A. loti* larvae	on *A. loti* pupae	host stage uncertain	*T. rufinus* pupae	*T. rufinus* adults	*T. rufinus* exit holes
1.1	0	0	0	0	0	0
1.2	0	0	0	0	0	0
1.3	0	0	0	0	0	0
2.1	1	0	0	0	0	0
2.2	0	0	0	0	0	0
2.3	0	0	0	0	0	0
3.1	0	0	0	0	0	0
3.2	0	0	0	0	0	0
3.3	0	0	0	0	0	0
4.1	0	0	0	0	0	0
4.2	0	0	0	0	0	0
4.3	1	1	0	0	0	0
5.1	0	0	0	0	0	0
5.2	3	0	1	0	0	0
5.3	2	0	0	2	0	0
6.1	1	3	2	3	0	0
6.2	0	0	2	0	0	0
6.3	1	0	0	0	0	0
7.1	0	0	0	0	0	0
7.2	5	3	0	0	0	0
7.3	4	1	2	0	0	0
8.1	0	0	0	0	0	0
8.2	1	0	1	0	0	1
8.3	0	0	0	0	0	1
9.1	0	1	0	0	1	0
9.2	0	0	0	0	0	0
9.3	0	0	0	0	0	0
10.1	0	0	0	0	0	0
10.2	0	0	2	0	0	2
11.1	0	0	0	0	0	0
11.2	0	0	0	0	0	0
Totals	19	9	10	5	1	4

Table 5.19 *Trichomalus rufinus* in seed pods of *L. corniculatus* collected at Eppleworth Quarry in 1978.

	T. rufinus larvae					
Sample	on *A. loti* larvae	on *A. loti* pupae	host stage uncertain	*T. rufinus* pupae	*T. rufinus* adults	*T. rufinus* exit holes
2.1	0	0	0	0	0	0
2.2	0	0	0	0	0	0
2.3	0	0	0	0	0	0
3.1	0	0	0	0	0	0
3.2	0	0	0	0	0	0
3.3	0	0	0	0	0	0
4.1	2	0	0	0	0	0
4.2	0	0	0	0	0	0
4.3	0	0	0	0	0	0
5.1	0	2	0	0	0	0
5.2	0	0	0	0	0	0
5.3	0	0	0	0	0	0
6.1	0	0	0	0	0	0
6.2	0	0	1	2	0	0
6.3	0	0	0	0	0	0
7.1	0	0	0	0	0	0
7.2	0	0	0	0	0	0
7.3	1	0	0	0	0	0
8.1	0	0	1	0	0	0
8.2	0	0	0	3	0	0
8.3	0	0	0	0	0	0
9.1	0	0	0	1	0	0
9.2	0	0	0	0	0	0
9.3	0	0	2	1	0	0
Totals	3	2	4	7	0	0

Table 5.20 *Entedon diotimus* in pods of *L. corniculatus* and the estimated initial percentage parasitism of *Apion loti*. Eppleworth Quarry, 1977

		Entedon diotimus			*Apion loti*	Estimated
Sample	larvae	pre-pupae	pupae	total	reaching pupation	% parasitism
2.1	-	-	-	0	1	0
2.2	-	-	-	0	0	-
2.3	-	-	-	0	0	-
3.1	-	-	-	0	1	0
3.2	-	-	-	0	0	-
3.3	-	-	-	0	1	0
4.1	-	1	1	2	11	15
4.2	1	-	-	1	2	33
4.3	1	-	-	1	10	9
5.1	1	1	3	5	2	71
5.2	5	2	4	11	15	42
5.3	2	7	5	14	24	37
6.1	3	6	30	39	39	50
6.2	1	-	1	2	9	18
6.3	-	1	1	2	5	29
7.1	1	1	2	4	4	50
7.2	9	7	35	51	66	44
7.3	10	3	27	40	60	40
8.1	2	-	6	8	16	33
8.2	-	-	35	35	59	37
8.3	-	-	4	4	12	25
9.1	1	-	38	39	52	43
9.2	1	1	16	18	25	42
9.3	-	-	11	11	33	25
10.1	-	-	3	3	22	12
10.2	-	-	3	3	16	16
11.1	-	-	6	6	7	46
11.2	-	-	8	8	25	24
Totals	38	30	239	307	517	37.3

Table 5.21 *Entedon diotimus* in pods of *L. corniculatus* and the estimated percentage parasitism of *Apion loti*. Eppleworth Quarry, 1978

		Entedon diotimus				
Sample	larvae	pre-pupae	pupae	total	*Apion loti* reaching pupation	Estimated % parasitism
4.1	-	1	-	1	1	50
4.2	1	-	2	3	6	33
5.1	-	-	-	1	15	6
5.2	-	-	1	0	3	0
5.3	-	-	-	0	2	0
6.1	-	-	-	0	2	0
6.2	1	1	3	5	2	71
6.3	1	1	1	3	11	21
7.1	-	-	1	1	5	17
7.2	-	-	3	3	6	33
7.3	1	-	4	5	7	42
8.1	-	-	-	0	1	0
8.2	1	-	7	8	9	47
8.3	-	-	2	2	1	66
9.1	-	-	6	6	7	46
9.2	-	-	-	0	0	-
9.3	-	-	3	3	9	25
Totals	5	3	33	41	87	32.0

example Hassell, 1971). Results from natural populations have often failed to detect this relationship, however, and Morrison and Strong (1980), after quoting examples where the intensity of parasitism varied independantly, negatively and positively with host density, concluded that, in the field, positive correlations are uncommon.

The survey of L. corniculatus seed pod inhabitants at Epplewerth Quarry provided an opportunity to relate the densities of A. loti with the levels of parasitism that were sustained. Host dispersion patterns often vary with the scale on which measurements are taken (Southwood, 1978) and parasites may have responses which also vary according to the scale of sampling units (Hassell and May, 1973). The densities of A. loti were compared at three different levels at Epplewerth Quarry, with sampling units that consisted of individual seed pods, the contents of randomly placed quadrats and adjacent areas of quarry floor.

The 'low growth habitat' at Epplewerth Quarry consists of a relatively flat area of low growing vegetation that is adjacent to the main sampling area. Two samples, each consisting of the contents of five 0.0929 m^2 quadrats, were collected in this area on 26.8.77 and 6.9.77. A. loti (including specimens that had died or had been replaced by parasites) was present at an average density of 24.1 per quadrat, a density considerably lower than the 61.3 per quadrat that was recorded at the main sampling area during the same period. A comparison of the levels of E. dictimus parasitism at the two sites (table 5.22) suggests that at this level the differences in the density of the host species did not significantly influence the degree of parasitism.

Individual L. corniculatus plants could not be separated reliably at Epplewerth Quarry because they were generally growing in contact with each other. The numbers of insects contained inside each quadrat (0.0929 m^2 in 1977, 0.025 m^2 in 1978) therefore provides the closest approximation to densities per plant that is available. Estimates of E. dictimus parasitism that are based

Table 5.22 *Entedon diotimus* parasitism of *Apion loti* at Eppleworth Quarry. A comparison of the levels of parasitism recorded at two different areas of the quarry.

	Areas	
	Low Growth Habitat	Main Sampling Area
Nos. of *E. diotimus* recorded	49	90
Nos. of *A. loti* pupae and adults	53	140
Estimated percentage parasitism	48.0	39.1

$\chi^2 [1] = 2.3, \ P > 0.05$

on the ratio of *A.loti* pupae and adults to *E.diotimus* larvae and pupae suggest a tendency for a higher proportion of *A.loti* to be parasitised in quadrats where the density of this species was high (table 5.23). The regression coefficients are not significant however.

Healthy *A.loti* larvae obtained during 1977 sampling weeks five to nine were dissected and the level of parasitism by *E.diotimus* larvae was recorded. 56.8% of the *A.loti* were found to contain *E.diotimus*, a rather higher value than the 43.6% obtained using the ratio estimate described above. Regression analysis using the data obtained by dissection confirms that a higher proportion of the *A.loti* larvae were attacked in quadrats containing a large number of hosts (table 5.24) and therefore that aggregation was occurring at this level.

Several *A.loti* can develop inside the same seed pod. In 1977 pods containing a number of *A.loti* larvae were more likely to contain *E.diotimus* (table 5.25a) but a lower proportion of the hosts were attacked (table 5.25b). In 1978 no significant relationships between *A.loti* density per pod and *E.diotimus* parasitism were recorded (table 5.25).

Examination of the responses of *T.rufinus* to changes in host density is limited by the relatively small numbers of this species that were present. In 1977, but not 1978, pods with several hosts were again more likely to be attacked (table 5.26a) but mortalities caused by *T.rufinus* were not significantly related to host density per pod in either year (table5.26b).

Results from Eppleworth Quarry suggest that *E.diotimus* responds to variation in the density of its host species by aggregating in those quadrats which contain the most hosts. Pods which contain greater numbers of host larvae are also more likely to be attacked but, despite these positive responses, more larvae escape parasitism in pods which contain several larvae. Morrison and Strong (1981) obtained similar results in a study of egg parasitism in the chrysomelid *Cephaloleia consanguinea* Baley.

Table 5.23 *Entedon diotimus* parasitism of *Apion loti* at Eppleworth Quarry in relation to host density per quadrat. Estimates of percentage parasitism are based on the relative proportions of *A.loti* pupae and adults and *E.diotimus* that are produced. Quadrat sizes were 0.025 m^2 in 1978 and 0.0929 m^2 in 1977.

	1977		1978	
Sample	total no. *A.loti*[1]	Estimated % parasitism	total no. *A.loti*[1]	Estimated % parasitism
4.1	-	-	8	50.0
4.2	-	-	11	33.0
4.3	-	-	-	-
5.1	39	71.0	19	6.0
5.2	127	42.0	7	0.0
5.3	191	37.0	3	0.0
6.1	146	50.0	2	0.0
6.2	36	18.0	16	71.0
6.3	19	29.0	20	21.0
7.1	31	50.0	8	17.0
7.2	164	44.0	10	33.0
7.3	164	40.0	21	42.0
8.1	30	33.0	2	0.0
8.2	110	37.0	24	47.0
8.3	17	25.0	3	66.0
9.1	99	43.0	16	46.0
9.2	44	42.0	-	-
9.3	48	25.0	17	25.0

Regression of arc sine transformed percentage parasitism on total no. *A.loti* per sample, $r\,[13] = 0.23$ (in 1977) and $r\,[14] = 0.46$ (in 1978), $P > 0.05$.

[1] Includes dead specimens and those destroyed by parasites.

Table 5.24 *Entedon diotimus* parasitism of *Apion loti* in relation to host density per quadrat (0.0929 m^2). Eppleworth Quarry, 1977. Parasitism estimated by dissection of *A. loti* larvae.

Sample	total no. *A. loti* [1]	*A. loti* larvae dissected	*E. diotimus* larvae		Estimated % parasitism
			present	absent	
5.1	39	15	7	8	46.7
5.2	127	65	38	27	58.5
5.3	191	102	68	34	66.7
6.1	156	46	22	24	47.8
6.2	36	19	10	9	52.6
6.3	19	4	1	3	25.0
7.1	31	19	6	13	31.6
7.2	164	50	27	23	54.0
7.3	164	27	18	9	66.0
Totals	927	347	197	150	56.8

$r_{\boxed{7}}$ (arc sine transformed) percentage parasitism on total no. *A. loti* per sample = 0.78, $P < 0.01$

---

[1] Includes dead specimens and those destroyed by parasites

Table 5.25 Parasitism of *Apion loti* by *Entedon diotimus* in relation to the number of *Apion loti* inside each seed pod. Eppleworth Quarry, 1977 and 1978.

A The numbers of pods in which *A. loti* was attacked by *E. diotimus*

1977

	A. loti density per pod [2]				
	1	2	3	>3	
Pods containing *E. diotimus*	137	103	31	7	
Pods with *A. loti* only[1]	891	380	123	43	X^2 [3] = 17.52, $P < 0.01$
% of pods with *E. diotimus* present	13.3	21.3	20.1	14.0	

1978

	A. loti density per pod [2]			
	1	2	>2	
Pods containing *E. diotimus*	25	7	5	
Pods with *A. loti* only[1]	145	31	17	X^2 [2] = 1.11, $P > 0.05$
% of pods with *E. diotimus* present	14.7	18.4	22.7	

B The numbers of *A. loti* individuals attacked by *E. diotimus*

1977

	A. loti density per pod [2]				
	1	2	3	>3	
E. diotimus produced	137	122	40	8	
Remaining *A. loti*[1]	891	844	422	217	X^2 [3] = 22.28, $P < 0.001$

1978

	A. loti density per pod [2]			
	1	2	>2	
E. diotimus produced	25	8	8	
Remaining *A. loti*[1]	145	68	79	X^2 [2] = 1.91, $P > 0.05$

[1] Includes all egg, larvae, dead specimens and those destroyed by parasites other than *E. diotimus*.

[2] Includes all *A. loti* present initially

Table 5.26 Parasitism of Apion loti by Trichomalus rufinus in relation to the number of Apion loti inside each seed pod. Eppleworth Quarry, 1977 and 1978.

A The numbers of pods in which A. loti was attacked by T. rufinus

1977

	A. loti density per pod[2]				
	1	2	3	>3	
Pods containing T. rufinus	15	22	5	4	
Pods with A. loti only[1]	1013	461	149	46	X^2 [3] = 17.98, $P < 0.001$
% of pods where T. rufinus was present	1.46	4.55	3.2	8.0	

1978

	A. loti density per pod[2]			
	1	2	>2	
Pods containing T. rufinus	9	2	2	
Pods with A. loti only[1]	161	36	20	X^2 [2] = 0.53, $P > 0.05$
% of pods where T. rufinus was present	5.3	5.3	9.1	

B The numbers of A. loti individuals attacked by T. rufinus

1977

	A. loti density per pod[2]				
	1	2	3	>3	
T. rufinus produced	15	24	5	4	
A. loti present[1]	1013	942	457	221	X^2 [3] = 4.61, $P > 0.05$
% Parasitism	1.46	2.48	1.08	1.77	

1978

	A. loti density per pod[2]			
	1	2	>2	
T. rufinus produced	9	3	4	
A. loti present[1]	161	73	73	X^2 [2] = 0.21, $P > 0.05$
% Parasitism	5.3	3.95	5.2	

[1] Includes all eggs, larvae, dead specimens and those destroyed by parasites other than T. rufinus.

[2] Includes all A. loti present initially

They found that as egg density per leaf increased, so did the likelihood of at least one egg being discovered. Among those leaves that had been discovered, the percentage of parasitised eggs fell with increasing density, however, and the net result was a decrease in the overall probability of parasitism as egg density increased. Several other studies of host-parasite interactions have also found that host clumping results in a lower level of parasitism (Morrison and Strong, 1981), but the reasons for this are still uncertain, although predator satiation and interferance have been suggested.

The L. corniculatus seed pod food web.

The trophic relationships found inside L. corniculatus seed pods are summarised in figure 5.1. The direction of the arrows follows Gallopin (1972) and points from the predators to their prey. The quantified results from four major sampling sites are given in tables 5.27 to 5.29, and the combined totals are summarised in the form of a matrix in table 5.30.

All the relationships shown in figure 5.1 were obtained during the four major sampling periods with the exception of those concerning Bracon sp., Callitula pyrrhogaster, Euderus albitarsis, Homoporus sp. and Pteromalus semotus (when feeding on C. compositella). These interactions were never frequent, and in total represented only fifteen individuals.

Sampling methods were different at the four localities. At Eppleworth (as described previously) the contents of randomly placed quadrats were examined. At Wharram Quarry individual plants could be distinguished more easily and this allowed the mature seed production of whole plants to be recorded. L. corniculatus was not as numerous at Fosson and Bulkington, and at these sites the seed pods were obtained as and where available.

The numerical values describing the trophic links are subject to the following limitations:

1. Parasite larvae which died before they could be identified have not been included.

FIGURE 5.1

Food web of the insects inhabiting L. corniculatus seed pods. Observations from all U.K. sampling sites are included.

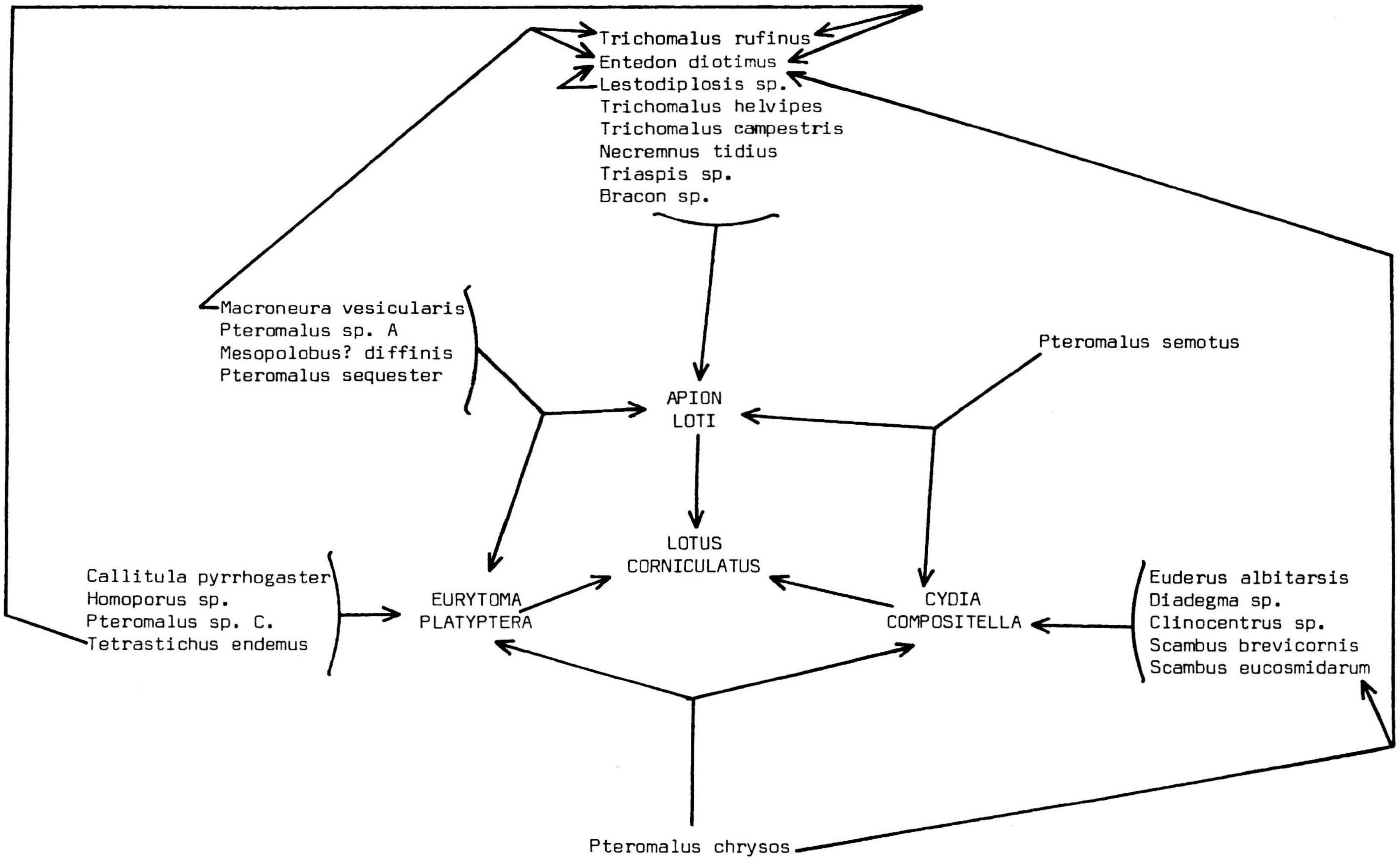

Trichomalus rufinus
Entedon diotimus
Lestodiplosis sp.
Trichomalus helvipes
Trichomalus campestris
Necremnus tidius
Triaspis sp.
Bracon sp.
Macroneura vesicularis
Pteromalus sp. A
Mesopolobus? diffinis
Pteromalus sequester
Pteromalus semotus
APION LOTI
LOTUS CORNICULATUS
Callitula pyrrhogaster
Homoporus sp.
Pteromalus sp. C.
Tetrastichus endemus
EURYTOMA PLATYPTERA
CYDIA COMPOSITELLA
Euderus albitarsis
Diadegma sp.
Clinocentrus sp.
Scambus brevicornis
Scambus eucosmidarum
Pteromalus chrysos

Table 5.27 The trophic relationships inside *L. corniculatus* seed pods at four localities in the United Kingdom and Norway. *A* Trophic levels one and two

Interacting species		Incidence and Location				
Herbivore	Green Plant	Eppleworth	Bulkington	Wharram	Fossen	Combined Totals
Apion loti	Lotus corniculatus	3004	1210	2470	165	6849
Eurytoma platyptera	Lotus corniculatus	155	185	5	70	415
Cydia compositella	Lotus corniculatus	107	46	4	0	157
Habitat units (seed pods) sampled		3916	1195	2392	430	7933
Sampling periods		1977-8	1975-6	Aug.1981	Aug.1979	

Table 5.28 The trophic relationships inside *L. corniculatus* seed pods at four localities in the United Kingdom and Norway. *B* Trophic levels two and three

Interacting Species		Incidence and Location				
1° Parasite	Herbivore	Eppleworth	Bulkington	Wharram	Fossen	Combined Totals
Entedon diotimus	Apion loti	1136	478	721	88	2423
Trichomalus rufinus	Apion loti	64	125	283	57	529
Tetrastichus endemus	Eurytoma platyptera	11	128	3	0	142
Pteromalus semotus	Apion loti	0	0	76	0	76
Pteromalus sp. C.	Eurytoma platyptera	6	6	0	3	15
Trichomalus campestris	Apion loti	0	0	14	0	14
Macroneura vesicularis	Apion loti	5	3	2	0	10
Triaspis sp.	Apion loti	0	0	9	0	9
Lestodiplosis sp.	Apion loti	6	0	1	0	7
Pteromalus sequester	Eurytoma platyptera	0	6	0	0	6
Pteromalus chrysos	Cydia compositella	0	5	0	0	5
Macroneura vesicularis	Eurytoma platyptera	4	0	0	0	4
Scambus brevicornis	Cydia compositella	4	0	0	0	4
Trichomalus helvipes	Apion loti	0	0	3	0	3
Scambus eucosmidarum	Cydia compositella	0	3	0	0	3
Pteromalus sequester	Apion loti	0	3	0	0	3
Necremnus tidius	Apion loti	0	0	2	0	2
Diadegma sp.	Cydia compositella	1	0	0	0	1
Clinocentrus sp.	Cydia compositella	1	0	0	0	1
Pteromalus sp. A	Apion loti	0	1	0	0	1
Pteromalus sp. A	Eurytoma platyptera	0	1	0	0	1
Mesopolobus ? diffinis	Apion loti	0	0	1	0	1
Mesopolobus ? diffinis	Eurytoma platyptera	0	1	0	0	1
Pteromalus chrysos	Eurytoma platyptera	0	1	0	0	1

Table 5.29 The trophic relationships inside _L. corniculatus_ seed pods at four localities in the United Kingdom and Norway. _C_ Trophic levels three and four

Interacting species		Incidence and Location				
2^{o} Parasite	1^{o} Parasite	Eppleworth	Bulkington	Wharram	Fossen	Combined Totals
Macroneura vesicularis	Entedon diotimus	1	5	0	0	6
Tetrastichus endemus	Entedon diotimus	0	4	0	0	4
Lestodiplosis sp.	Entedon diotimus	1	0	0	0	1
Tetrastichus endemus	Trichomalus rufimus	0	1	0	0	1
Macroneura vesicularis	Trichomalus rufimus	1	0	0	0	1
Pteromalus chrysos	Scambus eucosmidarum	0	1	0	0	1
Pteromalus chryses	Entedon diotimus	0	1	0	0	1

Table 5.30 The L. corniculatus seed pod food web matrix. The number at the top of each column refers to the consumer species and the number at the left of each row refers to the host species. Results are pooled from four localities, at Eppleworth, Bulkington, Wharram and Fossen.

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1	6849	415	157	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	2423	529	0	9	76	0	3	10	14	7	0	0	3	0	2	0	0	1	1
3	0	0	0	0	0	142	0	0	15	6	4	0	0	1	0	0	0	0	0	0	1	1
4	0	0	0	0	0	0	0	0	0	0	0	0	0	5	4	0	3	0	1	1	0	0
5	0	0	0	0	0	4	0	0	0	0	6	0	1	1	0	0	0	0	0	0	0	0
6	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

Key to Species

1 Lotus corniculatus
2 Apion loti
3 Eurytoma platyptera
4 Cydia compositella
5 Entedon diotimus
6 Trichomalus rufinus
7 Tetrastichus endemus
8 Triaspis sp.
9 Pteromalus semotus
10 Pteromalus sp. C
11 Pteromalus sequester
12 Macroneura vesicularis
13 Trichomalus campestris
14 Lestodiplosis sp.
15 Pteromalus chryses
16 Scambus brevicornis
17 Trichomalus helvipes
18 Scambus eucosmidarum
19 Necremnus tidius
20 Diadegma sp.
21 Clinocentrus sp.
22 Pteromalus sp. A
23 Mesopolobus ? diffinis

2. Where host records were uncertain the parasites concerned have not been included.

3. Mortality of larval Eurytoma platyptera may have led to an underestimate of the numbers of its endoparasite, Tetrastichus endemus.

4. Larvae of Cydia compositella move from pod to pod during development, and enter the ground to pupate. C. compositella (and associated parasites) are therefore under-represented in the tables.

5. The numbers of the abundant endoparasite Entedon diotimus have been obtained by calculation, with the ratio of E. diotimus pupae to A. loti pupae and adults assumed to represent the level of parasitism present inside the Apion loti larvae that were collected.

A. loti, E. platyptera and C. compositella were present at most of the sites where L. corniculatus pods were sampled (table 4.3) and were found at all the U.K. sites where extensive sampling was conducted. Several of the parasites have an equally wide distribution (table 5.2) and the community can be considered to have a high 'event probability' (Paine, 1980).

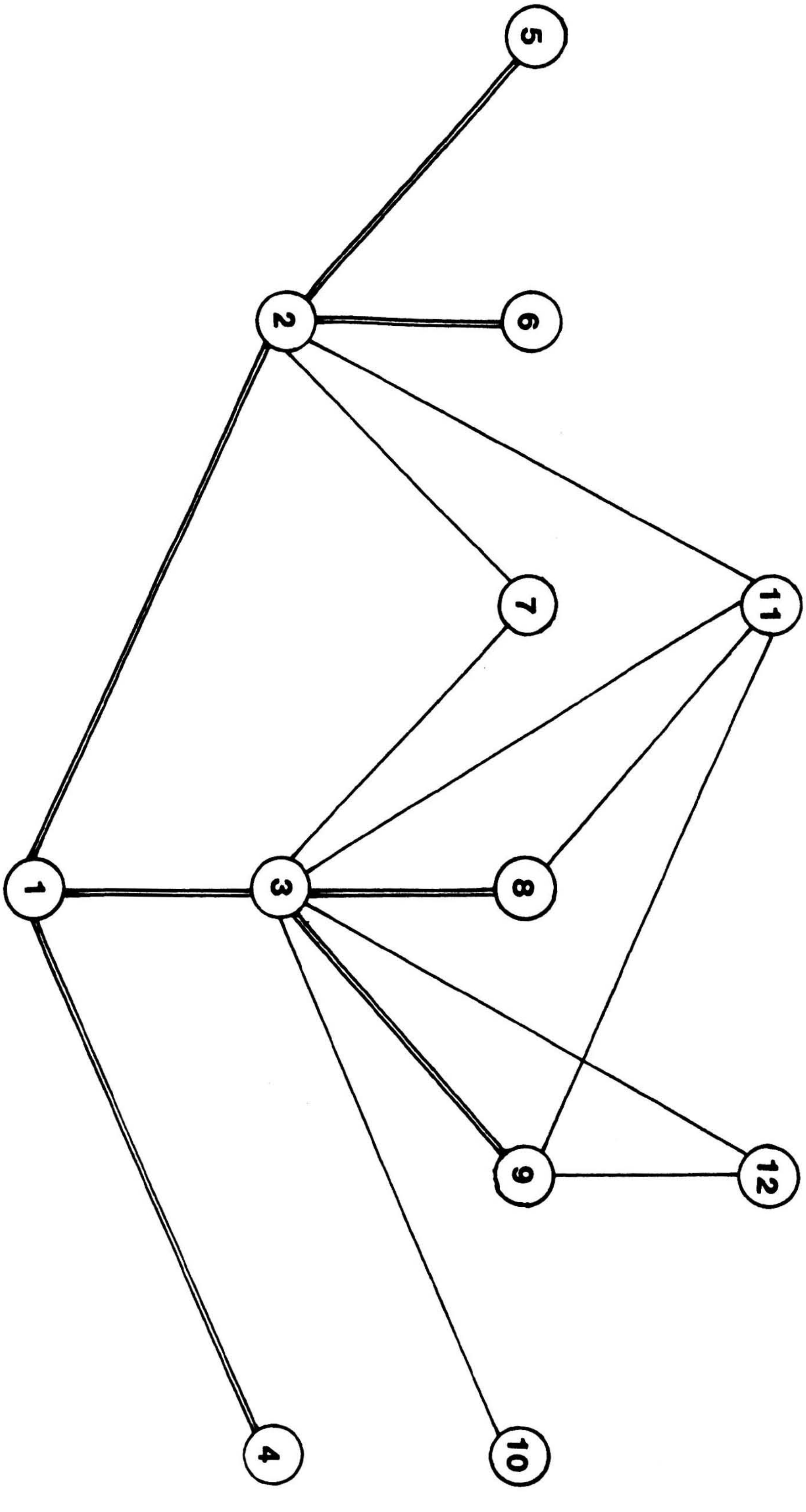
The relative abundance of each species does not vary greatly between sites (tables 5.27 to 5.29). The core species, consisting of L. corniculatus, three herbivores and four parasites, dominate the web and account for over 98% of the total linkages recorded at the four sites (figure 5.2). The addition of four other widespread parasites adds only 0.5% and the remaining 11 species represent only 1.1% of the total.

Previous investigations of the insects found in L. corniculatus pods have concentrated on the parasites of individual species. The parasites of A. loti were studied by Williams (1969) who found that T. rufinus and an Entedon sp. (presumably E. diotimus) were the only important parasites. In the U.S.A. Neunzig and Gyrisco (1959) surveyed the parasites of three Eurytoma species and recorded a total of seven parasites of E. platyptera. Batiste (1967) added an eighth species, Liodontomerus perplexus Gahan, reared from E. platyptera in L. tenuis pods. The most numerous parasites were found to be Tetrastichus bruchophagi and Pteromalus medicaginis, which may prove to be

FIGURE 5.2

Major elements of the *L. corniculatus* seed pod food web at Eppleworth, Bulkington, Wharram and Fossen. 98.9% of the observed links are represented, with 98.4% represented by the thickened lines alone.

1	*L.corniculatus*	7	*P.sequester*
2	*E.platyptera*	8	*T.rufinus*
3	*A.loti*	9	*E.diotimus*
4	*C.compositella*	10	*P.semotus*
5	*T.endemus*	11	*M.vesicularis*
6	*Pteromalus* sp. C	12	*Lestodiplosis* sp.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synonymous with the European *T. endemus* and *P. sequester*. *Macroneura vesicularis* was also reared from *E. platyptera* in the U.S.A., but the five remaining species have not been recorded from Britain. In Russia, Nikolskaja (1932) studied the parasites of *Eurytoma gibba* (which at that time included *E. platyptera*) and again recorded *T. bruchopagi* and *P. medicaginis* as the major parasites. *M. vesicularis* was again present, as was *T. tibialis* (a synonym of *T. endemus*). Mayr (1878) described *Eurytoma dentata* which he had reared from unripe pods of *L. corniculatus*, *Medicago falcata* L. and *Genista tinctoria* L. No examples of *E. dentata* were obtained from any of the samples collected during the present study and Parnell (1964) has found that *E. dentata* is associated with several species of *Ashphondylia* (Diptera).

A. loti and *E. platyptera* each support a dominant pair of parasite species which together outnumber the rest of the parasite community present in *L. corniculatus* pods. Each pair is composed of one ectoparasite and one endoparasite, both of which are effectively monophageous and in each case it is the endoparasite which is most successful in terms of numbers of reared individuals. A similar situation was recorded by Takado and Kamijo (1979) who studied the parasite complex of the leaf-mining *Phytomyza horticola* Gourea in Japan. They found that one endoparasite and two ectoparasites were the major parasites, with a further seventeen species recorded occasionally, and concluded that the parasite complex consisted of a few highly specialised species and a larger number of generalists that were adapted for feeding on a variety of leaf-mining insects. After a more extensive survey of parasite communities, Askew (1980) reached a similar conclusion and argued that because of intense competition each community can only support a limited number of specific parasites. A larger number of polyphagous species can be present because they have a broad range of host species which occur in different communities. This serves to reduce competition between them because each parasite will have different host preferences. The parasite complex inside

L. corniculatus pods provides further support for these conclusions.

Askew (1975) provided a detailed comparison of the chalcid communities found in Cynipid oak galls and deciduous tree leaf mines. The structure of the food web in L. corniculatus seed pods has more in common with the leaf mine communities, which probably reflects the ephemeral nature of seed pods that are liable to dehisce only weeks after they are first produced. Oak galls persist for much longer periods, allowing more structured communities to develop. Several characteristics of endophytic communities that were listed by Askew are evident inside L. corniculatus seed pods.

1. "Endoparasites attack their hosts earlier than ectoparasites". Entedon diotimus and Triaspis species oviposit in the eggs or early larvae of A. loti whereas all the ectoparasitic species attack mature larvae or pupae.

2. "Fewer species of endoparasites are present and they tend to be more host specific". Less than 25% of the species reared from L. corniculatus pods were endoparasites and of these only T. endemus attacks more than one host species.

3. "Endoparasites usually attack phytophages, only rarely their parasites". All secondary parasites, with the exception of T. endemus, were ectoparasites.

4. "Ectoparasites attack hosts irrespective of whether endoparasites are already present". A large number (sometimes the majority) of T. rufinus develop from hosts already containing E. diotimus. (See pages 203 and 205)

The L. corniculatus seed pod community also has many similarities with the Rhopalomyia gall community described by Force (1974). Endoparasites form a small proportion of the species in the Rhopalomyia parasite complex, but they are numerically very successful. Laboratory experiments demonstrated that Platygaster sp. (which was the most abundant parasite in natural communities) was a poor competitor and lost a large proportion of its population through multiparasitic competition with ectoparasites. Salt (1961) also found that when internal and external parasites are feeding on the same host it is the ectoparasite which normally survives and this general conclusion has gained additional support from the results of Askew (1975) and Zwoelfer (1979).

The importance of competition between parasites was also discussed by Price (1971) who emphasised its role in the organisation of the parasite complex associated with Neodiprion swainei Midd. Conversely however, Dean and Ricklefs (1979) concluded that there was no evidence of competition occurring between the parasites of some Canadian Lepidoptera.

In L. corniculatus pods E. diotimus is consistantly the most abundant parasite of A. loti, yet it clearly does very badly in direct competition with T. rufinus. Dissection of A. loti larvae confirmed that multiparasitism does occur, and on only one occasion was an E. diotimus larva observed to emerge successfully from a host larva which also had a T. rufinus larva feeding on it.

The empirical method described by Ehler (1979) provides a convenient means of detecting of effects of competition on parasite populations. Ehler defines competition as being present if the proportion of hosts parasitised by one species is reduced by the presence of a second parasite. The effects of competition on the success of E. diotimus can be examined by comparing the numbers that successfully developed inside pods which were shared with T. rufinus with those when T. rufinus was absent. Using this method it appears that at Eppleworth (table 5.31) competition was unimportant during both 1977 and 1978.

Competition is likely to be most intense when the densities of both T. rufinus and E. diotimus are high. A sample of L. corniculatus pods collected at Fossen (Norway) on 10 August 1979 contained unusually large numbers of T. rufinus and demonstrated that T. rufinus can have a marked effect on the success of E. diotimus (table 5.32). Under these conditions the majority of T. rufinus were developing from A. loti larvae shared with E. diotimus, although competition would have been avoided in some cases because T. rufinus also attacks the pupae of A. loti.

Despite its competitive weakness E. diotimus is usually more numerous

Table 5.31 The influence of the presence of *Trichomalus rufinus* on the success of *Entedon diotimus*. *L. corniculatus* pods collected at Eppleworth Quarry in 1977 and 1978.

a 1977

	L. corniculatus pods with *T. rufinus* Absent	Present
Entedon diotimus reared	294	13
Apion loti remaining	2296	78

$\chi^2 \; [1] \; = \; 0.75, \; P > 0.05$

b 1978

	L. corniculatus pods with *T. rufinus* Absent	Present
Entedon diotimus reared	41	0
Apion loti remaining	263	19

$\chi^2 \; [1] \; = \; 2.93, \; P > 0.05$[1]

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[1] See Chapter 4 for comment on the validity of the chi square statistic in contingency tables where one or more cells have a value of zero.

Table 5.32 Competition between parasites of <u>Apion loti</u> inside a sample of 265 <u>L. corniculatus</u> seed pods collected at Fossen (Jostedalen, Norway) on 10 August 1979.

	Apion loti				Parasites		Estimated Percentage parasitism			
	Healthy		Dead							
Trichomalus rufinus	Larvae	Pupae/adults	Larvae	Pupae/adults	Entedon diotimus	Trichomalus rufinus	Entedon diotimus	Trichomalus rufinus	Total	A. loti Mortality(%)
Present	0	1	2	0	7	51	11.5	83.6	95.1	98.4
Absent	1	7	6	1	42	-	73.7	-	73.7	86.0

than *T. rufimus* in samples of *L. corniculatus* pods. Inside *Rhopalomyia* galls the endoparasite *Platygaster* was also found to be more successful than its competing ectoparasites and Force (1974) attributed this success to a combination of intensive competition between the ectoparasites and to their limited reproductive capabilities. Ectoparasites other than *T. rufimus* occur relatively infrequently inside *L. corniculatus* pods and competition between them is not likely to be important. Superparasitism by *T. rufimus* larvae does occur, however, and this is probably the most frequent form of competition between ectoparasites. The success of *E. diotimus* is perhaps attributable to factors which make it inherently more difficult to search for a small number of mature larvae than for a larger number of eggs or relatively sedentary immature larvae.

The characteristics and properties of food webs have received considerable attention from mathematical ecologists, yet Cohen (1978) and Beddington and Lawton (1978) have commented on a lack of empirical data on the subject. 'Connectedness' food webs (*sensu* Paine, 1980), such as figure 5.1, are based on presence/absence (incidence) data and give the impression that communities have a high connectance (*sensu* May, 1973) and complexity. Beddington and Lawton (1978) have argued that this apparent complexity masks the relatively few density dependant key links that control the dynamics of each food web.

Energy flow webs quantify the linkages within communities and provide information on their relative importance. The exclusion of hosts that form only a small part of a predator's diet can considerably reduce food web complexity, but Pimm (1980) has stressed that such minor dietary constituents may ultimately prove to be of great significance. Paine (1980) has extended this argument and contends that energy flow webs are of little value. He maintains that functional webs, based on experimental manipulation of community structure, provide the most relevant insights into community organisation.

In relation to the number of individuals that are involved, the polyphagous species contribute a disproportionately high number of links in the *L. corniculatus* seed pod food web. These facultative secondary parasites appear to remove hosts in direct proportion to their likelihood of being encountered (table 5.33) and with sufficiently large sample sizes *Lestodiplosis* sp., *Pteromalus chrysos* and *Macroneura vesicularis* could probably be linked with almost all the other species found inside the pods. The relevance of such connections to the stability of the community must be negligable, however, and emphasises the need for linkage frequencies to be taken into account when the relationship between connectance and stability is considered.

Pimm and Lawton (1978) predicted that insect host-parasite systems might provide exceptions to their general conclusions that stable food webs are unlikely to contain many species that feed at more than one trophic level ('omnivores') and that omnivores are likely to feed at adjacent trophic levels. Pimm (1980) distinguished between 'same-chain' and 'different-chain' omnivery, and considered the distinction to be important because different-chain omnivery has little effect on the stability of model food webs whereas same-chain omnivery usually produces instability. *Pteromalus chrysos* feeding on *Scambus eucosmidarum* (Figure 5.1) is an example of same-chain omnivery because *P. chrysos* also develops directly from *Cydia compositella*. When *P. chrysos* attacks *E. diotimus* it provides an example of different chain omnivery because it was not recorded as attacking *A. loti*.

A total of four omniverous species were recorded inside *L. corniculatus* pods (*Macroneura vesicularis*, *Lestodiplosis* sp., *P. chrysos* and *Tetrastichus endemus*) and all were found to feed at adjoining trophic levels. Only four same-chain linkages were present, two of which were provided by *M. vesicularis*. This is a rather lower proportion than those recorded in the insect food webs analysed by Pimm (1980) and results from the large number of uncommon monophageous species in the seed pod food web.

Food webs usually contain only a small number of trophic levels, and

Table 5.33 The frequency of attacks by facultative hyperparasites in relation to the numbers of hosts that were available. Results are combined from L. corniculatus seed pod samples collected at four major sites. Note that the development of Tetrastichus endemus on E. platyptera is not included.

Host Species	No. of hosts	% of total hosts available	No. of parasite species	No. attacked by 2° parasites	% of total attacks
Apion loti	6849	66.0	2	22	46.8
Eurytoma platyptera	415	4.0	2	5	10.6
Cydia compositella	157	1.5	1	5	10.6
Entedon diotimus	2423	23.4	4	12	25.5
Trichomalus rufinus	529	5.1	2	2	4.2
Scambus eucosmidarum	3	0.03	1	1	2.1
Totals	10376			47	

are broad rather than long (Askew, 1975, Cohen, 1978). This feature, which enhances the stability of model systems (Pimm, 1980), is considered by Pimm and Lawton (1977) to result from constraints imposed by population dynamics rather than ecological energetics. The food chains inside L. corniculatus pods are short, and only four trophic levels are represented (discounting decomposers). Hyperparasites were found to be of minor importance in the Rhopalomyia community (Force, 1974) and in L. corniculatus pods this trophic level is similarly poorly represented, despite what appears to be a large pool of suitable hosts (figure 5.3).

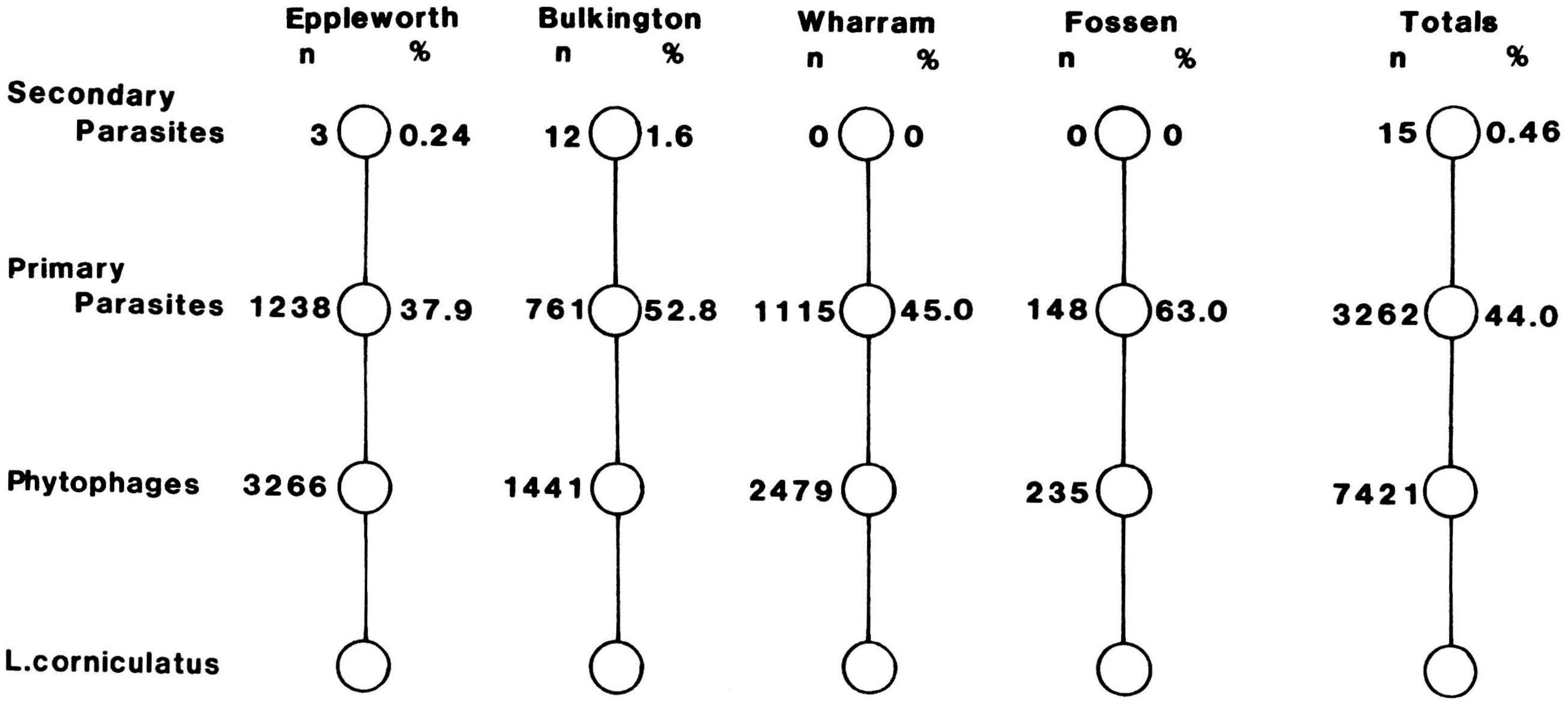
May (1974) found that the stability of complex model ecosystems could be improved by dividing the models into a series of loosely coupled subsystems. However, when the models were further refined by excluding biologically unreasonable phenomena it was found that compartmented models were no more stable than randomly organised ones (Pimm, 1979). The biological implications of these results were discussed by Beddington and Lawton (1978) and Pimm and Lawton (1980) and it was concluded that there was no evidence that natural communities were more compartmented than would be expected by chance.

Inside L. corniculatus pods the records from the four major sampling sites show that at the primary and secondary parasite levels 91.3% of the linkages were formed by monophagous species developing only on A. loti, 4.8% were formed by monophages of E. platyptera and 0.28% by monophages of C. compositella (Tetrastichus endemus has been treated as a monophage when developing on E. platyptera). Links formed by parasites feeding on two or more hosts account for only 3.6% of the total. This division is hardly surprising with each herbivore belonging to a different insect order, but it does show that compartmentisation based on host preference is present.

Natural communities may be divided into 'compartments' at one level and reticulate at another (Pimm and Lawton, 1980) and a comparison of the communities inside the seed pods of a number of legumes may reveal a considerable

FIGURE 5.3

The trophic levels inside L. corniculatus seed pods. Numbers of individuals and the percentage of the lower trophic level that this represents are indicated.


Eppleworth
n %
Bulkington
n %
Wharram
n %
Fossen
n %
Totals
n %
Secondary Parasites
3 0.24
12 1.6
0 0
0 0
15 0.46
Primary Parasites
1238 37.9
761 52.8
1115 45.0
148 63.0
3262 44.0
Phytophages
3266
1441
2479
235
7421
L.corniculatus

degree of overlap. Neunzig and Gyrisco (1959), for example, compared the parasite complexes of three closely related species of *Eurytoma* (including *E. platyptera*) and found that they were very similar.

A. loti and *E. platyptera* develop only in *Lotus* species, but *C. compositella* also feeds on *Trifolium* and probably supports broadly similar parasite complexes, irrespective of which plant it is feeding on. Limited sampling of *Trifolium pratense* L. flower heads has nonetheless demonstrated that this plant's parasite community is considerably different from that of *L. corniculatus*. A collection of *T. pratense* at Bulkington (27.8.78) produced specimens of *Pseudotorymus apionis* (Mayr) a well known parasite of *Apion* spp. in *Trifolium* (for example Richards 1935) that was never recorded from *L. corniculatus*. *Spintherus dubius* (Nees) is another parasite not found in *L. corniculatus* pods that attack *Apion* spp. in *Trifolium* (Graham 1969, Bouček, 1970) and it was reared from *T. pratense* collected at both Bulkington (27.8.78) and Eppleworth (4.9.78).

The degree of division into compartments that is found in the seed pods of legumes may not be representitive of their faunas as a whole. Reproductive structures are particularly diverse, both chemically and structurally, and this has probably resulted in greater speciation than, for example, in the leaf-chewing guild. A thorough investigation of several legume species growing at one site could provide the information that is necessary before any conclusions can be reached on this point.

CHAPTER VI

PRE-DISPERSAL PREDATION OF L. CORNICULATUS SEEDS

In recent years a considerable literature has appeared on the subject of 'seed predation' by animals, much of it stimulated by the publications of D.H. Janzen. Plants exhibit a complex pattern of responses to herbivory (Bentley and Whittaker, 1979) and the experimental removal of leaf tissue is often found to have only slight detrimental effects and can even lead to a stimulation in plant growth rates (Decker *et al*, 1960, Harris, 1972). Competitive interactions with other plants are likely to result in foliage removal being more damaging (Whittaker, 1979), but low levels of leaf damage may nonetheless have negligable consequences for the survival of mature plants. The effects of damage to reproductive structures are more readily quantified, because damaged seeds or ovules will almost invariably fail to develop. There is evidence that some compensation can occur, however, (Hendrix, 1979 , Smith and Bass, 1972) particularly if losses occur at an early stage. *L. corniculatus* produces a large excess of flower buds, many of which quickly abort (Chapter three). Whether this is influenced by flower or pod losses has not been established, but there would appear to be considerable scope for compensation to occur.

The seeds of many species of Leguminosae contain a range of secondary compounds, a number of which are believed to have a role in the defence of the seeds (Janzen, 1969). Krupe (1953) found that extracts of L. corniculatus seeds caused agglutination of Human blood cells, but Makela (1957) could not confirm this. L. corniculatus seeds are not cyanogenic (Jones, 1966) and the nature of their chemical defences (if any) remains in doubt.

Pre-dispersal predation of L. corniculatus seeds at Eppleworth Quarry was monitored by counting the numbers of healthy seeds and insects contained in each of the seed pods present in the sample quadrats (Chapters two and three). In addition during 1978 the length of each mature pod was measured, and the number of damaged and unhealthy seeds was recorded. Post dispersal predation was not investigated, but whereas in some cases this is known to exceed pre-dispersal predation in importance (for example Gardner, 1977) this is unlikely to be true for L. corniculatus, which has relatively small seeds (Janzen, 1971).

L. corniculatus seed production varies considerably between individuals (Albrechtsen et al, 1966 and Peacock and Wilsie, 1960) but under optimum growing conditions the plant can produce five to six pods per umbel, 15 - 20 seeds per pod (Seaney and Henson, 1970) and 18,000 seeds per plant, (Jones 1970). Seed predation can take the form of destruction or removal of whole umbels, individual pods or single seeds. The loss of complete umbels could not be detected within the sampling programme used and its relative importance remains unknown.

Results and Discussion

Flowers which fail to be pollinated successfully may wither and die, and losses of whole pods need not necessarily be due to predation. During both

1977 and 1978 the average number of seed pods per umbel (including pods which had dehisced) was only 1.8 (table 6.1), compared with a mean number of flowers per umbel of 2.0 in 1977 and 2.7 in 1978. The number of pods produced is therefore considerably below that which can be obtained under agricultural conditions, but most of the losses occur prior to the flowering stage (Chapter three). Observations suggested that few whole pods were being consumed by herbivores because pods chewed back to their sepals were rare. External damage to seed pods at Eppleworth Quarry was caused mainly by molluscs and chewing insects, and these rarely removed more than 25% of the pod tissue. Other factors that may have contributed to the low level of pod production include feeding by insects on the flowers and buds (Chapter three), insufficient pollination, and the poor health of the parent plants. Stem feeding by Homopterans can also have a considerable influence on seed production by legumes and Schoonhoven *et al* (1978) have shown that it can result in fewer pods being produced, a fall in the number of seed per pod, a reduction in individual seed weight and an increase in the number of pods which contain no viable seeds.

The *L. corniculatus* seed pods at Eppleworth Quarry contained an average of 3.44 healthy seeds in 1977 and 5.04 healthy seeds in 1978, an increase in per pod seed production of almost 50% (table 6.2). Healthy seed content was one of seven variables recorded for each of the seed pods and the relationships between these variables were examined using correlation analysis (table 6.3;only significant correlations are provided). Data in this form is well suited for multivariate analyses such as those carried out by Moore (1978b) in his study of seed predation in the shrub *Crotalaria*. A preliminary multivariate examination of the factors influencing healthy seed production by *L. corniculatus* pods (using the 'SPSS' package devised by Nie *et al*, 1975) revealed, however, that the recorded variables could explain only approximately 10% of the observed variance in 1977 and 20% in 1978. This form of analysis was therefore discontinued.

Table 6.1 The numbers of seed pods borne on *L. corniculatus* umbels collected at Eppleworth Quarry in 1977 and 1978. Note that dehisced pods are included.

Sample	1977		1978	
	No. of Umbels	Mean pods/ Umbel	No. of Umbels	Mean pods/ Umbel
1.1	40	2.2	-	-
1.2	72	1.9	-	-
1.3	39	2.0	-	-
2.1	70	1.9	16	1.2
2.2	39	1.8	18	2.1
2.3	50	2.0	40	2.3
3.1	94	2.1	9	1.2
3.2	47	2.3	11	1.1
3.3	65	1.4	20	2.3
4.1	65	1.8	8	2.5
4.2	69	1.8	8	1.9
4.3	60	1.9	0	-
5.1	26	1.9	29	1.7
5.2	58	1.7	8	1.4
5.3	93	2.0	32	2.2
6.1	103	1.7	6	1.2
6.2	23	1.3	21	2.4
6.3	13	1.5	31	1.6
7.1	13	1.5	19	1.8
7.2	85	2.0	30	1.7
7.3	81	1.8	68	1.8
8.1	34	1.9	18	1.4
8.2	84	1.8	33	1.1
8.3	13	1.6	8	1.4
9.1	70	1.7	29	2.3
9.2	24	1.7	5	1.8
9.3	51	1.5	8	3.0
10.1	35	1.1	-	-
10.2	38	1.3	-	-
11.1	13	1.2	-	-
11.2	30	1.2	-	-
Totals and means of total data	1538	1.8	475	1.8

Table 6.2 The average numbers of healthy seeds recorded from <u>L. corniculatus</u> seed pod samples collected at Epplewerth Quarry.

Sample	1977 No. of pods	1977 Mean healthy seeds per pod	1978 No. of pods	1978 Mean healthy seeds per pod
1.1	89	5.58	-	-
1.2	139	4.24	-	-
1.3	79	3.63	-	-
2.1	126	2.49	-	-
2.2	63	4.21	-	-
2.3	91	4.22	-	-
3.1	199	5.82	-	-
3.2	108	2.75	-	-
3.3	90	1.62	-	-
4.1	116	3.26	16	3.75
4.2	127	2.39	15	0.47
4.3	113	2.87	0	0
5.1	50	3.24	45	2.84
5.2	98	1.59	10	3.00
5.3	191	2.31	69	6.56
6.1	168	2.14	7	7.43
6.2	30	0.90	49	4.88
6.3	20	1.75	49	3.71
7.1	20	4.65	30	4.33
7.2	160	3.84	42	3.62
7.3	143	3.45	112	6.62
8.1	65	4.25	11	3.82
8.2	148	4.56	55	3.67
8.3	20	4.25	10	6.40
9.1	111	3.04	56	7.20
9.2	38	3.00	5	5.00
9.3	60	5.85	17	6.12
10.1	30	3.73	-	-
10.2	47	3.57	-	-
11.1	15	3.27	-	-
11.2	36	2.69	-	-
Totals and means of total data	2790	3.44	598	5.04

Table 6.3 Significant Pearson Correlation Coefficients among L. corniculatus seed pod variables. Degrees of freedom = 2788 in 1977 and 596 in 1978

A 1977	Pods per Umbel	External Damage	Healthy/ Unhealthy	Apion loti	Cydia compositella	Eurytoma platyptera	Healthy Seeds
Pods per Umbel	-	-	-	-0.047^{2}	-0.048^{2}	-	0.143^{3}
External Damage	-	-	-	-	-0.036^{1}	-	-
Healthy/Unhealthy	-	-	-	-0.10^{3}	-	-	-0.163^{3}
Apion loti	-0.047^{2}	-	-0.10^{3}	-	-0.156^{3}	-	-0.082^{3}
Cydia compositella	-0.048^{2}	-0.036^{1}	-0.156^{3}	-	-	-	-0.210^{3}
Eurytoma platyptera	-	-	-	-	-	-	-
Healthy Seeds	0.143^{3}	-	-0.163^{3}	-0.082^{3}	-0.210^{3}	-	-

B 1978 (Samples 4.1 - 9.3 only)	Pods per Umbel	External Damage	Healthy/ Unhealthy	Apion loti	Cydia compositella	Eurytoma platyptera	Healthy Seeds
Pods per Umbel	-	-0.085^{1}	-	-	-	-	-
External Damage	-0.085^{1}	-	-	-0.083^{1}	-	-	-0.137^{3}
Healthy/Unhealthy	-	-	-	-0.075^{1}	-	-	-0.241^{3}
Apion loti	-	-0.083^{1}	-0.075^{1}	-	-	-	-0.173^{3}
Cydia compositella	-	-	-	-	-	-	-0.151^{3}
Eurytoma platyptera	-	-	-	-	-	-	-
Healthy Seeds	-	-0.137^{3}	-0.241^{3}	-0.173^{3}	-0.151^{3}	-	-

$^{1}P < 0.05$

$^{2}P < 0.01$

$^{3}p < 0.001$

During 1977 healthy seed content was found to be positively correlated with pods per umbel and negatively correlated with unhealthy pod condition, *Apion loti* and *Cydia compositella*. No significant correlation with pods per umbel was present in 1978, but a fourth negative correlation, with external pod damage, was recorded. Significant correlations between the other variables were also obtained, although none involved *Eurytoma platyptera*.

Unhealthy and externally damaged pods were expected to contain fewer than average healthy seeds and indeed many of the unhealthy pods contained none at all (table 6.4a). In comparison, the effects of external pod damage were relatively minor, however, not even producing a significant reduction of seed content in 1977 (table 6.5a). Only two *C. compositella* and no *E. platyptera* were recorded from pods in these categories and they also contained fewer than normal *A. loti* (tables 6.4b and 6.5b). This suggests that the ovipositing females of the insects discriminate against unhealthy or damaged pods.

The significant relationship between pods per umbel and seed content per pod (1977 only, table 6.3a) could have been an indirect result caused by the negative correlation of pods per umbel with *A. loti* and *C. compositella*. Partial correlation of healthy seed content with pods per umbel (controlling for the presence of both insects), shows that this was not the case however (r [2785] = 0.131, $p < 0.001$).

Although feeding by the three endophytic insects did not result in whole pods becoming unhealthy there could have been some seed mortalities that resulted from the insects transmitting fungal or bacterial pathogens. There was no evidence that this was occurring, however, as the presence of *A. loti* (the most abundant species) did not increase the likelihood that a pod would contain mouldy seeds (X^2 [1] = 0.022, $P > 0.05$, with n pods = 451) and *A. loti* and mouldy seed content were not significantly correlated (Pearson Corr. [449] = -0.073, $P > 0.05$).

Estimates of seed losses caused by insects can be obtained by direct

Table 6.4 A comparison of the numbers of seeds and insects contained in healthy and unhealthy seed pods of L. corniculatus Eppleworth Quarry, 1977 and 1978.

A Healthy seed content

	1977 Seeds Present			1978 (samples 4-9 only) Seeds Present			
	0	1	>1	0	1	2-5	>5
Healthy pods	537	361	1892	54	40	243	228
Unhealthy pods	62	7	1	25	2	4	2
% represent by unhealthy pods	10.3	1.9	0.05	31.6	4.8	1.6	0.9

$X^2 [2] = 202.6, P < 0.001$ $X^2 [3] = 119.7, P < 0.001$

B Apion loti (including individuals represented by parasites)

	1977 A. loti absent	1977 A. loti present	1978 A. loti absent	1978 A. loti present
Healthy pods	1024	1696	553	225
Unhealthy pods	51	19	38	5

$X^2 [1] = 35.7, P < 0.001$ $X^2 [1] = 6.0, P < 0.05$

% Healthy pods colonised = 62.3% (1977) and 28.9% (1978)

% Unhealthy pods colonised = 27.1% (1977) and 11.6% (1978)

Table 6.5 The effects of external pod damage on the numbers of insects and healthy seeds contained in *L. corniculatus* seed pods. Eppleworth Quarry 1977 and 1978.

A Healthy seed content

	1977 Seeds Present				1978 (samples 4-9 only) Seeds Present			
	0	1	2-5	>5	0	1	2-5	>5
Undamaged pods	579	359	1168	617	66	40	234	224
Damaged pods	20	9	24	14	13	2	13	6
% represented by damaged pods	3.3	2.4	2.0	2.2	16.5	4.8	5.3	2.6

1977: $X^2 [3] = 3.1, P > 0.05$ 1978: $X^2 [3] = 21.3, P < 0.001$

B *Apion loti* (including individuals represent by parasites)

	1977 *A. loti* absent	1977 *A. loti* present	1978 *A. loti* absent	1978 *A. loti* present
Undamaged pods	1041	1682	555	226
Damaged pods	34	33	36	4

1977: $X^2 [1] = 4.3, P < 0.05$ 1978: $X^2 [1] = 6.8, P < 0.01$

% Undamaged pods colonised = 61.8% (1977) and 28.9% (1978)

% Damaged pods colonised = 49.2% (1977) and 10.0% (1978)

counts of damaged seeds or by comparing the numbers of healthy seeds in pods with or without the seed predators (Moore, 1978). Feeding by insects inside the seed pods of L.corniculatus often results in the virtual disappearance of some of the seeds and it was felt that the second of these methods would be likely to produce more reliable results. Using this method the estimated seed losses due to insects were 1.30 seeds per attacked pod in 1977 and 1.86 seeds in 1978. Because many more pods contained insects in 1977 this damage represented a loss of 20.03% of the seeds in 1977, but only 8.53% in 1978. Pods which had not contained insects produced on average 4.29 healthy seeds per pod in 1977 and 5.51 seeds per pod in 1978, while in the attacked pods the mean seed production values were 2.99 and 3.65 respectively (tables 6.6 - 6.8). Pods which had contained insects were more likely to fail to produce any viable seed and less likely to contain more than three (table 6.9).

This method of estimating seed mortalities assumes that the insects colonise the seed pods without regard for their seed content. In seven of the samples there was a greater average number of seeds in the pods containing insects than in those which did not (tables 6.6 and 6.7). Most of the samples with 'negative' seed mortalities were collected early in the season and, although none of the within sample differences in seed content are significant when examined by Chi square analysis, this strongly suggests that the insects were selecting pods which contained large numbers of seeds. Seed mortalities caused by insects will also have been underestimated because many of the larvae had not ceased feeding and the values of 20.0% removal in 1977 and 8.5% removal in 1978 must therefore be regarded as minimum damage estimates. A total of 451 of the mature seed pods collected during 1978 were scored for overall length and for any damaged or unhealthy seeds. Eighty five % of the seeds were found to be healthy, with 10.0% unhealthy and only 4.5% showing signs of damage. E.platyptera and C.compositella were rarely encountered,

Table 6.6 Estimates of seed losses caused by insects feeding inside seed pods of *L. corniculatus*. Epplewerth Quarry, 1977

Sample	Pods with insects		Pods without insects		Estimated seed losses	
	No.	Mean seeds/pod	No.	Mean seeds/pod	(a) Seeds per attacked pod	(b) % of initial production
1.1	48	5.81	41	5.32	-0.49	-
1.2	70	3.36	69	5.13	1.77	17.4
1.3	59	3.64	20	3.60	-0.04	-
2.1	80	2.61	46	2.28	-0.32	-
2.2	40	3.95	23	4.65	0.70	9.6
2.3	59	4.41	32	3.87	-0.54	-
3.1	88	5.74	111	5.89	0.15	1.1
3.2	79	2.71	29	2.86	0.15	3.8
3.3	72	1.24	18	3.17	1.93	48.7
4.1	89	3.26	27	3.26	0	0
4.2	98	2.01	29	3.69	1.68	35.1
4.3	94	2.77	19	3.37	0.60	14.8
5.1	30	3.47	20	2.90	-0.43	-
5.2	74	1.35	24	2.33	0.98	31.8
5.3	135	2.13	56	2.75	0.62	15.9
6.1	122	1.75	46	3.20	1.45	45.3
6.2	24	0.87	6	1.00	0.13	10.4
6.3	11	0.91	9	2.78	1.87	37.0
7.1	16	3.75	4	8.25	4.5	43.6
7.2	115	3.75	45	4.09	0.34	6.0
7.3	109	2.98	34	4.94	1.96	30.2
8.1	24	3.79	41	4.51	0.72	5.9
8.2	81	3.81	67	5.46	1.65	16.5
8.3	13	2.46	7	7.57	5.11	43.9
9.1	78	2.38	33	4.61	2.23	34.0
9.2	27	2.41	11	4.46	2.05	32.6
9.3	38	5.24	22	6.91	1.67	15.3
10.1	17	3.53	13	4.00	0.47	6.7
10.2	26	3.46	21	3.71	0.25	3.7
11.1	9	1.67	6	5.67	4.00	42.3
11.2	20	1.15	16	4.62	3.47	41.7
Totals	1845	2.99	945	4.29	1.30	20.03

Table 6.7 Estimates of seed losses caused by insects feeding inside pods of *L. corniculatus*. Eppleworth Quarry, 1978

Sample	Pods with insects		Pods without insects		Estimated seed losses	
	No.	Mean seeds/pod	No.	Mean seeds/pod	(a) Seeds per attacked pod	(b) % of initial production
4.1	6	4.67	10	3.20	-1.27	-
4.2	8	0.62	7	0.29	-0.33	-
4.3	0	-	0	-	-	-
5.1	17	3.29	28	2.57	-0.72	-
5.2	4	1.75	6	3.83	2.08	21.7
5.3	7	3.86	62	6.87	3.01	4.4
6.1	2	5.0	5	8.40	3.40	11.6
6.2	15	4.33	34	5.12	0.79	4.7
6.3	15	2.33	34	4.32	1.99	14.1
7.1	7	2.86	23	4.78	1.92	9.4
7.2	5	1.20	37	3.95	2.75	8.3
7.3	23	4.96	89	7.04	2.08	6.1
8.1	3	3.00	8	4.12	1.12	7.4
8.2	15	3.13	40	3.87	0.74	5.2
8.3	2	5.5	8	6.62	1.12	3.4
9.1	12	5.0	44	7.79	2.79	7.7
9.2	0	-	5	5.00	-	0
9.3	10	5.0	7	7.71	2.71	20.7
Totals	151	3.65	447	5.51	1.86	8.53

Table 6.8 A comparison of the numbers of healthy seeds in _L. corniculatus_ pods in the presence or absence of insects (_Apion loti_, _Eurytoma platyptera_ and _Cydia compositella_). Eppleworth Quarry, 1977 and 1978.

Healthy seeds per pod	1977				1978			
	Pods containing insects		Pods with no insects		Pods containing insects		Pods with no insects	
	No.	%	No.	%	No.	%	No.	%
0	479	26.0	120	12.7	29	19.2	50	11.2
1	268	14.5	100	10.6	22	14.6	20	4.5
2	259	14.0	100	10.6	17	11.3	33	7.4
3	194	10.5	122	12.9	12	7.9	51	11.4
4	158	8.6	124	13.1	17	11.3	46	10.3
5	136	7.4	99	10.5	14	9.3	57	12.7
6	88	4.8	52	5.5	10	6.6	34	7.6
7	81	4.4	65	6.9	8	5.3	36	8.0
8	62	3.4	56	5.9	9	6.0	30	6.7
9	47	2.5	36	3.8	7	4.6	24	5.4
10	36	2.0	22	2.3	1	0.7	12	2.7
11	5	0.3	21	2.2	3	2.0	14	3.1
12	11	0.6	8	0.8	0	0	12	2.7
13	10	0.5	4	0.4	2	1.3	7	1.6
14	5	0.3	6	0.6	0	0	4	0.9
15	4	0.2	0	0	0	0	6	1.3
16	2	0.1	3	0.3	0	0	6	1.3
17	0	0	2	0.2	0	0	1	0.2
18	0	0	2	0.2	0	0	1	0.2
19	0	0	1	0.1	0	0	2	0.4
20	0	0	1	0.1	0	0	1	0.2
21	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0
23	0	0	1	0.1	0	0	0	0
Totals	1845	100.0	945	100.0	151	100.0	447	100.0

Table 6.9 The effects of the presence of insects on the numbers of healthy seeds in the pods of L. corniculatus at Eppleworth Quarry.

A 1977 frequencies

	Healthy seeds per pod				
	0	1-2	3-5	6-10	>10
Insects present	479	527	488	314	37
Insects absent	120	200	345	231	49

X^2 [4] = 123.6, $P < 0.001$

1977 percentages

	Healthy seeds per pod				
	0	1-2	3-5	6-10	> 10
Insects present	26.0	28.6	26.4	17.0	2.0
Insects absent	12.7	21.2	36.5	24.4	5.2

B 1978 frequencies

	Healthy seeds per pod				
	0	1-2	3-5	6-10	>10
Insects present	29	39	43	35	5
Insects absent	50	53	154	136	54

X^2 [4] = 31.9, $P < 0.001$

1978 percentages

	Healthy seeds per pod				
	0	1-2	3-5	6-10	> 10
Insects present	19.2	25.8	28.5	23.2	3.3
Insects absent	11.2	11.9	34.4	30.4	12.1

and almost all the damage was attributable to A.loti. The 152 A.loti recorded in the pods were negatively correlated with total seed content (healthy, unhealthy and damaged seeds), with a Pearson Correlation Coefficient [449] of -0.88, ($P < 0.05$) and examination of the numbers of damaged seeds associated with individual A.loti shows that this negative correlation resulted mainly from 51 pods where A.loti was present, but no seed remnants were found. The failure to detect any damage in such a large proportion of the inhabited pods clearly confirms that direct counts of damaged seeds are particularly liable to underestimate seed losses in L.corniculatus pods.

The L.corniculatus pods contained an average of 3.44 healthy seeds in 1977 and 5.04 seeds in 1978 (samples 4 - 9 only). As there was no difference in the numbers of pods produced on each umbel (table 6.10a), this increase in seed content represents a considerable improvement in the reproductive output of the plants.

A comparison between the healthy seed production of plants collected in 1977 and 1978 indicates that amongst the pods which contained no insects there was a higher proportion containing large numbers of seeds in the second of the two years (X^2 [10] = 41.88, $P < 0.001$). There was no such difference amongst the pods which had contained insects (X^2 [10] = 12.14, $P > 0.05$), despite the higher density of A.loti per occupied pod in 1977 (table 6.10b). The proportion of unhealthy, externally damaged and pods which failed to set any seeds all increased in 1978, showing that these factors were not responsible for the increased seed output that year (table 6.11). A possible explanation is based on the observation that insects may preferentially select pods with large numbers of seeds (page 221). As a lower proportion of pods were colonised in 1978 this would have allowed more many - seeded pods to escape damage.

Plants grown as monocultures often suffer a higher degree of attack by specialist herbivores than do the same plants when they are grown under more

Table 6.10 The numbers of seed pods present on *L. corniculatus* umbels at Eppleworth Quarry and the densities of *Apion loti* that they contained.

a Seed pod frequencies (note that dehisced pods are included)

	Pods per Umbel				
	1	2	3	4	> 4
1977	822	421	222	104	24
1978	216	141	57	24	11

$$X^2 [4] = 6.99, P > 0.05$$

b The densities of *Apion loti* inside occupied pods

	Apion loti per pod				Mean density *A. loti*
	1	2	3	> 3	
1977	1028	483	154	50	1.56
1978	104	104	9	1	1.34

$$X^2 [3] = 39.1, P < 0.001$$

Table 6.11 The frequencies of various seed pod categories in *L. corniculatus* samples collected at Eppleworth Quarry in 1977 and 1978.

	1977			1978			$\chi^2[1]$	P
	Yes	No	%	Yes	no	%		
Unhealthy Pods[1]	70	2720	2.5	33	565	5.5	59.8	< 0.001
Externally Damaged Pods[1]	67	2723	2.4	34	564	5.7	18.4	< 0.001
Pods containing insects[1]	1845	945	66.1	151	447	25.2	340.0	< 0.001
Pods failing to set seeds	62	2728	2.2	14	584	2.3	0.03	> 0.05
Undamaged, healthy pods	799	1991	28.6	370	228	61.9	240.7	< 0.001
Pods containing *A. loti*[1]	1715	1075	61.5	139	459	23.2	290.7	< 0.001
Pods containing *C. compositella*[1]	142	2648	5.1	13	446	2.2	4.4	< 0.05
Pods containing *E. platyptera*[1]	59	2731	2.1	1	597	0.2	10.7	< 0.01

[1] These categories are not mutually exclusive

diverse conditions (Root, 1973, Bach, 1980). In natural populations Ralph (1977) has shown that a specialist seed eating bug, *Oncopeltus fasciatus* (Dall.), also displays this "resource concentration effect" and is present at higher densities per pod in areas where pod density is highest, while on a smaller scale Zimmermann (1980) found that pre-dispersal seed predation of *Polemonium foliosissimum* Gray was again density dependant, with more seeds being destroyed in ovaries that set many seeds.

At Epplewerth Quarry the density of *L. corniculatus* seed pods ranged from 15 - 199 per 929 cm^2 quadrat in 1977 and 5 - 112 per 250 cm^2 quadrat in 1978. *L. corniculatus* was growing almost continuously over much of the sampling area and the different quadrat densities reflect only very localised variation in pod production. This variation does not appear to have influenced the distribution of the insects feeding inside the seed pods as the per pod densities of neither *A. loti*, *E. platyptera* or *C. compositella* nor the degree of aggregation of *A. loti*, were significantly related to seed pod density per quadrat (tables 6.12 - 6.14; the numbers of *E. platyptera* and *C. compositella* were insufficient for analysis in 1978). The average healthy seed content of the pods was also independent of pod density (r [29] = 0.063, $P > 0.05$ in 1977 and r [15] = 0.26, $P > 0.05$ in 1978) as was the estimated level of seed predation in the pods (r [23] arc sine transformed percentage seed loss with pod density per quadrat = -0.285, $P > 0.05$ in 1977, and r [12] = 0.098, $P > 0.05$ in 1978 - quadrats with 'negative' seed losses were ignored).

The number of pods present on an umbel represents a smaller scale variation in pod density. Umbels bearing five or six pods contained a slightly lower density of *A. loti* (X^2 [1] = 4.5, $P < 0.05$ in 1977, and X^2 [1] = 3.2, $P > 0.05$ in 1978) but overall there was no significant relationship between pods per umbel and *A. loti* density (table 6.15a). *E. platyptera* density was also unrelated to pod number (table 6.15b), but more *C. compositella* were found on umbels that had only one or two pods (table 6.15c). *C. compositella* larvae

Table 6.12 The relationship between *L. corniculatus* seed pod density (per quadrat) and the densities of *Cydia compositella* and *Eurytoma platyptera* inside the pods. Eppleworth Quarry, 1977

Sample	No. of pods	Density per pod	
		E. platyptera	*C. compositella*
1.1	89	0	0
1.2	139	0.014	0
1.3	79	0	0.038
2.1	126	0	0.024
2.2	63	0	0.048
2.3	91	0	0.088
3.1	199	0	0.015
3.2	108	0	0.028
3.3	90	0	0.144
4.1	116	0.086	0.017
4.2	127	0.031	0.087
4.3	113	0	0.106
5.1	50	0.2	0
5.2	98	0.01	0.051
5.3	191	0.005	0.047
6.1	168	0.089	0.095
6.2	30	0.033	0.233
6.3	20	0	0
7.1	20	0.6	0
7.2	160	0.012	0.056
7.3	143	0.056	0.119
8.1	65	0.015	0.015
8.2	148	0	0.027
8.3	20	0	0.05
9.1	111	0.189	0.054
9.2	38	0	0
9.3	60	0	0.05
10.1	30	0.233	0
10.2	47	0.191	0.064
11.1	15	0	0
11.2	36	0.056	0
Totals	2790	0.038	0.051

r [20] Density of *E. platyptera* with pods per quadrat (Samples 4-11 only) = - 0.271, $P > 0.05$

r [29] Density of *C. compositella* with pods per quadrat = 0.129, $P > 0.05$

Table 6.13 The pattern of dispersion of *Apion loti* in seed pods of *L. corniculatus* collected at Epplewerth Quarry in 1977. Note that values include insects represented by their parasites.

Sample	No. of pods	Density of A. loti (per pod)	Aggregation ($S^2 / \overline{x}$)
1.1	89	0.809	1.540
1.2	139	0.676	0.926
1.3	79	1.241	1.079
2.1	126	1.016	1.150
2.2	63	0.794	0.738
2.3	91	0.857	0.949
3.1	199	0.578	1.071
3.2	108	1.269	1.526
3.3	90	1.000	0.876
4.1	116	1.216	0.727
4.2	127	1.016	0.781
4.3	113	1.496	1.040
5.1	50	0.780	0.747
5.2	98	1.296	1.117
5.3	191	1.000	0.842
6.1	168	0.869	0.765
6.2	30	1.200	1.63
6.3	20	0.950	1.493
7.1	20	1.550	1.662
7.2	160	1.137	0.957
7.3	143	1.147	0.933
8.1	65	0.462	1.223
8.2	148	0.743	1.082
8.3	20	0.850	0.778
9.1	111	0.892	0.843
9.2	38	1.158	0.818
9.3	60	0.800	0.881
10.1	30	0.867	1.411
10.2	47	0.511	0.839
11.1	15	0.933	0.837
11.2	36	0.917	1.269
Totals	2790	0.961	1.062

r [29] Density of pods per quadrat with $s^2/x = -0.292$, $P > 0.05$

r [29] Density of *A. loti* with No. of pods in each quadrat = -0.051, $P > 0.05$

Table 6.14 The pattern of dispersion of Apion loti in seed pods of L. corniculatus collected at Eppleworth Quarry in 1978. Note that values include insects represented by their parasites.

Sample	No. of pods	Density of A. loti (per pod)	Aggregation ($s^2 / \bar{x}$)
2.1	19	0.421	0.61
2.2	37	0.378	0.79
2.3	89	0.494	1.66
3.1	11	1.364	0.92
3.2	21	1.095	1.54
3.3	46	0.696	1.72
4.1	16	0.500	1.07
4.2	15	0.733	1.84
4.3	0	-	-
5.1	45	0.422	0.81
5.2	10	0.700	1.60
5.3	69	0.043	0.98
6.1	7	0.286	0.83
6.2	49	0.327	0.81
6.3	49	0.408	1.22
7.1	30	0.267	1.27
7.2	47	0.238	3.86
7.3	112	0.188	0.82
8.1	11	0.182	0.90
8.2	55	0.436	1.59
8.3	10	0.300	1.52
9.1	56	0.286	1.36
9.2	5	0.000	-
9.3	17	1.000	1.125
Totals	821	0.393	1.49

r [20] Density of pods per quadrat with $s^2/x = 0.047$, $P > 0.05$

r [21] Density of A. loti with no. of pods in each quadrat $= -0.299$, $P > 0.05$

Table 6.15 The relationship between the number of *L. corniculatus* seed pods present on each umbel and the intensity of colonisation by seed eating insects. Epplesworth Quarry, 1977 and 1978.

A *Apion loti*

	1977					1978				
	Pods on each umbel					Pods on each umbel				
	1	2	3	4	>4	1	2	3	4	>4
Pods available	794	831	660	413	91	216	281	171	96	56
A. loti present	790	840	599	389	62	86	134	54	37	12
A. loti / pod	0.99	1.01	0.91	0.94	0.68	0.40	0.48	0.32	0.38	0.21

1977: $X^2\ [4] = 7.06,\ P > 0.05$

1978: $X^2\ [4] = 9.13,\ P > 0.05$

B *Eurytoma platyptera*

	1977			
	Pods on each umbel			
	1	2	3	>3
Pods available	794	831	660	504
E. platyptera present	36	25	28	16
E. platyptera/pod	0.045	0.030	0.042	0.032

$X^2\ [3] = 3.26,\ P > 0.05$

C *Cydia compositella*

	1977			
	Pods on each umbel			
	1	2	3	>3
Pods available	794	831	660	504
C. compositella present	51	47	21	23
C. compositella/pod	0.064	0.057	0.032	0.046

$X^2\ [3] = 7.94,\ P < 0.05$

also feed in the flowers (and rarely the flower buds) of L. corniculatus (Chapter three) and are capable of moving from one flower to another. Movement is most likely to occur between flowers or pods on the same umbel and, if early feeding damage results in the loss of whole flowers or pods, this may account for the greater number of C. compositella on umbels that contained fewer than average pods.

The 451 mature seed pods collected in 1978 ranged in length from 10.5 to 31.25 mm. The mean of 20.3 mm was considerably lower than the 25.00 mm quoted by Seaney and Henson (1970) for commercial varieties. Longer pods did not contain a disproportionate number of the 152 A. loti that were present (Pearson Corr. r[449] $= 0.062$, $P > 0.05$) and the proportion of seeds that were either healthy, unhealthy (mouldy) or damaged was also unrelated to podlength (table 6.16). Seed losses were therefore independent of podlength, and because longer pods initially produce a greater number of seeds this resulted in healthy seed production being correlated with podlength (Pearson Corr. r [449] $= 0.63$, $P < 0.001$). Analysis of insect distribution and estimated seed losses at three different levels have therefore failed to detect any evidence for density related seed predation in the L. corniculatus population at Eppleworth Quarry.

Endophytic insects removed a minimum of 20·0% of the L. corniculatus seeds produced at Eppleworth Quarry in 1977, and 8·5 % of the seeds produced in 1978. This clearly represents a substantial proportion of the total reproductive effort of the plant and demonstrates that feeding by insects could have a significant influence on the population dynamics of L. corniculatus. Seedling recruitment may nonetheless have been relatively unimportant at Eppleworth Quarry because in the relatively heavy sward that was present the majority of seedlings would do badly in competition with well established plants and asexual reproduction may be responsible for the majority of new individuals that are produced.

Table 6.16 The relationship between the length of <u>L. corniculatus</u> seed pods and the survival of the seeds that they contain, Eppleworth Quarry, 1978.

	Podlength (length in mms)								Totals
	1	2	3	4	5	6	7	8	
	< 14.5	14.51-16.5	16.51-18.5	18.51-20.5	20.51-22.5	22.51-24.5	24.51-26.5	>26.5	
No. of pods	32	45	80	95	77	56	37	29	451
Healthy seeds	60	113	318	503	456	418	336	308	2512
Damaged seeds	5	2	17	18	33	20	17	22	134
Mouldy seeds	11	16	43	42	65	50	36	30	293
Total seeds	76	131	378	563	554	488	389	360	2939
% of initial seeds remaining healthy	78.9	86.2	84.1	89.3	82.3	85.7	86.4	85.6	85.5
% of suitable seeds damaged[1]	7.7	1.7	5.1	3.4	6.7	4.6	4.8	6.7	5.1

X^2 [7] Healthy seeds by total seeds = 14.75 $P < 0.05$
X^2 [7] Damaged seeds by total seeds = 10.63 $P > 0.05$
X^2 [7] Mouldy seeds by total seeds = 10.49 $P > 0.05$

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[1] Mouldy seeds are not included

Seed losses are likely to be of greatest significance when *L. corniculatus* is becoming established at a site where vegetational succession is at an early stage and there are numerous open spaces where seedlings can become established. Seedling and juvenile recruitment are in direct proportion to the number of seeds and seedlings that are produced by *Haplopappus squarrosus* H. and A. (Louda, 1982), for example, and if a similar pattern were present in *L. corniculatus* then an annual depletion of, let us say, 30% of the seed output could have dramatic consequences during a period of rapid population expansion.

Cavers (1973) quotes several examples of the successful control of weed species using seed predators, including the case of *Eurytoma attiva* Burks which halted the spread of black sage *Cordia macrostachya* Jacquin when it was introduced onto the island of Trinidad. Janzen (1969) has listed 31 traits that he considers may serve to protect legume seeds from attacks by bruchid beetles. Bruchids rarely feed on the seeds of *L. corniculatus* (at least not in the U.K.) and their niche has been exploited by *E. platyptera*. This species, together with *A. loti* and *C. compositella*, has obviously circumvented whatever defences are present in the pods and seeds of *L. corniculatus*. There is no evidence, therefore, that plant defences are limiting the numbers of these seed predators and seed losses would be even higher if it was not for the high rates of parasitism that all three seed predators regularly sustain.

To summarise this evaluation of *L. corniculatus* seed predation at Eppleworth Quarry:

1. *L. corniculatus* produced an average of 1.8 pods per umbel, with each pod containing an average of 3.44 healthy seeds in 1977 and 5.04 seeds in 1978.

2. It is estimated that a minimum of 20·0% of the seeds were removed by insects in 1977, and 8·5 % in 1978.

3. Pods that did not contain insects produced approximately the same numbers of seeds in 1977 and 1978, and this indicates that the decrease in the proportion of pods colonised by insects was responsible for the 46.5% increase in seed production during 1978.

4. There was no evidence that seed predation was related to seed density.

CHAPTER VII

INSECTS ASSOCIATED WITH THE VEGETATIVE STRUCTURES OF L. CORNICULATUS

Studies at Eppleworth, Bulkington and elsewhere were centred on the insects associated with the reproductive structures of L. corniculatus. At the same time, observations were made on other species found on the plants in order to provide a more complete picture of the insect communities which were present.

The animals associated with a particular plant species can be divided subjectively on the basis of feeding behaviour into groups of species corresponding to the 'guilds' described by Root (1967). A guild is a group of species which interact strongly amongst themselves for the use of resources, but only weakly with members of other groups (Joern and Lawlor, 1981). The parts of a plant which a species eats provides a convenient basis for initial guild seperation and suggests groupings of root, leaf, phloem and xylem, bud, flower and seed pod feeding species (Turnipseed and Kogan, 1976)

Phloem and xylem feeding species were not investigated, but it was noted that both adults and nymphs of the polyphagous *Philaenus spumarius* were often numerous on *L. corniculatus* at Eppleworth and Bulkington.

The Root-feeding guild

Although the root system of *L. corniculatus* is not cyanogenic, it has recently been shown to contain the phytoalexin Vestitol, which has insecticidal properties (Russell *et al*, 1978).

On 2 July and 1 September 1980 two adults of *Trachyphloeus aristatus* were collected on *L. corniculatus* at Wharram Quarry, using a D-Vac Suction Sampler. No further examples of this species were obtained and extensive sweep net sampling at Bulkington and Eppleworth did not produce any of the root-feeding beetles Walsh and Dibb (1975) give from *L. corniculatus* (*T. aristatus*, *T. olivieri*, *Tychius pusillus* and *Sitona waterhousei*). Although no specimens of *S. waterhousei* were obtained, several other species of this genus were collected on *L. corniculatus*, and *S. sulcifrons* occurred frequently on this plant at Wharram. This need not imply a close association however, as the leaf eating adults of this genus can be found on a wider range of legumes than their root-feeding larvae (Aeschlimann, 1979).

Species of the related genus *Phyllobius* also have root feeding larvae and these can reach densities sufficient to cause economic damage to grasslands (Bevan, 1962). Adults of *P. viridiaeris* and *P. roboretanus* feed on flowers of *L. corniculatus*, but this may not reflect their larval host relationships because the adults are again polyphagous (Witter and Fields, 1977).

Bembecia scopigera, the six-belted clearwing moth, was the only member of the root-feeding guild of *L. corniculatus* encountered at Eppleworth. The biology of this species has been described by Fibiger and Kristensen (1974) who list *Lotus*, *Anthyllis* and *Ononis* as the major host genera. A single adult female was found crawling through *L. corniculatus* vegetation on 12 July 1978, apparently after having only recently emerged. Yorkshire is at the northern limit of the range of B. scopigera in Great Britain (Amateur Entomological Society, 1946) and this species is probably rare in the county as there are few recent records of this very distinctive insect.

The Leaf Chewing Guild

Examination of the faunal list given for L. corniculatus in table 1.1 suggests that the leaf chewing insects constitute by for the largest of the guilds feeding on this plant. This predominance is not supported by field observations however and only 11 species were recorded. Furthermore, extensive defoliation was only observed during one period, (June, July and August 1978, at Bulkington) and was the result of feeding by large numbers of Zygaena larvae.

The eggs and larvae of a sawfly species (Hymenoptera, Symphyta) were collected from L. corniculatus leaves at Wharram Quarry during 1980 and at Leirdal, Gaupne, Fabergstolen and Nigardalen in the Jostedal Valley of S.W. Norway (details of Norwegian localities are given in Chapter 8). These were probably Tenthredo acerrima (Tenthredionidae), a univoltine species which is believed to be specific to L. corniculatus (Waterhouse and Sanderson, 1958, Waterhouse, 1964), but as none of the larvae survived the winter this cannot be confirmed.

In Norway, eggs were found on L. corniculatus throughout July and early August. These measured approximately 0.9 x 1.2mm and were laid in a very precise manner into the basal half of sub-terminal leaflets. Oviposition occurred from above (as shown by an inconspicuous curved brown scar) with the ovipositor pushed through the leaf tissue until coming to lie immediately above the lower epidermis, where the egg was laid. The first larvae emerged on 29 July and grew quickly, ceasing feeding and entering diapause in September. Mature larvae were bright green with a yellow stripe along the lower half of the trunk segments and across the anterior dorsal edge of the prothorax.

L. corniculatus is a food plant of several well known species of Lycaenid Butterflies. Larvae of the Common Blue (Polyommatus icarus) were abundant on L. corniculatus at Bulkington and Wharram, but with the exception of a single adult male seen in July 1978 and a single (hatched) egg found on 15 August 1978, this species was not encountered at Eppleworth. The Idas Blue (currently Plebejus argus idas (L.), but often considered as a distinct species, Lycaeides idas) has an interesting life history with the later larval instars living in the nests of ants (Higgins and Riley, 1970). This butterfly, which does not occur in Britain, was the most abundant species in the Jostedalen during 1979, being seen at Fabergstolen, Nigardalen and Vassdalen. L. corniculatus was presumably the larval food plant as this was the only legume present at these localities, but as no larvae were found this could not be confirmed.

Larvae of the Dingy Skipper (Erynnis tages) were common on L. corniculatus vegetation at Wharram Quarry, but were not found at the other sites. Also found only at Wharram was Syncopacma taeniolella (Gelechiidae), whose larvae were collected in spun shoots of L. corniculatus on 24 May and 11 June 1980. Adults subsequently emerged from these samples during late June and early July, and an additional adult was collected at Wharram on 28 July.

Zygaena trifolii and Zygaena filipendulae, the Five and Six-Spot Burnet Moths, were abundant on L. corniculatus vegetation at Spurn Point and at Bulkington where, in 1978, they caused extensive defoliation of both L. corniculatus and Lathyrus pratensis. Damage to the latter was presumably due solely to Z. filipendulae as Tremewan (1965) states that trifolii has never been found feeding on Lathyrus.

Hale Carpenter (1945) reared a large collection of Z. filipendulae cocoons and found an 18% level of parasitism, with the principal parasites being Phryxe magnicornis (Zett.) (Tachinidae), Casinaria orbitalis Grav. and a Gambrus sp. (both Ichneumonidae). Several Zygaena cocoons collected at Bulkington during July and August 1978 produced further examples of C. orbitalis a cocoon of which is illustrated by Shaw and Askew (1976). A parasitized Zygaena larva collected on L. corniculatus at Wharram Quarry in July 1978 produced a total of eleven Apanteles ?zygaenarum Marshall (Braconidae) and six Mestochorus sp. (Ichneumonidae) hyperparasites. Jones et al (1962) mentioned M. temporalis Thomson as a hyperparasite of A. zygaenarum and showed that the primary parasite contained Rhodanese whereas the secondary parasite did not. Because of the toxic effects of the cyanide in Zygaenid haemolymph it is likely that an unusually high proportion of their parasites will be specific to this genus - their unusual internal environment preventing the successful development of most generalist parasites.

Three other species of Lepidoptera were reared from L. corniculatus on one occasion only. A single larva of the polyphagous Broom Moth (Ceramica pisi) was collected at Gaupne, S.W. Norway on 3 July 1981, and an unidentified Noctuidae larva was found feeding on stock plants maintained at the University Botanic Gardens, Cottingham. Both pupated successfully after being fed exclusively on L. corniculatus. The third species, The Burnet Companion (Ectypa glyphica), developed from a group of six eggs collected on a grass stem growing amongst L. corniculatus at Bulkington on 10 July 1977. By 13 July four larvae had commenced feeding on young leaves and shoots of L. corniculatus and, after overwintering as pupae, adults finally appeared the following spring.

In the British Isles the insect fauna of L. corniculatus includes at least five species of leaf mining Lepidoptera: Trifurcula cryptella, Trifurcula eurema, Leucoptera lotella, Cnephasia incertana and Coleophora discordella. Trifurcula griseela Wolff may prove to be a sixth species (Emmet, 1975).

No examples were obtained of the polyphagous C. incertana, nor of T. eurema and L. lotella, which are associated specifically with Lotus species (Emmet, 1980).

Delucchi (1954) described the parasite Tetrastichus lotellae (later synonymised with T. amethystinus Ratz. by Dominichini, 1965a), from L. lotellae larvae collected in Germany. Several T. amethystinus were reared from mines of an alternative host species, Leucoptera laburnella (Stainton), (Askew, 1968) and these proved to be distinct from a second Tetrastichus species that is often present in the seed pods of L. corniculatus (Chapter five).

T. cryptella and T. eurema were place in the genus Levarchama Beirne in the second edition of the check list of British Insects (Bradley et al, 1972), but the recommendation of Borkowski (1972) that they be included in Trifurcula has subsequently gained general acceptance (A.M. Emmet, Pers. Comm.).

Leaves of L. corniculatus containing mines of T. cryptella were collected during June and July of 1977 and 1978 at Eppleworth Quarry, and in July 1978 at Hessle Quarry. Mines were widely scattered and were never found at high densities. Mature mines were most conspicuous, but finding them was made more difficult by the tendency for mined leaflets to become vertically orientated following upward folding at their stalks. The biology of T. cryptella at Eppleworth was in close agreement with the description given by Emmet (1976). Eggs were found attached to the underside of the leaflets and the mine began as a serpentine tunnel which was then enlarged into a blotch mine. From each mine a single larva subsequently emerged in either July or August, leaving via a slit on the ventral surface of the leaflet. By the next day a cocoon had been produced. Cocoons which were opened in late July and in December contained pupae, but no adults emerged until the following April or May, which confirms the univoltine breeding cycle of this species. During emergence the pupal case was typically left pretruding through the 'mouth' of the cocoon.

A single leaflet of L. corniculatus provides a very limited quantity of plant tissue for a developing larva. Most leaf-mining Nepticulidae feed on only one of the parenchyma levels, but T. cryptella, along with some other miners of small leaflets, removes the whole of the mesophyll. An intensive search for mines on 12 July 1978 at Eppleworth showed that T. cryptella has a preference for mining the terminal of the five available leaflets. Of the 33 mines collected, 25 were in the terminal, 6 in the (paired) lateral and only 2 in the (paired) basal leaflets. The advantage gained by mining the terminal leaflet was demonstrated by measuring the surface areas of leaflets from Anglesey stock plants kept at the University Botanic Gardens (table 7.1), using a Lambda I-3000 Portable Area Meter. Within each leaf the central leaflet is the largest and the basal leaflets are the smallest. Leaflet size also varies between leaves on the same plant and between plants, but the observed preference for the terminal leaflet will clearly help to increase the amount of leaf tissue available to the developing larva.

A total of four species of parasitic Hymenoptera were reared from the *T. cryptella* mines collected on 12 July. First to appear were one macropterous male and one micropterous female of *Hemiptarsenus fulvicollis* Westwood. These emerged from seperate mines on 1 August. Most older host records for this species are apparently of doubtful value because of confusion with *H. dropion* Walker (Bouček and Askew, 1968). Even the single record (Dowden, 1941) quoted by Bouček and Askew is suspect as the accompanying figure shows a macropterous female with the completely white clava of *H. dropion* and macropterous females of *H. fulincollis* are known to be rare (Askew, 1968). More recently, Bouček (1977) mentions that *H. dropion* has itself been reared from leaf-miners on *Lotus* and also gives *Phyllonorycter blancardella* (Fabr.) as a host for *H. fulvicollis*. Other confirmed hosts for *H. fulvicollis* are *Phytomyza ranunculi* (Schrank), (Dye, 1976) and *Stigmella dryadella* (Hofman) (Askew, Pers. Comm.). A third species of *Hemiptarsenus*, *H. waterhousii* Westwood, has also been reared from a leaf-miner on *L. corniculatus* (ex *T. eurema*, Szocs, 1965).

No adults of *H. fulvicollis* were detected during extensive sweep net sampling at Eppleworth, but several were collected on *L. corniculatus* at Wharram Quarry (1 female 2.7.80, 1 female 15.7.80, 1 female 1.9.80, 1 female and 1 male 28.8.81) where there are the open, dry conditions that are particularly favoured by this species (Askew, 1968). Females were also collected

Table 7.1 A comparison of the surface areas of L. corniculatus leaflets from 10 plants. Mean values are for 10 basal and lateral leaflets and 5 terminal leaflets per plant. Plants were maintained at the University Botanic Gardens from stock collected at Porthdafarch, Anglesey.

Clone	Mean Surface Area (Cm^2) Basal Leaflet	 Lateral Leaflet	 Terminal Leaflet
A8	0.144	0.207	0.260
A10	0.137	0.173	0.226
A12	0.091	0.139	0.186
A36	0.152	0.210	0.270
C2	0.123	0.188	0.268
C4	0.147	0.217	0.278
C31	0.135	0.198	0.252
C32	0.163	0.237	0.368
D31	0.205	0.257	0.394
E39	0.127	0.156	0.210
Overall Mean	0.142	0.198	0.271

at Bulkington (2.6.78 and 27.8.78) and North Newbald in East Yorkshire (9.8.80).

On 2 August 1977 a female of *Pnigalio pectinicornis* (L.) emerged from a *T. cryptella* mine collected on 12 July. This abundant species is a polyphagous ectoparasite that particularly favours leaf-mining Lepidoptera and Coleoptera as hosts (Bouček and Askew, 1968). The same species was reared on 25 July 1977 from a *Trifurcula* sp. mine on *L. corniculatus* collected at Bulkington 15 days earlier. Which species of *Trifurcula* was involved could not be established, because no adult moths were reared from this site.

The following spring two endoparasitic species emerged from overwintered *T. cryptella* cocoons collected at Eppleworth Quarry. A single female *Pediobius acantha* (Walker), another polyphagous species (Bouček and Askew, 1968), escaped on 7 June 1978 by chewing an irregular exit hole through the roof of the host cocoon. Adults of this common species were collected at both Bulkington (males on 2.6.78, 15.6.78 and 27.8.78) and Eppleworth (females on 23.8.78 and 12.9.78) and some were swept from *L. corniculatus*.

Finally, a male Braconid only identified to Opiinae, emerged on 20 June 1978. This is an unusual host record for a member of this subfamily, as they are usually reared from leaf mining Diptera (Askew, 1971). Another Braconid, *Acoelius subfasciatus* Haliday, has been reared from *T. eurema* on *L. corniculatus* (Shaw and Askew, 1976).

The species-group of *Coleophora* which includes *C. discordella* has recently been placed in the genus *Ardania* Capuse by Falkovitsh (1978), but I have retained the established classification here. *C. discordella* is the only Coleophorid known to develop on *L. corniculatus* although related (non-British) species have been described from other *Lotus* species (Hering, 1957 and Falkovitsh, 1978). Most reports suggest that *C. discordella* is specific to *L. corniculatus*, but it has also been recorded from *Medicago* by Benander (1939b).

C. discordella is widespread and occasionally abundant in Britain. I have collected larvae from Spurn Point, Flamborough, Wharram and Eppleworth in Yorkshire and from Chapel Farm and Bulkington in Warwickshire. Larval cases were also collected from L. corniculatus at sites in the Jostedalen, Norway on 28 July 1979 (Vigdal) and 5 August 1979 (Nigardalen). This species was rare at Eppleworth, where only one larval case was collected and the bulk of the following observations were made from Bulkington, where C. discordella was seen frequently.

The larval development of C. discordella follows the pattern typical of this genus with the young larva initially having a mine in a leaf of L. corniculatus which it then vacates, forming a protective case around itself. The structure of the case is species-specific and that of C. discordella has been figured by Toll (1962) who placed it as one of the "Lappensacke" cases.

Leaves containing small Coleophora larvae were collected at Bulkington between 12 June and 23 August 1977. The mines were short, often sinuate, and sometimes two individuals could be seen mining the same leaf. Occasionally a larva might vacate its mine, forming a new one in a nearby leaf. Construction of the initial case was achieved by tunnelling along the edge of a leaflet and then retreating and widening a short length of mine so that a blind-ending sac is formed. The epidermis at the boundary of this cleared area was chewed through, allowing the larva to detach itself while remaining enclosed in an arc of epidermal tissue. Feeding was often resumed on the same leaflet, producing the characteristic signs of Coleophorid damage - a small entrance hole, removal of the full depth of the mesophyll and an absence of any frass. As the larvae grow they periodically enlarge their cases. First an area of mesophyll at the edge of a leaflet is consumed and then the periphery of the leaf bordering this area is chewed open and the larva pulls its present case between the inner epidermal surfaces. After firmly adhering its case to the fresh leaf material, the epidermis in front of the larva is separated at the boundary with the non-mined area and the enlargement of the case is complete. Initially greenish, the new section quickly becomes dark brown. The structure of the cases of mature larvae suggests that enlargement occurrs at least five or six times, but the relationship between case enlargement and instar development was not observed.

After over-wintering, the larvae resume feeding in the spring. Specimens collected as miners in July 1977 did not pupate until July 1978, producing adults shortly after. This single generation each year is typical for Colephorids in Britain, where only *C. frischella* (L.) is believed likely to be bivoltine (Ffennell, 1976). Figure 3.1 summarises the life-history data obtained for *C. discordella*. Larval cases are present throughout the year, with some overlap of generations occurring during late July. The flight period for the species extends from June, when the first mines appear, to late August. Benander (1939) gave a similar flight period for this species in Sweden.

Table 7.2 records the contents of 165 mature *C. discordella* cases collected at Bulkington on 3 June 1977. A high level of parasitism was recorded with 76% of the *Coleophora* destroyed by hymenopterous parasites, almost all by an unidentified species of *Bracon* (Braconidae). Many of those *Coleophora* larvae not parasitized were dead and shrivelled.

Bracon sp. usually developed as a solitary ectoparasite, but in a few cases two, or even three, parasites developed successfully upon a single host larva. A similar observation was recorded by Coshan (1974) when rearing *Bracon osculator* Nees from *Coleophora serratella* (L.). Most of the *Bracon* sp. had already pupated when the cases were examined and the first adult emerged on 16 June.

The parasitized *Coleophora* were on newly mined leaves, showing that after over-wintering they had successfully resumed feeding. Parasitism must have occurred after this resumption because ovipositing *Bracon* females are known to paralyse their hosts (Benson, 1973). Healthy larvae (and pupae) were usually found firmly attached to the plant stems, having already completed feeding. If some *Coleophora* larvae move off *L. corniculatus* to pupate elsewhere they

FIGURE 7.1

Life-history summary for *Coleophora discordella*

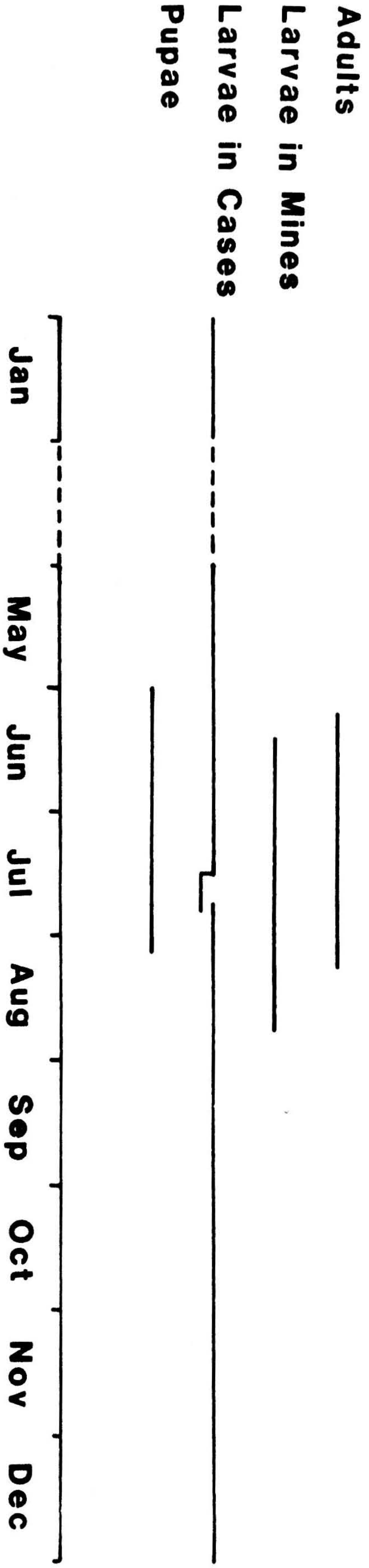
Adults
Larvae in Mines
Larvae in Cases
Pupae
Jan
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Table 7.2 The contents of 165 *Coleophora discordella* larval cases collected at Bulkington, Warwickshire on 3.6.77.

Healthy *Coleophora* larva/pupa	14
Dead *Coleophora* larva	26
One *Bracon* sp. larva/pupa	105
Two *Bracon* sp. larvae/pupae	11
Three *Bracon* sp. larvae/pupae	1
Pnigalio pectinicornis	5
Spaniopus dissimilis	3

would not have been found and this may have biased the estimate of the level of parasitism.

Benson (1973), working with laboratory populatians of Bracon hebetor Say, found that increasing the density of parasites per host larva also increased the proportion of males that were reared. Males were smaller and developed more quickly, giving them a competitive edge over female larvae at high densities. Comparison of the sex-ratios of the Bracon sp. reared from C. discordella gave the converse result however. A total of 27 gregarious Bracon were reared during the 1977 season at Bulkington and these were compared with 59 others reared singly. The sex-ratios were (female : male) 19 : 8 and 28 : 31 respectively, and these are significantly different at the 5% level of probability ($X^2[1] = 3.92$, $P < 0.05$, Yates' correction has not been applied).

Commenting on possible methods of ovipositing on Coleophora larvae, Sich (1923) suggested that parasitic Hymenoptera might pierce the case, or that minute species could squeeze through the valves at the apex of the case. I observed the technique of this Bracon sp. by placing a recently emerged female with several healthy host larvae in a petri dish. After searching the surface with her antennae for some time, she would climb to the top of the case and reach the host by forcing her ovipositor between the anal valves. The cue for ovipositing between the valves may have been the presence of frass there, as Vinson et al (1976) have shown that chemicals in the frass of the host are a major stimulus for probing behaviour in the related B. mellitor Say. The only Bracon adult reared from these cases (a male) appeared 25 days later. All the other host larvae offered were killed by the ovipositing female. Quednau (1970) has reported similar host mutilation in oviposition experiments using Agathis pumila (Ratz.) and Coleophora laricella (Hubner), but could not confirm that this was associated with the adult parasites feeding on their hosts. Host mutilation by ovipositing Bracon females would account for the number of dead C. discordella larvae in the 3 June collection, and further increases the mortalities that can be attributed to this species.

Parasites of C. discordella other than the Bracon sp. were relatively unimportant. Two males of Spaniopus dissimilis Walker were reared as 'Pseudohyperparasites' (Shaw and Askew, 1976) of Bracon and a female was reared directly from C. discordella. S. dissimilis has been reared before from a species of Coleophora (Askew, 1970) and there is also a previous record of this species (as Polyscelis modestus Gahan) feeding as a facultative hyperparasite (Gahan, 1933). Askew (1960) reared a single male of S. dissimilis from a gall of Diplolepis rosae (L.) but doubted whether the parasite was genuinely associated with this host.

On 20 May 1978 several D. rosae galls were collected a few metres from where S. dissimilis had been found parasitising C. discordella. Only the gall maker and its parasite Pteromalus bedeguaris (Thomson) emerged from the galls and any relationship between S. dissimilis and D. rosae cannot therefore be confirmed.

An adult male S. dissimilis was collected by sweeping in Thixendale, N. Yorkshire on 26 July 1980 and a second male was swept from Phragmites at Nymindegab in Jutland, Denmark on 22 August 1979. The latter is apparently the first example of this species obtained from Denmark. These records, in combination with those of Graham (1956) and Bouček (1972) suggest that S. dissimilis has a flight period which extends throughout the summer, from May through to September.

The only other parasites reared from the 3 June 1977 collection (table 7.2) were specimens of P. pectinicornis, with three females and two males emerging from seperate cases between 21 and 23 June. Morley and Rait - Smith (1933) have recorded four further species of parasitic Hymenoptera that have been reared from C. discordella.

Sericothrips bicornis (Karny)

As the precise feeding behaviour of S. bicornis has not been observed it currently cannot be placed in any particular guild. This species was considered synonymous with S. abnormis (Karny) in the check-list of British thrips given by Mound et al (1976) but Zur Strassen (1980) has since shown that S. abnormis is a separate species, which he has placed in the genus Neohydatothrips. L. corniculatus is the only host plant give by Mound et al (1976) and Ward (1973), but Priesner (1926-1928) and Morison (1972) list several other hosts for S. bicornis, including species of Trifolium.

L. corniculatus vegetation samples were collected at Eppleworth Quarry from July to September 1978 and occasional larvae and micropterous adults of S. bicornis were present throughout this period. Suction sampling at Wharram Quarry in 1980 revealed micropterous individuals only in July and these represented less than one per cent of the annual total. Larvae were only rarely found inside flowers of L. corniculatus, and no adults were recorded there. The larvae of S. variabilis (Beach) feed on the leaves of Soybeans and other legumes (Vance, 1974) and S. staphylinus Haliday is another chlorophyll feeder, living in the axils of gorse (Ulex sp.) spines. As none of the larvae of S. bicornis were seen with the characteristic green digestive tract that results from ingested chlorophyll this feeding pattern cannot be confirmed in S. bicornis.

CHAPTER VIII

GENECOLOGICAL STUDIES OF L. CORNICULATUS IN ANGLESEY AND NORWAY

1 PORTHDAFARCH

Introduction

The bay at Porthdafarch is situated on the south west coast of Holy Island, Anglesey (Grid Reference SH 234 799). In 1959 Jones (1963) found that at this locality there was a positive association between distance from the sea and the proportion of leaf cyanogenic L. corniculatus in a sample. The area investigated, which extends to about 250 metres inland, consists of three distinct zones, called the cliff, hollow and mound. The cliff supports a short turf, the hollow a taller sward, and the mound a heathland vegetation (Ellis et al, 1977b, Keymer, 1978). The frequency of cyanogenic plants in the three zones has been found to be relatively stable over a 16 year period (Ellis et al, 1977b) with averages of 25.7%, 74.2% and 68.00% cyanogenic on the cliff, hollow and mound respectively.

Ellis et al (1977b) showed that the cliff site received more airborne salt than the hollow or mound and suggested that this was probably the factor which was responsible for the observed scarcity of molluscs on the cliff. The most abundant species of snails at Porthdafarch were Helicella itala (L.) and Cochlicella acuta (Muller) and these were shown to prefer acyanogenic L. corniculatus in feeding trials (Keymer and Ellis, 1978). As L. corniculatus was known to be the preferred food plant of H. itala (Malen, 1973) in the area, there was good circumstantial evidence that selective grazing by the snails played a major part in the maintenance of the cline. This hypothesis was supported by further studies carried out along the south west coast of Holy Island, where it was shown that most cliffside areas had low proportions of cyanogenic plants and low densities of molluscs. At those cliff sites where mollusc densities were high (for example South Stack) there was a correspondingly high frequency of cyanogenic plants in the population and no cline was present.

On 11 June 1979 a survey of the L. corniculatus populations was carried out at Porthdafarch to observe whether the differences in mollusc numbers found by Ellis et al were reflected in the levels of damage sustained by the plants, to see if there were similar differences in the densities of insects, and to find if acyanogenic plants were subject to greater defoliation than their cyanogenic neighbours.

Methods

A sampling unit consisted of a flower umbel and an attached leafy stem. To reduce the chance of one clone being sampled more than once the sampling points were no closer than one metre apart. After collection the flowers were separated and stored at -10 C before being examined.

Flowers were scored for their keel colour, their inhabitants and the presence of damage, and then the petals were tested for cyanogenesis using the sodium picrate test. Any immature flowers were scored for keel colour only.

The numbers of damaged and undamaged leaves on each stem were counted and then the leaves were also tested for cyanogenesis.

Results

A total of 124 flower umbels and their associated stems were collected at Porthdafarch. The proportions of the cyanogenic and keel colour phenotypes are shown in table 8.1. Proportions of leaf cyanogenic plants from the hollow and mound are considerably higher than those reported by Ellis et al (1977b), an increase which has subsequently been confirmed by a more extensive sample collected in June 1980 (Beesley and Compton, unpublished). Values for the hollow may be misleading however, because only 12 plants were flowering, and results from this zone have not been included in further analyses.

The higher proportion of leaf cyanogenic plants on the mound, relative to the cliff, is repeated by the character of flower cyanogenesis, although at both sites more plants possess cyanogenic flowers than leaves. This pattern is not followed by the keel colour character, however, as there is no significant difference in the proportions of dark keeled flowers at the two sites (X^2 [1] = 1.09, $P > 0.05$).

As individual plants were scored for all three polymorphic characters, the frequencies of the combinations of phenotypes can be compared. No plant had cyanogenic leaves without having cyanogenic flowers (table 8.2) and there is clearly an excess of those plants with either both the leaves and flowers cyanogenic or with neither cyanogenic. No such relationship exists between keel colour and the expression of the cyanogenic polymorphisms, however.

The egg stage of Apion loti and the larvae of Hypera plantaginis were the most abundant insects in the flowers of L. corniculatus at Porthdafarch (table 8.3). Also present were small numbers of Aphid nymphs, Lepidoptera larvae, Odontothrips loti adults and a single Meligethes sp. larva. Both A. loti and H. plantaginis were much rarer on the cliff, with A. loti virtually

Table 8.1. Frequencies of *L. corniculatus* phenotypes at Porthdafarch. June 1979.

	LEAF CYANOGENESIS				FLOWER CYANOGENESIS				KEEL COLOUR			
Site	++	-	n	%++	++	-	n	%++	Pale	Dark	n	%Pale
Cliff	15	40	55	27.3	27	25	52	51.9	50	6	56	89.3
Hollow	12	0	12	100.0	12	0	12	100.0	9	3	12	75.0
Mound	53	3	56	94.6	38	1	39	97.4	53	3	56	94.6

Table 8.2 Frequencies of phenotypic combinations in the L. corniculatus populations at Porthdafarch.

Table 8.2a Leaf and Flower Cyanogenesis

		Leaf	Phenotype
		++	-
Flower	++	52	12
Phenotype	-	0	26

$X^2[1] = 50.0$, $P < 0.001$[1]

Table 8.2b Leaf Cyanogenesis and Keel Colour

		Leaf	Phenotype
		++	-
Flower	Pale	64	38
Phenotype	Dark	4	5

$X^2[1]$ with Yates' Correction, $= 0.52$, $P > 0.05$

Table 8.2c Flower Cyanogenesis and Keel Colour

		Flower	Phenotype
		++	-
Flower	Pale	22	61
Phenotype	Dark	4	4

$X^2[1]$ with Yates' Correction, $= 0.99$, $P > 0.05$

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[1] See Chapter four for comment on the validity of the chi square statistic in contingency tables where one or more cells have a value of zero.

Table 8.3 Insects present in *L. corniculatus* flowers at Porthdafarch, June 1979.

	Sample Size		*Hypera plantaginis*		*Apion loti*		Total Insects	
Site	Umbels	Flowers	n	Mean per flower	n	Mean per flower	n	Mean per flower
Cliff	56	167	15	0.09	1	0.006	28	0.17
Mound	56	169	72	0.43	29	0.17	112	0.66

absent there. On the mound the overall number of insects per flower was 0.66, a density which was over three times that recorded from the cliff and which resulted in noticeably higher levels of damage to the flowers (table 8.4). Significantly more umbels from the mound had flowers with damaged petals ($X^2[1] = 10.56$, $P < 0.01$) and damage to the young pods was also higher, although the difference was not significant ($X^2[1] = 2.96$, $P > 0.1$).

Leaf damage was scored on a presence or absence basis, with missing leaves being ignored. Damage was rarely intensive, with few of the leaves having more than a small amount of tissue removed (table 8.4). The proportion of leaves showing signs of damage was again much higher on the mound ($X^2[1] = 14.02$, $P < 0.001$), confirming that these plants suffer a higher herbivore lead than those growing on the cliff.

Comparisons between the levels of herbivory present on different phenotypes growing in the same area are hampered by the scarcity of acyanogenic morphs on the mound and the generally low numbers of dark keeled plants. Nonetheless, on the mound, the proportion of damaged leaves was significantly higher in the acyanogenic plants, with 25.4% of the leaves showing signs of damage, compared with only 12.1% of the leaves on cyanogenic plants (table 8.5).

Within site comparisons related to flower cyanogenesis are not possible from the mound, where only one acyanogenic flower was recorded. Results from the cliff suggest that there was no relationship between damage to the flowers and both leaf and flower cyanogenesis (table 8.6). Furthermore, acyanogenic plants did not contain significantly more insects. There was no indication of either animal distribution or flower damage being related to keel colour phenotype at either site (table 8.7).

Discussion

This study is supplementary to the research carried out previously at Porthdafarch by Ellis _et al_ (1977b) and by Keymer and Ellis (1978). The cline

Table 8.4 Levels of damage to leaves and flowers of L. corniculatus at Porthdafarch, June 1979.

Site	Leaves Damaged	Leaves n	Leaves % Damaged	Flower Petals Damaged	Flower Petals n	Flower Petals % Damaged	Immature Seed Pods Damaged	Immature Seed Pods n	Immature Seed Pods % Damaged
Cliff	205	4002	5.1	37	167	22.2	27	167	16.2
Mound	568	4552	12.5	65	169	38.5	40	169	23.7

Table 8.5 Leaf damage in relation to leaf cyanogenic phenotype. Porthdafarch June 1979

	Mound		Cliff	
	Leaf Cyanogenesis		Leaf Cyanogenesis	
	++	-	++	-
Undamaged leaves	3381	303	1088	2640
Damaged leaves	465	103	61	143

$X^2[1] = 55.9$, $P < 0.001$

$X^2[1] = 0.048$, $P > 0.05$

Table 8.6 Damage and Insect contents of L. corniculatus flowers in relation to cyanogenic phenotype. Cliff, Porthdafarch June 1979.

Table 8.6a Insects

	Leaf Cyanogenesis		Flower Cyanogenesis	
	++	-	++	-
Umbels with Insects	3	18	7	12
Insect Free Umbels	12	22	20	13

$X^2[1] = 2.89$, $P > 0.05$ $X^2[1] = 2.73$, $P > 0.05$

Table 8.6b Petal Damage

	Leaf Cyanogenesis		Flower Cyanogenesis	
	++	-	++	-
Umbels with petal damage	4	21	9	15
Undamaged Umbels	11	19	18	10

$X^2[1] = 2.94$, $P > 0.05$ $X^2[1] = 3.71$, $P > 0.05$

Table 8.6c Immature Pod Damage

	Leaf Cyanogenesis		Flower Cyanogenesis	
	++	-	++	-
Umbels with pod damage	11	26	7	8
Undamaged Umbels	4	14	20	17

$X^2[1] = 0.34$, $P > 0.05$ $X^2[1] = 0.24$, $P > 0.05$

Table 8.7 Insect numbers and flower damage in relation to Keel Colour. Porthdafarch 1979, Mound and Cliff sites combined.

Table 8.7a Colonisation by *Hypera plantaginis*

	Keel Colour	
	Pale	Dark
Umbels containing Hypera	43	1
Hypera - free umbels	60	8

$X^2[1]$ with Yates' Correction = 2.1, $P > 0.05$

Table 8.7b Petal damage

	Keel Colour	
	Pale	Dark
Umbels with petal damage	60	6
Undamaged umbels	43	3

$X^2[1]$ with Yates' Correction = 1.2, $P > 0.05$

in L. corniculatus leaf cyanogenesis that they described has been found to be mirrored by parallel changes in the proportions of flower cyanogenic plants. Scoring of individual plants for both polymorphic characters has shown that their expression is related, resulting in an excess of those plants which share a similar phenotype. A similar relationship was demonstrated by Jones and Crawford (1977) in an L. corniculatus population from near Birmingham.

Ellis et al (1977b) concluded that maintenance of the cline in leaf cyanogenesis at Porthdafarch was probably the result of plants from the cliff and mound supporting different degrees of herbivore pressure. Snail numbers were found to be high on the mound, giving cyanogenic plants an advantage, whereas on the cliff the number of snails was reduced and this allowed the acyanogenic plants to flourish. Comparison by direct counts of damaged leaves has confirmed that the differences in snail densities observed by Ellis et al are reflected in corresponding changes in the degree of leaf damage sustained by L. corniculatus. Plants growing on the cliff also had fewer damaged flowers than those on the mound and this was related to the smaller numbers of both phytophagous insects and molluscs on the cliff (table 8.4, $X^2[1] = 10.56$).

Several species of snail display a preference for feeding on acyanogenic L. corniculatus when tested in laboratory experiments, but field observations of selective feeding have been less conclusive. Jones (1966) for example, found only one year in three when significantly more of the acyanogenic plants in natural populations showed signs of damage. It is interesting therefore that within the mound population the acyanogenic plants suffered significantly more leaf damage, although it must be stressed that this is based on scores from only three acyanogenic plants, which had 25% leaf damage compared with a 10% average for the cyanogenic plants. Such a large difference in damage levels would appear to provide a potent selective force acting against acyanogenic plants growing on the mound.

There is no evidence to suggest that animals were also preferentially eating acyanogenic plants on the cliff. Acyanogenic flower umbels did not contain more insects (table 8.6a) and the levels of petal damage did not differ significantly between phenotypes (table 8.6b).

At Porthdafarch the possession of a particular keel colour appears to be independent of the cyanogenic phenotypes. Keel colour also has a quite different pattern of distribution, with the cliff and mound populations sharing a similar high proportion of pale keeled plants. Unlike cyanogenesis keel colour frequencies are clearly not influenced by the range of environmental conditions observed at this site.

The results of this survey have provided further evidence in support of the hypothesis that the cline in cyanogensis at Porthdafarch is at least partly the result of a higher level of herbivore activity on the mound. Both insects and molluscs are more abundant there, resulting in considerably more leaves and flowers being eaten and, as acyanogenic plants suffer proportionally more damage, this provides cyanogenic individuals with a selective advantage. The nature of the advantage that acyanogenic plants have when growing on the cliff remains to be established, although differences in salt tolerance has been suggested (Keymer and Ellis, 1978). Recent studies (Compton, Beesley and Jones, in preparation) have found that prior conditioning can have a marked influence on the responses of herbivores to cyanogensis. This may explain why molluscs appear to be selective grazers on the mound, but not on the cliff.

2 JOSTEDALEN

Introduction

The 1979 Hull University Expedition to Norway provided an opportunity for the research on L. corniculatus to be extended to Scandinavia. Six weeks during July and August 1979 were spent in the Jostedal Valley of the Indre Sogn region of south-west Norway. This was followed by a short return visit to the area during early July 1981.

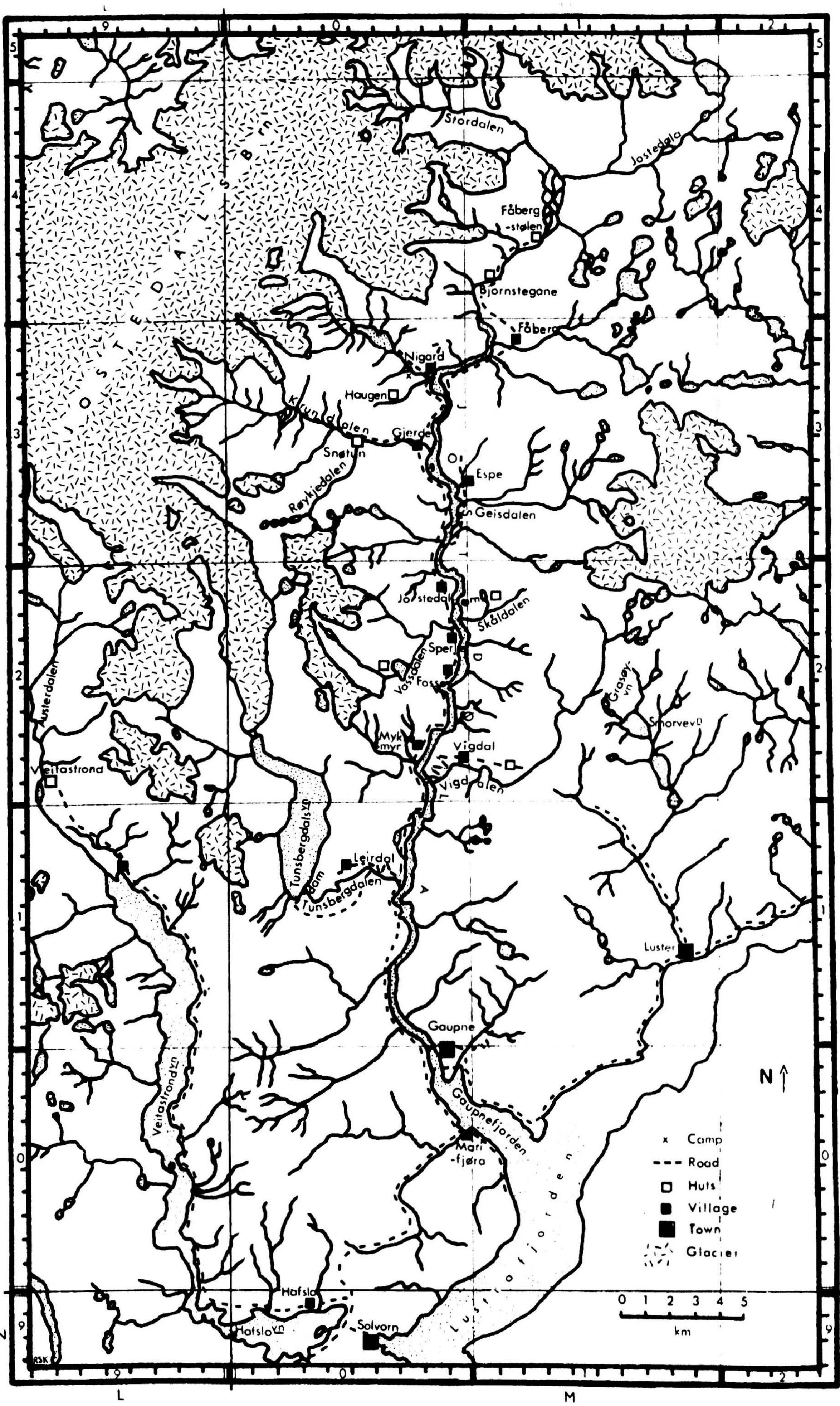
The Jostedalen is situated approximately 200 Km. north of Bergen, at latitude 61 N, longitude 7 E (figure 8.1). The main valley is approximately 50 Km. long and extends northwards from the town of Gaupne which is located on a branch of the Sogn Fjord. Several side valleys enter the Jostedalen, and one of these, the Nigardalen, is particularly interesting because the glacial tongue which it contains has been retreating rapidly since the little ice-age of the 17th Century and has left behind morraine deposits which have been accurately dated (Andersen and Sollid, 1971).

L. corniculatus is the most widespread species of its genus in Norway and is found as far north as Finnmark and at altitudes of up to 1380 metres (Hulton, 1950 and Lid, 1963). No previous studies of L. corniculatus polymorphism have been recorded from Norway, although populations elsewhere in Scandinavia have been investigated by Jones (1977) and Jones and Crawford (1977). They recorded very low levels of leaf cyanogenic plants in the populations (0 - 3%) with the major exception of a population at Eskilstuna in Swden, where 68.6% of the plants were cyanogenic. Dark keel colour was found to predominate in Sweden, ranging between 48% and 85% in the four populations studied, in contrast with the situation in Denmark, where a maximum of 50% of the plants had dark keels. It was likely, therefore, that L. corniculatus in Norway would be predominantly acyanogenic and dark keeled.

L. corniculatus is not generally recognised as a periglacial plant, (Stork, 1963 and Elven, 1974) yet this species is extremely abundant in the

FIGURE 8.1

The Jostedal Valley, S.W. Norway.


JOSTEDALSBRÆ
Stordalen
Jostedøla
Fåberg
-stølen
Bjørnstegane
Fåberg
Nigard
Haugen
Krundalen
Snøtun
Gjerde
Røykjedalen
Oi
Espe
Geisdalen
Jostedal
Skåldalen
Sperl
Vassdalen
Foss
D
Myk
myr
Vigdal
Vigdalen
Grasøy
vn
Smørvevn
Austerdalen
Veitastrond
Tunsbergdalsvn
Dam
Tunsbergdalen
Leirdal
A
Luster
Gaupne
Gaupnefjorden
Mari
-fjøra
Veitastrondvn
Lustrafjorden
Hafslo
Hafslovn
Solvorn
N
x Camp
Road
Huts
Village
Town
Glacier
0 1 2 3 4 5
km
P
N
L
M
RSK

Jostedalen and was found growing close to the retreating face of the Nigardsbreen, on soil only exposed this century. Whether the presence of L. corniculatus is unusual under such conditions remains to be seen, but it can be noted that a search of the nearby Austerdal Valley failed to detect this species.

Methods

Flowers were available throughout the 1979 visit to the Jostedalen, allowing a survey of both flower and leaf phenotypes to be completed. Within each population, plants were sampled at one metre plus intervals by removing a flower umbel and its associated leafy stem.

Leaf tissue was assessed for herbivore activity by counting the proportion of leaves which showed signs of damage and by scoring the three leaves subtended at the base of the flower head as being either healthy, damaged or absent.

All four leaf cyanogenic phenotypes were scored at sites examined in 1981. The + - phenotype was determined by adding one drop of B-glucosidase (extracted from linseed) to leaf material that had given a negative response in the Sodium Picrate test. If this produced a positive result then it was concluded that the phenotype was + -, and if there was no change then the phenotype was - - or - +. These two phenotypes were separated by including one drop of 20 mM linamarin (Calbiochem) in a further picrate test on material from the same source. A postive response showed that the phenotype was - +. Both enzyme and substrate deteriorate under warm conditions and therefore it was necessary to store them in the meltwater stream of the Nigardsbreen as a substitute for refrigeration.

L. corniculatus cuttings were kept in sealed plastic bags during transit. On arrival at Hull they were planted into a 50 : 50 Grit and Compost mixture and rooted in a mist unit. Leaf phenotypes were scored once the plants had become established and had reached sufficient size for leaf removal not to be damaging.

A soil sample was obtained at each of the seven sites visited during 1981. A small pit was dug immediately beneath an L. corniculatus plant and soil from the sub-surface layer was removed for subsequent analyses. These were carried out by Mr. D. Newsome of the Department of Geography at Hull University.

Results

In 1979 L. corniculatus populations were examined at a total of thirteen sites in the Jostedalen area. The frequencies of dark keeled and cyanogenic plants are given in table 8.8 and figures 8.2 and 8.3. Table 8.8 also provides brief descriptions of the habitats that were involved. The sample sites in table 8.8 and in the subsequent tables are ordered in decreasing latitude. An almost complete spectrum of phenotypic frequencies was present. Plants near the Gaupne car park were exclusively acyanogenic and had over 90% of their keels dark, in contrast with those from an exposed cliffside close to the Nigardsbreen, where all the plants were cyanogenic and less than 10% had dark keels.

These two extreme examples reflect a clear trend in that populations further north in the valley contain a higher proportion of cyanogenic and dark keeled plants. Analysis of this relationship using arc sine transformed percentage data and national grid northings gives the following correlation coefficients:

Leaf cyanogenesis $r\,[11] = 0.79$, $P < 0.001$
Flower cyanogenesis $r\,[11] = 0.79$, $P < 0.001$
Keel Colour (dark) $r\,[11] = -0.73$, $P < 0.01$

Sampling sites in the north of the Jostedalen were generally at higher altitudes than those further south, and a similar regression of the transformed percentage data with altitude provides the following significant coefficients:

Leaf cyanogenesis $r\,[11] = 0.62$, $P < 0.02$
Flower cyanogenesis $r\,[11] = 0.65$, $P < 0.02$
Keel Colour (dark) $r\,[11] = -0.60$, $P < 0.05$

Table 8.8 Polymorphism of <u>Lotus</u> <u>corniculatus</u> populations within the Jostedalen area 1979 (Continued on next page)

Sample	Location	Date	Habitat	Altitude (Metres)	Sample Size	Leaf Cyanogenesis (% +ve)	Flower Cyanogenesis (% +ve)	Keel Colour (% Dark)
1	Stordalen MP 118 472	22.7.79	Birch Scrub Understorey	560	56	87.5	96.4	46.4
2	Stordalen MP 121 471	22.7.79	Braided River Sediment	560	51	80.8	80.4	31.4
3	Fabergstolen MP 118 425	7.8.79	Birch Scrub Understorey	470	72/72/88	95.8	80.6	39.8
4	Nigardalen Mp 058 390	16.7.79	Cliffside	400	11	100.0	100.0	9.1
5	Nigardalen MP 069 384	2.8.79	Vaccinium Morraine	300	91	64.4	72.5	38.5
6	Nigardalen MP 077 377	5.8.79	Vaccinium Morraine	270	103	17.3	13.6	34.9
7	Nigardalen MP 087 368	30.7.79	Vaccinium Morraine	250	49	24.5	30.6	42.9
8	Espe MP 092 337	9.8.79	Roadside Verge	230	59/28/28	1.7	0.0	64.0
9	Fossen MP 089 249	30.7.79	Hay Meadow	120	57/56/57	7.0	7.1	28.1

Table 8.8 (Cont'd) Polymorphism of <u>Lotus</u> <u>corniculatus</u> populations within the Jostedalen area 1979

Sample	Location	Date	Habitat	Altitude (Metres)	Sample Size	Leaf Cyanogenesis (% +ve)	Flower Cyanogenesis (% +ve)	Keel Colour (% Dark)
10	Vigdalen MP 099 214	28.7.79	Roadside Verge	510	57	0.0	0.0	50.9
11	Leirdalen MP 048 171	24.7.79	Roadside Verge	360	85	5.9	20.0	56.5
12	Gaupne MP 091 091	19.7.79	Waste-Ground	10	30	0.0	0.0	93.3
13	Gaupne MP 091 089	19.7.79	Wet Meadow	5	76	1.3	0.0	92.1

FIGURE 8.2

The frequencies of plants with light or dark keeled flowers in Jostedalen populations of L. corniculatus. Summer, 1979.

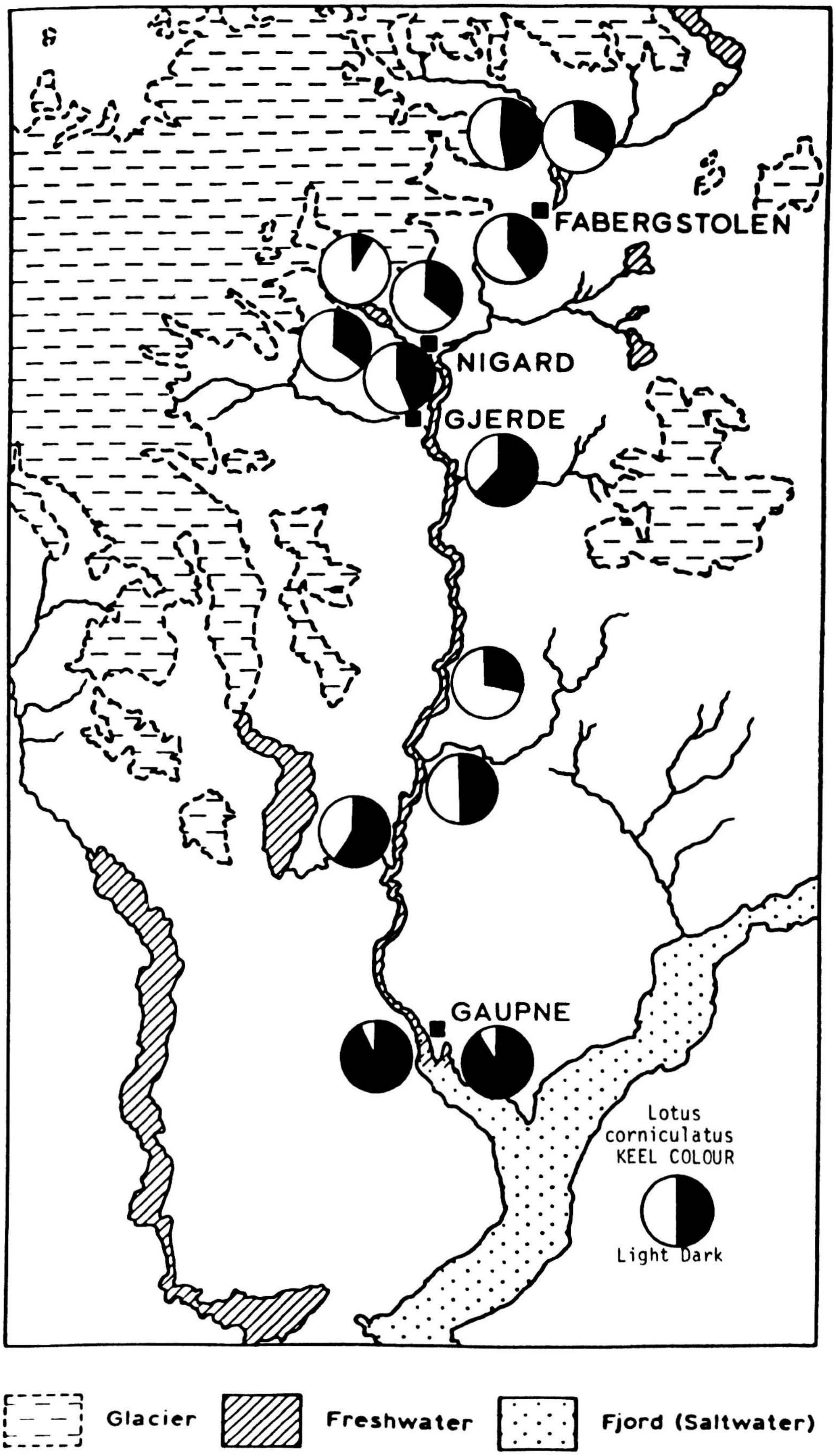
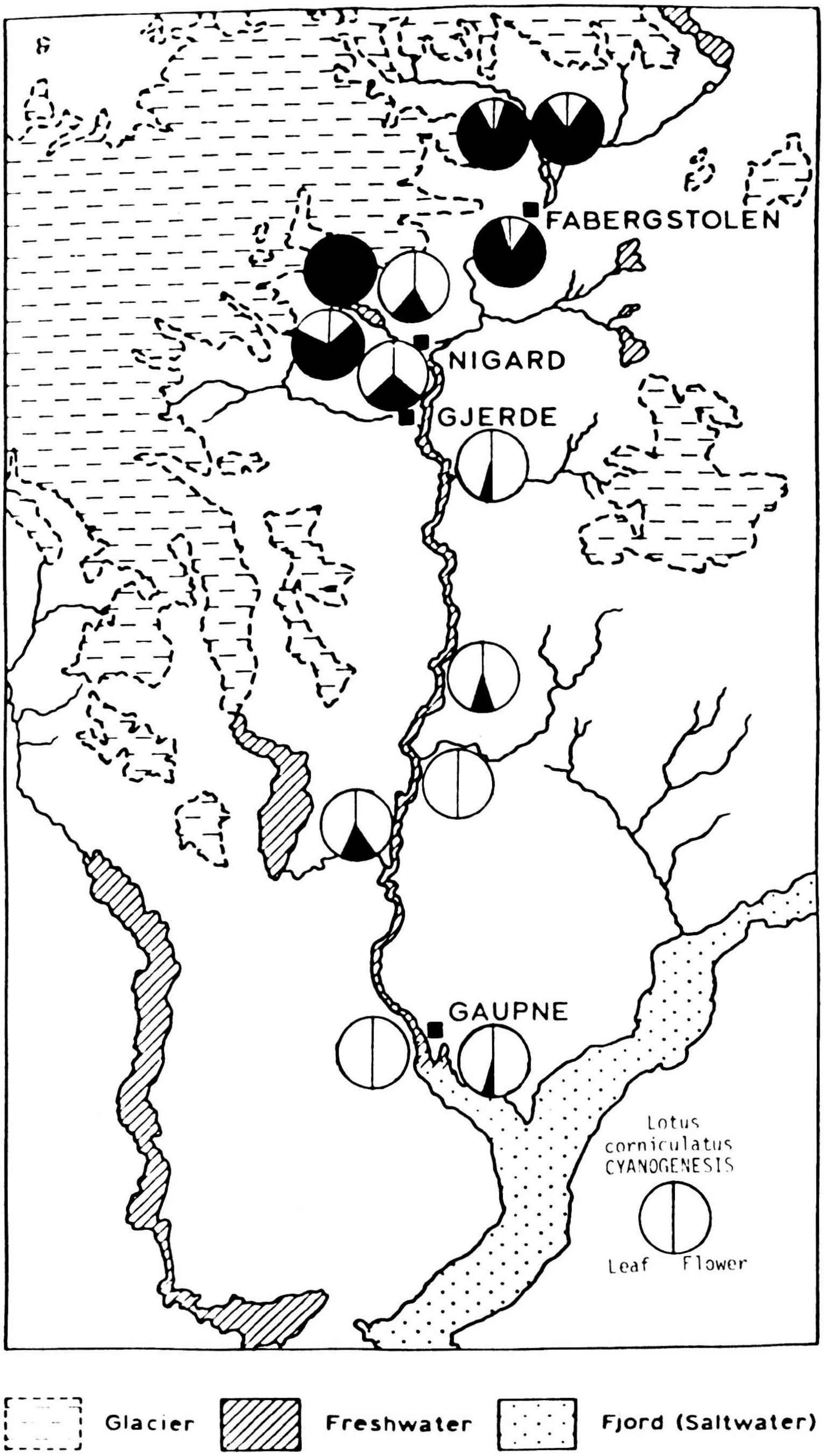

FABERGSTOLEN
NIGARD
GJERDE
GAUPNE
Lotus corniculatus KEEL COLOUR
Light
Dark
Glacier
Freshwater
Fjord (Saltwater)

FIGURE 8.3

The frequencies of leaf and flower cyanogenic individuals in Jostedalen populations of L. corniculatus. Summer, 1979.


8
FABERGSTOLEN
NIGARD
GJERDE
GAUPNE
Lotus corniculatus CYANOGENESIS
Leaf
Flower
Glacier
Freshwater
Fjord (Saltwater)

These analyses suggest that in the Jostedalen populations the phenotypic frequencies of the three polymorphisms are related. This is confirmed by correlating the transformed phenotypic percentages with each other:

Leaf: Flower cyanogenesis, $r\,[11] = 0.98,\ P < 0.001$
Dark Keel: Flower cyanogenesis, $r\,[11] = 0.69,\ P < 0.02$
Dark Keel: Leaf cyanogenesis, $r\,[11] = -0.67,\ P < 0.02$

The frequencies of leaf cyanogenesis at six of the original sites were re-tested in 1981, together with a population close to the retreating face of the Nigard Glacier (table 8.9). Results were generally in close agreement with those obtained previously and confirmed the pattern of distribution discovered in 1979. The leaf cyanogenesis cline in the Jostedalen populations can therefore be considered as effectively stable, as no marked changes had occurred between samples taken two years apart.

Over 90% of the cuttings taken on 5 and 6 July 1981 were successfully established, despite a noticeably higher mortality in the plants which had remained in transit for an extra day. Phenotypic frequencies again agreed with the pattern found in 1979 (table 8.10), although not as clearly as the 1981 scores taken in the field. The number of glucosidic individuals in each population was closely related to the frequency of cyanogenesis, with relatively few plants containing the substrate without the associated enzyme.

Phenotypic relationships can also be investigated within each population because during 1979 individual plants were scored for all three polymorphic characters. Chi square analysis was not appropriate at every site, however, because of low frequencies in one or more cells. At the remaining sites some of the phenotype ratios are extreme and this also prevents chi square analysis of the data when summed over location (Everitt, 1977). Within individual populations there are highly significant associations between the expression

Table 8.9 Frequencies of leaf cyanogenic phenotypes in Jostedalen *L. corniculatus* Populations. 1981.

Location	Date	Phenotypes				Percentage Cyanogenic	
		++	+-	-+	--		(1979)
Stordalen MP 118 472	2.7.81	42	5	0	0	89.4	(87.50)
Stordalen MP 121 471	2.7.81	34	3	9	1	72.3	(80.8)
Nigardalen MP 055 397	3.7.81	28	6	1	13	58.3	(——)
Nigardalen Mp 087 368	3.7.81	7	0	41		14.6	(24.5)
Fossen MP 089 249	5.7.81	2	1	8	37	4.2	(7.0)
Leirdalen MP 048 171	5.7.81	2	4	42		4.2	(5.9)
Gaupne MP 091 089	5.7.81	0	0	4	44	0	(1.3)

Table 8.10 Frequencies of leaf cyanogenic phenotypes in cuttings obtained from Jostedalen *L. corniculatus* populations.

Location	Date of collection	Date scored	Phenotypes ++	+-	-+	--	Percentage cyanogenic
Nigardalen MP 055397	5.7.81	18.9.81	14	3	19	23	23.7
Nigardalen MP 074385-093374	6.7.81	23.9.81	59	13	2	7	72.8
Nigardalen MP 087368	6.7.81	18.9.81	16	3	3	5	59.2
Fossen MP 089249	5.7.81	2.10.81	9	5	17	34	13.8
Leirdalen MP 048171	5.7.81	23.9.81	7	7	5	23	16.7
Gaupne MP 091089	5.7.81	2.10.81	1	2	7	40	2.0

of cyanogenesis in the leaves and petals at three of the sites, but not elsewhere (table 8.11). No significant relationship between combinations of keel colour and flower cyanogenesis is suggested (table 8.12) although there is a degree of heterogeneity and one population does provide a marginally significant chi square value.

The percentages of damaged leaves recorded at sites in the Jostedalen (table 8.13) show that during July 1979 damage was minimal at the more exposed northern sites, but reached quite high levels in the Gaupne and Leirdal populations. The two estimates of subtended leaf damage in table 8.13 give broadly similar results, but including all missing leaves as damaged gives, as expected, a slightly higher estimate. As the measures of subtended leaf and total leaf damage are strongly correlated ($r[4] = 0.97$ with estimate a, and $r[4] = 0.81$ with estimate b, using arc sine transformed percentages), counts of the subtended leaves alone may provide a convenient alternative to total leaf counts as a measure of herbivore pressure on <u>L. corniculatus</u>.

The flowers also showed signs of greater damage at the southerly sites (table 8.14). Thrips were the only insect group found consistantly in the flowers, with <u>Odontothrips loti</u> the dominant species. Also present, but in smaller numbers, were <u>Contarinia loti</u>, <u>Apion loti</u>, and a species of Aphid. <u>Hypera plantaginis</u> was apparently absent from the valley, although larvae were found nearby at the Hardangerfjord and any petal damage was probably caused by large chewing insects and molluscs rather than by the insects living inside the flowers.

Meaningful comparisons between the herbivore pressure sustained by different phenotypes are not possible for most sites because of the generally low degree of damage that was recorded and by the scarcity of particular phenotypes.

Table 8.11 L. corniculatus populations with individual plants scored for both leaf and petal cyanogenesis.

	Leaf ++		Leaf -		n	X^2[1] (Incl. Yates' Correction)	P
Petal	++	-	++	-			
Location							
Stordalen MP 121471	35	6	6	4	51	1.87	> 0.05
Fabergstolen MP 118425	56	13	2	1	72	0.02	> 0.05
Nigardalen MP 069384	44	14	21	11	90	0.63	> 0.05
Nigardalen MP 077377	10	8	4	81	103	28.52	< 0.001
Nigardalen MP 087368	11	4	1	33	49	24.21	< 0.001
Leirdal MP 048171	4	0	13	68	85	11.95	< 0.001

Table 8.12 *L. corniculatus* populations with individual plants scored for both keel colour and flower cyanogenesis.

	Light Keel		Dark Keel		n	X^2[1] (Incl. Yates' Correction)	P
Petal	++	-	++	-			
Location							
Stordalen MP 121471	27	8	14	2	51	0.75	> 0.05
Fabergstolen MP 118425	34	10	24	4	72	0.78	> 0.05
Nigardalen MP 069384	45	11	20	14	90	4.89	< 0.05
Nigardalen MP 077377	10	56	4	33	103	0.38	> 0.05
Nigardalen MP 087368	9	19	3	18	49	2.07	> 0.05
Leirdal MP 048171	7	30	10	38	85	0.05	> 0.05

Table 8.13 Estimates of leaf damage sustained by Jostedalen *L. corniculatus* in July 1979

Location	Date	n (stems)	Subtended leaf Damage (%) Estimate a[1]	Subtended leaf Damage (%) Estimate b[2]	Total Leaf Damage (%)
Stordalen Woods	22.7.79	23	4.3	0.0	2.0
Nigardalen (Sample 4)	16.7.79	10	0.0	0.0	3.4
Nigardalen (Sample 7)	30.7.79	24	5.6	4.2	4.8
Leirdal	24.7.79	26	17.9	12.2	11.9
Gaupne Waste Gnd.	19.7.79	12	16.7	3.4	13.9
Gaupne Meadow	19.7.79	18	25.5	24.0	17.2

[1] Estimate a scores missing leaves as damaged

[2] Estimate b ignores missing leaves

Table 8.14 Inhabitants and damage to *L. corniculatus* flowers, Jostedalen 1979.

Location	Date	Sample Size Umbels	Sample Size Flowers	% +ve Flower CN[1]	% Dark Keel[1]	% Umbels Damaged	Thrips Total	Mean Thrips Per Flower
Stordalen	22.7.79	25	101	100.0	40.0	4.0	10	0.09
Nigardalen	16.7.79	11	44	100.0	9.1	0.0	15	0.32
Nigardalen	30.7.79	25	84	36.0	32.0	9.5	4	0.05
Leirdal	24.7.79	27	109	22.0	70.4	16.5	99	0.91
Gaupne	19.7.79	15	56	0.0	93.3	8.9	10	0.18
Gaupne Meadow	19.7.79	20	68	0.0	85.0	14.7	3	0.04

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[1] These data are included within the general collections in Table 8.8

Analysis of the flower damage at Leirdal and Nigardalen (30 July sample), however, shows that this was not influenced either by keel colour (X^2 [1] = 1.89 and 1.14 respectively) or by flower cyanogenesis (X^2 [1]= 2.31 and 1.14 respectively, with Yates' Correction).

The pattern of leaf damage in the 30 July Nigard sample is interesting because a higher proportion of the cyanogenic leaves showed signs of injury. A low level of overall damage was present at this site, with only 8.0% of the cyanogenic and 3.25% of the acyanogenic leaves damaged, and this result was not repeated elsewhere.

The results of the soil analysis carried out by D. Newsome are given in table 8.15. Although the sites exhibited considerable variation in soil chemistry, this does not appear to be related to the frequencies of cyanogenesis found in the L. corniculatus populations as no significant correlations were found between any soil characters and leaf cyanogenesis.

Discussion

The initial intention of the field work in Norway was to study the relationship between insects and L. corniculatus in a region where individuals were predominantly acyanogenic. As cyanogenic plants were found to be numerous the emphasis of research was changed and priority was given to an investigation of the phenotypic frequencies in the Jostedalen populations.

Some individuals of L. corniculatus possess an unstable cyanogenic phenotype (Jones, 1977) and leaves scored as cyanogenic in July and August may be acyanogenic at other times. This instability would not have invalidated the comparisons between sites in the present study because all the samples were obtained within a six week period.

A series of clines clearly exist within the L. corniculatus populations of the Jostedalen, at least in the summer, with the proportions of leaf cyanogenic, flower cyanogenic and pale keeled plants all increasing with an increase in latitude. Several environmental variables show changes that may be correlated

Table 8.15 The soil chemistry of sites colonised by *L. corniculatus*. July 1981. Data of D. Newsome.

Locality	Ca Me/100g	Mg Me/100g	Na Me/100g	K Me/100g	PO4 Mg/100g	NH4 Mg/100g	NO3 Mg/100g	Total N Mg/100g	Organic % total soil wt.	pH
Stordalen MP 118472	1.48	0.35	0.33	0.22	0.05	3.22	0.0026	222.0	7.09	4.4
Stordalen MP 121471	0.57	0.06	0.18	0.06	0.71	0.83	0.0008	8.0	0.55	5.0
Nigardalen MP 055397	0.47	0.04	0.17	0.07	0.82	0.88	0.0017	5.7	0.74	5.1
Nigardalen MP 087368	0.72	0.08	0.28	0.14	0.03	0.92	0.0016	28.0	2.38	4.7
Fossen MP 089249	2.24	0.15	0.37	0.17	0.74	5.07	0.0017	591.0	10.49	4.6
Leirdal MP 048171	2.05	0.22	0.29	0.25	0.08	2.94	0.0029	275.0	6.54	5.2
Gaupne MP 091089	0.56	0.19	0.58	0.16	1.43	0.83	0.0000	34.0	1.03	6.0

with these clinal distributions, including temperature, droughting and herbivore activity.

L. corniculatus flowers have predominantly dark keels in the south of the Jostedalen and light keels in the north. The significance to the plant of possessing a particular phenotype is currently uncertain, but clearly the dark keeled plants have an advantage in the south of the valley which is lost further north.

Relationships between the cyanogenic and keel colour polymorphisms in the Jostedalen populations are broadly similar to those found at Porthdafarch. There is again an excess of plants sharing the same leaf and flower cyanogenesis phenotypes, but no excess of plants with a particular combination of cyanogenesis and keel colour. Expression of cyanogenesis in the leaves and flowers therefore appears to be related in some way, but occurrs independently of keel colour.

The populations that have high proportions of cyanogenic plants are situated in the more recently glaciated regions of the Jostedalen, on soils that are relatively newly formed. These young soils are strongly acidic and contain very low concentrations of metallic cations, nutrients and organic carbon. Similar soil conditions have been described from periglacial areas both elsewhere in Scandinavia and in North America. (Stork, 1963, Tisdale et al, 1966, Viereck, 1966 and Worsley and Ward, 1974). The sites with predominantly acyanogenic populations have soils which do not differ greatly from these periglacial soils, however, (table 8.15) and, since cyanogenic frequencies are not correlated with any of the soil characters that were investigated, it would appear that the observed cline is unlikely to be related to edaphic conditions.

Winter temperatures are the most important factor determining the distribution of cyanogenic Trifolium repens in Europe (Daday, 1954 ab). No similar role has been demonstrated with L. corniculatus, however, either in field population studies (Jones, 1977) or survival experiments (Ellis et al 1977a) and the preponderance of cyanogenic plants at higher altitudes and at more exposed sites in the Jostedalen is directly contrary to that found with T. repens. The high altitude sites in the south of the Jostedalen give further support to the view that temperature and altitude are not determining the frequency of cyanogenic L. corniculatus because their populations are typical of the nearby valley floor, and not the northerly sites at equivalent altitudes.

On the morraine deposits of the Nigard Valley, L. corniculatus was most numerous at the sides of streams and in other relatively damp situations. This distribution may have resulted directly from soil water limitations, because the low clay and organic carbon content of glacial soils generally results in very rapid drainage, even delaying colonisation on glacial outwash gravels (Ugolini, 1968). Alternatively, the more extensive moss cover of these damper areas may simply have provided better conditions for the germination and establishment of the plants.

Droughted conditions have been shown to increase the proportions of acyanogenic plants in Derbyshire L. corniculatus populations (Foulds and Grime, 1972), but the relationship between availability of water and cyanogenesis is evidently complex as drought conditions are known to increase the cyanogenic response of Trifolium repens (Rogers and Frykolm, 1937), Sorghum (Nelson, 1953) and Cassava (de Bruijn, 1973 and Butler et al, 1973). Nonetheless it is perplexing that it appears to be the drier sites in the Jostedalen which have the highest frequencies of cyanogenesis - in direct contrast to the findings from Derbyshire. This underlines the comments of Jones et al (1978) that it is the combination of a number of selective factors which determines the frequency of cyanogenesis in L. corniculatus populations and that each area must be examined individually in order to determine which factors are most influential.

The figures obtained in July 1979 would suggest that selective feeding by animals is unlikely to be of importance in maintaining the clines in cyanogenesis. Leaf and flower damage were highest at the sites where plants were mainly acyanogenic and cyanogenic plants did not appear to suffer less damage. Observations during 1981, however, revealed the presence of a potentially important herbivore whose distribution is likely to be limited to the areas where most plants are cyanogenic. Evidence of a very large population of Norwegian Lemmings (Lemmus lemmus L.) was found in Stordalen, particularly around site two (table 8.8). Many characteristic lemming runs were present (Corbet and Ovenden, 1980), piles of lemming dung measured up to several metres across, and the bodies of several dead lemmings (presumably killed during the winter) littered the area. Lemming numbers are notoriously variable (e.g. Semb-Johansson et al, 1979) and two years previously there was no sign of lemmings in this area.

Lemmings are usually restricted to the sub-alpine zone of birch and willow scrub, with animals only moving into the lowlands during migratory years (Marsden, 1964, Finerty, 1980). The presence of lemmings was not confirmed at any other sites where L. corniculatus was growing, but it is clear that they are more likely to encounter L. corniculatus in the north of the valley than elsewhere, and it is here that the plants are predominantly cyanogenic.

Lemmings eat mainly short growing mosses during the winter (when they continue to feed under continuous snow cover) and a combination of grasses and mosses during the summer (Kalela et al, 1961). Evidently Dicotyledons usually form only a minor part of their diet, although Baltruschat and Uberboch (1976) found that this was not always the case. L. corniculatus has not been recorded as a food item. In captivity, lemmings have been reared for many generations on a diet of mosses, rolled oats, apples and whole-wheat bread (Semb-Johansson et al, 1979).

Lemming activity was so intensive at Stordalen that even minor items of the lemmings' diet must have suffered extensive damage. In Stordalen the frequencies of cyanogenic L. corniculatus were the highest recorded in the Jostedalen (70%) and it is tempting to speculate that this has resulted from intensive (allbeit spasmodic) selection for plants which lemmings find distasteful. Microtus agrestris will preferentially eat acyanogenic L. corniculatus in feeding trials (Jones, 1962) and as Lemmings and Voles are closely related (Subfamily Microtinae) this may also be the case with L. lemmus.

The commitment of nitrogen for cyanoglucosides at the periglacial sites is particularly striking because nitrogen is likely to be in unusually short supply there. This is the result of a combination of low exogenous nitrogen levels, with low calcium and magnesium concentrations, low pH and low temperatures - all of which inhibit Rhizobium functioning (Vase and Jones, 1963, Vincent, 1962, Graham and Parker, 1964 and Pate, 1977). Jo et al (1980), for example, found that growth of L. corniculatus at pH 5 was only 55-72%, and root nodule weight was only 37%, of that obtained at pH 7. Although resources allocated to cyanoglucosides can be recovered relatively cheaply (Mckey, 1979), the degree of commitment found at these northern sites would suggest that a strong selective advantage must be gained by their retention.

Rhoades (1979) concluded that plant defensive compounds were allocated in proportion to the risk of tissue damage and the value of a particular tissue to the plant. Janzen (1974) and Mckey et al (1979) also developed this argument and have shown that plants growing in harsh environments may contain unusually high levels of protective compounds as a result of their tissues being hard to replace, and hence more valuable. The nutrient poor soils, low temperatures and short growing season (in early July 1981 snow cover was still extensive in Stordalen and Nigardalen) at the periglacial sites will limit the new growth that L. corniculatus can produce. This may be an important subsidiary factor in the selection for cyanogenic plants at these sites because any leaves or flowers lost through herbivory are clearly likely to be difficult to replace.

The following research will be necessary in order to establish whether feeding by lemmings is indeed a major factor in the maintenance of cyanogenic clines in the Jostedalen:

1. Carry out feeding trials in order to (a) estimate the relative palatability of L. corniculatus when compared with known major food items such as mosses and grasses, and (b) determine whether L. lemmus will distinguish between cyanogenic phenotypes.
2. Confirm that the distribution of lemmings is correlated with high frequencies of cyanogenic plants in the L. corniculatus populations.
3. Check in the field that L. corniculatus is eaten by lemmings and establish whether acyanogenic plants suffer greater damage.

CHAPTER IX

DISCUSSION

"The ultimate discussion of the cyanogenic glucoside content of Lotus leaves will have to include a discussion of Lotus root protection against nematodes through phytoalexin production, and how each defence is bought at the expense of the other, and how each kind of herbivory lowers the fitness of the plant rather than how much it lowers the yield of leaves or roots" - Janzen (1981).

The information gained in this study about the animal communities associated with *L. corniculatus* provides one of the necessary first steps in achieving this "ultimate discussion" of the genecology of the cyanogenic polymorphism in *L. corniculatus*. Because the plant, its herbivores and their parasites interact both directly and via the medium of the resource budget of the plant (Janzen, 1973), conclusions about the significance of any one particular selective pressure are likely to be distorted if they are considered in isolation. Considerations of the more important results described in this thesis have already been included in the relevant chapters, so here I shall restrict further discussion to an overview of cyanogenesis as a means of defence against herbivory in the light both of original and review articles and of my own research.

Jones (1979) has argued that cyanogenic glycosides may be primary metabolites and that cyanogenesis in plants has appeared via mutations in regulatory genes that have resulted in the extravagant production of these compounds. Small quantities of cyanogenic glycosides are therefore probably present in all L. corniculatus plants and the cyanogenesis which we can detect with the sodium picrate test is only distinguishing between the relative amounts of these compounds that are being produced. The fact that some herbivores respond differently to individuals scored as 'cyanogenic' or ' acyanogenic' nonetheless confirms that this distinction is ecologically meaningful.

Chemical defence is now considered to be the major function of cyanogenesis in L. corniculatus and T. repens (Jones, 1972a). Previous studies (Crawford - Sidebotham, 1972, Keymer, 1978) have concentrated on the relationship between molluscs and cyanogenesis, but Keymer (1978) and Dritschilo et al (1979) have both commented that insects could also prove to be important factors in the maintenance of the cyanogenic polymorphism in L. corniculatus.

The feeding experiments described in chapter three have provided the first examples of selective feeding by insects on L. corniculatus (notwithstanding a misquote by Culvenor, 1970). Subsequent experiments (Compton, in preparation) have shown that a third species of grasshopper (Chorthippus brunneus Thun.) also prefers to eat acyanogenic L. corniculatus flowers and that the Common Earwig (Forficula auricularia L.) selectively eats acyanogenic leaves and flowers.

The significance of these laboratory results is largely dependent on whether L. corniculatus is a regular item in the diet of these insects.

Phyllobius adults have been seen to feed on L. corniculatus flowers at several localities in the U.K., but casual observation has failed to confirm that any of the species of grasshoppers feed on L. corniculatus under natural conditions. All three species are considered to be primarily grass feeders, and Bernays and Chapman (1978) concluded that Chorthippus spp. were totally intolerant of the chemicals contained in broad-leaved plants. Kaufman (1965) tested the feeding responses of a large number of acridoids and found that even those species which normally feed on forbs (Oedipoda and Psophus spp.) did not touch L. corniculatus. Contrary observations were recorded by Clark (1948), however, and Richards and Wolff (1954) concluded that L. corniculatus can be moderately acceptable to some species. No account was taken of the polymorphism of cyanogenesis in any of these studies and their differing conclusions about the palatability of the plant may merely be the result of comparing responses to different morphs. These accounts also considered only the relative palatability of leaves to grasshoppers, and feeding on flowers has been mentioned rarely. The preference shown for L. corniculatus flowers in the feeding experiments suggests that this may be a significant omission in that flower feeding may prove to be more widespread than is usually believed. Nonetheless, it is unlikely that L. corniculatus forms a major item in the diet of any British grasshoppers, and selective feeding by these insects is more likely to be of importance to the plant in Southern Europe or parts of the U.S.A., where acridoids are more numerous and diverse.

F. auricularia, the adults of Phyllobius spp. and, to a lesser extent, the members of the Acrididae are generalist biting insects that feed upon a variety of plant species. These phytophages almost certainly lack specialised adaptations for feeding on L. corniculatus and can be considered as the ecological equivalents of many of the molluscs that are also known to be deterred by cyanogenesis. It is these, and other generalist species, that are likely to have an influence on cyanogenic frequencies in natural populations of L. corniculatus because the specialist leaf and flower chewing insects which regularly feed on this plant do not show selection when tested experimentally (Lane, 1962, Jones, 1966 and Compton in preparation).

Myrmeleotettix maculatus was only deterred from feeding on cyanogenic *L. corniculatus* after it had bitten, and therefore physically damaged, the plant tissues. This agrees with the results of Cooper-Driver and Swain (1976) and Woodhead and Bernays (1977) who found that it was the release of HCN, rather than the presence of cyanogenic glucosides, that was responsible for the inhibition of feeding by locusts on Bracken (*Pteridium aquilinum*) and *Sorghum* spp. Unfortunately *L. corniculatus* flowers that contained cyanogenic glucosides, but no β - glucosidase, were not available, and this prevented direct confirmation that feeding inhibition was caused by cyanogenesis *per se*. Exposure to HCN results in the inhibition of insect peripheral sensory responses (Levinson *et al*, 1973) and this may be one mechanism by which cyanogensis is detected because Blaney (1981) has shown that relative sensory input from the palps of locusts has an important role in the detection of unpalatable chemicals.

Some species of polyphagous molluscs and insects are capable of associating the symptoms of poisoning with the food plant on which they are feeding (Gelperin and Forsythe 1975, Dethier, 1980). Specimens which survive the toxins show 'food aversion learning' and subsequently avoid feeding on that particular plant species. β - glucosidase activity has been recorded from the digestive systems of both insects and molluscs (Kasturi *et al*, 1981, Dirzo and Harper, 1982), and Fowden and Lea (1979) have concluded that any cyanoglucosides that are ingested by phytophages will be rapidly hydrolyzed. Approximately 1% of the fresh weight of *T. repens* leaves is composed of cyananoglucoside (Collinge and Hughes, 1981) and as *L. corniculatus* leaves are more strongly cyanogenic (Jones, 1966), there is a possibility that feeding inhibition could also occur if animals that feed on *L. corniculatus* tissue suffer ill-effects from cyanide liberation and subsequently associated the illness with this food plant. A possible example of the toxic effects of consuming large quantities of cyanoglucoside was described by Fisk (1980) who showed that specimens of Peregrinus maidis produced less honeydew when maintained on artificially high concentrations of cyanoglucoside. The insects did not show any signs of distress, however.

Cyanogenesis is often considered as a prime example of the 'Qualitative' plant defenses that are typical of 'unapparent' plant species (for example Fox, 1981). Qualitative poisons are described as 'low-cost' defenses that are effective at low concentrations and can cause a serious reduction in the fitness of generalist phytophages. They also exert strong selective pressures on specialised phytophages and, by the process of 'co-evolution', it is relatively easy for specialists to develop effective defenses against them.

Humans, and mammals in general, are notoriously sensitive to cyanide (Feeny, 1976, Conn, 1979) and the entomologists' cyanide killing bottle effectively demonstrates the susceptability of insects to this poison. In insects as with other groups of animals, the toxic effects of cyanide exposure result from the inactivation of cytochrome oxidase (Keister and Buck, 1974). Several groups of insects are somewhat resistant to cyanide however (members of the Chrysomelidae, Meloidae and Zygaenidae - for example, Povolny and Weyda, 1981) and insects in general can tolerate and recover from much higher doses of cyanide than mammals (Bond, 1961).

Cyanide detoxification is believed to be carries out by the enzymes rhodanese and β - cyanoalanine synthase and Conn (1979) has suggested that the ability of animals to survive on cyanogenic plants should be correlated with the amounts of these enxymes that they contain. Other adaptations may also be necessary and Brattsen (1979) has concluded that the ability to feed on cyanogenic material for long periods may reflect a combination of modified respiratory enzymes, detoxifying enzymes and even sequestration into specialised organs. Parsons and Rothschild (1964) and Brattsen (1979) have shown that rhodanese is present in insects and a survey carried out recently by S.G. Beesley (Pers. Comm.) has shown that this enzyme occurrs in a wide variety of insect species. β - cyanoalanine synthase is also widespread, at least amongst the Lepidoptera (R. Davis, Pers. Comm.) and it is likely therefore that the majority of phytophagous insects possess at least some degree of resistance to HCN. The widespread distribution of these enzymes need not reflect a general need for cyanide detoxification because Volini and Alexander (1981) have argued that the traditional role of rhodanese as a sulphur donor to cyanide is only complementary to its routine function as a sulphur donor to proteins.

Despite cyanides 'well known toxicity to insects' (Dritschilo et al, 1979) there is no evidence to date that the amounts of cyanide released during cyanogenesis (an estimated equivalent of 0.5 - 1.0 μm HCN from Sorghum - Woodhead and Bernays 1977) or by subsequent digestion are acutely poisonous to insects. The specialist species which routinely feed on cyanogenic plants are evidently resistant, as are some polyphagous species, such as the Southern Armyworm (Spodoptera eridania Cram.) which was unaffected by cyanogenesis in L. corniculatus and Phaseolus sp. (Scriber, 1978 and see also Jones, 1981).

The question of cyanide toxicity is nonetheless most relevant in connection with those species which are known to be deterred by cyanogenesis, as it is assumed that these species are the 'targets' of this defense strategy. Molluscs that are maintained exclusively on cyanogenic L. corniculatus for long periods do not have a greater mortality rate then those feeding on the acyanogenic form (D.A. Jones, Pers. Comm.) and Dirzo and Harper (1982) found that when slugs were kept on cyanogenic T. repens they had only a slightly lower growth rate than controls kept on the acyanogenic morph. A reduced growth rate was to be expected as the slugs ate more of the acyanogenic T. repens and this result need not imply that chronic poisoning was taking place. Although the grasshoppers M. maculatus and O. viridulus are unable to survive for long periods on an exclusive diet of L. corniculatus (up to 50% die within three days) there is similarly no evidence that they die more quickly when kept on cyanogenic plants, while the earwig, F. auricularia can be maintained on cyanogenic L. corniculatus for periods of several weeks without any visible signs of ill-health (Compton, in preparation).

The animals that are deterred by cyanogenesis in L. corniculatus are therefore physiologically capable of coping with cyanide for far longer than they would need to under natural conditions, and it can be concluded that they would not be subject to acute cyanide poisoning if they failed to show selection and continued to feed despite cyanogenesis. This need not be the case when animals are feeding on plants with higher cyanoglucoside concentrations (for example the seeds of Vicia sativa L.) and in these situations generalist feeders might suffer acute poisoning. In general, however, it appears unlikely that the HCN liberated during cyanogenesis acts as an acute poison to unadapted phytophages and as such it cannot be considered as a typical 'qualitative' defence.

If generalist insects and molluscs are not poisoned by the cyanide liberated by L. corniculatus, why are they selective? Feeding on cyanogenic plants presumably has disadvantages, including subtle effects due to chronic cyanide exposure and the metabolic costs involved with detoxification, but these could be outweighed by the costs of deciding to "move-on" to another plant. L. corniculatus, in common with many other cyanogenic species, contains a variety of additional putative defensive compounds (Bernays and Chapman, 1975) and one explanation may be that cyanogenesis has a role that is analagous to the red and black warning colouration of aposematic insects and so warns generalist herbivores that a plant is potentially unpleasant. Cyanogenesis would appear to be well suited to such a role because it is recognised by a wide variety of animals (Mammals, Molluscs, Insects), it is relatively 'cheap', particularly for legumes (Mckey, 1979, Feeny, 1976, Janzen, 1981) and it is widespread amongst both flowering and non-flowering plants (Culvenor, 1970). Horn (quoted by Culvenor, 1970) has commented on the general distaste shown by herbivores for bitter-tasting plants and has even suggested that a form of mimicry could develop whereby non-toxic bitter-tasting plants could escape herbivory.

Studies of the insects associated with L. corniculatus, carried out at Eppleworth Quarry and elsewhere, have confirmed that this plant supports an extensive and diverse insect fauna. The number of species that are represented is nonetheless considerably smaller than that suggested by a review of the literature, particularly with respect to exophytic leaf chewing insects. This may be due in part to species being more or less restricted to Southern Britain and the fauna of L. corniculatus should prove to be even more diverse in that part of the country. With the exception of members of the Hemiptera and Heteroptera, which were not investigated thoroughly, the phytophagous insects that were regularly found on L. corniculatus were specialist species more or less restricted to this, and related, food plants, and generalist phytophages were poorly represented.

The L. corniculatus population at Eppleworth Quarry is effectively monomorphic for both leaf and flower cyanogenesis and is therefore unsuitable for an investigation of the responses of insects to cyanogenesis in the field. At Porthdafarch it was found that there was greater leaf and flower damage on the mound area and this agreed with the expectations of Ellis et al (1977b). The pattern of leaf damage was typical of that produced by grazing molluscs (with most of the damaged leaves having less than 25% of their surface area removed from their distal edge) and any leaf chewing by insects was insignificant in comparison. Much of the flower damage at Porthdafarch was attributable to feeding by larvae of Hypera plantaginis and because this species does not appear to be influenced by cyanogenesis (Chapter eight and

Beesley and Compton, in preparation) this probably accounts for the failure to detect a significant excess of damage to acyanogenic flowers. In the Jostedal valley the frequencies of cyanogenic plants in the L. corniculatus populations were not correlated with the observed levels of leaf and flower damage and, therefore, it again appears that selective feeding by insects is unlikely to play a major role in the maintenance of cyanogenic polymorphism there.

During the course of this study extensive defoliation of L. corniculatus by insects was only observed on one occasion (where there was an unusually high local concentration of Zygaena larvae) and in general the amount of leaf tissue consumed by insects was found to be relatively small in comparison with that which could be attributed to feeding by molluscs. Mature plants have a well documented resistance to leaf damage (MacCollan et al, 1982, for example, found that even when 38% of the leaves of Alfalfa were mined by an Agromyzid there was no detectable reduction in yield) and this suggests that even where insects do display selective herbivory they may not consume enough leaf tissue for selection to be of significance to a mature plant.

Feeding by snails can kill T. repens seedlings even 30 days after Cotyledon formation (Kalmbacher et al, 1979) and it has been postulated that reduction of grazing pressure at the seedling stage may be a particularly important role for leaf cyanogenesis (Jones, 1971, Crawford-Sidebotham, 1972, Ennos, 1981). Insects were never seen feeding on L. corniculatus cotyledons, however, and an examination of seedlings growing at Wharram Quarry revealed again that it was molluscs which were causing most of the damage.

Feeding by insects would appear to have its greatest impact on the sexual reproductive output of L. corniculatus. There is no evidence that any of the specialist insects which feed in L. corniculatus pods and flowers are influenced by flower petal cyanogenesis, however, and it is these species which cause most of the damage to the reproductive structures. Feeding by Hemiptera is a second major source of seed losses, but the mode of feeding of this group minimises their exposure to cyanogenesis. Nonetheless it is known that cyanogenic glucosides can be transported in the phloem of some plants (Clegg et al, 1979) and therefore any phloem-feeding species may be liable to come into contact with HCN liberated by their endogenous β-glucosidases. External damage to seed pods (much of which would have occurred while the immature pods were still surrounded by the petals) was a significant source of seed losses at Eppleworth Quarry. Larvae of Cydia compositella and Hypera planteginis were responsible for some of the damage, but the remainder was due to feeding by unidentified larger insects and by molluscs. It is as a deterrant to these generalist feeders that flower cyanogenesis is likely to be successful.

The presence or absence of cyanogenesis is only one of many factors which influence the degree of herbivory sustained by an L. corniculatus plant growing under natural conditions and it is therefore not surprising that studies of the deterrant value of cyanogenesis in natural populations have generally been less conclusive than parallel laboratory experiments. Studies with molluscs have shown that their pattern of response to cyanogenesis varies between individuals, with 'deviant' non-selective individuals occurring in typically selective species (Crawford-Sidebotham 1971, Dirzo 1980) and Jones (1981) has concluded that it may be necessary to consider herbivores as being polymorphic in terms of their response to cyanogenesis. Herbivores are also likely to become less selective as their hunger increases, and Voles, for example, were shown to be selective only when alternative foods were also available (Jones, 1966).

The intensity of herbivore damage sustained by individual L. corniculatus plants will also be influenced by the nature of their surrounding plant community. Dirzo and Harper (1982) showed that T. repens growing near nettles (Urtica dioica L.) suffered increased herbivory from snails, because the nettles acted as refuges for molluscs. Feeding trials have also shown that slugs from areas where certain unacceptable plants are present do not eat as much of these plants as 'naive' individuals collected from areas where the plants are absent (Whelan, 1982). On a similar basis it could be postulated that the degree of selectivity shown by herbivores from areas where *L. corniculatus* is predominantly cyanogenic will be more highly developed than that of individuals from mainly acyanogenic sites. If cyanogenic conditioning does have a significant influence on feeding responses then the situation could be highly complex because in chalk greasland there are at least four species that are polymorphic for cyanogenesis (*Achillea millefolium* L., *Centaurea scabiosa* L., *T. repens* and *L. corniculatus*). A relationship between cyanogenic frequencies in *L. corniculatus* and *T. repens* has already been demonstrated by Jones (1968) who showed that there were significantly fewer cyanogenic individuals in *T. repens* populations where *L. corniculatus* (cyanogenic) was also present than in nearby populations where *L. corniculatus* was absent.

Characteristics other than differential palatability have also been associated with cyanogenic polymorphism. Dritschilo *et al* (1979) concluded that cyanogenic *T. repens* were better competitors, and Dommee *et al* (1980) have provided a basis for this advantage by showing that cyanogenic *T. repens* display faster root growth. Under certain conditions the cyanogenic morph of *L. corniculatus* also shows better root growth (Keymer and Ellis, 1978) and preliminary results suggest that the acyanogenic plants at Porthdafarch (irrespective of cliff or mound origin) are less successful when transplanted into a dense sward (S.G. Beesley, Pers. Comm.). If an association between cyanogenic phenotype and competitive ability is confirmed then this will further complicate studies of the genecology of cyanogenesis. For example, at Wharram Quarry there is a significantly higher proportion of strongly cyanogenic *L. corniculatus* growing in areas of dense vegetation than in nearby more open areas (Beesley and Compton, unpublished). This distribution could be attributed to the higher density of large snails that are present in the dense sward, or to a possible greater competitive ability amongst the cyanogenic plants, or to a combination of the two.

The feeding choice experiments described earlier have shown that some insects prefer to eat acyanogenic *L. corniculatus*, but evidence that this is translated into a selective advantage in the field has not been obtained and the results that are available suggest that (at least in the U.K.) molluscs are more important herbivores than generalist insects. Deterrence of insect and mollusc feeding is likely to be complementary, however, and in situations where *L. corniculatus* is growing in dry or acid conditions selective feeding by insects may assume a greater significance.

Studies at Porthdafarch have shown that *L. corniculatus* plants are grazed more heavily by snails on the mound rather than the cliff and that the snails eat more of the leaves of acyanogenic plants. From this it has been concluded that on the mound, unlike the cliff, the degree of differential herbivory confers a selective advantage on cyanogenic individuals. Confirmation of this view, that it is primarily the distribution of molluscs which determines the frequency of cyanogenic plants, will require relatively long term examination of the plants at Porthdafarch. Reciprocal transplants of cyanogenic and acyanogenic *L. corniculatus* between the mound and cliff can provide one means of comparing the success of mature individuals of known phenotype growing in the two areas. It has been argued, however, that selective grazing may be particularly important at the seedling stage. Seedlings were observed only rarely at Porthdafarch and the introduction of seeds into artificially disturbed areas will probably be necessary before seedling mortality can be investigated. Problems arise, however, because with the complex inheritance of cyanogenesis and the self-incompatability of *L. corniculatus* it is currently impossible to produce seeds (and hence seedlings) of known phenotype.

Sequential removal of seedling sub-samples, or the scoring of individuals after germination, provide means of circumventing this difficulty, but neither method is entirely satisfactory.

The study of selection in natural populations is not readily compressed into the three year period allocated to most research programmes. In order to obtain a thorough understanding of the selective pressures operating on L. corniculatus populations it may be necessary to establish and to monitor carefully an isolated population of known genetic character for a period of several years. An ideal location for such a project would be a recently abandoned chalk quarry or similar site where native L. corniculatus are absent, but the species is likely to prosper once introduced. Early successional development could be speeded up by the provision of a well broken substrate (for example chalk rubble) which will favour seedling establishment and by seeding the area with examples of the local flora. Peripheral information would also be generated on topics like the establishment and development of the fauna associated with L. corniculatus and the interaction between plant, herbivores and parasites. A possible elaboration of such an experiment could involve the division of the transplants into zones where molluscs and/or insects could be eliminated by appropriate chemical treatments.

This thesis had the objective of describing the insect community associated with L. corniculatus and of providing a preliminary assessment of the likely importance of insects in the maintenance of cyanogenic polymorphism in natural populations. Insects nonetheless form only one component of the biotic environment of L. corniculatus and in order to assess the significance of insects in the genecology of cyanogenesis it will be necessary to consider their impact in combination with the other factors which together determine the relative success or failure of an individual plant.

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