Dynamics of the guild structure in the parasitoids and inquilines of an alien gall wasp, *Andricus quercuscalicis* Burgsdorf

by

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Abstract

Rapid and substantial changes have occurred in the parasitoid and inquiline community associated with the agamic galls of *Andricus quercuscalicis* in Britain since the insect arrived in southern England. Over the last 5 years the species composition converged to that recorded from galls from the native range.

High rates of attack by inquilines, virtually absent in previous surveys, were recorded in south-east England, but not at the edge of the invaded range. Inquiline abundance was positively correlated with parasitoid species richness, because most parasitoid species concentrated their attack on inquilines.

An examination of the guild structure sampled in different parts of the native and invaded range revealed continuous trends away from the native range in a number of community and food-web parameters.

The abundance patterns of 4 parasitoid species attacking the gall-maker, and 2 parasitoid species attacking inquiline larvae, were related to: 1) gall morphology; 2) the geographical location of the sample sites; and 3) the abundance of other members of the guild.

While parasitism of the agamic galls was low (<5% in Britain, <15 % in the native range), ten parasitoid species caused local mortalities up to 80% in the sexual galls of *A. quercuscalicis* collected in the native range. An analysis for spatial variation in density dependent abundance patterns showed both positive and negative density dependence as well as density independent relationships between parasitism and host density at all spatial scales and for all parasitoid species.

A comparison between the distributions of *A. quercuscalicis* and two other invading gall wasps, *Andricus kollari* and *A. lignicola*, showed that *A. quercuscalicis* was the only species positively associated with the presence of Turkey oak (an obligate host tree) and suggests that *A. quercuscalicis* exhibits the lowest rate of spread.

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1. Introduction

Communities might vary over time and space in species richness, abundance patterns or food web structure. Long-term variation is often difficult to examine, but invasions provide an excellent natural experiment to study such effects as species recruitment. Communities which might focus on an invader often begin from a known baseline (no species at all); and secondly, one can observe the community after different periods of residence of the invader along the invasion route.

The subject of this study is the community of parasitoids and inquilines attacking an invading cynipid gall wasp, *Andricus quercuscalicis*. Insect galls are particularly useful for community studies, because the whole population is stationary during the larval development inside the gall and it is therefore easy to census because every specimen which enters the gall, such as parasitoids, leaves a trace or remains which can usually be identified. Thus by the end of a season a mature gall might provide information about the timing and/or the cause of death of each of the inhabitants. These features have led to cynipids being used in a number of ecological studies. An example of metapopulation dynamics involving local extinctions by a natural enemy was described by Washburn and Cornell (1981); an example for competitive replacement was shown by Askew (1962); Cornell (1985) investigated the relationship between local and regional species richness using cynipid galls on oak; also early food web studies were based on cynipid galls (Askew 1961a, Schoenly and Cohen 1991). As an invading cynipid, *A. quercuscalicis* appears to be an ideal subject for community studies.

During the last 150 years four cynipid gall wasps were added the British cynipid fauna: *A. quercuscalicis, Andricus kollari, A. lignicola* and *A. corruptrix* demonstrating that the community of cynipid gall wasps in Britain was invasible after *Quercus cerris,* an obligate host tree for these species, was introduced. Since there is no indication of competitive exclusion of any of the native cynipid species by the invaders it appears that the species richness in these communities is not determined by niche pre-emption (May 1981, Lawton and MacGarvin 1986, Hails 1988). While *A. kollari* was intentionally introduced to Britain in about 1850, for the tanning and dying industry, the other three species spread naturally across continental Europe and arrived in Britain between the late 1950's and 1975 (Darlington 1974, Claridge 1962, Quinlan 1974). Of the four invasions the one by *A. quercuscalicis* has been most intensively studied (Collins *et al.* 1983, Hails *et al.* 1990, Hails and Crawley 1991, Stone and Sunnucks 1993, Schönrogge *et al.* 1994). Since *A. quercuscalicis* has been well established in Britain for the last 30

years, this species provides an opportunity to study the development of the guild of parasitoid and inquiline species associated with its galls (Hails and Crawley 1991).

1.1. Life-cycle of *Andricus quercuscalicis*

Andricus quercuscalicis is a gall forming cynipid. Like most other cynipid gall wasps *A. quercuscalicis* produces two generations each year. One generation consists only of females which reproduce parthenogenetically. By the end of February to the beginning of March these females oviposit into buds on Turkey oak (*Quercus cerris*) which contain male flowers where they induce the tiny galls of the second, sexual generation. The males and females of the sexual generation emerge by the end of May or beginning of June and oviposit into the female flowers of English oak (*Q. robur*) where they induce galls on the acorns, commonly called knopper galls, inside which the larvae of the parthenogenetic generation develop (see also Schönrogge *et al.* 1994). The host alternation between Turkey oak and English oak is obligate and determined much of the invasion history of this species (Stone and Sunnucks 1993).

1.2. Recruitment of native natural enemies by an invader

By invading new territory the invader might leave its natural enemies behind in its native range. Eventually, however, it will be detected and exploited by species native to its new range. The recruitment of native herbivores to introduced plants is comparatively well studied (Strong 1979, Auerbach and Simberloff 1988). These studies demonstrated a number of strong trends: 1. the native herbivore species recruited relatively quickly to invading plants; 2. the resulting assemblages were often less species rich compared with those in the native range of the invader; and 3. assemblages in the invaded range have a higher proportion of generalist species. Cornell and Hawkins (1993) examined these observations for local parasitoid communities focused on invading herbivore species by comparing them with parasitoid communities associated with native hosts. Invading hosts showed generally lower percentages of parasitism and a less species rich parasitoid guild than comparable native hosts. The number of parasitoid species contained in the guild of the invading herbivores showed only a slight tendency of increase over the first 150 years, also rate of increase varies considerably between host species (Cornell and Hawkins 1993).

1.3. The process of recruitment and the role of pre-adaptation

The ways in which individual species of natural enemies might be recruited to invading species were described by Strong *et al.* (1984) and Cornell and Hawkins (1993); these include the density of the invading host and/or the native enemy respectively, the area occupied by the invader, and the time of residence of the

invader. All these factors relate to the encounter frequency between the invading host and the native natural enemy (Strong *et al.* 1984).

Also important will be the degree of pre adaptation by the native to the invading host. The pre adaptations might be morphological, phenological or behavioural (Askew 1960, Sellenschlo and Wall 1984, McClure 1986). More important for native herbivores on invading plants might be a physiological pre adaptation which enables the herbivore to accept the chemical compounds in the new host. The degree of pre adaptation might then be reflected in terms which are easier to measure. Taxonomic isolation for instance, i.e. the relatedness of the invader to the native fauna or flora, might represent the similarity in the chemical compounds. Taxonomic isolation was shown to be important for the recruitment of herbivores to invading plants but less important for the recruitment of parasitoids to invading herbivores (Auerbach and Simberloff 1988, Hawkins and Lawton 1987). The wider search image of generalist species can be interpreted as an behavioural pre adaptation for colonising new hosts and might explain why parasitoid communities based on invading hosts have higher proportions of generalists.

There is evidence that morphological adaptation might be of particular importance for parasitoids attacking cynipid galls (Askew 1960, Cornell 1983, Weis and Abrahamson 1985, Weis *et al.* 1985). Price *et al.* (1987) reviewed, *inter alia*, the "enemy hypothesis", which attributes the evolution of galling and the subsequent diversification of gall shapes to the attack of natural enemies, and here in particular insect parasitoids. According to this hypothesis, galling species can gain parasitoid free space by building a physical (and sometimes chemical) barrier around them. Galling species and their parasitoids would then have entered into an "evolutionary arms race" in which the gall former evolved new shapes of galls and the parasitoids morphological means to circumvent the defence. However, evidence about the enemy hypothesis is still controversial (Price and Pschorn-Walcher 1988, Hawkins and Gagne 1989, Hawkins 1990). Price *et al.* (1987), for instance, argue that too much variability might actually minimise the differences in gall shape experienced by the parasitoids. Parasitoids might also show phenological adaptation by attacking the gall before it is sufficiently developed to provide any defence for the gall former whereby different shapes of the mature galls would not be important (Wiebes-Rijks and Shorthouse 1992, see also Chapter 4).

1.4. Previous work on the communities of the galls of *A. quercuscalicis*

Approximately 20 years after the arrival of *A. quercuscalicis* in Britain parasitism in the sexual galls was recorded with about 25% and has not changed dramatically since (Collins *et al.* 1983, Hails 1988). Also the number of parasitoid

species has remained constant. At the same time parasitism in the agamic galls was virtually absent and only in 1978 one specimen of the parasitoid *Syntomaspis cyanea* was recorded from knopper galls (Martin 1982). This record might represent an accidental oviposition or even be based on a misidentification since this species was never reared again from British knopper galls nor is it known from continental ones. However, during the 1980's a number of parasitoid species were found repeatedly and could be said unambiguously to have recruited to the guild of British knopper galls.

Collins *et al.* (1983) pointed out that there was a surprising lack of similarity between the parasitoid species lists recorded from knopper galls collected in continental Europe and in Britain since most of the parasitoid species were recorded in Britain as well, although from other cynipid hosts. This point was reiterated by Hails *et al.* as recently as 1990 after extensive rearings of knopper galls from Britain.

1.5. History of the invasion

The distribution of *A. quercuscalicis* was originally restricted by the distribution of one of its obligate host trees, *Quercus cerris*. When Turkey oak was extensively planted as an ornamental tree in parks and gardens throughout Europe about 300 years ago, *A. quercuscalicis* begun to extend its range (Stone and Sunnucks 1993). Knopper galls are very conspicuous and likely to be recorded very soon after the gall wasp became established in a new area. The earliest record from outside the native range dates back to 1631 (Gauss 1977 from the chronicles of the city Gera in Germany). Although the species had no taxonomic name by that time, the description by the unknown author is so vivid that mistaken identity is very unlikely. Since that time more records, further into the invaded range, have been published (Table 1.1).

Table 1.1: First published records of *A. quercuscalicis* from the invaded range in western Europe.

Year	Source	Region
1783	Burgsdorf(1787)*	Berlin (Brandenburg/Germany)
1882	Beijerink (1897)*	Netherlands
1892	Keßler (1895)*	Kassel (Hessen/Germany)
1898	Riedel (1910)*	Dresden (Sachsen/Germany)
about 1900	Hayhow (1983)	Channel Islands
1902	Dittrich (1909)*	Wraclaw (Poland)
1957	Pfützenreiter and Weidner (1958)	Hessen (Germany)
1958	Claridge (1962)	East Anglia (Britain)
1986	Nelson (personal communication)	Ireland
1989	Duty and Amelung (1990)	Rostock (Mecklenburg/Germany)
1992	Royal botanical garden (personal communication)	Copenhagen (Denmark)

* - these references are extracts from the reference collection of the late Dr. Haase (Halle/Germany) which were kindly provided by Mrs. L. Utech. Some of these references are unfortunately not complete. All information available is given in the Bibliography.

Since the galls were first recorded in East Anglia *A. quercuscalicis* spread through England and Wales (Hails and Crawley 1992) and was only recently in 1993 recorded for the first time from Scotland (P. Walker personal communication).

1.6. Contents of this thesis

Cynipid galls are characteristically associated with a number of parasitoid and inquiline species (Askew 1961a, 1984, Wiebes-Rijks and Shorthouse 1992). In this study the communities associated with the galls of *A. quercuscalicis* from its native range in south-eastern Europe to its western and northern distribution limits were examined and questions posed about spatial and/or temporal patterns in guild structure, species composition and population regulation. Chapters 2,3 and 4 are concerned with different aspects of the parasitoid and inquiline guild of the agamic galls of *A. quercuscalicis*. Chapter 5 discusses aspects of the parasitoids which attack the sexual generation of *A. quercuscalicis* in the native range and in central Europe, while Chapter 6 examines the cynipid community with particular emphasis on the invading species in Ireland which was invaded most recently.

In Chapter 2 temporal and spatial patterns in the recruitment of parasitoids and inquilines in Britain were examined, where these galls have been studied for now nearly 15 years (Collins *et al.* 1983, Hails *et al.* 1990, Hails and Crawley 1991, 1992, Schönrogge *et al.* 1994). The geographical distribution of parasitoid and inquiline recruitment were studied and the effect the recruitment of inquilines had on the species composition of the guild.

In Chapter 3 the guild structure across the sampled range has been investigated. Geographical trends in guild structure and the distribution of attack of individual parasitoid and inquiline species and links to the invasion history of *A. quercuscalicis* have been analysed. For the analyses a food web approach was employed to determine community properties. The difficulties of this approach are also discussed.

In Chapter 4 statistical modelling techniques have been employed to analyse the abundance/occurrence patterns of individual parasitoid species, species richness patterns, and the importance of gall shape. Further explanatory variables used in all these models were the geographical location of the sites from which the galls were sampled, to reflect the invasion history of *A. quercuscalicis*, and community variables (e.g. the abundance of other community members, particularly inquilines), to control for associations between community members. The results were also reviewed as to whether they produced new arguments for or against the enemy hypothesis (Price *et al.* 1987).

The subject of Chapter 5 are the parasitoids which attack the larvae of the sexual generation of *A. quercuscalicis* in its native range and in central Europe. Using a stratified sampling scheme (within trees across sites, between trees across sites and between sites) the spatial variation of patterns of density dependent parasitoid attack were examined (see also Hails and Crawley 1992). Accordingly, the possible impact of parasitism on the regulation of the population dynamics of *A. quercuscalicis* have been discussed and compared to previous work done in Britain (Hassell and Pacala 1990, Hails and Crawley 1991, 1992).

While the first four Chapters used mainly comparisons between Britain, regions in continental Europe which were invaded earlier and the native range, is Chapter 6 is concerned with Ireland, a region to which *A. quercuscalicis* spread to from Britain. The structure of the cynipid communities throughout Ireland including all cynipid species were examined, but special emphasis was given to the four invading species, *Andricus quercuscalicis, A. kollari, A. lignicola* and *A. corruptrix* and their relation to their host plants.

1.7. General statement to the production of this thesis

This thesis was funded by the Department of Environment and produced during a project on "Monitoring of invading insects". Chapters 2 to 6 represent manuscripts for publication in different journals which results in a certain amount of repetition and some stylistic differences. The project was conducted and the manuscripts produced in close collaboration with Dr. G.N. Stone and Dr. M.J. Crawley. The order of authorship for the manuscripts reflects the relative inputs of

the contributors. Chapters 2 - 4 and Chapter 6 are by Schönrogge, Stone and Crawley while the remaining manuscript is by Stone, Schönrogge and Crawley.

2. Alien herbivores and native parasitoids: rapid development of guild structure in an invading gall wasp, *Andricus quercuscalicis* (Hymenoptera: Cynipidae)

2.1. Introduction

Trophic guilds tend to be presented as if they were static in time and uniform in space (Schröder 1968, Cohen 1978). The importance of dynamic processes in structuring communities has been outlined on theoretical grounds but it is difficult to observe in the field (Pimm 1982, Pimm *et al.* 1991, DeAngelis 1992). The long term investigation of invading species and the development of the communities associated with them allows us to study rapid dynamics in both these aspects of community structure.

During the early period of an invasion the risk of extinction is high due to small population size (Lawton and Brown 1986). On the other hand, low mortalities in the invaded range might help to achieve a sufficient growth rate to overcome this period, especially if natural enemies were left behind in the native range of the invader. In this case, the invading species could be said to have entered 'enemy free space' (sensu Jeffrey and Lawton 1984). However, at some point the invader is likely to be exploited by natural enemies native to its new range. Possible mechanisms underlying the recruitment of native species onto invaders are described by Strong *et al.* (1984).

The analysis of the recruitment of herbivores onto alien plants and of parasitoids onto invading insects demonstrates that the duration of residence of the invader is generally a poor predictor of the development of the associated communities (Auerbach and Simberloff 1988, Strong *et al.* 1977, Strong 1979, Cornell and Hawkins 1993). While there is some evidence that communities associated with invaders tend to stabilise over a relatively short period of time (Strong 1979, Cornell and Hawkins 1993), it is difficult to predict the outcome of invasions for any given species. Species-area relationships are generally regarded as more important in predicting the size and composition of the guild supported by an invading species (Strong *et al.* 1984, Cornell and Hawkins 1993).

The invasion of Britain by four alien cynipid gall wasps, *Andricus quercuscalicis, A. kollari, A. lignicola* and *A. corruptrix,* provides us with an excellent natural experiment in which to study the changes to community structure that occur following invasions. The four species are currently at different stages in their invasion of Britain (P. Walker personal communication) and this may allow us carry out comparative studies in the future. However, one of the invaders, *A. quercuscalicis,* and its communities have been studied in detail since 1979 (Collins *et al.* 1983, Hails *et al.* 1990, Hails and Crawley 1991, Stone and Sunnucks 1993, Schönrogge *et al.* 1994). Here we describe the changes in species composition and

abundance that have occurred in the community associated with the agamic galls of this species over the last 15 years in different parts of Great Britain and Ireland. The results are discussed in comparison with studies of the same community in the native and invaded range of *A. quercuscalicis* in continental Europe (see Chapter 3 and 5). This allows further analysis of geographical patterns in community structure.

2.1.1. Natural history of the invader

A. quercuscalicis produces two generations each year. In spring asexual females oviposit into the male flowers of Turkey oak (*Quercus cerris*) where the hatching larvae induce the galls of the sexual generation. The males and females of the sexual generation emerge in late May - early June of the same year. The sexual females oviposit into the female flowers of English oak (*Q. robur*) where a characteristic gall, commonly known as a knopper gall, is induced on the acorns. The asexual generation overwinters inside the knopper galls, and emerges in the following spring. This study concentrates on the asexual generation; details of the community associated with the sexual galls can be found in Hails and Crawley (1991).

While *Q. robur* is widely distributed in Europe, the native range of *Q. cerris* is restricted to southern and eastern Europe. Human introduction of *Q. cerris* throughout western and northern Europe as an ornamental tree in parks and gardens over the last 300-400 years has created islands of Turkey oaks, from which Turkey oak has become locally naturalised. The history of the westward migration of *A. quercuscalicis* across Europe and the genetic bottlenecks through which the populations appear to have passed are described in more detail by Stone and Sunnucks (1993).

2.1.2. Earlier studies on the parasitoid and inquiline community

Nearly all of the parasitoid species known to attack *A. quercuscalicis* in its native range were known from native British cynipid galls, and it was expected that after a short time these parasitoids would discover and exploit *A. quercuscalicis* (Collins *et al.* 1983, Hails *et al.* 1990). While parasitism in the spring galls on *Q. cerris* in Britain has remained relatively constant at 20% since rearing began (Crawley 1986, Hails and Crawley 1991), very few parasitoids or inquilines were reared from the asexual knopper galls until the beginning of the 1980's (Martin 1982, Collins *et al.* 1983, Hails *et al.* 1990).

By 1988 a total of 11 parasitoid species had been obtained from knopper galls collected in various parts of England. Of these, only a few species, such as *Mesopolobus jucundus* and *M. amaenus,* were found regularly. Despite the fact that parasitism rates are still very low (rarely over 3%), species richness of the

guild in Britain has increased markedly over the last 10 years. As described in this paper, the size of the discrepancy in species composition between British guilds and those known from continental Europe (Hails *et al.* 1990), is now greatly reduced.

The species composition of the community associated with a cynipid gall is determined by the following factors: 1. the time of the year when the gall is found on its host plant; 2. the precise location of the gall on the plant; and 3. the detailed morphology of the gall. Knopper galls are unusual compared with the native British cynipid fauna in that they are the only cynipid gall to be induced on acorns, and the galls are larger than most British (but not continental) cynipid galls (Askew 1961a, Cornell 1983). Knopper galls grow on the acorn cup, in place of the acorns of *Q. robur*. The larval chamber is located centrally at the base of the gall, and is surrounded by a thick, corky wall covered by a sticky coating. Given the difference between this and the native British cynipids, some time lag in the recruitment of parasitoid and inquiline species to this novel host was perhaps to be expected (Askew and Neill 1993).

2.2. Methods

2.2.1. Sample sites

The results presented here are based on rearings of galls collected from 200 sites in Britain and 7 sites in Ireland (Figure 2.1). The location of each sample site was recorded on the national survey grid.

2.2.2. Rearings and dissections

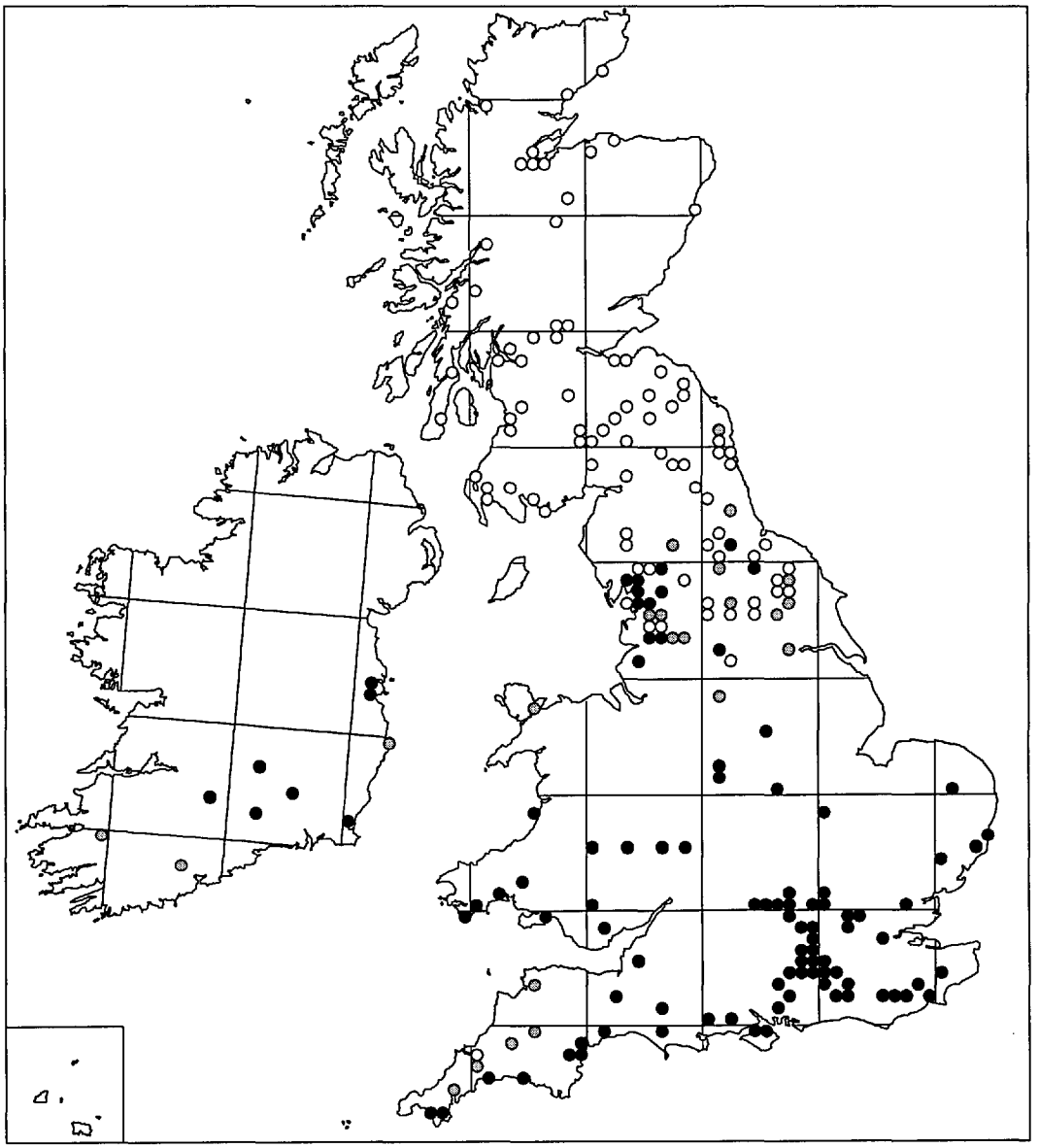
A total of 38,901 knopper galls were collected in 1990 and 1991, and reared in one of three different ways:

1. 28,174 galls from 181 sites, including 2,216 galls from 7 sites in Ireland, were kept in mass rearings. The number of galls per rearing container varied between 34 and 324 galls. To avoid complications due to variations in sample size in comparisons of species richness between sites (Karban and Ricklefs 1983) the number of galls in each container was standardised to 150 galls whenever possible. Larger collections were sub-sampled for that purpose.

2. 6,381 galls from 44 sites were kept individually to assess the variation of inquiline infestation and parasitism within samples.

3. 4,346 galls from 29 sites were opened and the gall wasp larval chamber separated from the outer wall. Both parts were then reared separately, thus determining the place of development for specimens which emerged (Hails *et al.* 1990).

Figure 2.1 : The distribution of *Andricus quercuscalicis* and of the sample sites (aggregated in 10km squares).



Solid Circles- Locations where samples were taken; Shaded Circles - knopper galls were found but not abundant enough for collections; Open Circles - No knoppers found.

All rearings were stored in an outdoor insectary and checked three times a week. Each insect that emerged was identified, and the species and the date recorded.

To determine the phenology of inquiline oviposition during gall development, samples of 50 galls were collected each week in Silwood Park from mid-July until mid-September 1992. The width and the height of the gall, and the diameter of the gall wasp's larval chamber, were measured, and the gall was subsequently dissected in order to count inquiline and parasitoid larvae. The oviposition period was then identified from the peak of the number of inquiline larvae per gall in a sample.

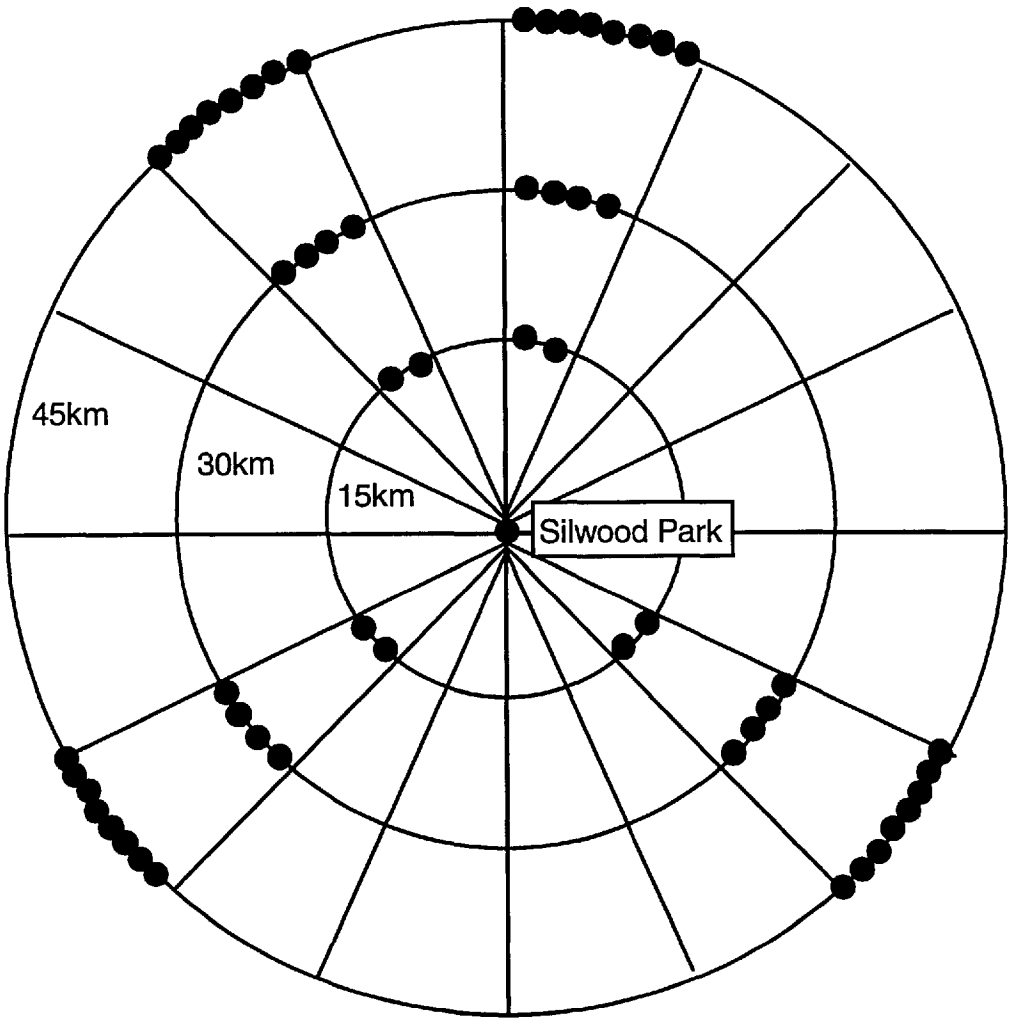
2.2.3. Analysis of the geographical surveys

In addition to collections throughout the study area, more systematic collections were undertaken to examine spatial variation in community structure in more detail. Schönrogge *et al.* (1994) suggested that inquiline infestation in knopper galls was highest in the south-east of England, and to obtain a clearer picture of the geographical distribution of inquiline attacks 56 samples were taken in four stratified random compass sectors at given distances (15km, 30km and 45km) away from Silwood Park (Figure 2.2). The number of samples was doubled with each step away from the centre in order to compensate for the increase in circumference with distance. The survey results were analysed using linear modelling. The response variable was the log transformed proportion of inquilines per gall (eqn. 1; where inq = number of inquilines emerged from a sample which varied from 0 to 344, n = number of galls in a sample; n varies between 80 - 100 galls) and the explanatory variable was distance from Silwood park fitted separately for each compass direction.

$$y = \ln\left(\frac{inq}{n} + 1\right) \qquad (1)$$

To test whether sites with high inquiline attack rates (mean number of inquilines per gall > 1) had a characteristic geographical distribution, the mean northerliness and the mean easterliness for these high inquiline sites were calculated and compared to the mean northerliness and the mean easterliness of all sample sites. The means were calculated using the British National Grid and the comparisons were performed as a 2-sample Wilcoxon rank-sum test.

Figure 2.2 : Collection scheme to establish dispersal from a point source (Silwood Park)



Parasitoid species richness was analysed in a generalised linear model with Poisson errors and a log-link function. Explanatory variables were the northerliness and easterliness of the sample site, sample size and inquiline infestation, the squares of these terms (to test for non-linearity) and their products (to test for 2 way interactions). Significance of the explanatory variables was assessed by stepwise deletion from the maximal model and using χ^2- or F - tests as appropriate to assess the significance of each term (Crawley 1993).

2.3. Results

2.3.1. Members of the community

The species identified as being members of the knopper gall community are listed in Table 2.1. The first two species, *Synergus gallaepomiformis* and *S. umbraculus*, are inquilines that develop within the wall of the gall. Variable numbers of inquiline larvae (from 0 up to 85 larvae) developed in an individual gall by feeding on gall tissue. Dissections of the British knopper galls produced no evidence to suggest that the presence of inquiline larvae did any harm to the gall former (this is in marked contrast to knopper galls collected from the native range; see Chapter 3).

Table 2.1: Parasitoid and inquiline species reared in Britain from the asexual galls of *A. quercuscalicis*.

Family	Genus	Species	(I)nner cell/ (O)uter wall
Cynipidae	*Synergus*	*gallaepomiformis*	O
		umbraculus	O
Pteromalidae	*Mesopolobus*	*jucundus*	I*/O
		amaenus	I (4) & O(17)
	Cecidostiba	*semifascia*	?
Eurytomidae	*Eurytoma*	*brunniventris*	O
	Sycophila	*biguttata*	I(48)&O(3)
Torymidae	*Torymus*	*nitens*	O
	Megastigmus	*dorsalis*	O
		stigmatizans	I
Eupelmidae	*Eupelmus*	*urozonus*	O
Ormyridae	*Ormyrus*	*nitidulus*	I
Gelidae (Ichneumonidea)	*Gelis*	*formicarius*	I

I - indicates that in separated rearings all specimens emerged from the larval chamber of the gall former; O - all specimens emerged from the gall wall; ( ) - the number of specimens emerged from each location; ? - none of the specimens reared emerged from the separated rearings.* *M. jucundus* was observed to attack the gall former by R.R. Askew (personal communication).

The remaining species in Table 2.1 are parasitoids which attack either the inquilines or the larva of the gall former. Based on rearings where the gall wasp larval chambers and the wall of the gall were kept separately it was possible to divide the members of the knopper gall guild into two reasonably distinct groups. 'I' indicates that all specimens obtained from these rearings emerged from separated inner cells, (i.e. were parasitoids of the gall former) while 'O' means that all specimens of this species were reared from the outer walls (i.e. were either inquilines or parasitoids of the inquilines). For those few species reared from both inner cell and outer wall the number of individuals that emerged from each part of the gall is given in parentheses. *C. semifascia* is marked with a question mark because all of the specimens emerged from the mass rearings, so there is no way of knowing where they developed and which species might have been the host.

During the dissections, all of the parasitoids were found to be solitary ectoparasitoids with the exception of *S. biguttata,* which is a solitary endoparasitoid. No remains of other parasitoid larvae, such as mandibles or skins, were found which indicates that hyperparasitism was not a major mortality factor in this guild.

2.3.2. Inquilines

2.3.2.1. Phenology of inquiline emergence

The emergence period of *S. gallaepomiformis* in 1991 started at the beginning of July: 50% of the specimens emerged within the next 2 weeks and the last specimens had emerged by mid-August. Cumulative emergence curves for *S. gallaepomiformis* (Figure 2.3a) show that males emerged 5-7 days earlier than females. Figure 2.3b shows that emergence of the same species in 1992, started nearly 3 weeks earlier. After the first week in July there was a break of about 2 weeks until emergence resumed, and emergence had finished by mid-August, as in the previous year.

S. umbraculus was much rarer in knopper galls than *S. gallaepomiformis* (but see Chapter 4 and Figure 4.3 for non-British distribution). Infestation rates (i.e. the mean number of inquilines per gall) were also much higher in *S. gallaepomiformis* (mean up to 5.32) than in *S. umbraculus* (mean up to 0.32). Of the 151 specimens of *S. umbraculus* that emerged from our rearings, 4 specimens eclosed earlier in May, 10 during June and all the others (=90%) within a 1 week period in mid-July. No emergence was recorded thereafter.

Figure 2.3 : Cumulative emergence of *Synergus gallaepomiformis* during a) 1991 and b) 1992

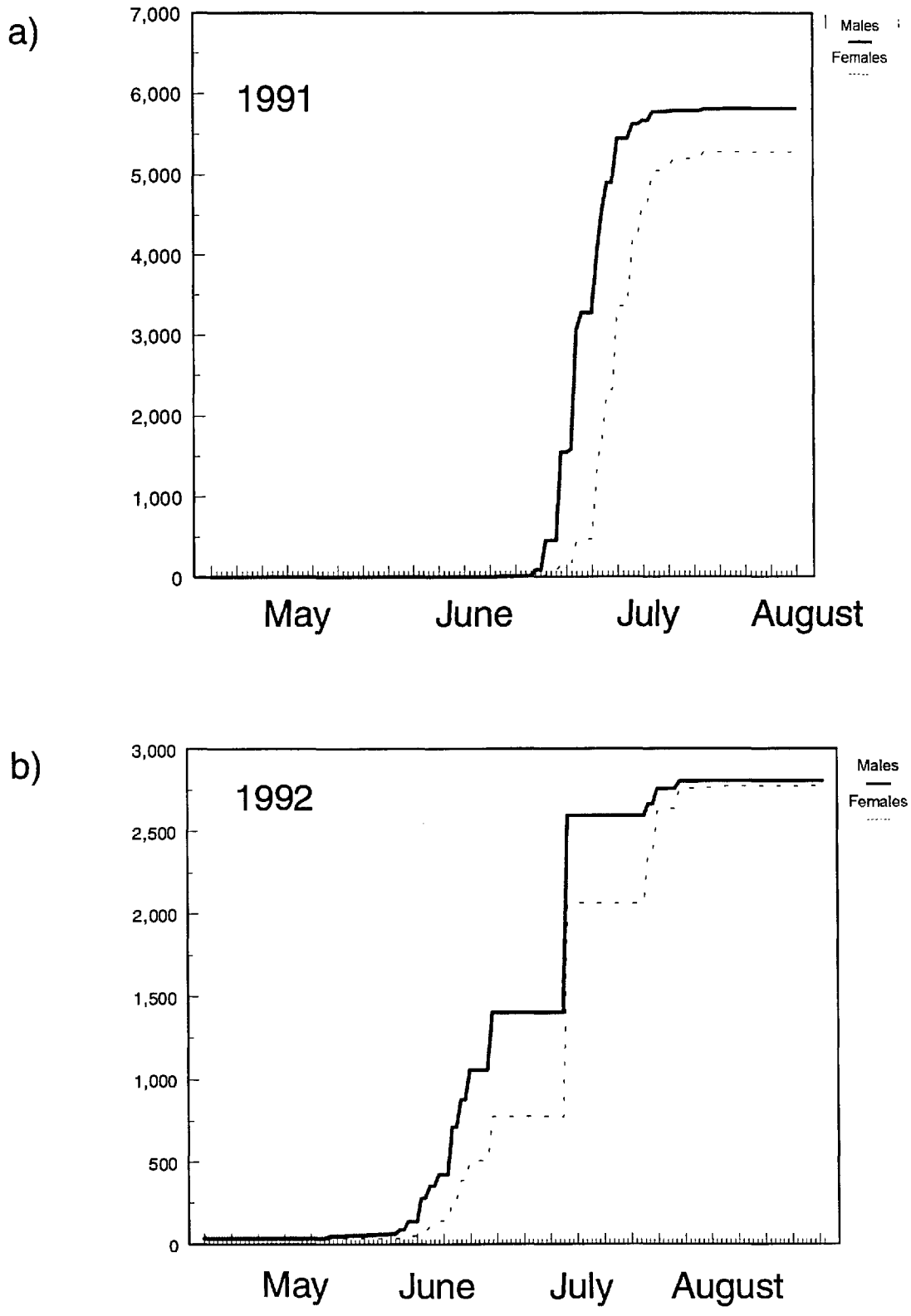
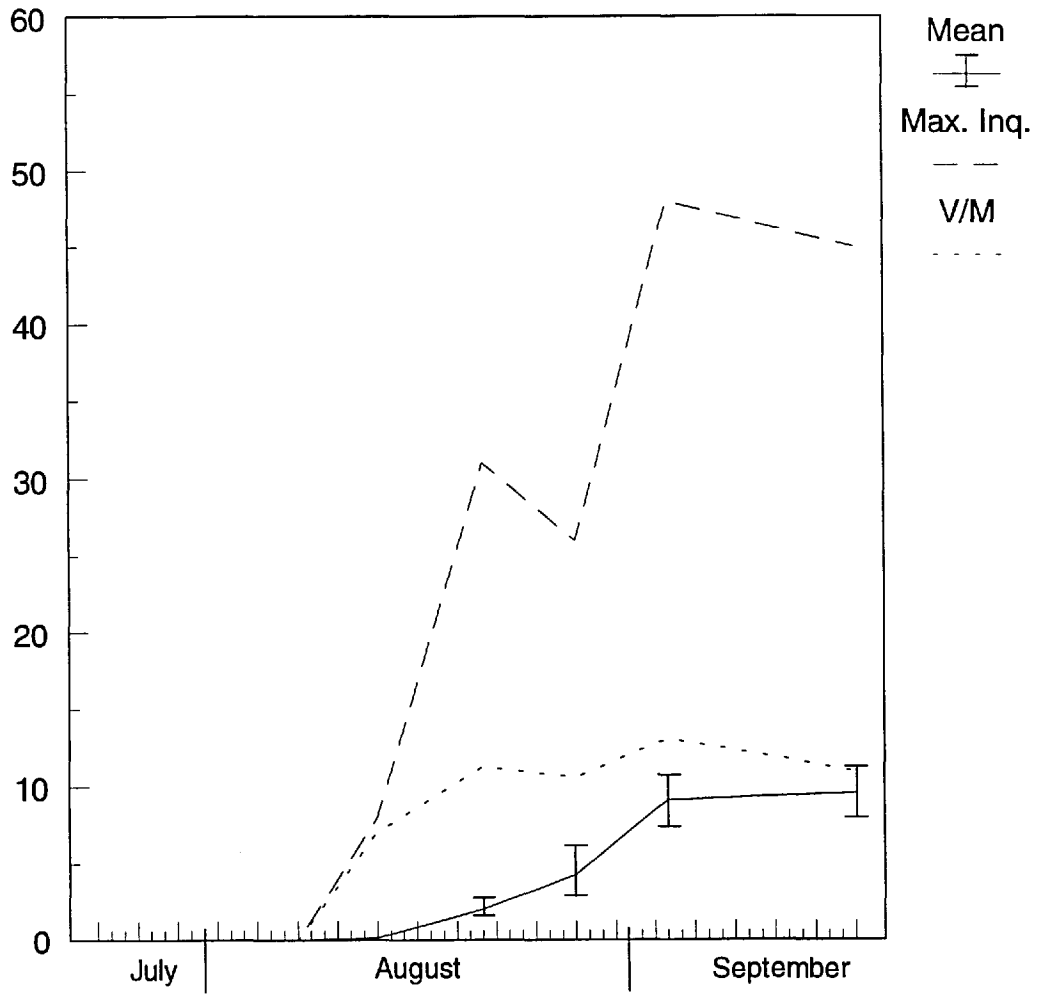


Figure 2.4 : Inquiline attack in knopper galls collected in Silwood Park from July to September 1992.



MEAN = Mean number of inquiline larvae per gall; MAX. INQ. = Maximum number of inquiline larvae found in an individual gall; V/M = Variance - Mean ratio.

In dissections it was not possible to distinguish between the larvae of the two *Synergus* species. Even though *S. gallaepomiformis* was the overwhelmingly dominant species in samples reared from Silwood Park, as far as the larvae are concerned they are referred to as *Synergus* spp.. The first larvae (<1mm length) were detected on the 1 August 1992 (Figure 2.4). The number of larvae increased over the next 4 weeks. An individual gall can be inhabited by as many as 45 larvae and the variance to mean ratio shows that the distribution of larvae is highly aggregated (Figure 2.4). After an initial period with increasing aggregation the variance to mean ratio stabilises despite increasing inquiline density (Figure 2.4).

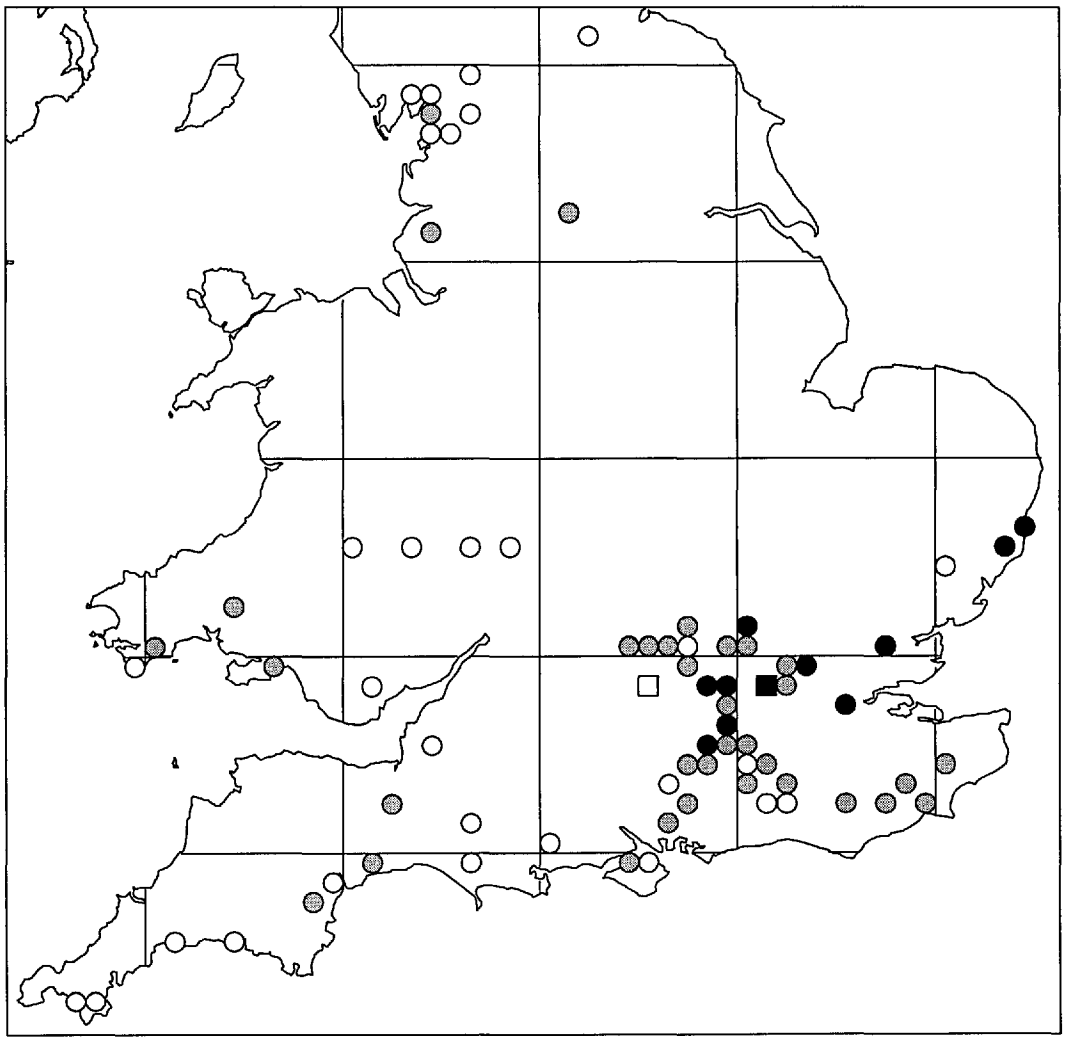
2.3.2.2. Geographical patterns of inquiline infestation in knopper galls

Of the two inquiline species, *S. gallaepomiformis* attacked knopper galls at 122 sites in Britain while *S. umbraculus* occurred in only 5. The following analysis is carried out using the data for *S. gallaepomiformis* alone.

S. gallaepomiformis was found most frequently and in greater abundance in samples from the south-east of England. In the transect survey around Silwood Park, inquiline abundance decreased significantly with distance in all directions except towards the north-east ($F_{(4,51)}=7.41$, $p<0.001$). Distance accounted for 63% of the deviance in inquiline attack rates.

Testing for a geographical concentration of sites with high inquiline attack rates (< 1 inquiline/gall) the geographical centre of these sites was found to be 55km east of the overall centre of all sample sites (i.e. west London; Figure 2.5; Wilcoxon rank-sum test: $Z = -2.58$, $p < 0.01$). There was no significant difference between the two centres on a north-south axis.

Figure 2.5 : Distribution of inquiline attack rates (aggregated in 10km squares).



Open Circles - No Inquilines reared; Shaded Circles - Attack rate < 1 inquiline per gall; Solid Circles - Attack rate > 1 inquiline per gall; Open Square - Geographical centre of all collections; Solid Square - Geographical centre of the heavily attacked collections.

2.3.3. Parasitoids

Of 181 mass rearings collected in Britain, representing 25,958 galls, 64% (=14,145 galls) produced no parasitoids at all. At least one specimen of a parasitoid species emerged from 65 samples. The maximum and average emergence rates per gall for all the parasitoid species are summarised in Table 2.2.

Of those parasitoids which attack the gall former (Table 2.1), *Sycophila biguttata* reached the highest attack rates (Table 2.2), while two species (*Megastigmus stigmatizans* and *Gelis formicarius*) were each represented by a single female in one sample.

Mesopolobus jucundus was the most numerous parasitoid of the inquilines (Table 2.2), although attack by this species was highly localised (see below). Three species (*Cecidostiba semifascia, Torymus nitens* and *Megastigmus dorsalis*) were found in only 1 or two samples.

With the exception of *Mesopolobus amaenus* and *G. formicarius*, all the parasitoid species were more abundant in our 1992 rearings than in earlier studies. Six of the species described here are new to British knopper galls. *M. amaenus* was the only (and the first) parasitoid record from Irish knopper galls.

Table 2.2: The number of specimens emerged per gall based on all mass rearings in comparison to earlier rearing results summarised in Hails *et al.* (1990) Parasitoid species which attack inquiline hosts, can have more than 1 specimen per gall, because each gall might contain multiple hosts. The average emergence per gall was calculated only over those samples in which the particular species was present.

Species	Highest average attack rate (specimens/gall)	Mean average attack rate (specimens/gall)	n (number of samples where present)	Max. average attack rates after Hails *et al.* (1990)
M. jucundus	1.401	0.189	31	0.037
M. amaenus	0.0133	0.0087	4	0.166
C. semifascia	0.0223	0.0223	1	-
E. brunniventris	0.360	0.0740	27	-
S. biguttata	0.0501	0.0151	33	0.004
T. nitens	0.0132	0.0094	2	-
M. dorsalis	0.0035	0.0029	2	-
M. stigmatizans	0.0050	0.0050	1	-
E. urozonus	0.101	0.0315	10	0.007
O. nitidulus	0.0261	0.0093	16	-
G. formicarius	0.0066	0.0066	1	0.03

2.3.3.1. Phenology of the parasitoid emergence

Most of the parasitoids emerged between March and July of the second year of the host gall (Figure 2.6). The exceptions may be *M. stigmatizans* and *O. nitidulus*,

which are both parasitoids of the gall former, and emerge from July until the end of August. Prolonged diapause of the gall former or the natural enemies appeared to be unusual in British samples, in contrast to galls of either the asexual or sexual generations collected in continental Europe (Schönrogge *et al.* 1994, see also Chapter 5).

Most of the parasitoids were recorded from samples collected in the south-east of England. *M. jucundus* was the most common parasitoid of inquilines and *S. biguttata* was the commonest parasitoid of the gall former. The parasitoid of the gall former might be expected to attack over a wider geographical range than the parasitoid of the inquilines, if the latter are restricted to places where inquilines occur at high densities within knopper galls (Figure 2.7).

Figure 2.6 : Emergence periods for Andricus quercuscalicis and its coinhabiting inquilines and parasitoids in 1992.

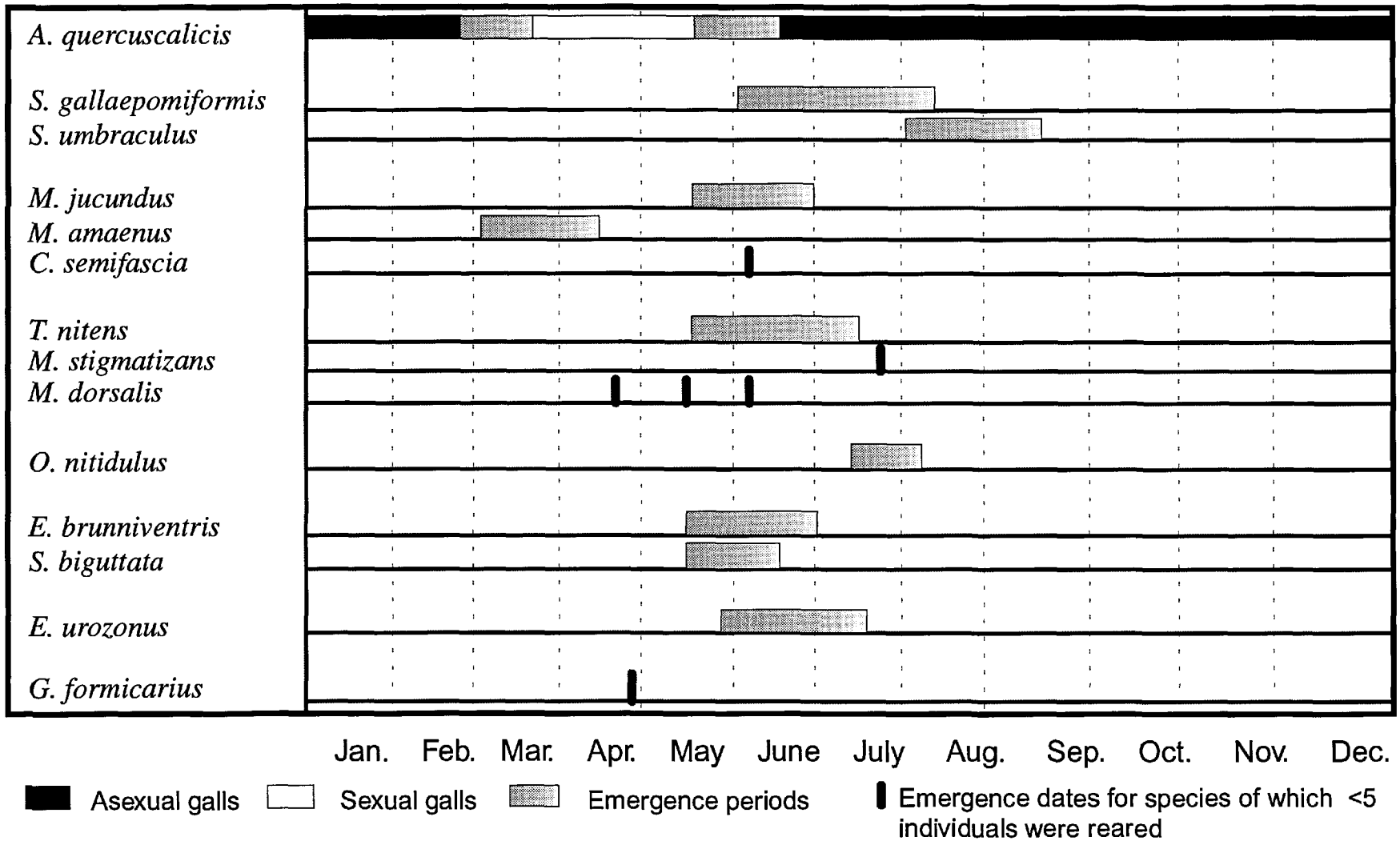
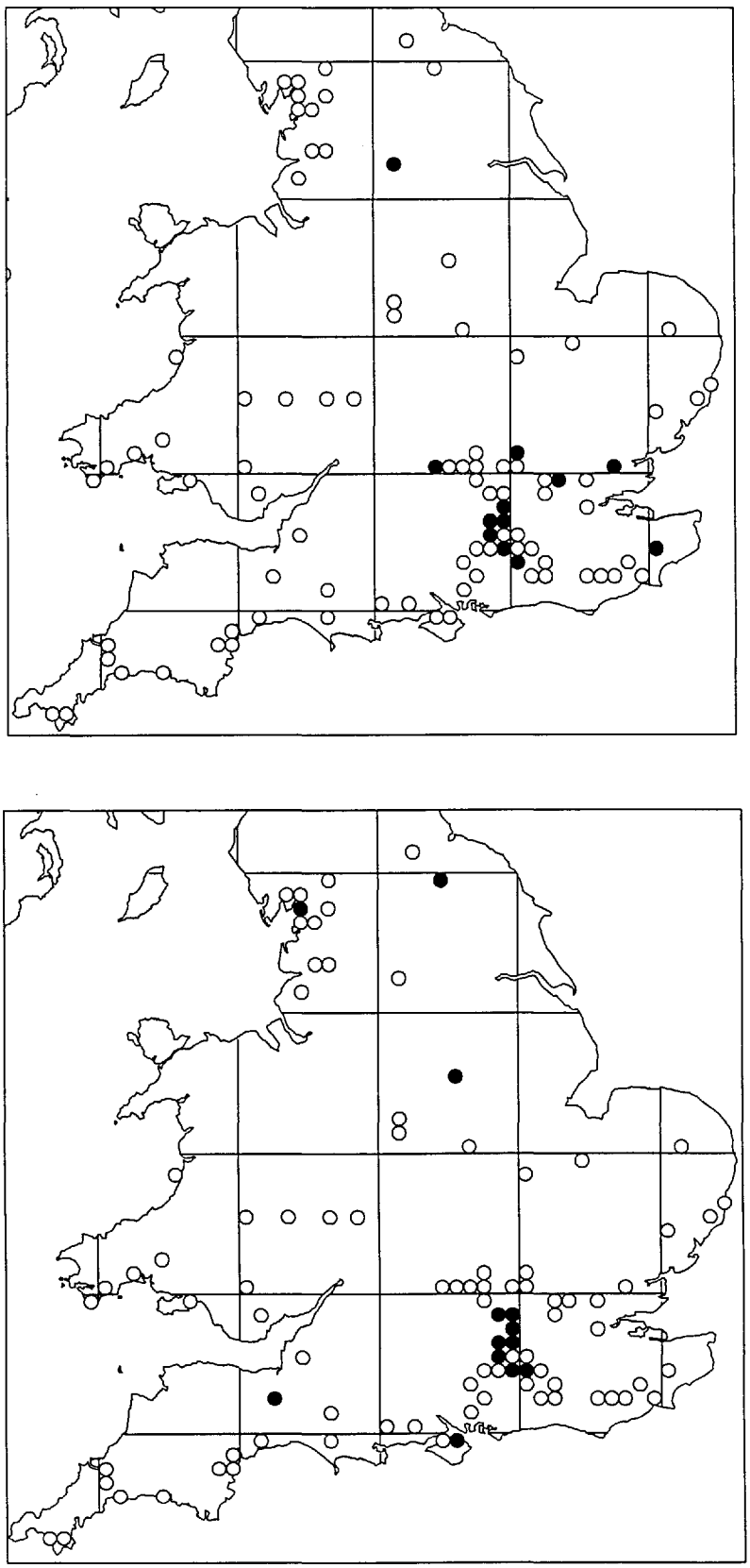


Figure 2.7 : Distribution of a) *Sycophila biguttata* and b) *Mesopolobus jucundus* in Knopper galls (aggregated in 10km squares).



Solid Circles - Present; Open Circles - no emergence.

2.3.3.2. Parasitoid species richness

Parasitoid species richness increased significantly towards the east and increased non-linearly with increasing inquiline abundance (significant negative slope for the quadratic term). This model accounted for 72% of the deviance in parasitoid species richness (Table 2.3).

Table 2.3: Significant parameter estimates of the log-linear regression of parasitoid species richness (GLIM with Poisson errors) against geographic location and inquiline density. Northerliness was not significant.

Explanatory Variable	Estimate	Standard Error	χ^2	d.f.
Intercept	-2.397	0.8372		
1.easterliness	0.0004754	0.0001809	7.45*	1
2.Inquiline infestation	0.03737	0.01117	12.31**	1
3. Inquiline infestation^2	$-1.01*10^{-5}$	$3.82*10^{-6}$	6.54*	1
easterliness x Inquiline infestation.	$-5.68*10^{-6}$	$2.11*10^{-6}$	8.46**	1
Residuals			32.85	41
Total			83.59	46

* - $p<0.05$; ** - $p<0.01$

2.4. Discussion

The results of this study need to be interpreted in the context of work done previously on the community of *A. quercuscalicis* (Hails and Crawley 1991, Collins *et al.* 1983, Crawley 1986, Hails *et al.* 1990, Schönrogge *et al.* 1994). Over a period of 15 years the knopper galls throughout Britain have accumulated 13 species of parasitoids and 3 species of inquilines.

The most striking pattern involves the rapid increase of inquiline abundance, a group that was virtually absent in all earlier studies (Martin 1982, Hails *et al.* 1990), but now present at high densities across south-east England. Abundant inquiline attack has brought with it a change in species composition in the guild, compared with the earlier studies, because of the occurrence of parasitoid species such as *Mesopolobus jucundus* and *Eurytoma brunniventris* which concentrate their attacks on inquilines of knopper galls. Despite the rapid increase in parasitism on the recently recruited inquilines, parasitoid attack on the gall former itself is still extremely low (< 6%).

There is little overlap between parasitoid species which attack the inquilines and those which attack the gall former, and this separation is unusual for parasitoid guilds associated with cynipid galls (Askew 1961a). The absence of detectable hyperparasitism is another unusual feature of this sort of community, but is not unexpected given the low rates of parasitism (Askew 1961a, 1975, Wiebes-Rijks 1982, 1992).

2.4.1. The distribution of inquiline attack

There are a number of ecological and historical factors which may contribute to the substantial geographical variation in inquiline attack rates in knopper galls within Britain. Regions with high attack rates by *S. gallaepomiformis* were East Anglia and the south-east of England, areas that have been inhabited by high concentrations of *A. quercuscalicis* for the longest period of time (Hails and Crawley 1991, Cornell and Hawkins 1993). This geographical pattern could be interpreted in terms of residence time, for it is here that the inquilines have had the longest time to adapt to the new host. Alternatively, the pattern might be the result of variation in host density, assuming that knopper galls reach higher densities in places where they have been present over a longer period of time (M.J. Crawley unpublished results). Both might result in an increased frequency of encounters between inquilines and the galls of the invader, in either time or space (Strong *et al.* 1984). In the present data, however, it is not possible to distinguish between these effects .

A third possibility is that the distribution patterns of inquiline attack rates are the result of an inquiline invasion from the continent rather than the result of recruitment of inquilines from native populations. It is possible that the *S. gallaepomiformis,* which attacks knopper galls in continental Europe (Fulmek 1968, see also Chapter 3), arrived in Britain by the same pathway as its host. Cynipids are known to disperse across the English Channel (Freeman 1945). The concentration of high inquiline attack rates in south-eastern England may be the result of higher abundance of immigrants from inquiline populations with a history of exploitation of knopper galls.

However, discrimination between these hypotheses is not possible on the basis of the data presented here. A population genetic comparison between populations of *S. gallaepomiformis* from the continent and from Britain, reared from knopper galls and from other British cynipid galls from which they could recruit, might make it possible to decide between the invasion and the native recruitment hypotheses (Stone and Sunnucks 1993).

The distribution of the sites with high inquiline attack rates suggest that they are located in a more or less continuous area where inquilines utilise knopper galls more often than elsewhere, and the results of the survey around Silwood Park indicates that it is located close to the boundary where inquiline attack rates decrease towards in the west and south-west. Whether these regions are actually distinct and whether the region of high inquiline attack rates is expanding is the subject of continuing research.

2.4.2. Recruitment of parasitoids in the asexual galls of *A. quercuscalicis* over time

The first parasitoid recorded from knopper galls was *Torymus cyanea* in 1976 from material collected in Devon (Martin 1982), but the species has never been reared from knopper galls subsequently. The next record, in 1979, was of *M. amaenus* (Hails *et al.* 1990). During the early 1980's the number of recorded parasitoid species increased, but the percentage of galls in a sample attacked by parasitoids generally remained less than 1%. Increasing parasitism rates were detected in 1987-9, when mortality due to *M. amaenus* reached a maximum of 16.6% (Hails *et al.* 1990).

Parasitoids which attack cynipid galls have been shown to be well adapted to the morphology of their host gall (Askew 1961b, 1965, 1984, Sellenschlo and Wall 1984). Hence it was curious that parasitoid species known to attack knopper galls on the continent, such as *E. urozonus, E. brunniventris, M. dorsalis* or *M. stigmatizans,* did not do so in Britain, even though some of them were common in other cynipid galls in Britain (Collins *et al.* 1983, Askew 1984). Further, Martin (1982) recorded *Torymus cyanea* and Hails *et al.* (1990) two more parasitoid species (*Mastrus castaneus, Spilomicrus stigmaticalis*) which had never been detected in knopper galls from continental Europe (Fulmek 1968, see also Chapter 3). These species were not found in the present study, and it is possible that all three species were rare accidental ovipositions, detected due to the large samples sizes employed (c. 1000 galls). Only a single female of *M. stigmatizans* was reared in the present study and previous workers might have missed this species in spite of their large sample sizes.

The lack of parasitoids of inquilines in earlier studies, such as *E. brunniventris, M. dorsalis, E. urozonus* and *M. jucundus,* can be explained by the previous scarcity of inquilines. Since the abundance of inquilines in knopper galls has increased these parasitoid species can be found in knopper galls as was predicted (Collins *et al.* 1983, Hails *et al.* 1990, Askew and Neill 1993).

While the number of species recorded in this study (11 species) is not markedly greater than the number reported by Hails *et al.* (1990) (10 species), the identities of the species recorded in this study are rather different. Our species include more of those recorded from the native range on the continent (Fulmek 1968, Collins *et al.* 1983, Schönrogge *et al.* 1994), including records of *M. stigmatizans, M. dorsalis, O. nitidulus* and *E. brunniventris* which were previously not recorded from British knopper galls. Likewise, several of the parasitoids recorded by Hails *et al.* (1990), such as *Mastrus castaneus, Torymus cyanea, Spilomicrus stigmaticalis* and *Arthrolytus ocellus*, were not found in the present extensive study.

How does the community associated with knopper galls compare with those associated with the other invading cynipids, *Andricus kollari, A. lignicola* and *A. corruptrix*? There are no published parasitoid or inquiline records for the galls of *A. corruptrix*, although we have material in rearing at present. The community associated with the agamic galls of *A. lignicola,* commonly called the cola nut gall, is still poor in parasitoid species and attack rates are low (P. Walker personal communication). Askew and Neill (1993) emphasise that in continental Europe the communities associated with cola nut galls and marble galls (*A. kollari*) are similar in species composition. This is not unexpected as they have similarities in gall structure and phenology. In Britain, however, the parasitoid and inquiline species associated with *A. lignicola* represent a rather small subset of those recorded from galls of *A. kollari*. Marble galls were established in Britain about 100 years earlier than the other three invading species (Darlington 1974), and now support a relatively large natural enemy fauna (16 species; see Askew 1961a, Askew and Neill 1993).

2.4.3. The communities of *Andricus quercuscalicis* in the future

Mesopolobus amaenus is the first parasitoid record from Irish knopper galls, where the gall wasp invaded probably in the middle of the 1980's (see also Chapter 6). It is intriguing that this was also one of the first species to be recorded as a parasitoid of British knopper galls (Hails *et al.* 1990). The absence of inquilines from Irish knoppers also matches the pattern observed in Britain, and suggests that the process of parasitoid recruitment in Ireland could mirror the situation present in Britain about 10 years ago.

The knopper gall community in Britain is rapidly converging towards to the community known to attack this gall in continental Europe, confirming the predictions of Collins *et al.* (1983), Hails *et al.* (1990) and Cornell and Hawkins (1993). The strong correlation between inquiline abundance and parasitoid species richness suggests that the mode of species recruitment follows what is described as "encounter-frequency" or "frequency of exposure" (Southwood 1961, Strong *et al.* 1984), i.e. the more abundant the host the higher the probability that the host species will be detected and exploited by parasitoids.

If and when the region of high inquiline infestation spreads from south-eastern England, a similar pattern of increasing numbers of inquiline parasitoid species and a convergence in species composition throughout the country could be expected. Even though it is not clear whether the community convergence is also true for the parasitoids of the gall former, the increasing number of parasitoids from knopper galls may begin to couple the dynamics of the invader with the dynamics of native gall species which share the same natural enemies. To date, there has been little

interaction between *A. quercuscalicis* and native cynipids, because none of the natives attack the acorns of *Q. robur* or the male flowers of *Q. cerris* and there has been no apparent competition through high rates of attack by shared natural enemies.

2.4.4. Inquiline and parasitoid phenology

S. gallaepomiformis in Britain is closely synchronised with the development of the knopper galls. The oviposition period occurs when the host gall has reached its final size and provides a maximum of space and protection for the inquilines. The time of emergence of *S. gallaepomiformis* from knopper galls (in July-August) also makes it likely that females emerging will find new knoppers in the right state of development for oviposition. This emergence pattern of British *S. gallaepomiformis* from knopper galls is interesting because the species is described in the literature as having two or three generations each year on its other cynipid host galls (Askew 1961a, Eady and Quinlan 1963, Wiebes-Rijks 1979, Nieves Aldrey and Villar 1986). From these descriptions *S. gallaepomiformis* would be expected to emerge from knopper galls in April and May rather than July and August. It is possible that knopper galls have characteristics which prolong the development of the inquiline larvae, for example the high concentration of tannins in the gall parenchyma, which in *A. quercuscalicis* account for 25%-33% of the dry weight (Berland and Bernard 1951).

The high level of aggregation of inquilines in knopper galls suggests that the individual females lay their eggs in clutches rather than distributing them more regularly over the available galls. Females ovipositing later in the season may avoid galls which already contained inquiline larvae; evidence for this is indirect, and is based on the fact that the variance-mean ratio does not increase as the mean inquiline burden increases (Figure 2.4). This behaviour may minimise intraspecific competition or mortality caused by positive density dependent parasitism as found for the attacks of a pteromalid parasitoid, *Cecidostiba adana,* on *Synergus gallaepomiformis* in continental Europe (see also Chapter 4).

The emergence period of most parasitoid species begins in May and finishes by the end of June. Since the galls of *A. quercuscalicis* are not developed by that time these parasitoid species are likely to need at least one additional host species from which a subsequent generation may return to attack knopper galls later in the year (July - September). Exceptions to this rule are *M. stigmatizans* and *O. nitidulus*, both parasitoids of the gall former, which emerged at the appropriate time of the year in July and August. Although little is known about the life span of the parasitoid females in the field it is plausible that these two species could persist by attacking knopper galls alone.

2.4.5. Coexistence with other cynipid galls

All but one of the parasitoid species reared from knopper galls (*S. biguttata*) are ectoparasitic species which kill or terminally paralyse their host in the process of oviposition (Askew and Shaw 1986). Such insect parasitoids characteristically have a relatively wide host range (Askew and Shaw 1986, Hawkins *et al.* 1990) and often dominate the parasitoid communities based on endophytic hosts such as cynipid galls (Askew 1975, Hawkins 1990). The British gall forming cynipid species show a wide overlap of inquiline and parasitoid species (Askew 1961a). Now that parasitoids and inquilines develop more abundantly in the galls of *A. quercuscalicis,* they may begin to interact with the native fauna via shared parasitoids or inquilines (i.e. apparent competition (Holt 1977 \ as when a native leafhopper was driven to virtual extinction by another, invading leafhopper species as a result of mortality inflicted by a shared parasitoid \ Settle and Wilson 1990).

Whether or not such a scenario is likely to apply to *A. quercuscalicis* and the British cynipid fauna is the subject of current research. We predict, however, that the most important process is unlikely to be parasitism, since the parasitoids appear to be egg limited (Askew 1975, B. Cockrell unpublished data). It is possible that the inquilines which kill the gall former in some other oak cynipid galls (Askew 1961a) might have more important effects.

2.4.6. Conclusions

The guild of parasitoids, inquilines and parasitoids of inquilines in the asexual galls of *A. quercuscalicis* has changed dramatically in species composition and in species abundance over the last 15 years. After an initial rapid increase in species richness during the 1980's a substantial turnover resulting in changes in the species composition was observed. This process has resulted in an increasing similarity between British communities and continental communities where knopper galls are native (Stone and Sunnucks 1993, see also Chapter 3). The most pronounced changes have been in abundance of inquilines (from zero to an average of more than one inquiline per gall). Subsequently, parasitoid species attacking the inquilines have increased in distribution and abundance. This is a parallel development to the guild associated with another alien gall-former *A. lignicola* (Askew and Neill 1993).

While it is not clear whether the inquilines and parasitoids which develop in knopper galls can affect the population dynamics of native cynipid species in subsequent generations, the present low mortality caused by the parasitoids of the gall former makes it unlikely that they currently affect the dynamics of the invader.

3. Spatial and temporal variation in guild structure: Parasitoids and inquilines of *Andricus quercuscalicis* Burgsd. (Hymenoptera: Cynipidae) in its native and alien ranges

3.1. Introduction

Patterns in the structure of food webs have been the focus of considerable interest over the last 15 years (Cohen 1978, Pimm *et al.* 1991). Analyses of food web structures have resulted in a number of empirical generalisations about the way communities are organised: food chains are typically less than 5 trophic levels in length; the product of the number of species in a web and network connectance is roughly constant; the ratio between predator and prey species in a food web is roughly constant (between 1 and 3) and the fractions of top predators, intermediate species and basal species are independent of the total number of species in the food web (Sugihara *et al.* 1989, Pimm *et al.* 1991, but see Martinez 1991, 1993a,b). Very little is known, however, about the way in which these patterns originate. Most published food webs represent a static snapshot of the identity of the species and of the links between them taken from one point in space and frozen in time. The tacit implication is that the species and the links between them are invariant in time and space. Invading species provide a good model system of guild structures that are both spatially and temporally variable.

By extending its range, an invading species may leave its natural enemies behind and enter 'enemy free space' (Holt 1977; Jeffries & Lawton 1984; Holt and Lawton 1993). Sooner or later, however, the invader is likely to be discovered and exploited by generalist predator species endemic to its invaded range and a novel community, focused on the invader, may develop (Strong 1984; Cornell & Hawkins 1993). Invasions provide interesting information about the development of communities in two dimensions: 1) by studying the system over long periods of time changes can be observed directly; 2) by re-tracing the route by which the invader spread from its native range one can observe different successional stages.

One example of a well studied insect invasion is the cynipid gall wasp *Andricus quercuscalicis* (Collins *et al.* 1983, Hails *et al.* 1990, Hails and Crawley 1991, Stone and Sunnucks 1993). This species has obligate, annual host alternation, involving an agamic generation on English oak (*Quercus robur* Linnaeus) and a sexual generation on Turkey oak (*Q. cerris* Linnaeus), an alien plant over most of western Europe. In this study we concentrate on the galls of the agamic generation, commonly known as knopper galls.

Because Turkey oak is an obligate host plant of *A. quercuscalicis,* the distribution of the gall wasp was once restricted to south-eastern Europe, the post-glacial native distribution of this host. Turkey oak has been planted extensively

outside its native range from the 17th century onwards, allowing the gall wasp to spread (Huntley & Birks 1983; Stone & Sunnucks 1993). The invasion history of *A. quercuscalicis* is relatively well documented. First records from within the invaded range date back as far as 1631 (eastern Germany; Gauss 1977). Great Britain and Ireland were invaded most recently and form the western limits of the distribution (Collins *et al.* 1983; see also Chapter 3). A detailed description of the life cycle and biogeography of *A. quercuscalicis* and the history of its invasion are given by Stone and Sunnucks (1993).

While the communities associated with knopper galls in Britain have been studied since the galls were first recorded (Collins *et al.* 1983, Hails 1988, Hails *et al.* 1990), the information available from continental Europe is sparse and scattered (Pfützenreiter and Weidner 1958, Fulmek 1968, Gauss 1977). At first, the parasitoid species records from Britain were not consistent with those from continental Europe (Collins *et al.* 1983, Hails and Crawley 1991), but more recent results indicate that the communities associated with knopper galls in Britain are rapidly converging towards those of continental Europe (see also Chapter 2).

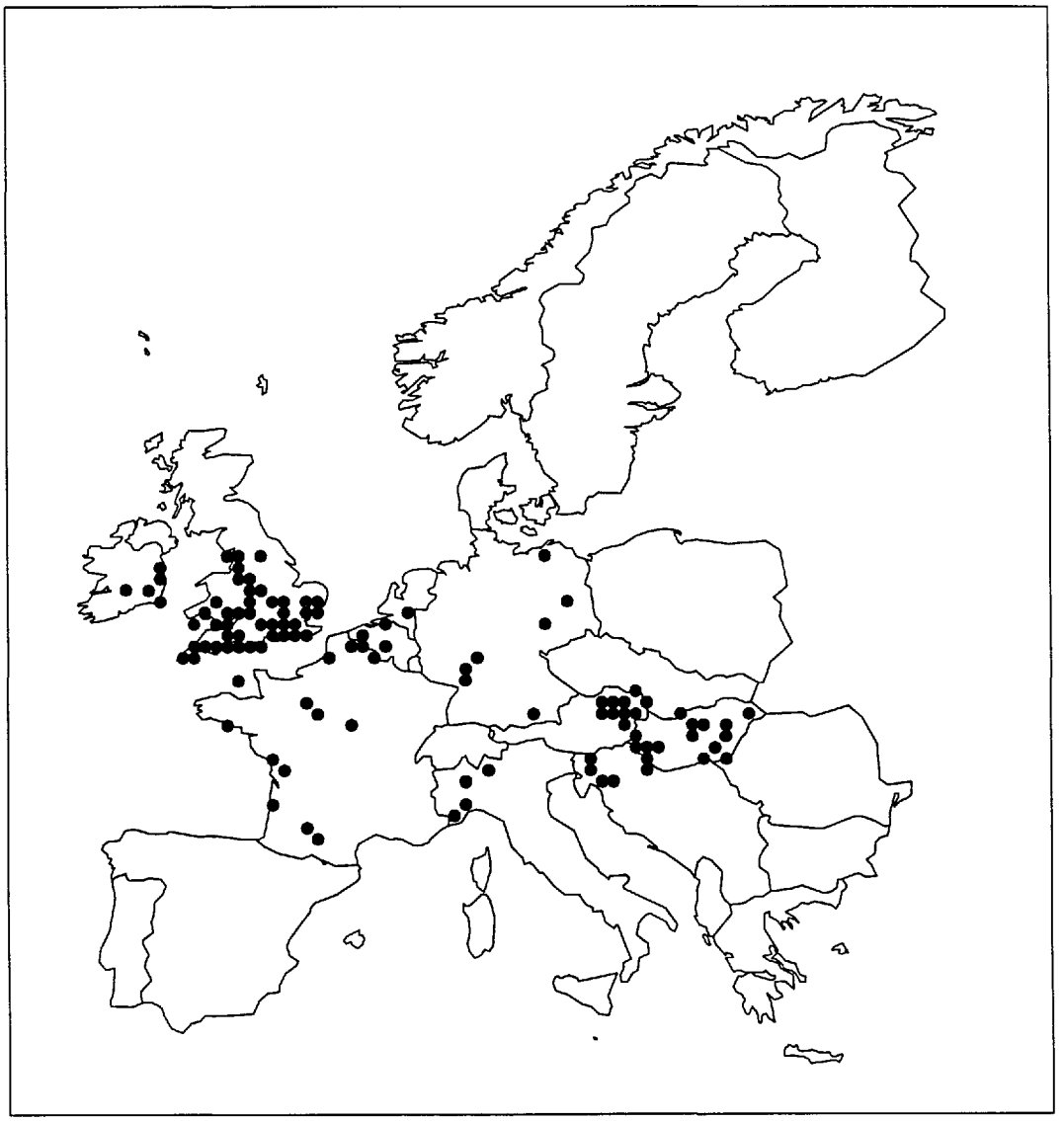
In Chapter 2 the temporal and geographical dynamics of the community associated with the agamic galls of *A. quercuscalicis* in Britain over the last 15 years were discussed. Here the communities associated with knopper galls along a transect from the native range to the edge of the invaded range in Europe are described to address the following questions: 1) What species are associated with knopper galls, only (or mainly) in continental Europe? 2) How are the communities of parasitoid and inquiline species structured in the different regions of the sampled range? 3) How variable are the communities throughout the range? 4) Is there a characteristic pattern of change in community structure which reflects the invasion history of *A. quercuscalicis*?

3.2. Methods

3.2.1. Sample sites

Knopper galls were collected throughout the western part of the known range of *A. quercuscalicis* in Ireland, Britain, Belgium, France, Germany, the Czech Republic, Austria, Hungary, Slovenia and Italy (Figure 3.1). The last five countries are regarded as forming part of the native range while the others were invaded after human dispersal of Turkey oak.

Figure 3.1 : Geographical location of the collection sites in Europe.



3.2.2. Rearings and Dissections

In total, 64,562 Knopper galls were collected in 1990 and 1991, and reared in one of three different ways:

48,308 galls from 293 sites were kept in mass rearings. The number of galls per rearing container varied between 34 and 500 galls. To avoid complications due to variations in sample size in comparisons of species richness between sites (Karban and Ricklefs 1983) the number of galls in each container was standardised to 150 galls whenever possible. Larger collections were sub-sampled for that purpose.

10,764 galls from 76 sites were kept individually to assess the variation in inquiline infestation and parasitism within samples. 50 galls from each set of single rearings were dissected at the end of 1992 to determine host-parasitoid relationships and causes of mortality other than parasitism. The results of these dissections were also used to create the food webs.

5,490 galls from 41 sites were opened and the gall wasp larval chamber separated from the outer wall. Both parts of the gall were then reared separately, to determine in which part of the gall the specimens which emerged had developed (Hails *et al.* 1990).

All rearings were kept in an outdoor insectary and checked three times a week. Each emerging insect was identified and the emergence date recorded.

3.2.3. Community structure statistics

The mean density of inquilines per gall, the geographical location (eastings and northings) and the presence/absence of other parasitoid or inquiline species were used as explanatory variables in a logistic regression with presence/absence for a given parasitoid or inquiline species as the response variable. Model simplification involved deletion of terms from the maximal model; terms that were significant on deletion were added back to the model, until a minimal adequate model was obtained for each coinhabiting species which contained only significant terms (Crawley 1993).

3.2.4. Food web properties

To allow comparisons with other food web studies, the following food web properties (defined below) were calculated: the number of species, connectance, links per species, percentage top-predators, percentage intermediate species, percentage basal species, prey-predator ratio, percentage top-basal links, percentage intermediate-basal links and percentage top-intermediate links. These properties were used by Schoenly *et al.* (1991) in the analysis of 95 insect food webs including several webs from other cynipid gall wasp communities (e.g. Askew 1961).

The units in our food web are taxonomic species. Links are of the "positively identified A eats B" kind. Because the larvae of the two inquiline species could not be distinguished we assume that all parasitoids which feed on one of them also feed on the other. Top predators are those species which are not fed upon by other members of the knopper gall guild. Basal species are those which do not feed on any other species (i.e. here *Q. robur* the oak host of the gall wasp). All other species are defined as intermediate.

Connectance is the ratio of the number of links observed to the number of links possible (every species linked to every other). A logistic regression was carried out using the fractions of top-, intermediate- and basal species as the response variable, with the number of species constituting each food web and the residence time of *A. quercuscalicis* (i.e. the first published record from each of the regions listed in Stone and Sunnucks 1993 and Chapter 6 for Ireland) as explanatory variables. Significance was assessed by deletion from the minimal adequate model.

3.3. Results

3.3.1. Parasitoids and inquilines

A total of seventeen species was found in the galls of *A. quercuscalicis,* feeding either on gall tissue (inquilines) or as parasitoids of the gall former or inquiline species (Table 3.1).

Table 3.1: Parasitoid and inquiline species reared from knopper galls collected throughout Europe (P- Parasitoid species; I - Inquiline species).

Superfamily	Family	Genus	Species	(P)arasitoid/ (I)nquiline
Chalcidoidea	Pteromalidae	*Mesopolobus*	*jucundus*	P
			amaenus	P
		Cecidostiba	*adana*	P
			semifascia	P
	Eurytomidae	*Eurytoma*	*brunniventris*	P
		Sycophila	*biguttata*	P
	Eupelmidae	*Eupelmus*	*urozonus*	P
	Torymidae	*Torymus*	*nitens*	P
		Megastigmus	*stigmatizans*	P
			dorsalis	P
	Ormyridae	*Ormyrus*	*nitidulus*	P
	Eulophidae	*Aulogymnus*	*trilineatus*	P
		Baryscapus	*berhidanus*	P
Ichneumonidea	Gelidae	*Gelis*	*formicarius*	P
Cynipoidea	Cynipidae	*Synergus*	*gallaepomiformis*	I
			umbraculus	I
Tortricoidea	Tortricidae	*Pammene*	*amygdalana*	I

3.3.1.1. Inquilines

Three species, *Synergus gallaepomiformis* (Boyer de Fonscolombe), *S. umbraculus* (Olivier) (both Hymenoptera: Cynipidae) and *Pammene amygdalana* (Duponchel) (Lepidoptera: Tortricidae) are inquilines and feed mainly on the parenchymatic tissue of the galls. It was rare for either of the two *Synergus* species to kill the gall former. Death tended to occur when the inquilines oviposited relatively early in gall development, when the larval chamber of the gall former was small and still unprotected by a sclerenchymatic shell. Because the inquiline larvae tend to grow faster than the gall former, the larval chamber eventually collapses, killing the larva of the gall wasp inside.

In contrast, the moth *Pammene amygdalana* usually killed the gall wasp larva. At some point during its development in the wall of the gall, the tortricid larva bites a hole into the larval chamber of the gall wasp and kills the gall former. Subsequently the moth returns to feed on the parenchymatic tissues. *P. amygdalana* should be regarded as a lethal inquiline rather than a predator because there is no evidence that the tortricid larva feeds on the gall wasp larva. It is possible that by killing the gall causer, the inquiline moth prevents the lignification of the gall parenchyma and thereby prolongs the duration of high food quality (P. Lalonde personal communication).

3.3.1.2. Parasitoids

Ten of the parasitoid species were found to be solitary, larval ectoparasitoids (Table 3.1). There were two species of endoparasitoids; *Sycophila biguttata* (Swederus) is solitary, but up to 28 larvae of *Baryscapus berhidanus* Erdös were found inside the larval skin of a single gall former. *Gelis formicarius* (Linnaeus) (1 female reared) and *Cecidostiba semifascia* (Walker) (4 males reared) were reared from knopper galls but were never observed during gall dissections.

On two occasions a tunnel was observed between two inquiline chambers produced by larvae of *Eurytoma brunniventris* Ratzeburg . Askew (1975) stated that this species is able to supplement its diet with plant tissue if its insect host does not provide enough food.

3.3.2. Distribution

Both inquilines of the genus *Synergus* (Table 3.1) attacked knopper galls throughout the native and alien ranges. Three species (*Baryscapus berhidanus*, *Pammene amygdalana* and *Aulogymnus trilineatus* (Mayr)) were found only in the presumed native range (Austria, Czech Republic, Hungary, Slovenia, Croatia and Italy; see Table 3.2).

Table 3.2: Distribution of parasitoid attack in knopper galls throughout Europe.

		Parasitoids of the inquilines								Parasitoids of the gall-former						
	Galls collected	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	I1
Britain	38406	+		+	+	+	+	+	+	+	+	+			+	
Ireland	2216								+							
Belgium	628		+													
Netherlands	585		+	+												
France	2113		+	+	+							+				
Germany	3156		+	+	+			+		+		+				
Czech Rep.	317		+	+						+	+		+			+
Austria	4672	+	+	+	+	+		+		+	+	+	+			+
Hungary	8565	+	+	+	+	+		+		+	+	+	+			+
Slovenia	983		+	+	+					+	+	+				
Italy	1371		+	+	+	+				+	+	+		+		+

+ indicates presence; empty cells indicate that the species was not reared from samples collected in these countries.

P1 = *Mesopolobus jucundus*; P2 = *Cecidostiba adana*; P3 = *Eurytoma brunniventris*; P4 = *Eupelmus urozonus*; P5 = *Megastigmus dorsalis*; P6 = *Cecidostiba semifascia*; P7 = *Torymus nitens*; P8 = *Mesopolobus amaenus*; P9 = *Sycophila biguttata*; P10 = *Ormyrus nitidulus*; P11 = *Megastigmus stigmatizans*; P12 = *Aulogymnus trilineatus*; P13 = *Baryscapus berhidanus*; P14 = *Gelis formicarius*; I1 = *Pammene amygdalana* (lethal inquiline)

Another three species (*Mesopolobus amaenus* (Walker), *Cecidostiba semifascia* and *Gelis formicarius*) were reared only from galls collected in Britain and Ireland, the countries most recently invaded by *A. quercuscalicis*. *M. amaenus* was the only relatively common member of this group, and the records of *C. semifascia* and *G. formicarius* are likely to be due to the much larger sampling effort in Britain compared to the other countries. Patchiness in collection effort will also account for some of the gaps in our distribution data (e.g. *Sycophila biguttata* was detected in British galls and in those collected in Germany and further east, but not in Belgian, Dutch or French galls).

3.3.3. Community structure

All but four species were significantly associated with the presence/absence of other parasitoid or inquiline species (Table 3.3). Four of the seven parasitoids which attack mainly inquilines were more likely to be found at high inquiline abundance, while none of the parasitoids of the gall former showed a significant association with the number of inquilines in a sample. Furthermore, the presence/absence of 8 species were significantly correlated with the geographical location of the collection site.

Megastigmus dorsalis (Fabricius) and *Sycophila biguttata* were the only two species which showed no significant associations with any other species and no geographical trend in their distribution (i.e. their pattern of presence/absence appears to be independent of other parasitoids or inquilines; Table 3.3).

Three pairs of species were identified which generally tended to occur together; namely *C. adana* Askew -*M. stigmatizans* (Fabricius), *O. nitidulus* (Fabricius) -*S. umbraculus* and *A. trilineatus* (Mayr) -*P. amygdalana*. In contrast *E. urozonus* Dalman was generally less likely to be present where *O. nitidulus* occurred and vice versa. *E. urozonus* was also less likely to be found where *S. umbraculus* was present. These were the only two significant negative associations in the presence/absence patterns of community members (Table 3.3).

Table 3.3 : Associations between parasitoid and inquiline species.

	Parasitoid species attacking inquilines							Parasitoids attacking the gall-former				Inquilines		
	M. jucundus	*C. adana*	*M. amaenus*	*E. brunni-ventris*	*E. urozonus*	*T. nitens*	*M. dorsalis*	*S. biguttata*	*O. nitidulus*	*M. stigma-tizans*	*A. trilineatus*	*S. gallae-pomiformis*	*S. umbraculus*	*P. amyg-dalana*
M. jucundus					+									
C. adana									+	+				
M. amaenus														
E. brunniventris	+									+				
E. urozonus									+					
T. nitens					+				-					
M. dorsalis														
P. amygdalana				+							+			
S. biguttata														
O. nitidulus					+								+	
M. stigmatizans		+												
A. trilineatus												+		+
S. gallaepomiformis														
S. umbraculus					-				+					
Inquiline abundance	+		+		+	+						/	/	/
easterliness	-	+	-	+	+								+	+
northerliness					+					-			-	

+/- marks positive/negative associations which are significant ($p < 0.05$), while empty cells indicate non-significance. The shaded areas indicate species which have no significant association with any of the other species. +/- for inquiline abundance shows whether that species was more likely to be found at high/low inquiline abundance. +/- for easterliness and northerliness indicates that the species was more likely to be reared from samples collected in the east/west and north/south of the range.

3.3.4. Food webs

The trophic relationships shown in Figure 3.2 are based on data gathered during dissections. The results of dissections of galls from Hungary, the Czech Republic, Austria and Slovenia are gathered under the title of "native range" (Table 3.4). The data from France were pooled with those from the Netherlands and Belgium. British galls were recorded as coming from the "range of high inquiline abundance" (i.e. South-east England) and from the "range of low inquiline abundance" (i.e. the rest of England and Wales). The differences between these two regions were shown in Chapter 2). By regrouping the observations in this way the number of galls dissected for each group is better balanced (Table 3.4).

No remains of parasitoid larvae (mandibles or skin), which might indicate the attack of another parasitoid, were detected during dissections. *Pammene amygdalana* larvae may kill inquilines and/or their parasitoids, because they hollow out most of the gall wall, but if this happened, the destruction was too complete to find any remains of parasitoid or inquiline larvae. For the calculation of food web properties, it is assumed that *P. amygdalana* does not feed on the inquilines or their parasitoids, although it is possible that it kills them in the same way that it kills the gall former (see above; Figure 3.2a).

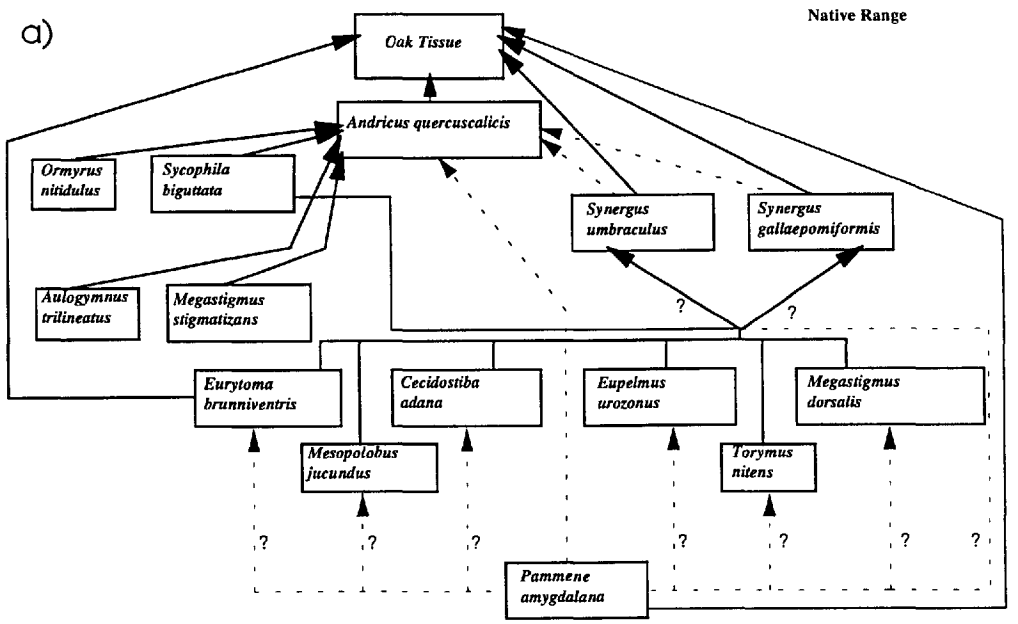
The trophic relationships in galls from the native range are the most complex and involve the highest number of species (Table 3.4). With increasing distance away from the native range, the food webs become progressively simpler and less species-rich. Species richness and complexity within Britain are higher in the south-east within the range of high inquiline abundance where they approach levels close to the those observed within the native range (Table 3.4).

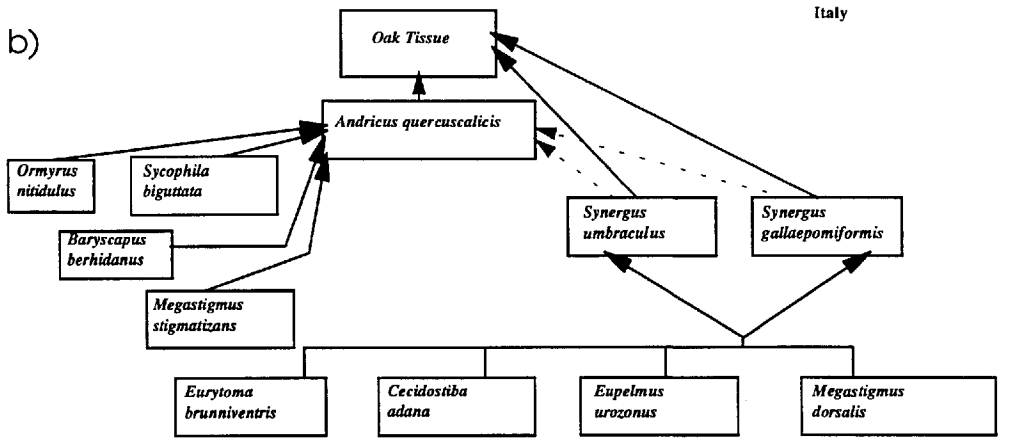
The percentage of top species is significantly correlated with the number of species in the food web ($\chi^2 = 4.26$, 1 d.f., $p < 0.05$, slope = 0.16 ± 0.075). Similar analysis for the percentage of intermediate and basal species showed no significant relationships.

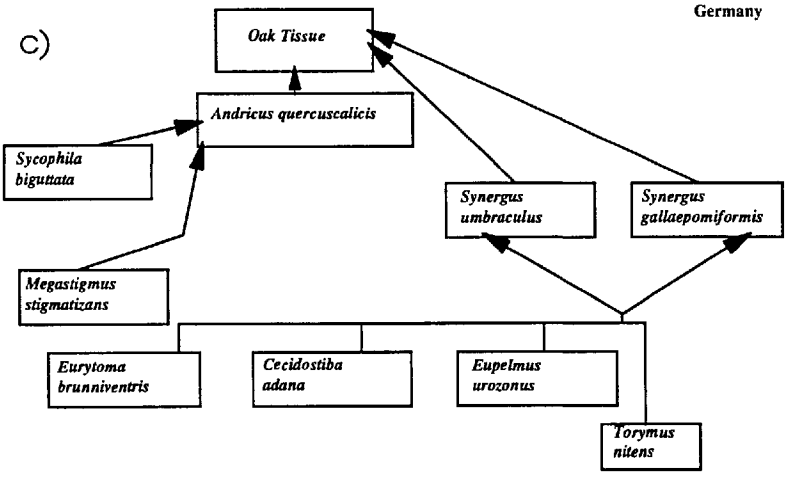
Table 3.4: Properties of the food webs in knopper galls from the native and invaded range (Britain inquilines high/low refers Chapter 2; see also text). n = Number of galls dissected; S = Species in the web; L = Total number of links in the web; L/S = Links per species; %Top = Percentage top predators; %Inter = Percentage intermediate species; %B = Percentage basal species; Pr/Pr = Prey-Predator ratio; %TB = Percentage top-basal links; %TI = Percentage top-intermediate links; %IB = percentage intermediate-basal links; C = Directed connectance ($C = L/S^2$).

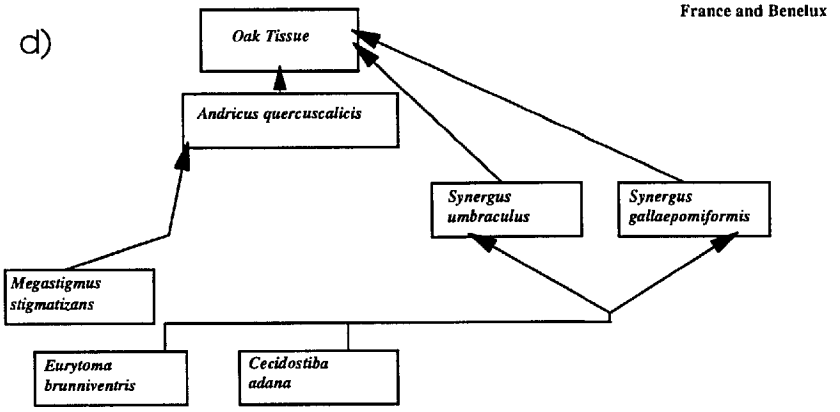
	Native range	Italy	Germany	France and Benelux	Britain Inquilines high	Britain Inquilines low	Ireland
n	400	150	300	200	650	350	100
S	15	12	10	7	13	7	3
L	24	15	13	8	19	8	2
L/S	1.6	1.3	1.3	1.1	1.5	1.1	0.7
%Top	73.3	66.7	60.0	42.9	69.2	42.9	33.3
%Inter	20.0	25.0	30.0	42.9	23.1	42.9	33.3
%B	6.6	8.3	10.0	14.3	7.7	14.3	33.3
Pr/Pr	0.3	0.4	0.4	0.7	0.3	0.7	1
%TB	8.3	-	-	-	-	-	-
%TI	79.2	80.0	76.9	62.5	84.2	62.5	50
%IB	12.5	20.0	23.1	37.5	15.8	37.5	50
C	0.11	0.10	0.13	0.16	0.11	0.16	0.22

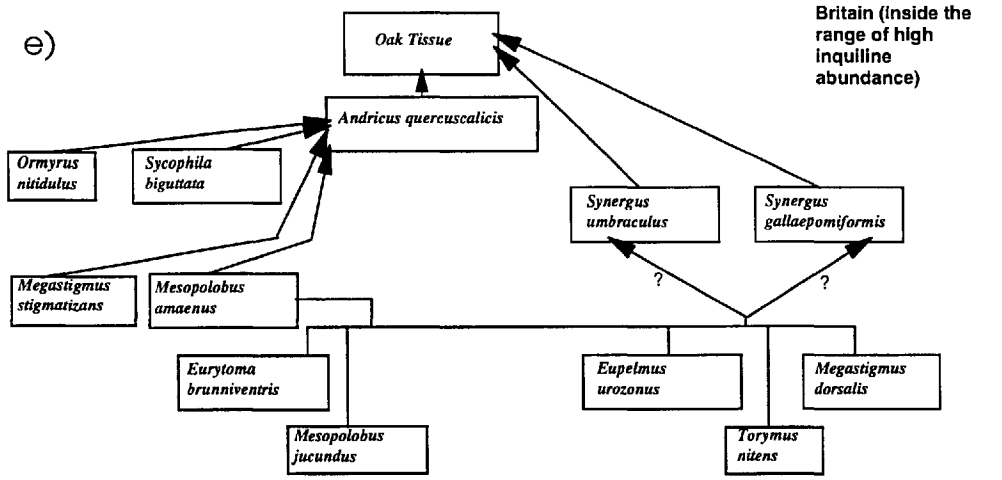
Figure 3.2a-g : Trophic relationships in the knopper gall guild from 7 areas within the collected range. Arrows point from predator to prey. Dotted lines indicate a directed but not feeding relationship (i.e. the "prey" gets killed but not fed upon; see also text). ? - indicates uncertainty (see text).

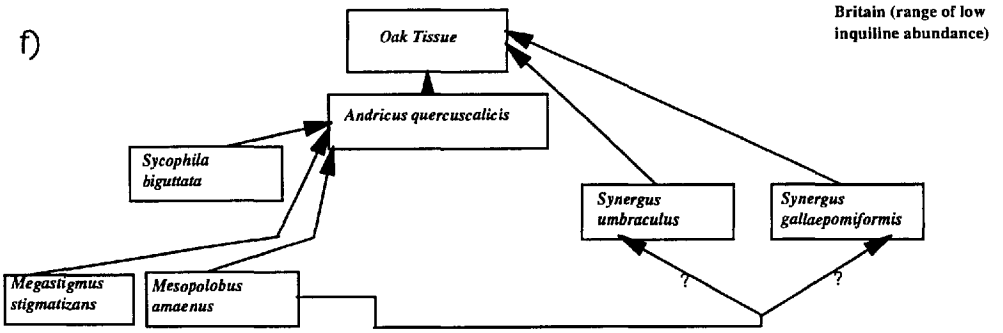


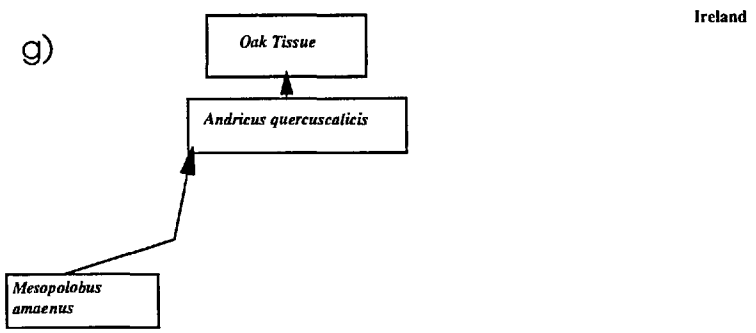

b)
Italy
Oak Tissue
Andricus quercuscalicis
Ormyrus nitidulus
Sycophila biguttata
Baryscapus berhidanus
Megastigmus stigmatizans
Synergus umbraculus
Synergus gallaepomiformis
Eurytoma brunniventris
Cecidostiba adana
Eupelmus urozonus
Megastigmus dorsalis


c)
Germany
Oak Tissue
Andricus quercuscalicis
Sycophila biguttata
Megastigmus stigmatizans
Synergus umbraculus
Synergus gallaepomiformis
Eurytoma brunniventris
Cecidostiba adana
Eupelmus urozonus
Torymus nitens


d)
France and Benelux
Oak Tissue
Andricus quercuscalicis
Megastigmus stigmatizans
Synergus umbraculus
Synergus gallaepomiformis
Eurytoma brunniventris
Cecidostiba adana


e)
Britain (inside the range of high inquiline abundance)
Oak Tissue
Andricus quercuscalicis
Ormyrus nitidulus
Sycophila biguttata
Synergus umbraculus
Synergus gallaepomiformis
?
?
Megastigmus stigmatizans
Mesopolobus amaenus
Eurytoma brunniventris
Eupelmus urozonus
Megastigmus dorsalis
Mesopolobus jucundus
Torymus nitens


f)
Britain (range of low inquiline abundance)
Oak Tissue
Andricus quercuscalicis
Sycophila biguttata
Synergus umbraculus
Synergus gallaepomiformis
?
?
Megastigmus stigmatizans
Mesopolobus amaenus


g)
Ireland
Oak Tissue
Andricus quercuscalicis
Mesopolobus amaenus

3.4. Discussion

The community of parasitoids and inquilines associated with knopper galls shows considerable geographical variation in its species richness and composition throughout the invaded range. Differences in species richness and species composition between communities Britain and continental Europe were suggested by Collins *et al.* (1983) and reiterated by Hails *et al.* (1990). Five years later, however, these differences are much less pronounced (as shown in Chapter 2). In addition to this rapid temporal variation, our results show that there is also distinct spatial variation within continental Europe. The knopper gall guild is richest in the native range and becomes poorer with increasing distance into the invaded range.

3.4.1. Food web properties

Food webs from parasitoids and inquiline guilds in Cynipid galls are source food webs (Schoenly *et al.* 1991). Source food webs are less informative than community food webs since they include only a subset of consumers based on one producer. The food webs presented here are restricted because they do not include birds, pathogens and fungi which would appear as top predators or the cynipid galls that might provide alternative hosts for the parasitoids and inquilines (Hails and Crawley 1991). Nonetheless we think that our results show interesting patterns contributing to the understanding of the development of food web structures.

The parameters for the food web of the guild in knopper galls from the native range fall well within the range of those given by Schoenly *et al.* (1991) for 11 cynipid guilds native to Britain. For instance, prey-predator ratios range from 0.25 in *Neuroterus albipes* (Schenk) to 1 in *Andricus ostreus* (Hartig) (Schoenly *et al.* 1991). The mean prey-predator ratio of all eleven gall food webs was 0.66 which would place the knopper gall guild (0.3 in the native range; see Table 3.4) at the lower end of the spectrum, indicating that the predators are relatively specialised (see also Schönrogge *et al.* 1994, see also Chapter 2).

Residence times of *A. quercuscalicis* in the regions from which the food webs in this study were constructed ranged from tens of thousands of years in the native range to about 10 years in Ireland (Stone and Sunnucks 1993, see Chapter 6). Schoenly and Cohen (1991) analysed 16 food webs which were observed over periods of time ranging from 30 days to 5 years. It is intriguing that all these food webs show the same trends over time in the fractions of top-, intermediate- and basal species as do the webs for *A. quercuscalicis*. The percentage of top species increases with time while the percentage of intermediate and basal species both decrease.

The exception to this trend is south-eastern Britain (Britain - Inquilines high; Table 3.4). We believe that the increased observational effort increased the species

richness and thus makes it appear as if this region is very similar to Italy and the native range. Instead we believe that the increase in species richness of the guild towards the centre of the native range is the outstanding feature of the food web in knopper galls.

Food web parameters were originally believed to be independent from the number of species in the web ('scale invariance'; Cohen 1978, Sugihara *et al.* 1989). However, this view has recently been challenged (Martinez 1991, 1993a,b, Martinez and Lawton 1994), leading to predictions that the percentage of top- and basal- species should decrease, and percentages of intermediate- species increase, as the number of species in the food web increases (Martinez and Lawton 1994). The results from the knopper gall food web are not consistent with these predictions. Scale dependencies might be different for source food webs, as shown here, and community food webs, as described by Martinez and Lawton (1994).

Community complexity can be measured as the proportion of the observed number of links between species to all theoretically possible links in the community (=connectance; see Pimm 1982). In food webs which involve only a small number of species the number of possible links is small and hence connectance is likely to be high, while food webs with many species are likely to be less complex for the same reason. Connectance may be the most interesting food web parameter since it is the least confounded with species richness (Martinez 1992). Even though there might be a positive bias in connectance of food webs with small numbers of species (Martinez 1992), all the food webs presented here (except the one for Ireland) fall well inside the confidence limit of the mean connectance calculated from 175 food webs of various sizes (mean connectance 0.14±0.06 from Martinez 1992).

Judged by the degree of connectance, Italy appears to be part of the native range (see also Stone & Sunnucks 1993) although the species composition of the guild is different. Pimm (1982) states that community complexity is negatively correlated with community stability. Since connectance decreases towards the native range one would expect the communities in the invaded range to become more species rich, less complex and hence more stable, although the species composition remains variable.

3.4.2. Associations between species and their distribution

The analysis of the association of parasitoid and inquiline species in the communities of knopper galls combines some species with similar distributions into species pairs. *Aulogymnus trilineatus* and *Pammene amygdalana,* for instance attacked knopper galls only within the native range where both were commonly found. *Cecidostiba adana* and *Megastigmus stigmatizans* attacked knopper galls

widely throughout the native range and almost throughout the invaded range. However, *C. adana* was not detected in Britain nor Ireland while *M. stigmatizans* was not found in Ireland and was very scarce in Britain.

While positive associations indicate similar distributions between species, negative associations indicate little if any overlap between distributions. Though both *Synergus umbraculus* and *Eupelmus urozonus* were significantly more likely to be present in eastern collections (see also Chapter 4), *Synergus umbraculus* was more likely to be found in southern samples while *E. urozonus* occurred more in northern collections.

It is intriguing that some of the species which were not reared from the intermediate range (Germany, France, Belgium and Holland), such as *Sycophila biguttata, Ormyrus nitidulus* or *Mesopolobus jucundus* (Walker), were detected in British galls (further from the native range). However, the sampling effort in Britain was more than three times as high as in any other country, and it is possible that these species remain to be detected in the intermediate invaded range. All the species are endemic to these areas in other cynipid galls (Fulmek 1968) and it is possible that these parasitoid species attack knopper galls in variable intensity and are likely to be missed in collections from sites where they occur at low densities.

3.4.3. Conclusion

The present results, together with earlier studies of the development of the knopper gall guild in Britain (Collins *et al.* 1983; Hail *et al.* 1990; see also Chapter 2) suggest that communities in the invaded range are becoming richer in parasitoid and inquiline species over time. The species composition at a particular place within the range will be determined by the pool of species available and by the length of time knopper galls have been established (see also Chapter 4). Particular roles in the gall community may be occupied by different species in different areas. For example, *Cecidostiba adana* is the main parasitoid of inquilines in continental Europe, while *Mesopolobus jucundus* fulfils this role in Britain. This suggests that the diversity of niches in the guild of knopper galls may be limited (Schönrogge *et al.* 1994).

The geographical distribution of parasitoid attack suggest that most of the species are present throughout Europe (see also Fulmek 1968). The distribution gaps in attacks of individual species may mean that there is no rule for the time a parasitoid population at a given place needs to detect a new host (Cornell & Hawkins 1993).

Knopper gall communities in the invaded range are becoming more similar to the community observed within the native range in the way they are structured. This process, however, must be a very slow one; even in the regions with the

longest residence time, the guilds associated with knopper galls are considerably different to those in the invaded range.

4. The abundance and species richness of the parasitoid and inquilines of an invading gall wasp: *Andricus quercuscalicis* (Hymenoptera: Cynipidae)

4.1. Introduction

Communities tend to be viewed as a fixed set of species linked to one another in a fixed pattern (Askew 1961a, Odum 1983, Krebs 1985, Ricklefs 1990). Dynamic changes in community structure and composition are assumed to be important over evolutionary time or, in ecological time in the course of succession. While successions of plant- and herbivore communities have been relatively extensively studied, dynamic changes in a community of natural enemies have rarely been the subject of research (Anderson 1986).

The community of parasitoids and inquilines of the invading gall wasp *Andricus quercuscalicis* showed characteristic patterns of variation in species composition and attack rates on a temporal and geographical scale and provides an excellent opportunity to study the dynamics of species establishment in a community of natural enemies following invasion of an alien herbivore (Collins *et al.* 1983, Hails 1988, Hails *et al.* 1990).

Andricus quercuscalicis has invaded northern and western Europe over the last 400 years from its native range in south eastern Europe (Gauss 1977, Stone and Sunnucks 1993). This gall wasp has two generations each year. In spring small sexual galls form on the male flowers of Turkey oak (*Quercus cerris*). In early summer the sexual females oviposit into the female flowers of Pedunculate oak (*Q. robur*) where the galls of the agamic generation are formed on the acorns during summer and autumn. *A. quercuscalicis* has spread through Britain since it arrived in the late 1950's, and is now also widespread in Ireland (Hails and Crawley 1991, Chapter 6). The acorn galls, known as knoppers, are the subject of this study. The community in the sexual galls is considered elsewhere (Stone *et al.* in prep.).

In this study the impact of a set a factors shall be quantified which earlier work indicated affect the occurrence and/or abundance of members of the community (i.e. might be important in structuring the community). The factors investigated here can be described in three categories: 1) gall morphology; 2) geographical locations of sample sites which also reflect the invasion history of *A. quercuscalicis*; and 3) interactions between community members.

There are two aspects to relationships between parasitoid/inquiline abundance and gall morphology. First, parasitoids and inquilines may select host galls on the basis of morphology (Askew 1961b, 1965). Price *et. al.* (1987) put forward "the enemy hypothesis" which describes how parasitoid attack might have driven the diversification of gall shapes. The gall formers would gain "enemy free space" by excluding parasitoids if the different gall shapes require certain levels of pre-

adaptation from the parasitoid species (Jeffries and Lawton 1984, Weis and Abrahamson 1986). The enemy hypothesis is still controversial (Askew 1961a, Price and Pschorn-Walcher 1988, Hawkins and Gagne 1989, Hawkins 1990). Alternatively, parasitoids may also affect gall morphology directly by killing the larva of the gall former. Attack on the gall former typically halts gall formation within a matter of hours (Wiebes-Rijks 1982, Askew 1960, 1961a) so if the gall wasp larva is killed in an early stage of gall development the gall is likely to stay small.

The geographical location where a sample was taken reflects the period of time for which *Andricus quercuscalicis* has been part of the local gall community. These periods vary between several thousand years in the native range to about 10 years in the most recently invaded regions (C. Nelson personal communication).

Interactions between the different members of cynipid gall communities via auto- and/or hyperparasitism have commonly been observed (Askew 1961a, 1975). Further, due to the polyphagy and the phenology of the parasitoids, these interactions might be important in structuring the guild within the galls of *A. quercuscalicis*, and also affecting the way it interacts with the guilds of other cynipid galls.

The aim of this study was the construction of statistical models to explain the variation in the abundance/occurrence of the parasitoids and inquilines of the asexual galls of *A. quercuscalicis* and to understand the determinants of parasitoid species richness, using gall height, gall width, gall shape, geographical location and the abundance of other guild members as explanatory variables. Several combinations and transformations were used and procedures from general linear modelling employed (Crawley 1993) in order to assess the importance of each of the factors in structuring the guild of knopper galls in the native and invaded range.

4.2. The guild of inhabitants associated with knopper galls

The inhabitants of the autumn galls of *A. quercuscalicis* on *Q. robur* can be split into four reasonably distinct groups: 1) the gall former; 2) inquilines, which develop in varying numbers in the wall of the knoppers feeding on gall tissue; 3) parasitoids which attack the gall former; and 4) parasitoids which attack the inquilines (Chapter 3).

Only the 8 commonest parasitoid and inquiline species were included in the statistical analyses of species abundance, but analyses of parasitoid species richness included a further 9 rare species which occurred in the rearings. Of the three inquiline species associated with knopper galls two, *Synergus gallaepomiformis* and *S. umbraculus*, were included in the analyses, both of which belong into the

tribe Synergini (Cynipidae). All of the common parasitoids in knopper galls belong to the superfamily Chalcidoidea (Table 3.1).

The common parasitoid species which attack inquiline larvae are *Cecidostiba adana* (Pteromalidae) in continental Europe and *Mesopolobus jucundus* (Pteromalidae) in Great Britain. Parasitoids attacking the larva of the gall former itself are *Megastigmus stigmatizans* (Torymidae), *Ormyrus nitidulus* (Ormyridae), and *Aulogymnus trilineatus* (Eulophidae). All these species are solitary, ectoparasitic parasitoids. *Sycophila biguttata* (Eurytomidae) is a solitary endoparasitoid.

4.3. Methods

4.3.1. Sites

Agamic galls of *A. quercuscalicis* were collected from 60 sites throughout their European range (Figure 4.1), including the historic native range and the invaded range as far north as the German Baltic coast and as far west as the current invasion front in Great Britain and Ireland.

4.3.2. Rearing techniques

Species richness and species abundance in the *A. quercuscalicis* guild were established using two different rearing techniques.

1. The species richness of the knopper gall guild at 60 sites results from mass rearings of 150 galls from each site. To avoid contamination of rearings by species outside the guild all galls were cleared of debris and removed from acorns and acorn cups before rearing in outside insectaries. Gall dimensions for mass rearings were not recorded.

2. A total of 2100 galls from 42 locations were reared individually and later dissected to determine the abundance of the individual species and the causes of mortality suffered by the gall causer and inquilines. Inhabitants unemerged at the time of dissection were identified as larvae or reared to adults in gelatine capsules.

Figure 4.1: Sites in Europe from which knopper galls were dissected.



4.3.3. Local cynipid species richness

At each site the local gall fauna was surveyed to compile a presence/absence list of the cynipids on oak. At least three investigators searched all oak species for thirty minutes. Because the surroundings in which we collected the galls were varied (including parks, forests and field edges), the number of trees surveyed differed between sites. Where possible, at least five trees were searched at each site to compensate for between-tree heterogeneity of cynipid species diversity (Askew 1962, Crawley and Akhteruzzaman 1988). Possible observer bias was tested (and found to be minimal) by searching the same stand for the same period of time and comparing the species observed. No significant differences were obtained.

4.3.4. Modelling

Variation in species richness and in the abundance of parasitoid and inquiline species was modelled in terms of gall size, geographic location and guild structure..

A. Geographical location: Geographic patterns were analysed using two types of variables:

1. The latitude and longitude of each sample site (easterliness and northerliness).

2. A categorical variable, dividing the sampled range into 6 regions (appropriate on the basis of historical and population genetic data Stone and Sunnucks 1993): the native range includes samples from eastern Austria, Hungary and Croatia; the other five regions are: Germany, France, Italy, the Netherlands and Belgium and Great Britain. The regions are separated by natural geographical barriers, such as the Alps and the English channel, and have been occupied for different periods of time.

B. Gall morphology is described by the width and the height of the gall. Gall width was measured as the maximum diameter at the base of the gall excluding the thin, corky ridges (inquilines were never found in these ridges). Gall height was measured from the base to the apex of the gall.

C. Abundance of other species: Where species occurred with only one individual per gall a category variable was used to indicate presence/absence; elsewhere the abundance of each species was used as an explanatory variable in the model.

For continuous variables, like gall size, easterliness and northerliness, quadratic terms were included to test for non-linearity, and product terms were included to test for interaction effects. For each response variable, all potential explanatory variables and interactions terms were added to create a maximal model., then a minimal adequate model was generated by stepwise simplification; non-significant

model terms were deleted until all remaining explanatory variables explained a significant amount of deviance (Crawley 1993).

Two types models were employed. For solitary parasitoids attacking the gall former there is one host per gall, so it is appropriate to model this kind of parasitism on the basis of presence/absence using logistic regression with the presence of the parasitoid (1=present, 0=absent) as a binary response variable.

A Poisson error structure with a log-link function corrected for overdispersion provided the best model for species richness (count data). The number of hosts was introduced to the model as a covariate to control for sample size (Karban and Ricklefs 1983). To ensure an acceptable distribution of residuals in the minimum adequate model, a variety of error structures, link functions and transformations of the explanatory variables was tried; and the combination giving the best distribution of standardised residuals was selected.

Logistic regression was used to analyse for spatial density dependence (e.g. parasitoids of the inquilines) as described by Hails and Crawley (1992).

4.4. Results

4.4.1. Geographic trends in the explanatory variables

Local cynipid gall species richness was positively correlated with the number of oak species present at a particular collection site ($b=0.204\pm0.064$) and this effect became significantly more pronounced towards the centre of the native range (i.e. eastwards: $b=4.37*10^{-4}\pm1.06*10^{-4}$).

Average knopper gall shape changed from east to west and from south to north (Table 4.1). Galls were generally taller in the south of the range than in the north, and wider in the east than in the west of the sampled range.

Table 4.1: Geographic trends in gall size ($p<0.05$).

	Estimates	S.E.	$F_{(1,40)}$	r^2
Width				0.21
Intercept	13.33	1.119		
easterliness	0.0010	0.0003	10.51	
Height				0.16
Intercept	22.00	2.691		
northerliness	-0.0029	0.0010	7.75	

4.4.2. Parasitoids

Certain differences in gall shape were associated with whether or not the gall former was killed early in its development by parasitoids (Figures 4.2a-b). The category marked (H) shows the average volume of galls from which adults of *A. quercuscalicis* emerged and represents a standard of a "normally developed" gall.

4.4.3. Parasitoids of the gall former

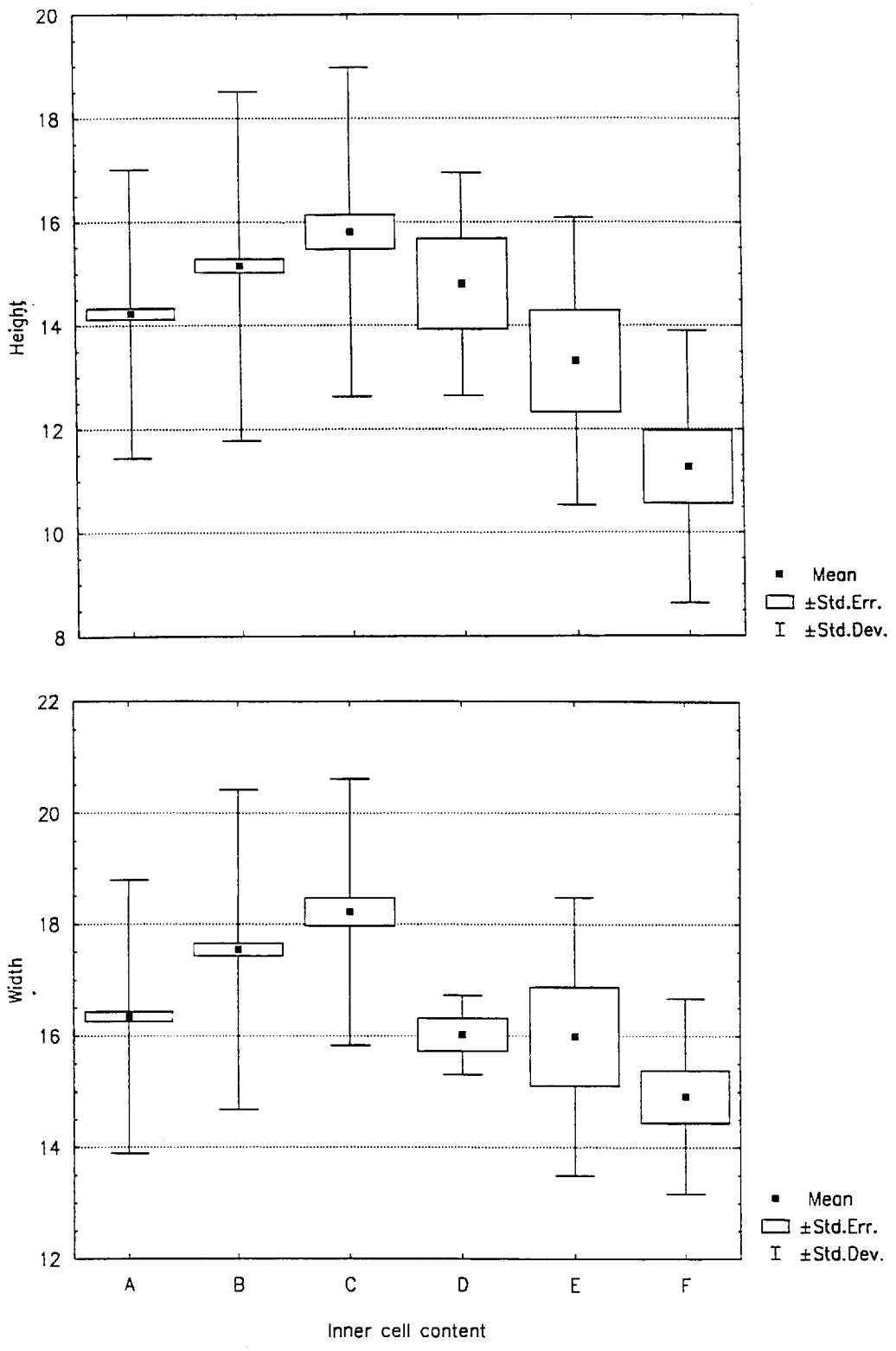
Mortality from parasitism of the gall former was generally low. The 100 galls from Germany which were dissected did not contain any of the four main parasitoid species (Table 4.2). In the invaded and native range *Megastigmus stigmatizans* was the commonest parasitoid which attacked the gall-maker (Table 4.2).

Table 4.2: Overall percentage parasitism in the 6 regions for four parasitoid species which attack the gall former.

	Native range	Germany	France	Netherlands and Belgium	Italy	Britain
	%	%	%	%	%	%
Megastigmus stigmatizans	6.5	-	13.0	8.0	-	-
Sycophila biguttata	0.7	-	-	-	2.0	-
Ormyrus nitidulus	1.3	-	-	-	1.3	0.2
Aulogymnus trilineatus	2.0	-	-	-	-	-
No. of galls dissected	400	100	200	200	150	1050

M. stigmatizans required the most complex model (Table 4.3). The inclusion of the logarithms of gall height and gall width in the minimal adequate model suggests that *M. stigmatizans* responded to the volume of the galls, though this relationship varies in strength between regions. In France, the Netherlands and Belgium, attacked galls were taller on average than unattacked galls, but this was not the case in the native range (Table 4.4). *M. stigmatizans* was also the only species which was significantly more likely to be present in galls which contained large numbers of inquilines (Table 4.3 & 4.4). Intriguingly, this correlation was particularly strong for galls from the Netherlands and Belgium where inquilines were relatively rare (on average 1.1±0.24 inquilines per gall compared to 3.7±0.34 in the native range and 4.8±1.1 in France).

Figure 4.2 a-b: Average gall width and gall height according to the content to gall wasps larval chamber:



A - *A. quercuscalicis* has emerged; B - Diapausing females of *A. quercuscalicis*; C - *Megastigmus stigmatizans*; D - *Sycophila biguttata*; E - *Ormyrus nitidulus*; F - *Aulogymnus trilineatus.*

Table 4.3: Significant parameters ($p<0.05$) which determine the likelihood of the presence of the 4 parasitoid species which attack the gall former. Regions is a categorical variable which represents the countries listed in Table 4.1 (region(4) = the Netherlands and Belgium). Only galls from those regions in which the individual parasitoid species was detected were included in the analyses (n = number of galls dissected).

	Megastigmus stigmatizans		*Sycophila biguttata*		*Ormyrus nitidulus*		*Aulogymnus trilineatus*	
n	800		550		1600		400	
	χ^2	d.f.	χ^2	d.f.	χ^2	d.f.	χ^2	d.f.
width	5.6	1	-	-	7.0	1	-	-
width^2	-	-	-	-	7.6	1	-	-
ln width	5.8	1	-	-	-	-	-	-
height^2	-	-	-	-	-	-	-	-
ln height	-	-	-	-	-	-	-	-
width*height	-	-	-	-	-	-	7.5	1
regions	-	-	-	-	7.9	1	-	-
regions x height^2	-	-	8.72	1	-	-	-	-
regions x ln height	13.4	2						
inquilines	17.7	1	-	-	-	-	-	-
inquilines x region(4)	23.8	1	-	-	-	-	-	-

The only significant term which affected the likelihood of finding *Sycophila biguttata* in a gall was the interaction between gall height squared and region (Table 4.3). *S. biguttata* was only recorded during the dissections from galls collected in the native range or in Italy. Galls from the native range which contained the larva of this parasitoid species were smaller on average than those without, whereas the situation in Italy was reversed (Table 4.4). Note also that galls from Italy were on average the widest (17.75±0.19mm) and tallest (18.90±0.20mm) galls from any of the regions.

The likelihood of finding a larva of *Ormyrus nitidulus* was significantly correlated with gall width and with region (Table 4.3). While the width of knopper galls ranged from 7.2mm to 32mm, *O. nitidulus* was only found in galls from a narrow band of widths (13.4mm to 17.2mm; see also Table 4.4). Attacked galls were on average narrower than those which were not attacked (Table 4.4). This was true for galls from the native range and from Italy, but for knopper galls collected in Britain there was no difference in width between attacked and unattacked galls. However, parasitism by *O. nitidulus* was much rarer in Britain than in Italy or other parts of the native range (Table 4.2).

Aulogymnus trilineatus was found only in galls from the native range, and the only parameter required in the model was a negative term for the product of gall height and gall width (Table 4.3), showing that *A. trilineatus* is most likely to be found in smaller galls.

Table 4.4 : Mean gall size (height and weight ±S.E.) and mean number of inquilines (±S.E.) in attacked and not attacked knopper galls for the four parasitoid species which attack the gall former.

		Native range	France	Netherlands and Belgium	Italy	Britain
Megastigmus stigmatizans						
mean width (mm)	attacked galls	18.21±0.53	18.37±0.29	18.18±0.56	-	-
	non attacked galls	17.88±0.16	16.66±0.22	18.27±0.17	-	-
mean height (mm)	attacked galls	13.93±0.63	15.40±0.53	18.12±0.54	-	-
	non attacked galls	13.93±0.18	13.76±0.26	15.38±0.23	-	-
mean number of inquilines	attacked galls	7.35±2.29	17.15±5.29	7.56±0.14	-	-
	non attacked galls	3.40±0.33	3.03±0.90	0.61±2.01	-	-
Sycophila biguttata						
mean width (mm)	attacked galls	18.97±0.94	-	-	16.23±1.42	-
	non attacked galls	17.89±0.15	-	-	17.78±0.23	-
mean height (mm)	attacked galls	17.03±1.16	-	-	14.50±1.27	-
	non attacked galls	13.91±0.17	-	-	18.99±0.22	-
mean number of inquilines	attacked galls	10.00±2.52	-	-	1.33±1.33	-
	non attacked galls	3.61±0.35	-	-	0.31±0.10	-
Ormyrus nitidulus						
mean width (mm)	attacked galls	15.10±0.50	-	-	15.40±1.00	16.33±0.87
	non attacked galls	17.94±0.15	-	-	17.78±0.23	16.03±0.08
mean height (mm)	attacked galls	13.98±2.14	-	-	14.40±2.80	12.33±1.51
	non attacked galls	13.93±0.16	-	-	18.97±0.23	13.90±0.09
mean number of inquilines	attacked galls	0.00±0.00	-	-	0.00±0.00	9.00±8.02
	non attacked galls	3.71±0.35	-	-	0.33±0.10	1.50±0.17
Aulogymnus trilineatus						
mean width (mm)	attacked galls	14.98±0.91	-	-	-	-
	non attacked galls	17.96±0.15	-	-	-	-
mean height (mm)	attacked galls	11.68±1.04	-	-	-	-
	non attacked galls	13.98±0.17	-	-	-	-
mean number of inquilines	attacked galls	3.50±2.17	-	-	-	-
	non attacked galls	3.66±0.35	-	-	-	-

Samples from Germany were omitted since none of the four parasitoid species were detected in those.

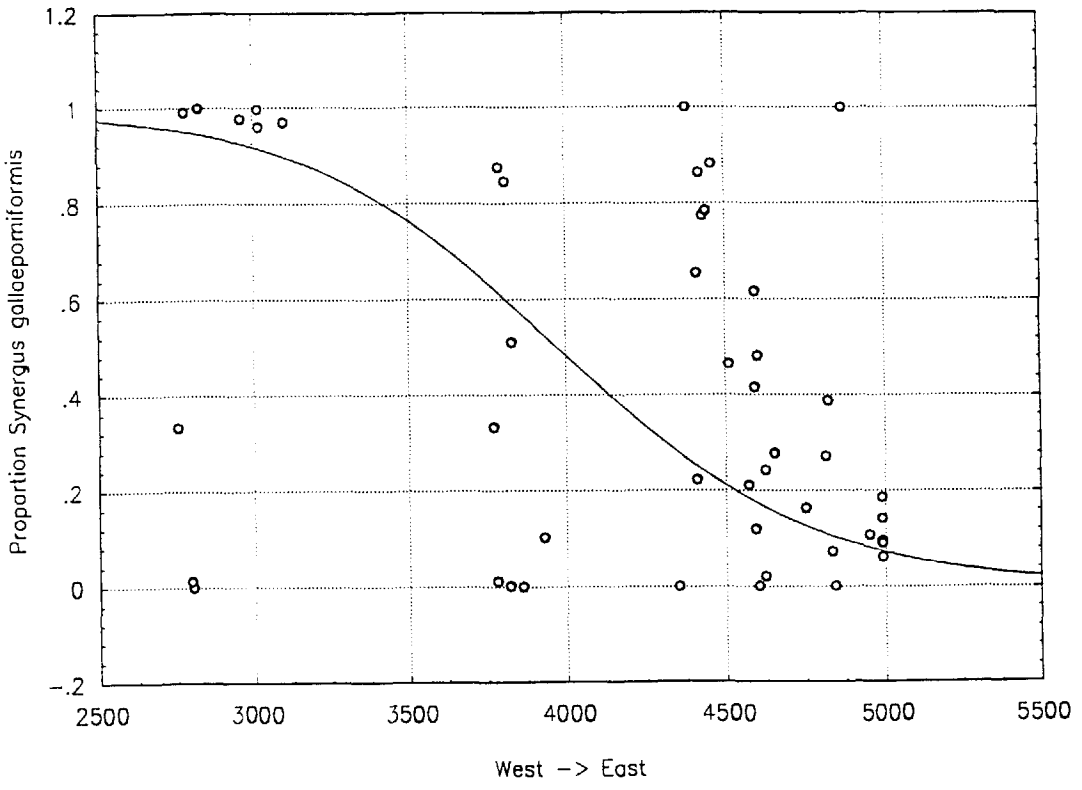
4.4.4. The inquilines

The two inquiline species *S. gallaepomiformis* and *S. umbraculus* can form many cells in the outer wall of a single gall. Each larva develops in its own cell and there can be up to 80 cells in a single knopper gall. Based on rearing data it appears that the proportion of galls infested by *S. gallaepomiformis* decreases, while *S. umbraculus* becomes more dominant towards the east (Figure 4.3)

In the dissections it was not possible to distinguish the larvae of these two inquilines, but it is likely that most of the larvae in galls collected in the east were *S. umbraculus* larvae and in the west were *S. gallaepomiformis*. Because no differences in the biology of the parasitoids attacking the inquilines in the west or east was found (i.e. all parasitoid species were solitary ectoparasitoids and there was no evidence for hyperparasitism) we assumed that the two *Synergus* spp. are equivalent as hosts for the inquiline parasitoids in knopper galls.

To analyse inquiline abundance, we used averages of gall width and height. None of the geographic variables or their interactions turned out to be significant, and the only parameter retained in the minimum adequate model was the mean width of the galls ($F_{(1,39)}$=8.8, $p < 0.01$, b =0.441±0.0929). Not surprisingly, wider galls were likely to contain larger numbers of inquiline larvae.

Figure 4.3: The proportion *Synergus gallaepomiformis* of the number of inquilines emerged from samples collected across Europe (GLIM regression with binomial errors, corrected for overdispersion, b=-0.0023±0.0005)



4.4.5. The common parasitoids of inquilines

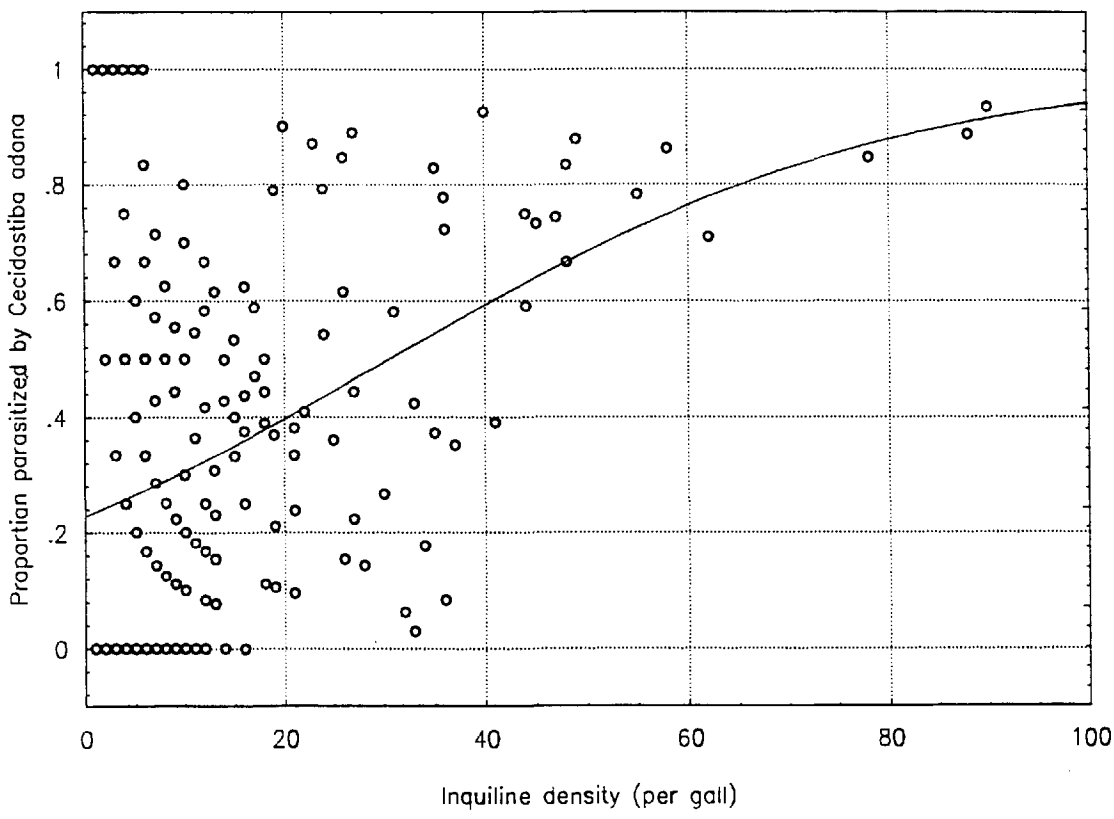
The two most common parasitoids attacking inquilines in knopper galls were *Cecidostiba adana* and *Mesopolobus jucundus*. The first species is dominant in the native range and in long-invaded parts of the alien range within continental Europe, while *M. jucundus* is the common parasitoid of inquilines in Great Britain (it attacks inquilines in knopper galls on the continent only rarely and just 3 individuals were reared from thousands of continental galls containing inquilines).

The varying number of inquiline hosts was used as the binomial denominator in a model to test for patterns of density dependence employing the same gall shape and geographical variables as before using inquiline density (and log inquiline density) as an explanatory variable (Hails and Crawley 1992).

For *C. adana*, the only significant explanatory variable was host (inquiline) density. Figure 4.4 shows the slight but only marginally significant positive relationship ($F_{(1,365)} = 3.87$, $p<0.05$) between host density and percentage attack by *C. adana*.

None of the model terms or interactions had any significant explanatory power for variation in the attack rate of *M. jucundus* in British knopper galls.

Figure 4.4: Positive density dependence of *Cecidostiba adana* on its inquiline hosts (GLIM regression with binomial errors; corrected for overdispersion: b=0.039± 0.00319; a=-1.216)



4.4.6. Species richness of the *A. quercuscalicis* parasitoid guild

Parasitoid species richness declined significantly with distance away from the native range (Table 4.5). Likewise, there were more cynipid species (potential alternative hosts for the parasitoids) in the native range than anywhere in the invaded range. The strength of the association between the local cynipid species richness and the number parasitoid species in the knopper galls varied with geographic location of the sample site (as indicated by the significant interaction term in Table 4.5).

Species richness of parasitoids was positively correlated with inquiline abundance (Table 4.5). In a model with Poisson errors which accounts for 65 percent of the deviance in parasitoid species richness.

Table 4.5: Significant terms ($p<0.05$) of the regression on species richness of parasitoid species attacking the larva of the gall maker (GLIM regression with Poisson errors).

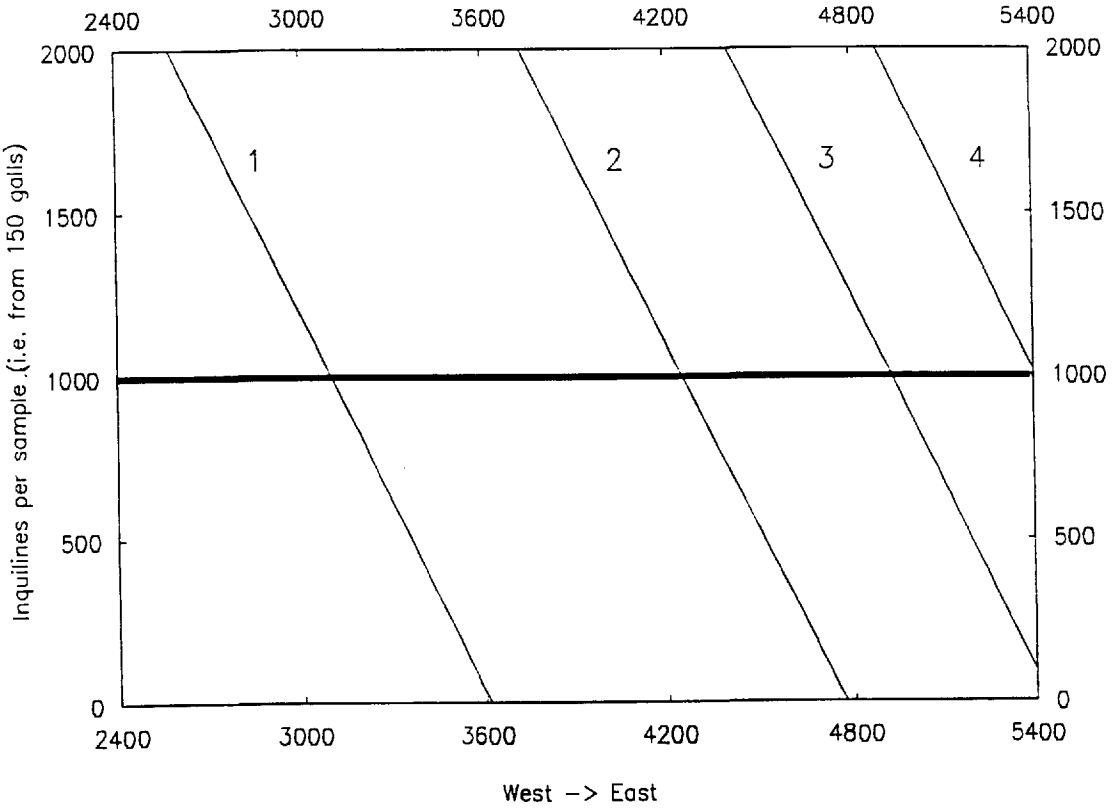
Variables	Estimate	S.E.	χ^2	d.f
intercept	-5.957	1.179		
easterliness	0.0013	0.0003	43.84	1
Cynipid gall richness	0.7261	0.1835	4.586	1
Inquiline load	0.0005	0.0001	8.10	1
easterliness. Cynipid gall richness	-0.0002	0.0000	11.95	1
Error			36.88	55
Total			105.37	59

4.4.7. Species richness of the inquiline parasitoid guild

Species richness of inquiline parasitoids was affected only by the east-west location of the sample site and by sample size ($F_{(1,56)} = 26.28$; $p < 0.05$; Poisson errors, corrected for overdispersion). Figure 4.5 shows the number of inquiline parasitoid species expected at different locations along the west-east axis for a given abundance of inquiline hosts in a fixed sample of galls.

The thick horizontal line demonstrates that in samples with 1000 inquiline hosts, for instance, one would expect to find only one parasitoid species attacking the inquilines in galls from Britain (easterliness 2500-3300) whereas a sample with the same number of inquiline hosts from Hungary (easterliness 4500-5150) is expected to yield between two and four parasitoid species.

Figure 4.5: Predicted number of inquiline parasitoid species according to the geographical location and the available number of hosts (GLIM regression with Poisson errors, corrected for overdispersion, $b_{easterliness}$=0.0006±0.0001, $b_{host\text{-}density}$=0.0003±0.0001, a=-2.167±0.560).



4.5. Discussion

The abundance of individual parasitoid species and the species richness of the guild in knopper galls were both affected by the geographical location of the sample (which is likely to be linked to the invasion history of *A. quercuscalicis*); the presence and abundance of gall inhabitants; and gall size as measured by the width and height of the knopper galls.

4.5.1. Parasitoid and inquiline abundance and gall morphology

Relationships between gall size and the occurrence of parasitoids which attack the gall-maker can be determined in two different ways:

Parasitoids might attack the gall-maker early in its development. When the gall former is killed immediately, gall development halts within hours resulting in a smaller than average size of the attacked galls (Wiebes-Rijks 1982). This appears to be the case for *Aulogymnus trilineatus*.

Alternatively, parasitoids might select larger galls for oviposition. In *A. quercuscalicis*, gall size and gall wasp size are positively correlated (G. McGarvin, unpublished data, Collins *et al.* 1983). If parasitoid fecundity is a correlate of parasitoid size, and parasitoid size is positively correlated with host size, then the selection of large hosts is of obvious selective value for the female. *M. stigmatizans* appears to select for larger knopper galls.

Ormyrus nitidulus also seemed to select galls above a minimum size (about 13mm in width) and to ignore galls which were smaller (about 10% of all the galls which were measured). It may be that the ovipositing female thus assures a minimum size of the host larva, sufficient for the successful development of the parasitoid larva. Because the gall maker is then killed immediately, galls attacked by *O. nitidulus* were smaller than average by the end of the season.

In contrast, the positive relationship between gall size and the number of inquilines which develop inside a gall is determined by the ability of the inquiline larvae to alter the tissues which surround them and to contribute actively to the growth of the gall (Shorthouse 1980, Askew 1984, Stille 1984, Wiebes-Rijks and Shorthouse 1992); this made it also more likely to find *M. stigmatizans* associated with galls which contained numerous inquilines since this species occurred more often in larger galls.

4.5.2. Parasitoid and inquiline abundance and geography

All four parasitoid species which attack the gall maker, were recorded almost throughout the range which was sampled here (Fulmek 1968). It appears, however, that *O. nitidulus* and *A. trilineatus* are considerably rarer in western Europe than towards the native range of *A. quercuscalicis* and hence it is likely that these species encounter knopper galls infrequently (Table 4.2, see also Askew 1960).

One reason might be that many of the other cynipid galls which are exploited by these two species are restricted to eastern Europe (Buhr 1965, Fulmek 1968, Ambrus 1974).

M. stigmatizans, in contrast, was more often found in galls from the invaded range than from the native range of *A. quercuscalicis.* This species is recorded from 18 different cynipid galls throughout Europe (Fulmek 1968). In the invaded range, however, the only other galls attacked by *M. stigmatizans* were *Andricus kollari* and *A. lignicola.* Both species show the same host-alternation between Turkish oak and English oak as *A. quercuscalicis,* and are invaders of western Europe themselves. *M. stigmatizans* might therefore be an example for a parasitoid species which extended its geographical range by following its hosts.

The same pattern can be found for the inquiline *Synergus umbraculus* which is recorded in Britain only from galls of *A. quercuscalicis, A. kollari* and *A. lignicola* but is found in another 19 cynipid galls in continental Europe, many of which are only known from the native range of *A. quercuscalicis* (Askew 1961a, Buhr 1965, Fulmek 1968, Askew and Neill 1993).

The results of the analysis of the abundance of the two inquiline parasitoids *Cecidostiba adana* and *Mesopolobus jucundus* are particularly interesting because of their geographic separation. While *C. adana* showed positive density dependence in attacking its inquiline hosts, none of the explanatory variables were significant for *M. jucundus.* It is possible that important factors were not recorded, but it is also possible that the inquiline parasitoid species in Britain are only now beginning to exploit the new resource, and have not yet had time to establish characteristic patterns of abundance (e.g. there were no records for *M. jucundus* from knopper galls collected in Britain before 1986 despite intensive rearing; Hails *et al.* 1990).

4.5.3. Patterns of parasitoid species richness

Species richness of parasitoids attacking the gall wasp larva is greatest in the native range where the greatest richness of potential alternative hosts is also found (Eady and Quinlan 1963, Fulmek 1968, Ambrus 1974). Intriguingly, however, *A. quercuscalicis* was attacked by *fewer* parasitoid species in places in the native range with higher cynipid diversity than in places where there were only a few other gall species present. It could be that an increasing number of alternative host galls might divert ovipositing parasitoid females away from knopper galls. We do not yet know the relative importance of different gall hosts in determining parasitoid abundance, but for *Mesopolobus* parasitoids of the sexual generation of *A. quercuscalicis* does it appear that *A. quercuscalicis* is an inferior host, producing exclusively smaller, male parasitoids (Hails and Crawley 1991).

Parasitoid species richness is also positively correlated with inquiline density and obviously the presence of inquilines is a prerequisite for the presence of a number of parasitoid species which concentrate their attacks on inquiline larvae. This becomes particularly clear at sample locations close to the invasion front, where inquilines are just beginning to exploit knopper galls (see also Chapter 2). Our results also show that the higher the abundance of inquiline larvae the more parasitoid species are recorded. Furthermore, since inquilines can actively increase gall size, high inquiline density increases the likelihood of finding parasitoid species which select larger galls for oviposition (e.g. *M. stigmatizans*, see Table 4.4).

According to the "enemy hypothesis" gall morphology could provide protection for the gall former against natural enemies (Price *et. al.* 1987). In the evolutionary arms race parasitoids might have adapted to the new shapes and sizes of galls, and this could result in relatively specialised parasitoid species which attack only galls of relatively similar shape. Here we have shown that gall shape was often altered by parasitoid and inquiline attack and that the gall never grows large enough to provide protection from natural enemies. Of those parasitoids considered here, only *Megastigmus stigmatizans* possesses an ovipositor which is long enough to penetrate the wall of a mature knopper gall. Although this species might appear to specially adapted to attack galls of the size of knopper galls it is also recorded from the much smaller agamic galls of *Andricus lignicola* and from galls of *Andricus caput-medusa* whose shape is quite different from knopper galls (Fulmek 1968, Sellenschlo and Wall 1984).

We have shown substantial variation in gall size and shape in different parts of the geographic range, but there is nothing to suggest that these changes in gall morphology are caused by, or have important consequences for natural enemies.

5. Patterns of mortality in galls of the sexual generation of the cynipid gall-wasp *Andricus quercuscalicis* (Hymenoptera; Cynipidae)

5.1. Introduction

Andricus quercuscalicis is a cynipid gall-wasp which has been extending its range across western Europe for between 3 and 4 hundred years (Stone and Sunnucks 1993) following human dispersal of one of its host plants, the Turkey oak (*Quercus cerris*). The history of the spread of this species from its native range in central and south-eastern Europe is well documented (Stone and Sunnucks, 1993) and particularly in Britain where the invasion has been the subject of considerable ecological study.

In common with several other invading cynipids of oak (Askew 1984), *Andricus quercuscalicis* has two generations each year; one generation develops on the acorns of pedunculate oak (*Quercus robur*), giving rise to characteristic knopper galls. All the gall-wasps emerging from these galls in the following spring are asexual females. These disperse to Turkey oak, where they lay their eggs in the male flower buds, giving rise to tiny galls on the catkins in May. The generation which emerges is sexual; the mated females disperse to pedunculate oak, where they lay their eggs on the female flowers, thus completing the life cycle.

A. quercuscalicis reached Britain in the late 1950's, and is now widespread in Ireland (see Chapter 6). The development of parasitoid and inquiline communities associated with this species has been studied for more than a decade (Collins *et al.* 1983; Hails 1988; Notton 1988; Hails & Crawley 1991, 1992; Schönrogge *et al.* 1994). In contrast, very little is known about the community associated with this gall-wasp in its native range. This study examines patterns of mortality in the sexual generation in continental Europe. Mortality and community composition in galls of the agamic generation in the native range are considered elsewhere (see Chapter 2, 3 and 4).

5.1.1. Causes of mortality in the sexual generation of *A. quercuscalicis*.

Five parasitoid species are known to attack the sexual galls of *A. quercuscalicis* in Britain (Hails 1988; Hails and Crawley 1991). This parasitoid guild is unusual in comparison to other guilds known from oak cynipids, because there have been no inquilines recorded from these galls nor had there been any evidence for hyperparasitism (Askew 1961a, 1984, Hails 1988). No gall ever yielded more than a single adult insect.

A relatively constant 20-30% overall mortality was caused each year by three principal parasitoids, all species of *Mesopolobus*, (*M. fuscipes* [Walker 1934], *M. xanthocerus* [Thomson 1878] and *M. tibialis* [Westwood 1833], (Hymenoptera; Pteromalidae) (Hails and Crawley 1991). Two other species, *Mesopolobus dubius*

(Walker 1834) and *Aprostocetus (= Tetrastichus) aethiops* (Zett.) caused a total of less than 0.6% mortality. All of these species were found to be pupal parasitoids, attacking the gall-wasp during the brief period in May between pupation and adult emergence. Further mortality was attributed to bird predation. A significant number of galls (9-35.5%) failed to produce any adult insect, and Hails (1988) demonstrated that at least a part of this mortality could be attributed to failed parasitoid attack, leading to the death of the pupae. The only parasitoid known at the time from the sexual generation of *A. quercuscalicis* in continental Europe was *Mesopolobus tibialis* (Pfützenreiter & Weidner 1958).

5.1.2. Patterns of parasitoid-induced mortality in sexual galls

The total numbers of sexual galls of *A. quercuscalicis* on a single Turkey oak can be extremely high, and this may explain the ability of this species to spread even where its host tree is rare and patchily distributed (Stone and Sunnucks 1993). The impact of natural enemies on the sexual generation has been studied in detail in Britain by Hails and Crawley (1991, 1992), who looked for evidence of spatial density dependence in attack by parasitoids. They found that the relationships between parasitoid induced mortality and host density were both complex and variable.

The proportion of flowers galled, the percentage of galls parasitised and the rank order of percentage parasitism by each *Mesopolobus* species were all found to vary considerably between trees in a given year. Hails (1988) found no density dependence for any *Mesopolobus* species when host galling rates were universally low, although in years with higher density, density dependence was detected for *M. fuscipes, M. xanthocerus* and *M. tibialis*. Even when host densities were manipulated to artificially high levels, patterns of density dependence remained weak, variable and non-uniform over a range of different spatial scales (Hails 1988; Hails & Crawley 1992).

This study examines patterns of mortality in the sexual generation for 11 sites in Germany, Hungary, Austria and the Czech republic. The sites in Germany lie in the central part of the invaded range for this species, while the remaining sites lie within the native range (Stone and Sunnucks 1993). We describe the community composition in the sexual gall, and examine variation in mortality patterns at three spatial scales: within trees at a site, between trees at a site, and between sites.

5.2. Methods

5.2.1. Sampling methods

Hails & Crawley (1992) searched in detail for density dependence at a range of spatial scales from catkins, through buds, shoots and twigs. Because of the wide

geographical area covered in the present study and the short period of time for which the catkin galls are available for sampling, collections were made at only 3 spatial scales.

1. Large scale geographic variation. A total of 1000 catkins was collected from 5 trees at each of 11 sites in central and eastern Europe. Catkins from each site were reared together in a single mass rearing.

2. Variation between trees within sites, and between samples within trees. At three sites in the native range (Tausendblum in eastern Austria, Valdice in the Czech Republic, and Zalaegerszeg in western Hungary) we made hierarchical collections of 20 samples from each of 5 trees at each site. Each sample consisted of 30 catkins, giving a total of 3000 catkins per site. The collection of samples in this way allows the analysis of patterns within trees within sites and of patterns (using tree means) between sites.

At all sites, samples were removed from the trees with a 5.0m pole pruner. Within the limits imposed by this reach, small branches were removed from a range of heights and aspects. For the three sites studied in greater detail, each sample consisted of 30 catkins taken from a length of growth measuring 20cm from the tip, thus standardising the size of the sample unit. Within the 20cm length, the structural complexity varied from bushy growth to a straight single shoot. To account for the differences in growth structure the numbers of twigs, shoots and catkins were recorded (as defined by Hails & Crawley 1992) and used in the analyses as covariates.

5.2.2. Rearing methods

All samples were checked to ensure that no galls other than *A. quercuscalicis* were included. Catkins were stored in muslin-covered containers in an outside insectary. Good ventilation of the samples was found to be essential if extensive fungal attack was to be avoided. Because earlier work suggested that parasitoids such as *Aprostocetus aethiops* only emerged in the second year after completion of gall development (Hails 1988), catkin samples were left undisturbed for 16 months after collection in May 1992. Because of degradation of the samples, only emerged insects could be collected from the mass rearings (1000 catkins), and total numbers of galls and flowers per sample, and mortality prior to adult emergence, proved to be impossible to record. In contrast, all catkins from the three sites sampled in detail were sorted under a dissecting microscope. The total number of galls was recorded for each catkin, with separate totals for those from which insects had eclosed, those which had reached full size but produced no adult insect, and those which were stunted and unopened. All unopened galls were dissected in order to determine the fate of the gall former. Parasitoid larvae and pupae still in

development were transferred to gelatine capsules to allow eventual adult eclosion and identification. Adult parasitoids were identified using identification keys by Graham (1969; 1987) and Askew (1961a), and the identity of voucher specimens was confirmed by Dr. R.R. Askew.

5.2.3. Detection of density dependence.

Measures for host density were obtained for the three sites which were studied in detail, Tausendblum, Valdice and Zalaegerszeg. Density dependence for a given mortality factor was examined by analysis of the number of individuals dying as a function of host density, using logistic regression (Hails & Crawley 1992; Crawley 1993). Logit mortality (ln(parasitized/non-parasitized individuals) was regressed against host density in a weighted regression, using the gall density as the weight. Gall density within a sample unit was estimated as the product of the mean number of galls per catkin over the 30 catkins and the number of catkins recorded within a sample unit. Two different analyses were used which reflect different patterns of host availability to the parasitoids.

a. 'Total galls' includes those galls which did not yield living adult insects. This would be appropriate for parasitoids which attack early in gall development. Because the *Mesopolobus* species encountered in this study are known to attack only host pupae, this measure of host density is probably not appropriate for these species. Some of the galls included in this measure were already stunted or dead by the time healthy hosts had reached the pupal stage, and would probably be ignored by ovipositing *Mesopolobus* females. This measure was used because the phenology of attack by the other species is uncertain.

b. 'Total viable galls'. Because each gall produces only a single insect, this parameter was estimated by summing the total number of adults and diapausing larvae and pupae of all species reared from a sample. This measure of host density involves the following important assumptions, discussed by Hails & Crawley (1991a).

1. All galls are available for parasitism, except those stunted and dying as larvae. Because the sexual galls of *A. quercuscalicis* only ever yield a single adult insect, the total host availability is then the total number of galls giving rise to diapausing or adult insects of any type. This will be an underestimate of host density if any gall-wasp larvae died as a result of failed parasitoid oviposition or feeding.

2. Parasitism by all species occurs at the same time, and parasitoids act independently of each other. This assumption would be violated if there were differences between parasitoids in the timing or specificity of oviposition. For example, *M. xanthocerus.* and *M. fuscipes* may attack earlier than *M. tibialis*

because they become active earlier in the spring (Askew 1961b). Overestimates might then be made of the number of hosts available to the later parasitoid. The assumption also implies that the parasitoids are not host-limited in their attack and can distinguish between parasitised and non-parasitised host galls, or that the parasitoids can be facultatively hyperparasitic.

3. In addition to these assumptions, it should also be noted that density dependence for a given parasitoid species may be obscured if numbers of the parasitoid are significantly altered by hyperparasitism.

Total viable galls seems a more appropriate measure of host density given what is known for *Mesopolobus* species in other cynipid galls (Askew 1961a). There is very little information on the host life stages attacked by *Aprostocetus* (Askew 1961d; Graham 1987), while *Cecidostiba adana* is recorded as a larval parasitoid by Askew (1961c). In the absence of detailed phenological data, both measures of host abundance were fitted for all parasitoid species. When analysing the frequency of death before emergence and total mortality (pre-emergence death and parasitoid-induced mortality) only the total number of host galls was used.

Analyses were carried out as nested analyses of variance or covariance. A maximal model was fitted for each mortality factor, containing the selected host density term, numbers of shoots, twigs and catkins in the sample, their squares (to test for non-linearity) and all two-way interactions. Model simplification proceeded by step-wise elimination of non-significant terms (Crawley 1993). In all cases, the distribution of standardised residuals was examined to check that the error distribution used was appropriate. Overdispersion was corrected if necessary by rescaling the error variance after fitting the full model.

5.3. Results

5.3.1. The parasitoid guild found in the sexual galls of *A. quercuscalicis*.

11 parasitoid species were reared from the sexual galls of *A. quercuscalicis*; *Mesopolobus fuscipes, M. xanthocerus, M. tibialis* (Pteromalidae), *Ormocerus vernalis* Walker (Pteromalidae), *Cecidostiba adana* Askew (Pteromalidae), *Aprostocetus aethiops, A. viridinitens* Graham, 1987, *A. cerricola* (Erdös), *Aulogymnus gallarum* L. and *Aulogymnus kelebiana* (Erdös) (Eulophidae), and *Torymus nitens* Walker (Torymidae). *Mesopolobus dubius,* found in British samples by Hails (1988), was not detected in our rearings. As in England, no inquilines were reared.

5.3.1.1. The 1000 catkin rearings.

The results of the rearings of 1000 catkins from the 11 central European sites are shown in Table 5.1. The total number of insects emerging from the 1000 catkin

samples ranged over two orders of magnitude from 17 at Felsötarkany (Hungary) to a maximum of 3439 at Ludwigsburg (Germany) in the invaded range. Because the total numbers of galls in these samples could not be determined, mortality due to parasitoids is expressed as a percentage of the total number of emergent insects. The mortality attributable to parasitoids over the three German sites ranged between 0.4 and 6.0%, while total rates of parasitism in Hungary (the native range of *A. quercuscalicis*) varied between 0.0% at very low host abundance (Felsötarkany) and 42.0% at the highest host abundance (Szarvas). The parasitoid causing highest overall mortality in these rearings was *Aulogymnus kelebiana,* which reached a maximum of 32% of the emerging insects. The three *Mesopolobus* species caused a maximum of 22% mortality between them, sometimes distributed evenly across the species (e.g. Ajka, Hungary) and sometimes contributed mainly by a single species (e.g. *M. tibialis* at Szarvas or *M. fuscipes* at Nagybanisza, both in Hungary).

Table 5.1: Number of sexual galls of *Andricus quercuscalicis* collected from sites in central Europe which produced adult gall-wasps or parasitoids and percent mortality due to parasitism. All rearings contained 1000 catkins gathered at random (see also text).

Site	Total emerged adults	*A. quercus -calicis* %	*A. kelebiana* %	*M. fuscipes* %	*M. xantho-cerus* %	*M. tibialis* %	*C. adana* %	Total para-sitism %
Germany								
Ludwigsburg	3439	99.7	-	0.3	-	0.1	-	0.4
Stuttgart	95	96.8	-	2.1	-	-	2.7	3.2
Munich	562	94.0	1.4	2.3	2.1	0.2	-	6.0
Hungary								
Gödöllõ	341	88.9	9.7	-	0.6	0.3	0.4	11.1
Nagybanisza	50	96.0	-	4.0	-	-	-	4.0
Ajka	40	60.0	32.5	2.5	2.5	2.5	-	40.0
Szarvas	1663	58.3	31.0	0.7	0.7	9.1	0.1	41.7
Tiszakurt	574	65.7	15.0	7.7	4.7	4.5	2.4	34.3
Vysoka	60	61.7	16.7	5.0	-	16.7	-	38.3
Miskolc	37	78.4	2.7	16.2	-	2.7	-	21.6
Felsötarkany	17	100.0	-	-	-	-	-	0.0

Cecidostiba adana was found in both Hungary and Germany at low frequency. 2 individuals of *Aulogymnus gallarum* were obtained, one from Gödöllö and a second from Szarvas, both in Hungary. The single male of *Torymus nitens* was reared from Szarvas. *Ormocerus vernalis,* found in the more detailed rearings described below, was not found in the 1000 catkin rearings.

5.3.1.2. Rearings from Tausendblum, Valdice and Zalaegerszeg.

At these sites the mean galling rates per catkin were relatively low compared to those recorded by Hails (1988) in Britain, with 2.2 galls per catkin at Tausendblum (range 0-11.4) and 0.4(0-2.6) and 0.8(0-4.2) for Valdice and Zalaegerszeg. Surprisingly, in none of the samples examined was there any evidence of bird predation, of the kind described by Hails & Crawley (1992), even though the galls were collected only just before the emergence period of the gall-wasp started. The only identifiable causes of mortality were the parasitoids described below. The mean proportion of galls at a site giving rise to either gall wasps or parasitoids (including diapausing larvae and pupae) ranged between 53% and 62% (Table 5.2). Of galls which failed to emerge, very few were stunted while the majority were fully developed although no remains of any inhabitant could be detected. The species list obtained from these rearings differs from the 1000 catkin rearings in the absence *Torymus nitens* and records for 4 additional species (*Ormocerus vernalis, Aprostocetus aethiops, A. viridinitens* and *A. cerricola*).

Again, the parasitoid species causing the highest mortality was *Aulogymnus kelebiana* (maximum of 65% mortality of total viable galls at Tausendblum, Table 5.3). A variable proportion (a mean of c. 25% at Zalaegerszeg) of *A. kelebiana* were found diapausing as fully formed larvae or pupae within the gall (Table 5.3). Galls containing diapausing *A. kelebiana* were characterised by thickened and strengthened gall walls. The presence of larvae suggests that this parasitoid can remain in diapause for at least two years.

The mortality caused by the three *Mesopolobus* species varied considerably between species and between sites. *M. fuscipes* was relatively abundant in Tausendblum and Zalaegerszeg, but was very rare in Valdice (present in only a single tree). *M. xanthocerus* caused up to 40% mortality in Zalaegerszeg, but a maximum of only 6% in the remaining sites. *M. tibialis* was the rarest of the three *Mesopolobus* species (0.5% in Tausendblum and 2.2% in Zalaegerszeg), and was completely absent from Valdice .

Six other parasitoid species were present in the rearings at low frequencies (0-7%, e.g. *Aprostocetus cerricola, A. aethiops, A. viridinitens, Aulogymnus gallarum, Cecidostiba adana* and *Ormocerus vernalis*). In addition to having the highest galling rates and overall mortality rates, Tausendblum also had the highest species richness (10 parasitoid species recorded). Zalaegerszeg, with lower galling rates than Tausendblum (Table 5.2), lacked *Cecidostiba adana*, but had the other five rare species at low frequency. Valdice, with the lowest overall galling rates and overall mortality rates, produced only the three principal parasitoid species (Table 5.3) with *O. vernalis* from a single tree.

Table 5.2: Total numbers of galls per tree, galling rates and the percentage of galls yielding living inhabitants for three sites (Tausendblum, Valdice, Zalaegerszeg). Totals (rows) refer to 3000 collected catkins.

	Total galls in sample	galls per catkin	% galls viable
1. Tausendblum (Austria)			
Tree 1.	688	1.14	56
Tree 2.	4151	6.91	55
Tree 3.	362	0.60	56
Tree 4.	1059	1.76	70
Tree 5.	270	0.45	68
Total	**6530**	**2.18**	**61**
2. Valdice (Czech Republic)			
Tree 1.	763	1.27	67
Tree 2.	161	0.27	77
Tree 3.	205	0.34	24
Tree 4.	12	0.02	25
Tree 5.	54	0.09	36
Total	**1195**	**0.40**	**53**
3. Zalaegerszeg (Hungary)			
Tree 1.	311	0.52	65
Tree 2.	146	0.24	73
Tree 3.	546	0.91	47
Tree 4.	354	0.59	73
Tree 5.	1065	1.77	58
Total	**2422**	**0.81**	**62**

Table 5.3: Percent parasitism by the three principal parasitoid species of the sexual generation of *A. quercuscalicis*. The proportions are of the total number of emerged insects (total viable galls; column 1). The percentage of all *A. kelebiana* found as larvae but which were still alive is given in parentheses.

	Total viable galls	*A.quercus-calicis* %	*A. kelebiana* (% in diapause) %	*M. fuscipes* %	*M. xantho-cerus* %	% Total mortality by parasitism
1. Tausendblum (Austria)						
Tree 1.	394	24.3	64.7 (11.9)	7.3	0.9	75.6
Tree 2.	2197	36.9	34.6 (6.6)	18.5	6.0	63.1
Tree 3.	190	20.3	72.8 (13.7)	1.8	-	80.8
Tree 4.	716	12.8	83.7 (33.7)	1.4	1.2	87.1
Tree 5.	157	11.8	76.9 (17.5)	10.5	-	88.2
Total	**3654**	**21.5**	**65.0 (19.2)**	**7.9**	**1.7**	**78.6**
2.Valdice (Czech Republic)						
Tree 1.	541	85.1	8.2 (0)	0.6	6.0	14.9
Tree 2.	116	61.7	37.5 (0)	-	-	38.3
Tree 3.	65	89.7	4.1 (49.0)	-	6.1	10.2
Tree 4.	5	-	-	-	-	-
Tree 5.	22	28.6	71.4 (28.0)	-	-	71.4
Total	**749**	**77.1**	**18.6 (9.1)**	**0.25**	**3.8**	**22.9**
3. Zalaegerszeg (Hungary)						
Tree 1.	207	20.3	21.6 (39.3)	8.8	40.7	79.7
Tree 2.	102	46.7	14.4 (4.2)	10.4	22.0	53.3
Tree 3.	285	33.1	21.6 (32.4)	17.9	17.9	66.8
Tree 4.	266	23.5	35.7 (19.3)	4.3	25.8	76.5
Tree 5.	632	36.7	34.4 (26.4)	7.5	13.1	63.3
Total	**1492**	**31.9**	**25.8 (25.6)**	**9.9**	**23.5**	**68.0**

5.3.1.3. Sex ratios of emerging parasitoids.

The sex ratio of emerging *A. quercuscalicis* was indistinguishable from 50% (49.5% male, a mean over 198 sample sex ratios).

The data obtained in this study support the observation by Hails (1988, 1989) that the sex ratios of all three *Mesopolobus* species emerging from sexual *A. quercuscalicis* were heavily male biased. All emerging *M. tibialis* and *M. xanthocerus* were males, and 90.4% (n=87 individual sample sex ratios; mean of percentages from each sample, rather than ratio over all emerged insects) of emerging *M. fuscipes* were male. The other two pteromalids had less markedly biased sex ratios, with 80.5% (n=6) male for *C. adana* and 61.8% (n=39) male for *O. vernalis*.

In contrast to the pteromalids, the eulophid parasitoids all showed slightly female biased sex ratios of 40.6% (n=172) males in *Aulogymnus kelebiana*, 40.2% (n=18) males in *Aprostocetus aethiops* and 38.9% (n=9) males in *A. cerricola*.

5.3.2. Variation in mortality between trees within sites and between sites (Tausendblum, Valdice and Zalaegerszeg).

Nested analysis of deviance showed that for almost all of the parasitoid species a high proportion of the variation in parasitoid attack rate was due to differences between trees within sites and differences between sites (Table 5.4). This was true whichever measure of host density was used. For *A. kelebiana*, *M. fuscipes*, *M. xanthocerus* and *O. vernalis*, spatial variation explained between 44 and 56% of the deviance in attack rates. The only clear exceptions were *A. cerricola* and *M. tibialis*, where there was no significant differences between sites, and significant differences between trees within sites was for total viable galls alone (30% of deviance explained).

Table 5.4: F- and p values for analyses of differences in attack rates between sites and between trees (nested within sites). Included in the analyses were samples from Tausendblum, Valdice and Zalaegerszeg. Results are given for both measures of host density (see text)

y variable	$F_{(2,12)}$ Between sites		$F_{(12,30)}$ Between trees within sites	
	Total galls	Total viable galls	Total galls	Total viable galls
A. kelebiana	4.7*	56.1***	12.0***	30.9***
Diapausing larval *A. kelebiana*	0.9 n.s.	1.1 n.s.	66.4***	24.9***
A. cerricola	4.16*	3.7 n.s.	1.0 n.s.	0.9 n.s.
A. viridinitens + *A. aethiops*	1.7 n.s.	1.7 n.s.	3.2**	3.8**
M. fuscipes	4.3*	3.9*	11.7**	16.0***
M. xanthocerus	7.9**	8.2**	8.1***	6.65***
M. tibialis	2.4 n.s.	2.3 n.s.	1.2 n.s.	2.2*
O. vernalis	24.5***	22.2***	3.6**	4.2***
C. adana	11.7**	12.5**	5.8***	7.0***
Total parasitoids	9.9**	16.1***	6.5***	7.5**
Non-emergence	0.47 n.s.		3.2**	
Total mortality	13.08***		5.1***	

n.s. = non-significant, * = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$

Differences between sites and between trees within sites were also highly significant for total rates of parasitism (67% of the deviance explained for total viable galls and 52% for total galls) and total mortality (58.5% deviance explained for total galls). Non-emergence mortality showed significant differences between trees, but not between sites. The effects of these factors are controlled for in the following analyses of density dependence by the nested design.

5.3.3. Analyses of density dependence within trees within sites

Analysis of relationships between the attack rates of the parasitoids and host density were carried out for the three parasitoid species which were most abundant in the sexual galls of *A. quercuscalicis, Aulogymnus kelebiana, Mesopolobus xanthocerus* and *M. fuscipes*. All models were nested within trees within sites using total galls and total viable galls as the binomial denominator of the logistic regression.

5.3.3.1. *Mesopolobus fuscipes*

Mesopolobus fuscipes was chosen as an example because significant relationships were detected in both models for total galls and total viable galls. The significant explanatory variables ($p < 0.05$) and the signs of the partial correlations for the minimal adequate models are shown in Table 5.5. *M. fuscipes* was found in galls from all five trees in Tausendblum and in Zalaegerszeg but only in galls from tree1 in Valdice, where the attack rate was also the lowest and no significant relationships could be detected (Table 5.3 and Table 5.5).

Although the number of significant terms in both minimal adequate models is almost the same (9 for Model1, total galls, and 8 for Model2, total viable galls), Model1 includes more product-terms while Model2, has more significant quadratic terms (Table 5.5). Further, slightly fewer than half of the significant partial correlations in Model1 were positive (44 significant partial correlations 18 of which were positive) while 24 of the 35 significant terms in Model2 were positive. Particularly in those terms representing host density (total galls and total viable galls) Model1 had five negative and 3 positive relationships, while all 3 significant partial correlations with the attack rates of *M. fuscipes* in Model2 were positive (Table 5.5).

Considering the relationships within individual trees both models also differ dramatically in the results for at least two trees. Tree1 in Tausendblum shows six significant partial correlations in Model1 but none in Model2 while, in contrast, tree3 in Zalaegerszeg had only three significant relationship in Model1 but seven in Model2. There doesn't seem to be any easy explanation since both trees were rather intermediate in terms of galling rate (Table 5.2) and attack rates (Table 5.3) within their sites.

Table 5.5: Density dependencies in attack rates by *Mesopolobus fuscipes*, showing the signs of the partial correlations from the minimum adequate model (GLIM with binomial errors; nested within trees within sites). The columns identify the trees within the sites (sites: 1= Tausendblum, 2 = Valdice, 3 = Zalaegerszeg). All parameters shown are significant ($p < 0.05$).

			Sites														
			1					2					3				
			Trees														
	χ^2	d.f.	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Model1 (total galls)																	
Total galls	38.5	5	-	+	-				-					+	+	-	-
Total galls^2	22.6	5		+	-									-	+		
Catkins	47.3	4		-											-		+
Catkins^2	42.0	4	-	+			-							-			
Shoots	27.9	4	-		+												+
Twigs	136.7	5		-			-						+	+			+
Galls*Catkins	56.4	6	+	-	-		+						+	+		+	
Galls*Shoots	42.7	5	-	+			-							+			+
Catkins*Shoots	55.2	6	+		-								-	-			-
Model2 (total viable galls)																	
Total viable galls	19.6	3		+										+	+		
Total viable galls^2	37.3	5		-			+						+	-	+		
Catkins	59.8	4		-										+	-		+
Catkins^2	68.3	5		+		+								-	+		-
Shoots	36.6	5		+		+	-							+			-
Shoots^2	51.2	5			+	-	+								+		+
Twigs	25.0	3			+										+		+
Catkins*Twigs	47.8	5		-	-								+		+		+

Both models involve various combinations of significant structural terms (i.e. catkins, shoots and twigs) as explanatory variables. While both models include different terms and the signs of the partial correlations are not consistent across the trees, these significant terms indicate that the structural complexity within a part of a branch of 20cm length mediates the relationships between host density and parasitoid attack rate. Since each of the structural variables also occurs in either its squared form or a product-term with another variable these relationships never seem to be linear.

5.3.3.2. *Aulogymnus kelebiana*

The equivalent minimal adequate model for the *A. kelebiana* is shown in Table 5.6. None of the variables tested proved significant in the model with total viable galls for *Aulogymnus kelebiana*.

A. kelebiana was the most abundant parasitoid species in all three sites and the model with total galls was the most complex one. All the variables tested here, their squared terms and the product terms between them explained a significant proportion of the variation in the attack rate of this species.

Table 5.6: Density dependencies in attack rates by *Aulogymnus kelebiana* and *Mesopolobus xanthocerus* showing the signs of the relationships from the minimum adequate model (GLIM with binomial errors; nested within trees within sites). The columns identify the trees within the sites (site: 1= Tausendblum, 2 = Valdice, 3 = Zalaegerszeg). All parameters shown are significant ($p < 0.05$).

			Sites														
			1					2					3				
			Trees														
	χ^2	d.f.	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Aulogymnus kelebiana (total galls)																	
Total galls	111.3	9	+	-	+	+	-		+	+			+		+		
Total galls^2	126.4	6		-		+		-	+						-		-
Catkins	129.7	8	+	+				+					-		+		
Catkins^2	111.3	8		-	+	+									-	-	-
Shoots	108.5	5	+		-	+		-	-						-	-	+
Shoots^2	127.0	8	-		+	-							-	+	-	-	-
Twigs	151.0	6	-	-		-	-	-									-
Twigs^2	73.8	5	-	-		-									+	-	
Galls*Catkins	94.5	7	-	+		-	+	+					-		-		
Galls*Shoots	42.2	2		-		+											
Galls*Twigs	152.5	6		+		-			-					-	-		+
Catkins*shoots	109.0	8	-	-		-	-						+		+	+	+
Catkins*Twigs	44.1	3	+					-	+								
Shoots*Twigs	145.5	5	+	+		+		+								+	
Mesopolobus xanthocerus (total galls)																	
Total galls	61.8	6		+		+	-			+				+			-
Total galls^2	23.6	2				+							-				
Catkins^2	82.2	7	-	+		+		-					-	+			-
Shoots	64.5	3				+		+					+			+	
Shoots^2	97.0	5	+			+							+		+	+	
Twigs	43.2	2													+	-	
Galls*Catkins	59.9	5		-		-		+						-			+
Catkins*Twigs	58.4	4	+			-								+		+	
Shoots*Twigs	94.3	6	-					-						-	-	+	+
Mesopolobus xanthocerus (total viable galls)																	
Total viable galls	60.3	3	-	+												+	
Total viable galls^2	67.3	4	+											+		-	+
Shoots	33.3	3	+			+							+				
Shoots^2	59.3	5	-			-							-	-			+

Within sites, trees with low galling rates tended to have fewer significant relationships, although this is only clear for trees with the lowest gall densities. Tree3 and tree5 at Tausendblum had the lowest galling rates at this site and had only 4 significant terms compared with 11 on tree1 and tree2 and 12 on tree4 at the same site. Valdice was the site with the lowest galling rates and all 5 trees had relatively few significant parameters while tree4 and tree5 (0.02 and 0.09 galls per catkin) had none at all (Table 5.6). Interestingly, tree2 at Tausendblum which had an exceptional high gall density (6.91 galls per catkin; Table 5.2) was not the tree which had the most significant relationships nor was the pattern distinctly different from those of trees with medium gall densities.

While there was a bias towards positive density dependent attack rates (significant in 7 trees), there were two trees for which the partial correlation of host density were negative. Both trees were at Tausendblum and had the highest (tree2) and the lowest (tree5) galling rate at that site.

For only one explanatory variable, the number of twigs, all significant terms was negative. Generally the response to any one of the explanatory variables was extremely complex, since the functional response was often curvilinear and, more important, they all interacted with each other. All structural variables included in the minimal adequate were also present as quadratic terms and in product terms which often showed opposing signs for their partial correlations. The response to any one of them is extremely complex and difficult to visualise in a conventional, two dimensional plot of percent parasitism against host-density.

5.3.3.3. *Mesopolobus xanthocerus*

With total galls as the measure of host density the minimal adequate model for *M. xanthocerus* was relatively complex including host-density and host-density squared, two structural variables and their squared terms as well as three product terms. Using total viable galls as the host density measure, the minimal adequate model was much simpler including only host density, the number of shoots and the squared terms of both variables (Table 5.6).

M. xanthocerus was most abundant in Zalaegerszeg where this species reached 40% parasitism rate on an individual tree (23.5% averaged over all 5 trees; Table 5.3) in Tausendblum and Valdice attack rates were considerably lower (1.7% and 3.8% mean attack rate respectively). The differences in attack rates are reflected in the number of significant relationships detected at each site (Table 5.6). In contrast to the models for *M. fuscipes*, however, both models for *M. xanthocerus* showed a bias towards positive density dependencies (4 positive and 3 negative relationships for total galls, and 4 positive and 1 negative relationships for total viable galls; Table 5.5 and Table 5.6).

5.3.3.4. Total parasitoid-induced mortality.

To model the total mortality of *A. quercuscalicis* caused by parasitism the attacks of all parasitoid species were added together. Mortality which was not attributable to any of the recorded parasitoid species was excluded.

In both models, using total galls and total viable galls as host-density measures, none of the variables tested proved significant, which suggests that the relationships found for the individual species might compensate each other.

5.4. Discussion

Ten parasitoid species were recorded from sexual galls of *A. quercuscalicis* collected in the native and invaded range in continental Europe. Patterns of density dependent attack rates, which were analysed for the 3 most abundant parasitoid species, *Aulogymnus kelebiana*, *Mesopolobus fuscipes* and *M. xanthocerus*, were shown to be highly variable on three different spatial scales. These results are in line with those obtained for parasitism in the sexual galls of *A. quercuscalicis* in Britain, where they were studied for a much longer period of time (1982-1993; Hails 1988, Hails and Crawley 1991, 1992, Walker and Crawley unpublished results). This study also confirms the observation that virtually all individuals of the *Mesopolobus* species were male and thus refutes the assertion that this biased sex-ratio reported for Britain might be an 'invasion effect' (Hails 1989).

5.4.1. Parasitoid sex-ratios

Based on a model of sex allocation in parasitic wasps by Charnov *et al.* (1981) Hails (1989) tested the two predictions for the parasitoid species, *Mesopolobus fuscipes, M. xanthocerus* and *M. tibialis*, which attack the sexual galls of *A. quercuscalicis* : 1) the sex ratio of the progeny should vary as a functions of host size, and 2) the response of the parasitic wasp to a particular host size will depend upon the other sizes available. Since *A. quercuscalicis* is one the smallest galls, if not the smallest gall, in the host range of the three *Mesopolobus* species, it was expected that the sex ratio of the offspring should be male biased. Virtually all offspring reared of the three parasitoid species were male supporting Charnov's theory (Hails 1989). There was, however, no evidence to support the second prediction, that the parasitoid female would be flexible in its response.

One of the criticisms of this test concerned the fact that the host, *A. quercuscalicis*, was only present in Britain for a relatively short period of time. It could be that the male-biased sex ratio did not reflect the choice in sex allocation by the ovipositing female but rather a lack of adaptation of the parasitoid to the novel (inferior) host in spite of its size (Hails 1989, Godfray 1994). However, since the same male biased sex ratios for *Mesopolobus fuscipes, M. xanthocerus*

and *M. tibialis* from sexual galls of *A. quercuscalicis* were found in the native range this possibility can be disregarded.

Two more parasitoid species, *Cecidostiba adana* and *Ormocerus vernalis*, were also found to produce more male than female offspring. Both species have approximately the same size as the three *Mesopolobus* species, while the sex ratios for the smaller, eulophid parasitoid species, *Aulogymnus kelebiana, Aprostocetus aethiops* or *A. cerricola*, were slightly female biased. A sex allocation rule of thumb related to the body size of the parasitoid female would result in a fixed response in contrast to the second prediction from Charnov *et al.* (1981).

5.4.2. Mortality by parasitism in the sexual galls of *A. quercuscalicis*

The total mortality due to parasitoids in Britain in studies by Hails (1988) and Hails and Crawley (1991) varied between 20 and 31%. There were significant differences between trees in the density of galls, the total parasitoid-induced mortality, and the order of importance of particular parasitoids. The total mortality due to parasitoids in continental Europe in the 1000 catkin rearings showed low mortality in Germany, and a uniformly greater mortality, with a mean of 24%, over the 8 Hungarian sites. Because it was not possible to dissect the galls in these rearings, and appreciable mortality is known to be attributable to diapausing *Aulogymnus kelebiana*, these are almost certainly substantial underestimates. The 3000 catkin rearings show that at the two sites with high galling density, total mortality due to parasitoids may reach very high levels (a mean of 78.6% at Tausendblum, and 68.0% at Zalaegerszeg).

Total mortality, mortality attributable to parasitoids and the contributions of other mortality factors differed significantly between trees within sites and between sites, in line with the high levels of spatial heterogeneity detected in British populations (Hails & Crawley 1992).

Mortalities due to *Aulogymnus kelebiana, Mesopolobus fuscipes* and *M. xanthocerus* all showed significant host density-dependence, but for all three parasitoids significant within-tree patterns included both positive and negative density dependence. Furthermore, there was no significant relationship between the sign of a correlation and mean host density for the tree; positive density dependence for a given parasitoid occured in trees of both high and low host densities.

5.4.3. Density dependent parasitoid attacks.

Density dependent relationships between parasitoid attack rates and host density have received a great deal of attention as one of the mechanisms to stabilise host populations. Originally it was suggested from work in population theory as

well as in optimal foraging, that positive density dependence should be common in host-parasitoid systems in which host populations are regulated by their parasitoids (Hassell and May 1973, Hassell 1980, Charnov 1976, Cook and Hubbard 1976). Later it was implied that the stability criteria in host-parasitoid models depended more on a negative density dependence between parasitoid abundance and attack rates on hosts (Walde and Murdoch 1988). Recent studies have indicated that negative density dependence between host density and parasitism rates as well as spatial heterogeneity in host mortality, which might be density independent, can also contribute to the regulation of host populations (Hassell 1985, Walde and Murdoch 1988, Hassell and Pacala 1990).

The importance of scale was first emphasised by Heads and Lawton (1983). Particularly in host-parasitoid systems in which the hosts are stationary, such as galls or leaf-miners, patterns of density dependent parasitoid attack rates result exclusively from the foraging behaviour and oviposition decisions of the ovipositing female. Therefore, density dependence should be analysed at the functional scale, i.e. the scale on which the parasitoid female can experience the host density (Hassell 1987). Since it usually not known what the functional scale of a parasitoid is, the next best way to approximate that scale is hierarchical sampling as was carried out here.

The significance of the structural variables, twigs, shoots and catkins, indicates that the foraging pattern of an ovipositing female might be affected by the structural complexity of a branch. If one considers male flower-buds which hold the catkins with galls as the patches between which a parasitoid female moves, then a more bushy structure might allow the female to from one patch to the next more quickly than when the buds are more spaced out as in a linear structure. The time a female needs to get from one patch to the next is only one possible way in which the parasitoid female might evaluate its environment. That the parasitoids of the sexual galls of *A. quercuscalicis* might do this on the smallest scale seems likely since *Mesopolobus* females as well as many other parasitoids of cynipid-galls are known to move around the canopy of a tree by walking and jumping rather than by flying longer distances (Askew 1961b, Sellenschlo and Wall 1984). The effect of environmental heterogeneity in the form of structural differences between samples on the statistical models presented here suggests that although the host-density measured in the sample might have been similar, the perception by the ovipositing female might be different, and the complex response to the structural variables shown in all the minimal adequate models suggests that the way they affect an ovipositing female might be far from simple.

The results presented here were in agreement with findings by Hails (1988) for *M. fuscipes, M. tibialis* and *M. xanthocerus*. Apart from the variation in the strength and sign of density dependence of the parasitism rates between sites and between trees within sites, it was also found density dependence for a particular species at a given site to vary between years (Hails 1988). Hails and Crawley (1992) concluded that any species may show almost any pattern, with no overall relationship between death rates and host density.

In the case of *A. quercuscalicis*, however, it is not clear whether parasitoid attack is an important factor which affects the population dynamics of this species. In Britain it was shown that population regulation was probably due to the limitation in oviposition sites for the sexual females during the 'low years' of the acorn cycle (Hails and Crawley 1991, Crawley and Long 1995). Although parasitism rates on Turkey oak in the native range were shown to reach much higher levels than in Britain it would be necessary to evaluate the importance of parasitism for the overall dynamics of this gall-wasp. For a species, such as *A. quercuscalicis*, with two generations which suffer different mortality by parasitism and differing degrees of resource limitation the long term regulation of population needs urgently to be considered by the development of appropriate theoretical models. Hails and Crawley (1991) made a start, by pointing out the unknown mortality suffered during the two annual migrations from one host to the other, but the extent of the spatial heterogeneity in parasitoid-induced mortality is simply too great to ignore. Not only do trees differ consistently in their rates of galling and mean rates of parasitoid attack, but a tree which shows positive density dependence in one year can show negative density dependence the next (Hails and Crawley 1992, P. Walker personal communication). The development of theoretical models incorporating realistic levels of heterogeneity in parasitism presents an exciting challenge for theoretical population ecology.

6. The distribution and abundance of alien, host-alternating *Andricus* spp. (Hymenoptera: Cynipidae) on oak in Ireland.

6.1. Introduction

The history of the invasion of Ireland by the alien, host alternating cynipids is not well documented. The first records of *Andricus kollari* (1983 in O'Connor *et al.* 1990), *A. lignicola* (O'Connor and O'Connor 1993a), *A. quercuscalicis* (1986; C. Nelson, personal communication) and *A. corruptrix* (O'Connor and O'Connor 1993b) are all relatively recent, but it is not clear how precisely these records date the establishment of the species. The collection of Irish distributional data on gall-forming cynipids has been undertaken only since 1989 (J.P. O'Connor, personal communication).

The four alien insects all have obligate, annual host-alternation, involving an agamic gall on native *Quercus* spp. (*Q. robur*, *Q. x rosacea* and/or *Q. petraea*) and a sexual generation on the alien Turkey oak (*Q. cerris*). All the cynipids are bud gallers in the agamic generation with the exception of *A. quercuscalicis* whose knopper galls destroy the acorns of *Q. robur* and *Q. x rosacea*. Likewise, the sexual generations form tiny galls in the winter buds of *Q. cerris*, with the exception of *A. quercuscalicis* which forms galls on the male flowers of Turkey oak. The invasion of Britain, particularly by *A. quercuscalicis*, has been studied for 15 years (Collins *et al.* 1983; Hails and Crawley 1992; Crawley and Long 1995), and study of the invaders in Ireland provides an opportunity to assess the generality of the patterns observed in Britain.

We are interested in the following questions: how far have the 4 alien cynipids spread within Ireland; to what extent is their spread linked to the local abundance of Turkey oaks; and how is their spread influenced by the native cynipid community? We want to understand the pattern of dispersal of the two generations of each gall wasp, their dependence on the distribution of host plants (especially the alien Turkey oak), and the extent to which the species compete with one another for resources in each generation. We leave the question of apparent competition with native cynipid species through shared natural enemies (Holt 1977, Holt and Lawton 1993) to a later paper. There are no parasitoid records in the present paper.

6.2. Methods

The field work was carried out between 29 August and 10 September 1993. A transect of roughly figure-eight shape was driven clockwise, starting and ending in Dublin. An average of 10 sites per day was assessed by 3 collectors. At each site the size and abundance of 4 oaks (*Q. robur*, *Q. petraea*, *Q. x rosacea* and *Q. cerris*) were noted. It can be difficult to distinguish hybrid oaks in Ireland, so we

employed a pragmatic definition; a tree was recorded as the hybrid *Q. x rosacea* if it differed from *Q. robur* or *Q. petraea* in two or more of the attributes listed in Table 6.1.

Table 6.1. The characters used to determine the identity of *Q. x rosacea*. Any plant failing two or more of the characters that would assign it to good *Q. robur* or *Q. petraea* was recorded as *Q. x rosacea*. The system is easily learned and is consistent across different investigators. Knopper galls of *A. quercuscalicis* are found commonly on *Q. robur* and *Q. x rosacea* but almost never on *Q. petraea*. Other gall-formers appear to be indiscriminate across species (e.g. *A. kollari*), but highly discriminating between individual trees within species.

Character	*Q. robur*	*Q. x rosacea*	*Q. petraea*
Peduncle length	long (>2 cm)	medium - long (1 - 9 cm)	short (<2 cm)
Peduncle width	thin	thick	thick
Peduncle hairy?	no	sometimes	yes
Leaf base (shape)	cordate	very variable (2 sides of same leaf may differ)	cuneate
Leaf hairs (underside)	none	present, on leaf veins below simple, sometimes stellate	stellate hairs
Leaf shape	3-6 lobes large, deep, irregular	intermediate and variable	5-8 lobes small, shallow, regular
Upper vein of leaf	narrow, greenish yellow	intermediate	broad, yellow
Petiole length	short (0-7 mm)	variable (2-40 mm)	long (13-25 mm)

The buds, foliage, acorns, bark and roots of each tree were searched and all cynipid gall species were noted for each kind of oak. For agamic *A. quercuscalicis* the number of knopper galls per acorn cup was counted for 100 acorn cups, and the number of acorn cups on 100 shoots was assessed (using binoculars for smaller trees and telescope for larger trees). With heavy infestations, up to 8 knopper galls can be found on one acorn cup, so the average number of knopper galls per shoot can be greater than the number of acorns per shoot. These data allow an estimate of the percent acorn cups galled (a rough assessment of the mortality suffered by acorns, since few galled acorns are capable of producing a viable seedling; Crawley, unpublished results), and of knopper gall density (acorn cups per shoot x galls per acorn cup). A heavy acorn crop is defined as an average of more than 0.5

acorns per shoot (the maximum value on a single shoot might be 6 acorns for *Q. robur* and 12 for *Q. petraea*).

In the statistical analysis, the presence of each cynipid species, the presence of each oak species, distance from nearest Turkey oak, and the geographic location (eastings and northings) were used as explanatory variables in a logistic regression of presence/absence for each invading species. Model simplification involved deletion of each explanatory variable in turn from the maximal model; significant terms were retained in the minimal adequate model for each gall wasp (Crawley 1993). In the first analysis of cynipid species richness we used a log linear model (Poisson errors) with easterliness, northerliness and oak species richness as explanatory variables. In the second analysis, oak species richness was replaced by a category variable for the presence/absence of each of the 4 kinds of oak (*Q. robur*, *Q. x rosacea*, *Q. petraea* and *Q. cerris*).

Two kinds of oak habitat were sampled: 1) parks, gardens and arboreta where Turkey oaks were likely to be planted; and 2) roadside, hedgerow and woodland oaks well away from gardens. The rationale was to obtain sites at a range of distances from Turkey oak in the hope assessing the relative dispersal ability of the 4 cynipid species. The positions of all Turkey oaks seen outside gardens were noted; distance in km from a sampling site to 'the nearest Turkey oak observed' was used as a category variable in the modelling: Turkey oaks within the same site were scored as level 1; Turkey oak seen outside the location but within 20 km of the site were level 2; and Turkey oak not seen within 20 km were level 3 of the factor. We have found from work in Britain that at a more local scale (e.g. 10's of metres), *Q. robur* phenology and genetic susceptibility appear to be more important determinants of knopper galling than proximity of *Q. cerris* (Hails and Crawley 1991).

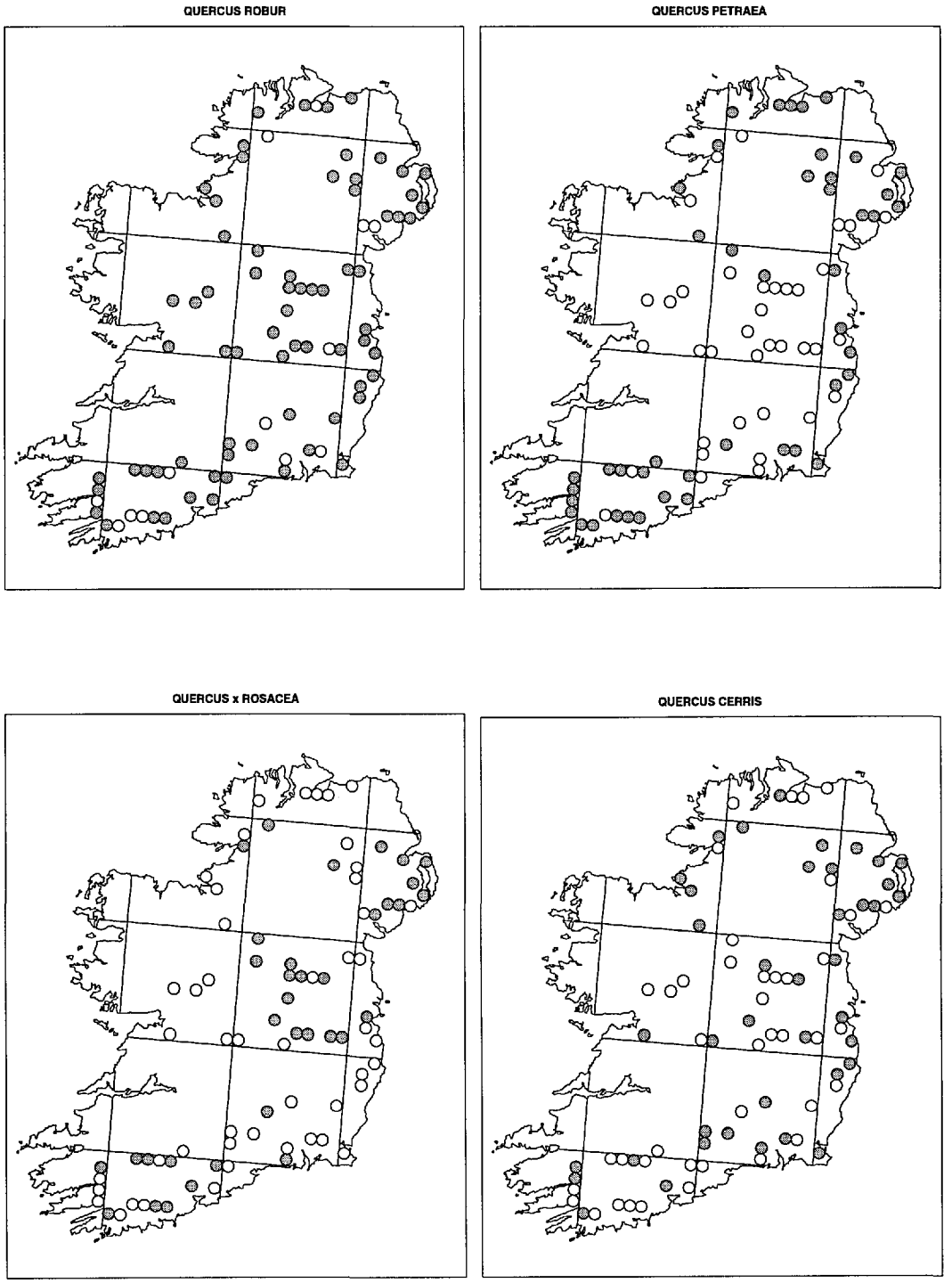
6.3. Results

6.3.1. Oaks

Ireland is essentially an oak-free country. All but tiny fragments of the primeval oak forest have long since been felled, and few commercial hardwood forests have been planted to replace them. The common hedgerow and wayside trees of Ireland are ash and sycamore, and even scattered oaks are absent from large areas of the north and centre of the island (in our driven transect, the longest length of oak-free roadside was 75 km between Coleraine and Lough Neagh in County Antrim). That all 4 oaks can grow extremely well in Ireland is witnessed by the many fine oak park lands surrounding large country houses and the splendid growth of oaks in arboreta. The trend of oak depopulation appears to have been reversed in recent years, and many estates have extensive plantings of young (< 10 years) *Q. robur*.

The distributions of the four oaks along our sampling transect are shown in Fig. 6.1. These maps highlight the difficulty of predicting abundance from distributional data; *Q. robur* is virtually ubiquitous, yet oaks are extremely rare (<1 per km of roadside) over large areas of the north and centre of the country. *Q. petraea* forms native forest in the south-west, and is planted in the majority of estates in the east (although less abundantly than *Q. robur* or *Q. x rosacea*), but it is rare in central Ireland. *Q. x rosacea* gives the appearance of always having been planted (none of the natural regeneration we saw was of the hybrid), and has a broadly eastern and southern distribution. This is consistent with its having been planted since the large park land estates also have an eastern and southern distribution. Turkey oak *Q. cerris* turned out to be more widely distributed than we anticipated (Fig 6.1d) and while it was most common in the large estates of the east and south, it was seen in all but 1 of the 13 100-km squares in which we sampled.

Figure 6.1: Distribution of the host tree species, a) *Quercus robur*, b) *Q. petraea*, c) *Q. x rosacea* and the introduced d) *Q. cerris*.



Shaded symbols = present; open circles = not found.

6.3.2. Cynipids

6.3.2.1. Distribution

The distributions of the 4 alien host-alternating cynipids are shown in Fig. 6.2 and the records of the 12 native species are shown for each county in Table 6.2.

Abundance

The abundance of all the cynipids was highly variable from site to site, from tree to tree within sites and from shoot to shoot within trees (Crawley and Akhteruzzaman 1987, Hails and Crawley 1992). Because of this, interpretation of variation in average gall density needs to be made with caution.

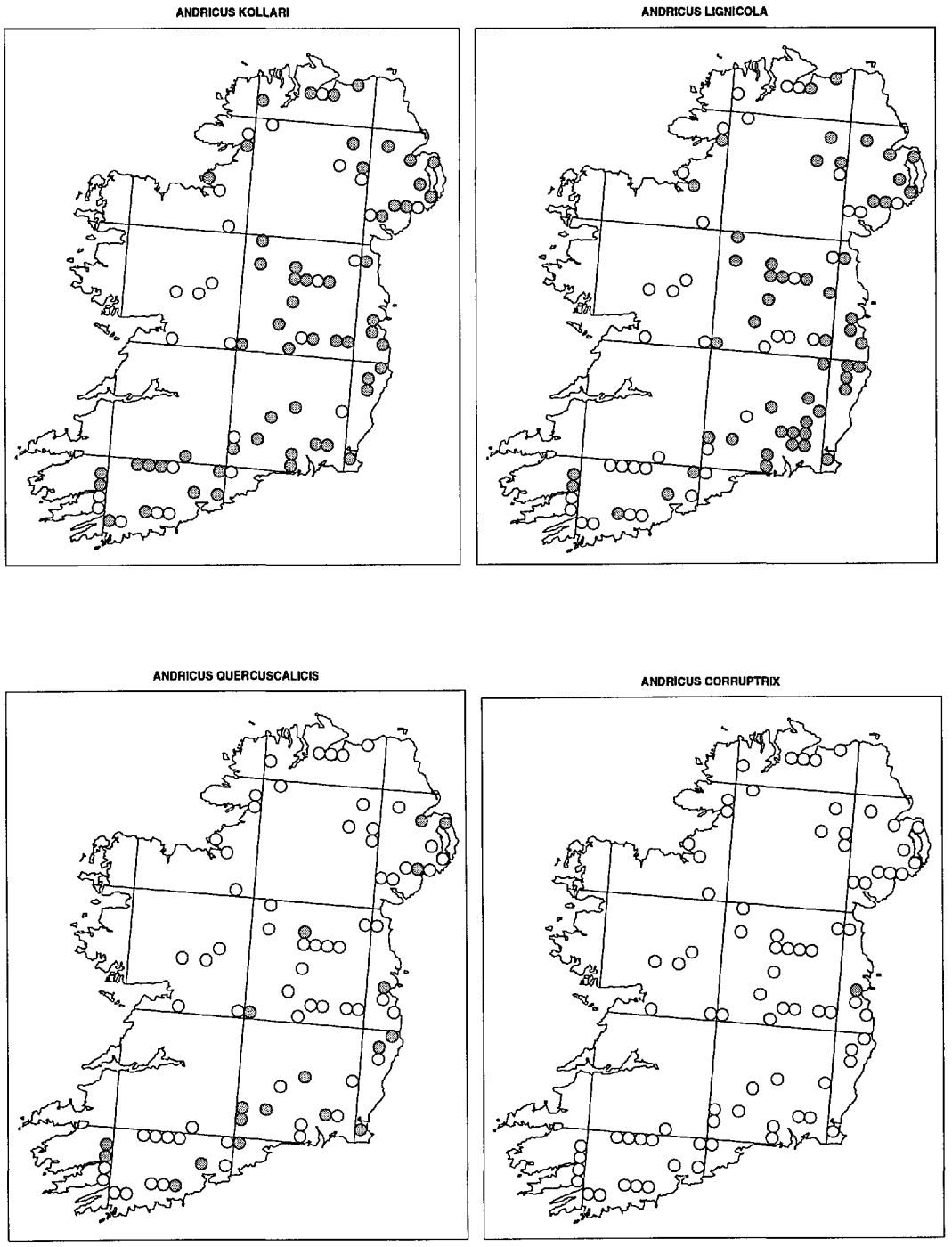
Even the most widespread species *N. quercusbaccarum* showed substantial site-to-site variation in abundance: in some cases only one or two leaves on a mature tree were infested, while in other cases, the galls were so crowded onto individual leaves that they overlapped one another. Thus, the apparently uniform distribution of *N. quercusbaccarum* (Table 6.2) masks considerable variation, and this variation is largely inexplicable in terms of the variables we have measured in this short-term study (e.g. genetically-based differences in susceptibility to galling between individual oaks might be an important factor; Crawley and Akhteruzzaman 1987)

Table 6.2: Distribution of the native Cynipid galls in Ireland.

	C. q-f.	C. long.	C. div.	N. q-b	N. num	N. alb.	A. fec.	A. anth.	A. curv.	A. infl.	A. alb.	A. sol.	A. q-r.	B. pall.
Dublin	-	l	-	c	p	-	l	c	c	-	-	-	-	p
Wicklow	p	p	c	c	c	p	c	c	c	-	-	-	-	-
Wexford	p	p	l	c	l	l	c	c	l	l	-	-	-	-
Waterford	-	-	p	c	l	p	l	-	-	-	-	-	-	-
Tipperary	-	-	p	c	p	-	l	l	-	-	-	-	-	-
Cork	l	p	c	c	l	p	c	c	-	-	-	-	-	-
Kerry	p	-	c	c	-	-	c	l	p	-	-	-	-	-
Kilkeny*	-	-	p	p	p	p	-	p	p	-	-	-	-	-
Laois*	-	-	-	p	p	-	-	-	-	-	-	-	-	-
Offaly	-	-	c	c	c	-	c	c	c	p	-	-	p	p
Galway	-	p	c	l	l	-	l	c	l	-	-	-	-	-
Longford*	-	p	p	p	-	-	-	p	p	-	-	-	-	-
Roscommon*	-	p	p	p	p	-	-	-	p	-	-	-	-	-
Sligo	p	-	-	p	p	-	p	p	c	-	-	-	-	-
Leitrim*	p	p	p	p	p	-	-	p	p	-	-	-	-	-
Donegal	p	-	l	c	l	-	c	c	p	-	p	-	-	-
Londonderry	p	p	l	c	l	-	l	c	l	-	-	p	-	-
Antrim	-	-	c	c	c	p	c	c	c	-	-	-	-	p
Tyrone*	-	p	p	p	-	-	p	p	-	-	-	-	-	-
Armagh	-	-	p	c	c	-		p	c	-	-	-	-	-
Down	p	-	p	c	l	-	l	c	l	-	-	-	-	p
Meath	-	-	p	c	c	-	-	p	c	-	-	-	p§	-
Westmeath	-	-	c	c	l	p	-	c	l	-	-	-	-	p
Louth*	-	-	-	p	p	p	-	p	-	-	-	-	-	-
Kildare	-	-	p	c	p	l	-	l	c	p	-	-	-	-

p = present, l = local; c = common. In counties marked with * only one site was surveyed. Records marked with § after O'Connor and O'Connor (1993). Counties which were not visited: Carlow, Limerick, Clare, Mayo, Fermanagh, Monaghan, Cavan. Abbreviations for the species: C. q-f = *Cynips quercusfolii*; C. long = *C. longiventris*; C. div. = *C. divisa*; N. q-b. = *Neuroterus quercusbaccarum*; N. num. = *N. numismalis*; N. alb. = *N. albipes*; A. fec. = *Andricus fecundator*; A. anth. = *A. anthracinus*; A. curv = *A. curvator*; A. infl. = *A. inflator*; A. alb. = *A. albopunctatus*; A. sol. = *A. solitarius*; A. q-r. = *A. quercusramuli*; B. pall. = *Biorhiza pallida*.

Figure 6.2: Distribution of the four alien Cynipid species in Ireland: a) *Andricus kollari*, b) *A. lignicola*, c) *A. quercuscalicis* and d) *A. corruptrix*.



Shaded symbols = present; open circles = not found.

6.3.2.1.1. Andricus kollari

Marble galls are virtually ubiquitous where ever oak occurs in Ireland, and were found at sites where no Turkey oak was seen in the vicinity. We did not find marble galls in the central west (Fig 6.2a) but this is an area where all kinds of oaks are uncommon. The abundance of different year-classes was highly variable, and the 1992 marble galls were much more abundant than the 1993 cohort at most of the sites we visited. Marble galls tend to be present at higher densities (galls per shoot) on young plants and on epicormic sprouts and regrowth shoots on older trees. Emergence times also vary from site to site (agamics had emerged by early September 1993 at some of the sites), and work in Britain (P. Walker, unpublished results) shows that emergence time is also highly variable and year to year.

Table 6.3. Statistical modelling for 4 different response variables: (a) presence/absence of *Andricus quercuscalicis*; (b) presence/absence of *A. kollari*; (c) presence/absence of *A. lignicola*; (d) abundance of *Andricus quercuscalicis*. Analysis based on logistic regression with a binary response variable. Explanatory variables were the presence/absence of all other cynipid species, the proximity of *Quercus cerris* (a 3-level factor; see text), northerliness (kilometres from 0,0), easterliness (kilometres from 0,0), the presence of *Quercus robur*, *Q. petraea* and *Q. x rosacea*. Modelling was by step-wise deletion from a maximal model containing all terms. Terms included in the Table all caused significant ($p < 0.05$) increases in deviance when deleted from the minimal adequate model. Parameter estimates (p.e.) and standard errors (s.e.) are in logits.

	(a) A. qc.		(b) A. k.		(c) A.l		(d) A qc. abundance	
Explanatory variable	p.e	s.e.	p.e.	s.e.	p.e.	s.e.	p.e.	s.e.
C. divisa	-	-	-2.11	0.73	1.83	0.65	-	-
N. numismalis	-	-	1.47	0.67	-	-	-	-
A. lignicola	-	-	3.11	0.78	-	-	-	-
A. curvator	-	-	1.90	0.74	-	-	-	-
A. kollari	-	-	-	-	2.35	0.68	-	-
A. quercuscalicis	-	-	-	-	1.56	0.83	-	-
Q. robur	-	-	-	-	1.78	0.97	-	-
Q. cerris distance	-4.16	1.27	-	-	-	-	-	-
easterliness	0.02	0.01	-	-	0.02	0.01	-	-
northerliness	-0.02	0.01	-0.01	0.00	-	-	-0.01	0.01

Analysis of the presence/absence of marble galls showed 5 significant explanatory variables (Table 6.3). *A. kollari* was more likely to be found at southern sites and in places where *N. numismalis* and *A. curvator* were also present. There was a strong positive association between the likelihood of finding *A. kollari* at a site and the presence of *A. lignicola* (another host-alternating alien). Marble galls were significantly *less* likely to be found at sites where *C. divisa* was present. This was the only significant negative association between species in the entire data set relating to the alien gall-formers.

6.3.2.1.2. Andricus lignicola

Cola-nut galls were widespread in Ireland and cover a somewhat greater fraction of the range of *A. kollari* than is the case in Britain (P. Walker unpublished results). They were absent from parts of the west, but otherwise were almost as widely distributed as *A. kollari* (Fig. 6.2b). As with the marble gall, their annual cohorts were highly variable in abundance, and 1992 galls were more common than 1993 galls at most of our sample sites. The galls were more numerous in the east and the south than elsewhere, but were found at considerable distances from the closest known Turkey oak. At a site within the range of both *A. kollari* and *A. lignicola* an oak was somewhat more likely to support *A. lignicola* (i.e. the within-range frequency of *A. lignicola* was higher than *A. kollari*).

A model for the presence/absence of *A. lignicola* contained 5 significant terms. There was a positive association with marble galls (see above), but *A. lignicola* was more likely to be found in the east, and at sites where *Q. robur* and *A. quercuscalicis* were present. Unlike *A. kollari*, the cola-nut galls showed a *positive* partial correlation with the presence of *C. divisa*.

6.3.2.1.3. Andricus quercuscalicis

Knopper galls show a strongly eastern and southern distribution and were rarely found outside large estates where mature Turkey oaks were established (Fig. 6.2c). They were absent from apparently suitable estates in many parks containing Turkey oaks in central and north-western Ireland. Knopper galls can attack extremely high proportions of the acorn crop on *Q. robur* and *Q. x rosacea*, but were never observed on the acorns of *Q. petraea*. This is consistent with our information from Britain and continental Europe, where knopper galls have been found on sessile oak only once in 15 years (on one tree from Gweek in Cornwall; M. Crawley unpublished results). Attack rates varied between 0 and 100% and acorn crop sizes varied between <0.001 and 0.5 acorns per shoot. As with the British data, there is a hint of inverse density dependence; the percentage galling tends to decline as acorn crop size increases (Hails and Crawley 1991 but see Crawley and Long 1995). Some trees with very low acorn crops can have all their

acorns galled by *A. quercuscalicis*, and very high loads of galls per acorn cup (up to 8 with a mean of more than 3) were observed in sites where the proportion of acorns galled exceeded 90% (as at Kilkenny Castle). *Q. robur* appears to be the most important host for agamic *A. quercuscalicis* in Ireland, but we know from work in Silwood Park that some *Q. robur* are completely immune to attack. It is clear from the present study in Ireland that acorns of certain *Q. x rosacea* are highly susceptible to attack by knopper galls.

The model for presence/absence of knopper galls contains a significant term for proximity to Turkey oak (knopper galls were less likely to be found if there was no Turkey oak at the sampling site itself). The analysis quantifies the impression from the map of *A. quercuscalicis* distribution (Fig. 6.2c); knopper galls are significantly more likely to be found in the south and the east. A model for the abundance of knopper galls (acorn crop multiplied by proportion galled) contained only one significant term: knopper gall densities were higher in the south than the north. In the model, a term for proximity to Turkey oak showed a declining but non-significant trend in gall density with increasing distance from the nearest Turkey oak.

6.3.2.1.4. Andricus corruptrix

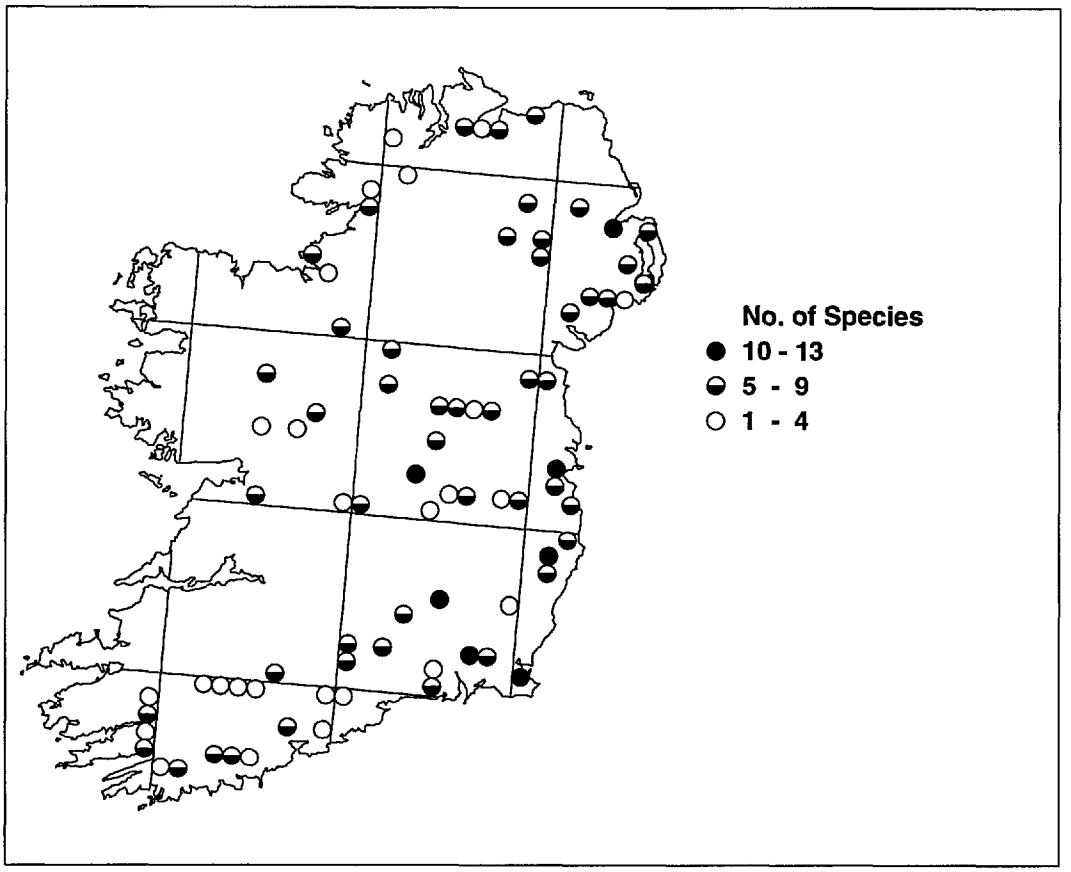
This gall is still extremely rare and local within Ireland. It was present in only 1 of our 95 sites (in Phoenix Park, Dublin) and was restricted here to young plants on which it may have been imported as nursery stock from Britain or Holland (the first Irish record (O'Connor *et al.* 1993b) was from Kerry in the south-west). The agamic gall is sufficiently small that it may have been under-recorded, but we can say with confidence that it has the most restricted distribution of the 4 alien cynipids. This is also the case in Britain, where the gall is restricted to south-eastern England (*A. quercuscalicis* reaches the Scottish border, *A. lignicola* reaches central Scotland and *A. kollari* reaches the north coast of Scotland; P. Walker personal communication).

6.3.3. Cynipid species richness

The total number of cynipid galls (native and alien) at each sampling site is shown in Fig. 6.3. Analysis of the species richness data (GLIM with Poisson errors) shows significant terms for easterliness (χ^2 = 5.01, df=1) and for oak species richness (χ^2 = 30.63, df=1): there are more gall species in the east than in the west of Ireland and more gall species at sites where there are more oak species present. Of the 4 oak species, it is *Q. robur* (χ^2= 9.40, df=1) and the alien *Q. cerris* (χ^2= 12.07, df=1) which contribute most to cynipid species richness. There is no evidence in our data to support the hypothesis that herbivorous insects are more

abundant or more species rich on hybrid host plants (i.e. on *Q. x rosacea* rather than *Q. robur* or *Q. petraea*).

Figure 6.3: Cynipid species richness (native and alien species together) at the surveyed locations.



6.4. Discussion

The four alien gall wasps are much more widespread in Ireland than was previously thought. It seems likely, therefore, that they have been present in Ireland for substantially longer than the first published records suggest.

6.4.1. Dispersal

The wide distributions of *A. kollari* and *A. lignicola* compared with *A. quercuscalicis* indicate that the dispersal ability of the sexual generation is relatively high in these species and relatively low for *A. quercuscalicis*. Indeed, the marble galls of *A. kollari* are sometimes found so far away from Turkey oaks that it was formerly believed that the sexual generation on Turkey oak could be skipped (i.e. there was no obligate host alternation). Results of experiments in which agamic *A. kollari* were bagged directly onto a range of *Q. robur* genotypes indicate, however, that this is not the case; only sexual *A. kollari* from galls on *Q. cerris* are capable of producing marble galls on *Q. robur* (see also Marsden-Jones 1953; Folliot 1964). We never found knopper galls at sites where we did not also find mature (i.e. flowering) Turkey oak.

The other factor promoting the wider distribution of *A. kollari* and *A. lignicola* could be their transport via commercial horticulture. Young oaks in nurseries often support agamic galls of both these cynipids, but *Q. robur* can not support *A. quercuscalicis* until the trees are sexually mature. Furthermore, it would only support the gall during a part of the year during which tree planting is unlikely, because the trees carry female flowers (and hence knopper galls) only between May and September. Similarly, the bud galls of *A. kollari* and *A. lignicola* can attack young nursery stock of Turkey oak and their tiny bud galls would not be noticed. In contrast, the sexual generation of *A. quercuscalicis* is only on the tree from March to May, and so could only be transported on mature, flowering Turkey oak in early spring. Of course, introduction on nursery stock does not guarantee establishment; this would require annual recruitment from a sexual generation on *Q. cerris*. Thus, although it is plausible that galls might be introduced on nursery stock, observation of agamic galls on older or non-planted *Q. robur* is evidence of dispersal from a sexual generation on *Q. cerris*.

6.4.2. Intraspecific and interspecific competition

The very high loads of knopper galls per acorn cup (up to 8 with a mean of more than 3) at sites where the proportion of acorns galled exceeded 90% suggest that there is strong intraspecific competition for access to acorns in *A. quercuscalicis*. It also demonstrates that there is considerable scope for compensating for low acorn density by increasing the gall burden per acorn cup.

Preliminary studies suggest that the fitness cost of multiple galling are not great (Collins *et al.* 1983).

The densities of the agamic galls of *A. kollari* and *A. lignicola* were generally low in the present study, and although we did find one example of a cola-nut gall fused to the side of a marble gall, there was nothing to suggest that there is intense interspecific competition in the agamic generation. However, both *A. kollari* and *A. lignicola* are extremely sensitive to the phenological condition of the buds on *Q. robur* at the time of egg-laying, and so any assessment of the availability of suitable buds is likely to be difficult (the differences between suitable and unsuitable buds are certainly not evident to the human eye). Studies in Britain (P. Walker in preparation) point to competition between these two species during the sexual generation on Turkey oak as being a potentially important process. This remains to be studied in Ireland.

Statistical analysis shows only positive associations between the local distributions of the alien gall wasps and there is no evidence for differential habitat selection. *A. lignicola* was significantly more likely to be found at a site that had both *A. quercuscalicis* and *A. kollari* (Table 6.3), but the distribution of *A. quercuscalicis* was independent of the distribution of the other two common host-alternators. The generally positive partial correlations demonstrate that a good place for one alien gall species tends to be a good place for the others, while the asymmetry in the response of knopper galls suggests that *A. quercuscalicis* is presently absent from a number of apparently suitable sites.

The distribution maps (Fig 6.1) coupled with information on proximity to the nearest Turkey oak (Table 6.3) suggest that the dispersal abilities of the sexual generations can be ranked as follows: *A. lignicola* >= *A. kollari* > *A. quercuscalicis* > *A. corruptrix*. This ranking from the Irish data set is entirely consistent with the geographic distributions and relative frequencies of the species in Britain (*A. kollari* is more widespread than *A. lignicola* but has been present in Britain much longer; at a given site within the range of *A. lignicola* in Britain the probability of finding *A. lignicola* is greater than the probability of finding *A. kollari*). We do not know enough about the relative dates of introductions of the different gall wasps in the two islands to allow us to factor out any differences that might exist in the time since invasion.

6.4.3. Cynipid species richness

Two of the factors we measured were associated with increased cynipid species richness. The greater diversity of galls in eastern Ireland probably reflects the greater average population density of oaks in that part of the island. The greater species richness at sites where there are greater numbers of oak species is

interesting, and suggests that even though the agamic galls of most cynipid species can occur on *Q. robur*, *Q. x rosacea* or *Q. petraea*, there are preferences or differences in insect performance which mean that certain oak species are more influential than others in determining gall diversity. Of the 3 native oaks, it is the presence of *Q. robur* at a site which increases gall species richness while the presence of *Q. cerris* at a site increases the likelihood of finding 2 of the 4 alien cynipids (*A. lignicola* and *A. quercuscalicis*; see above).

7. Discussion

The invasion of *A. quercuscalicis* provides the opportunities to study a community which is variable in space and changing and time (Elton 1958; but see Hairston 1989 on the limitations of 'natural experiments'). Changes in time of species richness and composition within the guild of knopper galls could be studied directly in Britain where galls were reared for the last 15 years (Martin 1982, Collins *et al.* 1983, Hails *et al.* 1990). To study changes over longer periods of time the guild of knopper galls was investigated in regions in continental Europe where *A. quercuscalicis* invaded from about 80 years ago to as early as 300 years ago. Since these regions are separated by distances up to several hundred kilometres, geographical variability in guild structure had to be taken into consideration and it proved difficult to distinguish effects of the residence time of the invading host and from effects due to regional variation.

During this study of the guild of knopper galls in Britain 4 parasitoid species were recorded for the first time. All but one of these four species were also found to attack knopper galls in continental Europe and hence the guilds in both places appear to be more similar than before. This trend was also found across the invaded range in continental Europe indicating a convergence towards a guild similar to that found in the native range of *A. quercuscalicis*.

7.1. A community in development

Changes in the community associated with knopper galls were examined in Britain over a period of more than 15 years. Previous studies as well as those presented here showed that the community of inquilines and parasitoids associated with the knopper galls in Britain is still changing (Collins *et al.* 1983, Hails *et al.* 1990). These changes might be divided in to two phases which are not necessarily completely separated in time. The first phase involves the enrichment in species of the knopper gall guild (see also Strong *et al.* 1977, 1984, Cornell and Hawkins 1993). Until 1988 the 12 inquiline and parasitoid species had been recorded from knopper galls collected in Britain, compared with 13 species during this study (Hails *et al.* 1990). Collins *et al.* (1983), reiterated by Hails *et al.* (1990), stated that it was curious that the species composition of the guild in knopper galls from Britain was so different to the guild known from continental Europe, since most of the parasitoid and inquiline species known to attack knopper galls in the native range were also known from Britain. The results presented here show that the guild of the knopper galls in Britain appears to have entered a second phase. While the number of recorded parasitoid and inquiline species in Britain has not changed dramatically a turnover in species has led to a species composition which is more similar to that in the native range. The 13 parasitoid and inquiline species recorded

from Britain compare to 15 species recorded from knopper galls collected from the native range. However, the bigger sampling effort in Britain does not allow a direct comparison. Analyses using standardised sample sizes demonstrate that the local species richness is not only highest in the native range, but decreases with distance, probably reflecting the invasion history of *A. quercuscalicis*.

7.2. The invasion of *Andricus quercuscalicis* and time as a determining factor for guild structure

7.2.1. The guild in knopper galls from Britain

Cornell and Hawkins (1993) analysed data of the recruitment of parasitoid species for many invading insect species and found that the time over which the invader kept recruiting parasitoid species was very variable with a tentative mean of about 150 years. The recruitment is described as a relatively continuous process determined by the periods of time that individual parasitoid species might need to adjust to the new host, and/or by the progressing invasion which might bring the invader in contact with more parasitoid species, and larger numbers of individuals of common, widespread parasitoid species.

An example for the continuous recruitment of parasitoids comes from the chestnut gall-wasp, *Dryocosmus kuriphilus*, which invaded Japan around 1940 and probably a second time in 1960 (Moryia *et al.* 1989a). The number of parasitoids, native to Japan, rose from 5 species in the early stages of the invasion to 12 species in 1973 and 15 species by beginning of the 1980's (Moriya 1989a, Askew 1984). None of the parasitoid species native to Japan was able to regulate the population of *D. kuriphilus* which caused considerable damage to chestnut trees and was therefore of economic importance (Otake *et al.* 1982). Only when *Torymus sinensis* was introduced, a parasitoid species which attacks the chestnut gall-wasp in its native range in China, was it possible to reduce the population levels of the pest insect (Otake *et al.* 1984, Moryia *et al.* 1989b). The reason why the native parasitoid species failed and the introduced species was successful in reducing the population density of *D. kuriphilus* was a much higher degree of synchronisation between the phenologies of the pest and the introduced parasitoid species than with any of the native species (Moryia *et al.* 1989a).

In the knopper gall guilds parasitoid species were recruited between 1980 and 1993 at relatively continuous rate of roughly one new parasitoid species per year. The change in inquiline abundance (i.e. an additional host, Chapter 2), however, resulted in a rapid change in species composition. About half of the parasitoid species which were reared from knopper galls from the native range were parasitoids of inquilines. Sudden phases of rapid community changes might be characteristic for well structured communities, such as the guild in knopper galls,

when species are recruited which serve as hosts (or prey) for relatively specialised consumers.

Many of the successful insect invasions come from the field of biological control when for instance insects were transferred between continents and became pests because they escaped their natural enemies (Jeffries and Lawton 1984, Greathead 1989). *A. quercuscalicis*, on the other hand, never really escaped from the parasitoid species which attack its galls in the native range since most of these species were recorded in Britain attacking other cynipid galls before it arrived (Kloet and Hinks 1975). The British populations of these species, however, may well have been naive towards the new host and their host searching image apparently did not include the new galls (e. g. their host searching behaviour did not lead them to the acorns of *Q. robur*). The lag in the appropriate host searching behaviour might have lead to the 20 year delay during which knopper galls were virtually free from parasitism.

7.2.2. The guild in knopper galls in continental Europe

The considerable variability in guild structure through the invaded range in continental Europe, where *A. quercuscalicis* has been present for up to 300 years, is difficult to interpret in terms of residence time, because base-line data are not available. Only on the basis of 15 years rearing data has it been possible to say that there were continuous changes in the guild of British knopper galls. The guilds in knopper galls from continental Europe might have stopped changing, and the observed variability could be caused by unmeasured local factors. Two arguments indicate that this is not entirely true. First, the parasitoid and inquiline guilds associated with other cynipid galls are reported to be stable and very similar over large geographical scales, and so the kind of geographical variability observed here would be relatively unusual (Schröder 1968, Stille 1984). Second, the distance of the sample sites from the native range (easterliness) was shown to have a significant impact on the species richness of the guilds. Although less clear, the trends in food web parameters along the invasion route also indicate that the guilds in the invaded range on the European continent are still converging towards the structure observed in the native range.

Many of the parasitoid and inquiline species in knopper galls also attack other cynipid galls and might require these host species to complete their annual life-cycle. The numbers of cynipid species which were recorded at the sample sites decreased with distance from the native range towards Britain and was found to have a significant impact on the species richness of the parasitoid and inquiline guild in knopper galls (Chapter 4). In the same model, however, easterliness

explained a significant part of the variation in the species richness in the knopper gall guild, independently from local cynipid richness (Table 4.5).

Not all members of the guild of knopper galls from the native range extend their distribution throughout Europe, and this also contributes to the geographical variation in guild structure. Species which were apparently left behind when *A. quercuscalicis* extended its range left vacant niches in the guild structure of the knopper galls in the invaded range. The process of filling these niches may be slower if the new species is not as well adapted as the original occupant. We found only one example of this kind of substitution when *Mesopolobus jucundus* became the dominant parasitoid of the inquilines in Britain in the absence of *Cecidostiba adana*.

Examples for apparently vacant niches over most of the invaded range are those occupied by *Aulogymnus trilineatus, Baryscapus berhidanus* and *Pammene amygdalana* in the native range. *A. trilineatus* and *B. berhidanus* both have very different life histories. The first is a solitary ectoparasitoid while the latter is a gregarious endoparasitoid, but both attack the gall former. *P. amygdalana* feeds on the tissue of the outer wall, but regularly kills the gall former, probably to secure the food quality which is needed by the larva, which is much bigger than any of the other inhabitants, to complete its development. All three species seem to be well adapted to attack and develop in knopper galls in their own way and it will be for the future to see whether species with similar characteristics will enter the guild of knopper galls in regions where these three species are not present.

The importance of morphological adaptation for parasitoids which attack galls was demonstrated by Askew (1965) and Weis *et al.* (1985) and was discussed in Chapter 1 and 4. Once parasitoids and inquilines have begun to exploit the new host the complex structure of the knopper galls might give the morphologically better adapted species the advantage over other more opportunistic inhabitants, along with other factors such as the synchronisation of phenologies (an example was given with the success of *Torymus sinensis* in controlling *Dryocosmus kuriphilus*; Section 7.2.1), etc..

The function of gall shape is the subject of an ongoing debate and is interesting in the context of knopper galls, because gall size increased significantly with distance away from the native range (Askew 1961a, Price and Pschorn-Walcher 1988, Hawkins and Gagne 1989, Hawkins 1990). The results presented in Chapter 4 showed that, at least in the guild of knopper galls, parasitoid and inquiline species tend actively to alter the gall shape rather than respond to it.

In summary, there is evidence that the guild associated with knopper galls in Britain is in the process of converging towards a structure and composition similar

to that observed in galls from the native range. The discussion of the results for regions in the invaded range of continental Europe indicates that the guilds might also be changing (after up to 200-300 years), but that local factors may determine how similar these guilds become to those in the native range.

7.3. Parasitism in the sexual generation of *A. quercuscalicis*

High rates of parasitism are not unusual in cynipid galls and sometimes exceed 80% (Askew 1975, Schröder 1967). The gall wasp *Xanthoteras politum* was locally driven to extinction in California by two inquilines *Ceroptres* sp. and *Synergus* sp. both of which kill the gall causer (Washburn and Cornell 1981). Thus it appears, that parasitoids and/or inquilines can affect their host's population dynamics at least in some cynipid guilds.

In *A. quercuscalicis* both generations are exploited by parasitoids and in the agamic galls the gall former is killed by one of the inquilines, *Pamene amygdalana*. Mortality of the gall former in knopper galls from parasitism or attack by the inquiline moths was low in the invaded range as well as in the native range, where parasitism rates exceeded 15%.

Density dependence of parasitism in the sexual generation was examined in British populations between 1982 and 1993 (Hails 1988, Hails and Crawley 1991, 1992). Mortality varied with spatial scale and was probably not important in regulating the population densities of the gall wasp. In Britain the most important regulating factor was the availability of oviposition sites for the sexual females (i.e. the number of flowers on *Q. robur* which produce acorns). It was not possible, however, to predict the population size in the next generation with any precision since it is not possible to predict the size of the acorn crop on *Q. robur* (Hails and Crawley 1992, Crawley and Long 1995).

During the examination of parasitism in sexual galls from the native range of *A. quercuscalicis* 10 parasitoid species were identified, and these attacked up to 80% of the available galls, compared with 25-30% in Britain (Hails and Crawley 1992). Attack rates were variable on all spatial scales at which they were examined.

Interestingly, the mean galling rates per site corresponded with the total mortality caused by parasitism (Valdice < Zalaegerszeg < Tausendblum) which would indicate a positive density dependent relationship on a geographical scale. The importance of the spatial scale on which to measure heterogeneity in parasitism was emphasised earlier (Heads and Lawton 1983, Hassell 1987). Since patterns of density dependence in parasitism on stationary hosts, such as galls, result only from the host searching behaviour and decision making of the ovipositing parasitoid female the appropriate spatial scale should be the functional

scale of the parasitoid female (Hails 1988). Because the geographical distances between the sample sites mentioned above is not likely to be on the functional scale of a parasitoid female and the described trend is more likely to be caused by other differences between those sites, such as the densities of alternative cynipid hosts, resulting in local population dynamics of parasitoid and host (Walde and Murdoch 1988).

Significant positive *and* negative density dependent relationships between host density and parasitism rates were found on all spatial scales, for all major parasitoid species and in all three sites. Because the signs of the correlations were variable at all spatial scales, as they were in Britain over several years (Hails and Crawley 1991), direct population regulation by parasitoids appears to be unlikely. That there were significant density dependent relationships suggest, on the other hand, that refugia exist in either the high density or the low density patches from which the host population might recover (Hassell 1985). Considering the results for al parasitoid species, only 2 out of 15 trees examined showed no significant density dependence with any of them underlining the point that these refugia are common and could contribute to stabilising the populations of *A. quercuscalicis*. To confirm that there is no direct population regulation by parasitism or that refugia have the stabilising effect data over several generations and possibly manipulative experiments would be needed.

Moreover, density dependence in parasitism might not be necessary to regulate the population dynamics of *A. quercuscalicis* (see Section 5.4.2). Hails and Crawley (1991) stated, if *A. quercuscalicis* were univoltine and non-host alternating then the spatial heterogeneity found in Britain would be sufficiently high for non-density-dependent processes to regulate its population dynamics (see CV^2-rule in Hassell and Pacala 1990). This could also be true for populations in the native range, but models of spatial heterogeneity and population regulation have not yet been developed for host-alternating, bivoltine insect species.

7.4. Further questions and future research

7.4.1. The future of the invasion

It appears that *A. quercuscalicis* is still extending its range within the British Isles, and only recently knopper galls were found for the first time in southern Scotland (P. Walker personal communication). It is interesting to note that of the other three invading cynipids *Andricus lignicola* has spread considerably further than *A. quercuscalicis* even though both arrived in Britain at about the same time. *A. lignicola* was found almost throughout Ireland and halfway up through Scotland (Chapter 6, P. Walker personal communication). This leads to three predictions about differences in the mode of dispersal between these two species: 1) *A.*

lignicola is a better disperser and the adults spread further than those of *A. quercuscalicis*; 2) host utilisation; while *A. quercuscalicis* is virtually monophagous in both generations, *A. lignicola* uses *Quercus robur* and *Q. petraea* as host trees for the agamic generation and this should make it easier to spread through areas where *Q. petraea* is the dominant species and *Q. robur* is rare (Chapter 6, Folliot 1964); 3) human aided dispersal; there is a considerable horticultural trade in oak trees throughout Europe (P. Walker personal communication). Most of these trees are imported and planted while they are still young. Since *A. quercuscalicis* attacks only mature, flowering trees it is unlikely that galls of this species have been moved unintentionally. *A. lignicola* on the other hand oviposits into the buds of even the youngest host trees and is often recorded on nursery stock.

During the survey throughout Ireland only *A. quercuscalicis* showed a positive association with the presence of *Q. cerris* (Table 6.3). This indicates that at least the females of the sexual generation of *A. lignicola* and *A. kollari* can disperse further than those of *A. quercuscalicis*. The wider host ranges of *A. lignicola* and *A. kollari* might then reinforce this difference in dispersal ability and explain why *A. quercuscalicis* has not yet spread as far as *A. lignicola*.

Currently further work is beeing carried out on two spatial scales to obtain evidence for the different dispersal abilities of two of the three invading species. On a small scale the dispersal within one generation will be studied using mark and recapture technics. On a larger scale the population genetics of *A. lignicola* throughout Europe is currently under investigation to be compared to data obtained for *A. quercuscalicis* (Stone and Sunnucks 1993). Populations of *A. quercuscalicis* showed a significant, non-random decrease in genetic variability with distance from the native range. If *A. lignicola* would have dispersed considerably further between generations one would expect an increased gene-flow and a less distinct pattern if at all. Particularly if the oak trade throughout Europe was an important factor for the spread of *A. lignicola* a continuous change in genetic variability would not be expected.

7.4.2. Interactions with native cynipid species in Britain

There is no evidence that *A. quercuscalicis* is competing for resources with any other cynipid species in Britain. The possibility of apparent competition between *A. quercuscalicis* and native cynipid species via shared natural enemies was thought to be not important, since the agamic generation was virtually free of parasitism and parasitoids emerging from the galls of the sexual generation were virtually all males (Holt 1977, Jeffries and Lawton 1984, Hails 1989, Hails and Crawley 1991).

Since 1989, however, the number of inquilines and parasitoids emerging from knopper galls has increased generally and in certain sites by more than 100-fold (Chapter 2). If *A. quercuscalicis* enters into an apparent competition with any of the native cynipid species it appears to be more likely that the shared enemy would be the inquiline *Synergus gallaepomiformis* than a parasitoid species, as discussed in Section 2.4.5. *S. gallaepomiformis* was the most numerous species which emerged from knopper galls.

S. gallaepomiformis attacks native cynipid galls such as *Neuroterus quercusbaccarum* and *Biorhiza pallida* in which, unlike in knopper galls, the gall former is killed by the inquiline (Askew 1961a). Because the inquiline is not a mortality factor for *A. quercuscalicis,* one might expect this asymmetric competition to have important effects.

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