

Organization of a parasitoid community associated with a complex of galls on *Atriplex* spp. in southern California

BRADFORD A. HAWKINS and RICHARD D. GOEDEN Division of Biological Control,
Department of Entomology, University of California, Riverside, California

ABSTRACT. 1. *Atriplex canescens* (Pursh) Nuttall and *A. polycarpa* (Torrey) Watson (Chenopodiaceae) support twelve morphologically distinct gall types in southern California. Thirty-seven common species of parasitoids, predators and inquilines are associated with these galls.

2. The galls incited by eight members of the *Asphondylia atriplicis* Cockerell (Diptera: Cecidomyiidae) species complex are linked into a single, interacting community through shared hymenopterous parasitoids and inquilines.

3. Cluster analysis (UPGMA) grouped the fifteen most common species of Chalcidoidea into three host guilds of five species each: (1) specialists in tumour stem and blister leaf galls on *A. canescens*, (2) specialists in woolly stem galls on *A. polycarpa*, and (3) generalists that attack all galls. Guild 1 dominated the galls with which it was primarily associated, while guild 3 dominated the remainder.

4. The abundances of the parasitoids of the tumour stem and blister leaf galls were negatively correlated with the abundances of two organizer species, a gall-forming inquiline, *Tetrastichus cecidobroter* Gordh and Hawkins, and an internal, larval–pupal parasitoid, *Tetrastichus* sp. B. The abundances of nine of the twelve most common chalcidoids were not correlated with the abundances of all co-occurring species in six other galls.

5. Host seasonality partly determines parasitoid population dynamics and guild structure. Parasitoid dominance increased with gall duration, suggesting that parasitoid competition depends on resource stability. The two continuously available galls were dominated by their specialist guild, while all seasonal galls were dominated by generalists. The sub-dominant specialists of woolly stem galls may represent competitively inferior species that utilize those galls opportunistically, because of the gall's widespread distribution and 9–10 month yearly availability.

6. Sites in the Colorado Desert and chaparral that supported several gall types showed stable relative abundances of the major parasitoid species, whereas sites in the Mojave Desert that supported only woolly stem galls had unpredictable parasitoid species assemblages.

7. The competitive success of *Atriplex* gall parasitoids may depend primarily on voltinism (multivoltine species dominated univoltine species) and mode of feeding (phytophagous, mixed entomophagous–phytophagous and facultatively hyperparasitic species in general dominated strict primary parasitoids).

Key words. *Atriplex*, gall parasitoids, community structure, guilds, phenology, resource stability.

Correspondence: Dr Bradford A. Hawkins, Department of Entomology, Texas A & M University, College Station, TX 77843, U.S.A.

Introduction

The degree to which parasitoid communities are structured by competition has recently been questioned (Dean & Ricklefs, 1979, 1980; but see Bouton *et al.*, 1980; Force, 1980), as part of a larger re-evaluation of the importance of competition in nature (Strong, 1980; Schoener, 1982). However, studies of parasitoid complexes frequently provide at least some evidence of competition (Parnell, 1964; Price, 1970, 1971; Force, 1970, 1974; Ehler, 1978, 1979; Zwölfer, 1979), and there is at least one well-documented case of the competitive exclusion of one parasitoid by another (DeBach & Sundby, 1963).

In this paper we examine the insect community associated with galls on *Atriplex* spp. (Chenopodiaceae) in southern California. First, we describe the trophic relations of the gall formers, inquilines, predators and parasitoids. Then we examine the parasitoid complex to determine basic community organization based on niche relationships, and we identify host guilds that partition the gall community into interacting sub-communities. Parasitism patterns within these sub-communities are examined to determine to what extent they are structured and if patterns indicative of competition exist. Lastly, we examine the effects of host seasonality on parasitoid community organization and discuss the biological attributes responsible for dominance and factors affecting parasitoid resource utilization strategies.

North America is one of three major centres of diversification of the genus *Atriplex* (Osmond *et al.*, 1980). Two of the more common of the thirty-two species found in California are *A.canescens* (Pursh) Nuttall and *A.polycarpa* (Torrey) Watson. These woody perennials are sympatric and widespread on California deserts, where each often grows in large, solid stands. *Atriplex polycarpa* is restricted to the interior deserts, but *A.canescens* also occurs in coastal sage scrub and chaparral habitats.

We have identified twelve distinct galls on these saltbushes in southern California: two caused by *Neolasioptera willistoni* (Cockerell) (Diptera: Cecidomyiidae), one caused by *Ophiomyia atriplicis* Spencer (Diptera: Agromyzidae) and nine caused by eight members of the *Asphondylia atriplicis* Cockerell (Diptera: Cecidomyiidae) species complex. The galls are formed on leaves, stems, buds, flowers and fruits. Descriptions of the galls and the taxonomy, biology and ecology of the *Asphondylia* spp. will be presented elsewhere. These midges form the ecological basis for this study.

Materials and Methods

After preliminary sampling in 1978 and early 1979, systematic sampling was conducted bi-weekly from 14 July 1979 to 5 July 1980 at eight sites in the southern Mojave Desert, western Colorado Desert (Coachella Valley) and the chaparral on the southern face of the San Jacinto Mountains (Table 1). Up to 150

TABLE 1. Sampling locations in southern California and the species of *Atriplex* at each site.

Site	<i>A.canescens</i>	<i>A.polycarpa</i>
Mojave Desert (San Bernardino Co.)		
Victorville (VIC)	X	X
Hodge (HOD)		X
Barstow (BAR)		X
North Lucerne Valley (NLV)		X
Colorado Desert (Riverside Co.)		
Palm Desert (PLD)	X	
nr Thermal (THR)	X	X
Torres Martinez Indian Reservation (SLT)		X
Chaparral (Riverside Co.)		
nr Valle Vista (VLV)	X	

galls of each type present were collected at each site, depending on gall densities. When possible at least fifteen plants of each *Atriplex* sp. were sampled.

The insects were reared in glass desiccators over NaCl-saturated water at 75% r.h. and room temperature. After all adult insects had emerged (6–8 weeks), the galls were dissected and their contents (e.g. dead larvae) recorded. Additional samples of all galls were taken during 1980–82 to verify developmental and trophic characteristics.

During preliminary sampling it became apparent that parasitoid/host relationships were complex and highly variable, and that some parasitoids had widely differing abundances in the various galls. To quantify these differences and to determine if general feeding relationships existed, the data were initially analysed using niche analysis techniques. Once general patterns were identified, the emphasis of the analysis was to examine factors potentially responsible for these patterns. Specific techniques and indices were selected for their relative simplicity and widespread use, or because of their empirical properties.

The niche dimensions that affect interacting species are varied, but most animals partition components of time, place and food (Schoener, 1974). The niche dimensions recognized in this study were time (in 2-week intervals), macrohabitat (eight sites) and gall type (eight *Asphondylia* galls), the latter being a composite of microhabitat and food (host). All the galls considered here are caused by morphologically indistinguishable midges. The midges are so closely related taxonomically and biologically that differences in host quality are probably minimal, and there is no distinct food dimension.

Niche overlaps between species pairs were calculated using Pianka's (1973) symmetrical measure

$$O_{jk} = O_{kj} = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum p_{ij}^2 \sum p_{ik}^2}}$$

where p_{ij} and p_{ik} are the proportions of each species in the i th unit of the resource set. This measure is bounded by 0 (no overlap) and 1 (total overlap).

Because absolute estimates of overlap are

affected by non-uniformity of units within resource sets (e.g. differences in absolute resource abundance), all parasitoid numbers were converted to the number of parasitoids/100 hosts in each sample before calculating proportions. This was done because sample sizes did not necessarily reflect absolute host abundances in each gall type or at each site, and because we were interested in the relative efficiencies of parasitoids in each resource unit rather than in absolute numbers of individuals. This also prevents the analysis from being dominated by large samples.

Niche breadths of individual species were measured using a modification of Simpson's (1949) diversity index

$$B = 1/\sum p_i^2 s$$

where p_i is the proportion of a species in the i th unit of the resource set, and s is the number of units. This measure is scaled between 1 (the species equally distributed in all units) and $1/s$ (all individuals in a single unit).

Dominance was measured as $1-J'$ (see Brower & Zar, 1977), with J' (Pielou, 1966) defined as

$$J' = H'/\log(s)$$

where s is species richness and H' is the Shannon-Wiener (Shannon & Weaver, 1949) diversity index ($-\sum p_i \log p_i$).

Parasitoid guild structure was examined using cluster analysis. In complex communities where relationships between species are not clear, community dendrograms based on niche overlaps can identify groups of ecologically similar species, or guilds (see Cody, 1974). To analyse guild structure in *Atriplex* galls, we selected the fifteen most important Chalcidoidea (eleven primary parasitoids, two facultative hyperparasitoids and two inquiline). These species accounted for 99.3% ($n = 8705$) of the total number of individuals reared. Niche overlap matrices based on all species pairs were generated in each niche dimension and in all niche dimensions considered simultaneously. The overlap matrices were then subjected to cluster analysis using the unweighted pair-group method using arithmetic averages (UPGMA) (see Sneath & Sokal (1973) for a discussion of cluster techniques).

Results

Trophic structure

Fig. 1 depicts the trophic relationships among the gall-inhabiting insects. Each species is coded by shape for a major type of feeding relationship, and species on each trophic level are grouped horizontally. Each gall trapezoid represents a distinct gall-forming species; in two cases each form two gall morphotypes (Gagné & Hawkins, 1982; Hawkins, unpubl.). Predators and parasitoids

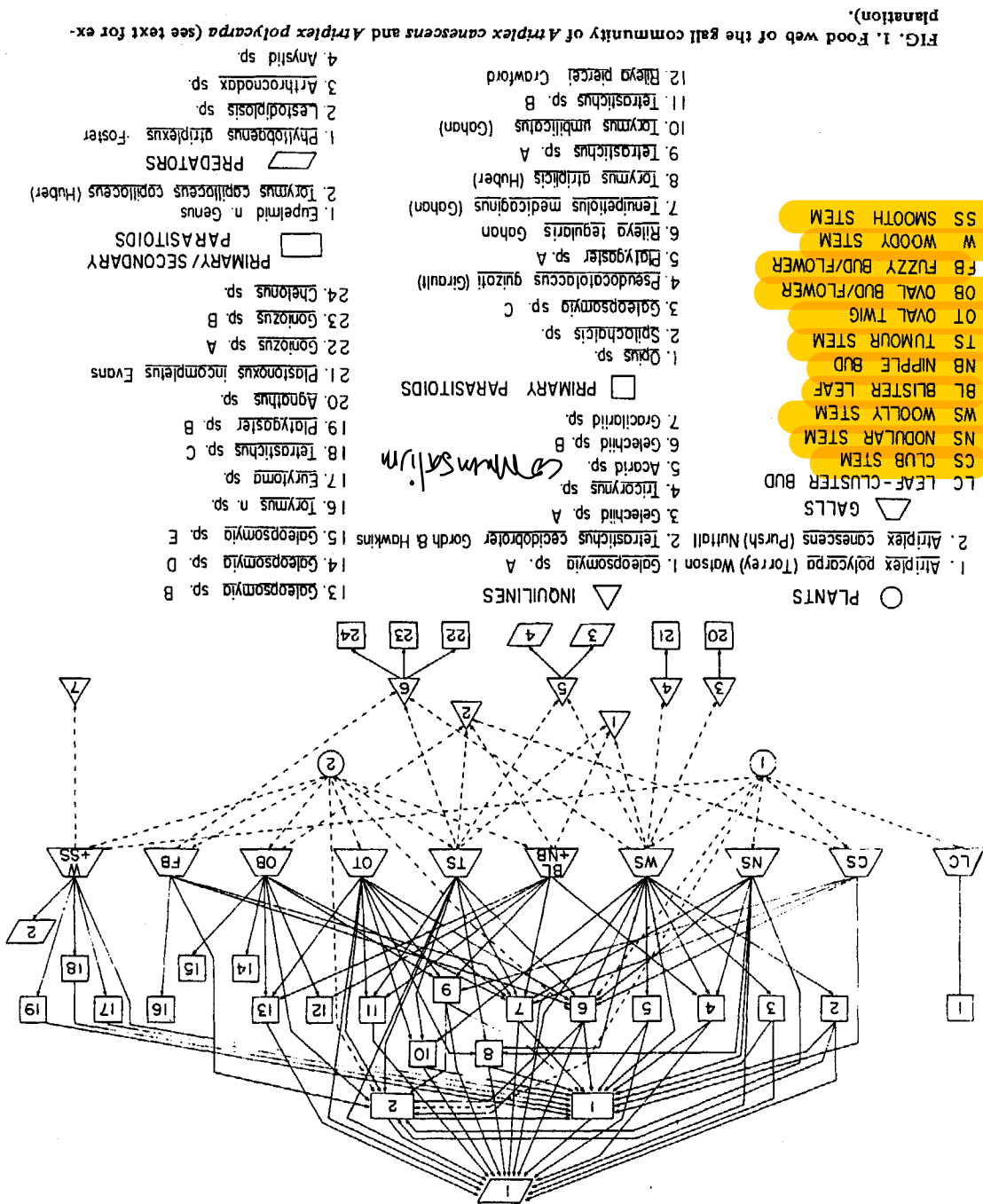


FIG. 1. Food web of the gall community of *Atriplex canescens* and *Atriplex polycarpa* (see text for explanation).

of the gall formers are shown above the line of galls, while inquilines and their natural enemies are shown below. The arrows indicate the direction of energy flow; solid lines show entomophagy, and dashed lines, phytophagy.

The food web (Fig. 1) has been simplified in several ways. Very rare species and those that do not at least potentially interact with the gall formers (e.g. successori) have been omitted. The web shows only forty-seven of the sixty-one species reared from *Atriplex* galls. Second, interactions accounting for less than 5% of the observations for a species are not shown. Third, suspected interactions not directly observed are not included. Fourth, cases of indirect mortality are not considered. This represents primarily the effects of inquilines on the gall-formers and their parasitoids.

Despite the conservative nature of this food web, several observations concerning the general structure of the *Atriplex* gall community are possible. (1) There is extensive overlap of parasitoids in the galls, with most galls having several parasitoids in common. The woody and smooth stem galls, both formed by *Neolasioptera willistoni*, support a fairly distinct parasitoid complex. The

leaf-cluster bud gall, formed by *Ophiomyia atriplicis*, is attacked by a single braconid, *Opius* sp., which does not interact with the remainder of the parasitoid community. All remaining galls, which are formed by the *Asphondylia* spp., share at least two parasitoids, creating a trophic network. (2) The parasitoid trophic system, although broad, is shallow. Only two species, *Torymus capillaceus* (Huber) and the undescribed eupelmid sp., are confirmed facultative hyperparasitoids; however, *Torymus atriplicis* (Huber) and *Torymus umbilicatus* (Gahan) are suspected facultative hyperparasitoids. (3) The upper trophic levels comprise species that feed on several trophic levels simultaneously. *Torymus capillaceus* feeds on gall tissue, gall midges and primary parasitoids, and the eupelmid sp. feeds on midges, primary parasitoids and *T. capillaceus*. The absence of fourth trophic level specialists has also been observed in oak-gall and leaf-miner communities and may be generally true for parasitic communities on concealed hosts (Askew, 1975; but see Luck, 1976).

The top predator, *Phyllobaenus atriplexus* Foster (Coleoptera: Cleridae), although widely distributed in *Atriplex* galls, is known only from this plant genus (Foster, 1981).

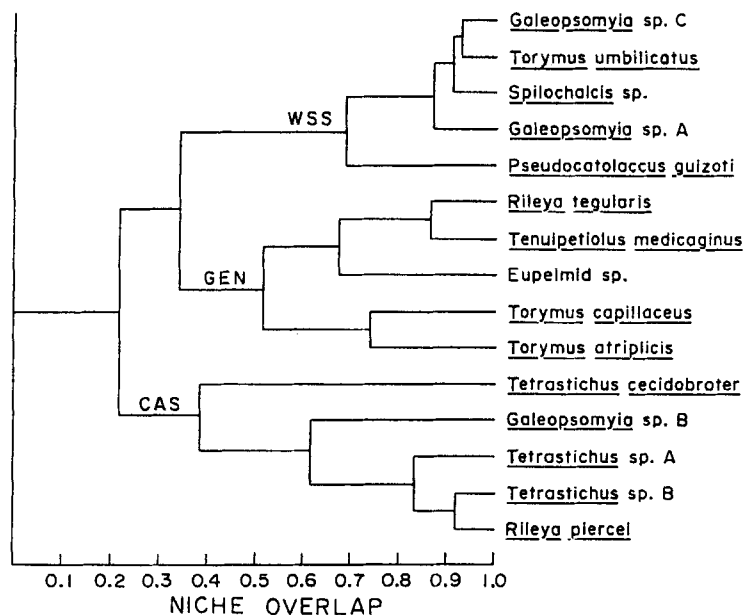


FIG. 2. Parasitoid community dendrogram based on gall type niche dimension. (CAS = *canescens*-specialists, GEN = generalists, WSS = woolly stem gall specialists).

First instar larvae chew into galls and eat any insect encountered. The beetle has been observed in up to 20% of the galls in a sample, although infestation rates are typically less than 10%.

Parasitoid guild structure

Cluster analysis based on gall type grouped the parasitoids into three clusters of five species each (Fig. 2). Each cluster represents a group of species that have high niche overlaps with each other, but low overlaps with species in other clusters. These clusters, then, represent guilds which partition the host (gall type) spectrum. The distributions of the major species in each gall type are shown in Figs. 5–7, but Fig. 3 provides a generalized view of the host associations for each parasitoid guild.

The three parasitoid guilds partition the eight *Asphondylia* galls into three basic gall 'types'. Fig. 3A shows the proportion of the total number of individuals of each guild occurring in each of these basic types, measured as the number of parasitized hosts for gregarious species. The uppermost guild (in Fig. 2) comprises species associated primarily with the woolly stem gall (WS) on *A. polycarpa*, as 83% of the individuals occurred in this gall. This guild is termed the woolly stem gall specialist (WSS) guild. The bottom guild represents species associated primarily with the tumour stem gall (TS) and the

blister leaf gall (BL) on *A. canescens*, in which 82% of the individuals occurred. Because these species concentrated on galls on *A. canescens*, we term this guild the *canescens*-specialist (CAS) guild.

The species in the middle guild (in Fig. 2) were not concentrated in any particular galls, but occurred in all galls. However, a plurality (45%) of these parasitoids were reared from the remaining five galls not used appreciably by the species in the specialist guilds. We refer to these galls collectively as RARE galls because of their restricted spatial or temporal distributions. We term this parasitoid guild the generalist (GEN) guild, because it represents species attacking all hosts (Fig. 3A).

Niche breadths further suggested a specialist-generalist dichotomy between the guilds. Mean niche breadths of the *canescens*-specialist guild and the woolly stem gall specialist guild were similar ($\bar{x} = 0.290$, $2SE = 0.038$ and $\bar{x} = 0.229$, $2SE = 0.066$, respectively), but both guilds had significantly narrower niche breadths than the generalists ($\bar{x} = 0.457$, $2SE = 0.114$).

Fig. 3B is the inverse of Fig. 3A and shows the relative importance of the three guilds in each gall 'type'. In terms of abundance, the generalists strongly dominated the RARE galls, accounting for 73% of the total number of parasitoids that emerged from these galls. The tumour stem and blister leaf galls were dominated by their specialists, which

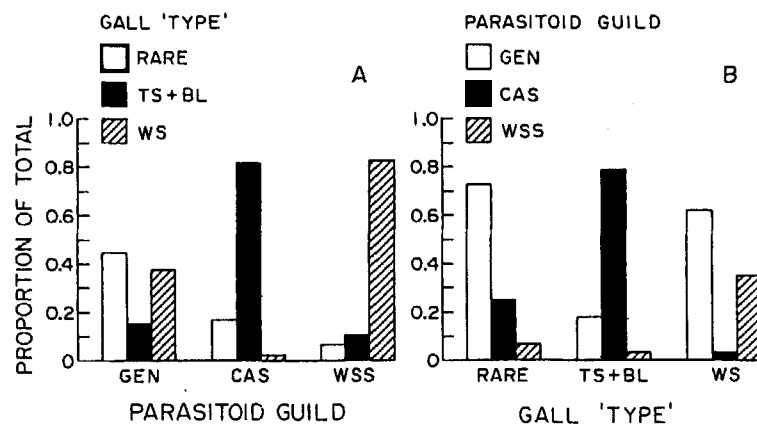


FIG. 3. Associations of parasitoid guilds in basic *Atriplex* gall 'types'. (A) Proportion of the total number of individuals of each guild emerging from each gall 'type'. (B) Proportion of total number of parasitoids emerging from each gall 'type' belonging to each guild. (RARE = rare galls, TS = tumour stem gall, BL = blister leaf gall, WS = woolly stem gall, GEN = generalists, CAS = *canescens*-specialists, WSS = woolly stem gall specialists.)

accounted for 79% of the total parasitoid complex. The woolly stem gall specialists, however, were not the dominant species in the woolly stem galls, representing only 37% of the total number of parasitoids.

The parasitoid complex, then, consists of a specialist guild (CAS) associated with two gall types (TS + BL) which strongly dominates those galls, a specialist guild (WSS) primarily associated with one gall (WS), but accounting for a minority of the total parasitoid complex utilizing the gall, and a generalist guild which attacks all galls and which dominates all but two.

The significance of the cluster analysis was not tested directly, but the possibility that the niche overlaps on which the cluster analysis was based could have arisen randomly was tested against two null hypotheses. The first assumed that the niche overlaps themselves represented values from a random distribution. The observed values were tested against a uniform distribution ranging from 0 to 1, and were found to deviate significantly from expected ($\chi^2_9 = 27.1$, $P < 0.005$). The second hypothesis assumed that the distribution of each parasitoid species was random and independent of other species. Using Monte Carlo simulation, the observed numbers of individuals of each species were randomly distributed among the eight gall types. From these distributions an expected niche overlap distribution for all fifteen species was generated. The observed niche overlaps differed significantly from expected ($\chi^2_8 = 652.7$, $P < 0.001$). Therefore the pattern of overlaps between the parasitoids represents non-random partitioning of the gall types.

We have identified guild structure only in terms of host relationships, without regard to the effects of time and habitat. The basic organizing force for parasitoids are their hosts. Time and place act only as mediating factors superimposed upon communities structured around hosts. That macro-habitat *per se* is not of major importance is suggested by the widespread distributions of the parasitoids. Thirteen of the fifteen species occurred in all three major habitats. *Galeopsomyia* sp. A. did not occur in the chaparral, and *Tetrastichus* sp. B was found only in the Colorado Desert. Also, the

niche overlaps of parasitoids based on the site dimension did not differ significantly from a random (uniform) expectation ($\chi^2_9 = 12.1$, $0.10 < P < 0.50$).

Differences in parasitoid phenologies suggest that the temporal dimension plays a role in guild structure. Furthermore, niche overlaps along this dimension were non-random ($\chi^2_9 = 33.0$, $P < 0.005$). The significance of phenology in guild structure will be discussed in a subsequent section.

Cluster analysis using three niche dimensions modified host-guild structure (Fig. 4). The *canescens*-specialist guild remained unchanged, but the woolly stem gall specialist and generalist guilds were no longer distinct, reflecting the relatively great overlap between the guilds at sites and times when generalists and woolly stem gall specialists simultaneously attacked woolly stem galls. For example, the middle cluster (in Fig. 4) represents those species attacking galls primarily in the spring, while the top cluster represents both generalists and woolly stem gall specialists that were associated either in place (e.g. *Spilochalcis* sp. and eupelmid sp. in the Mojave Desert) or time (e.g. *Torymus capillaceus*, *Galeopsomyia* sp. A, *Rileya tegularis* (Gahan) and *Tenuipetiolus medicaginus* (Gahan) in the autumn or the year

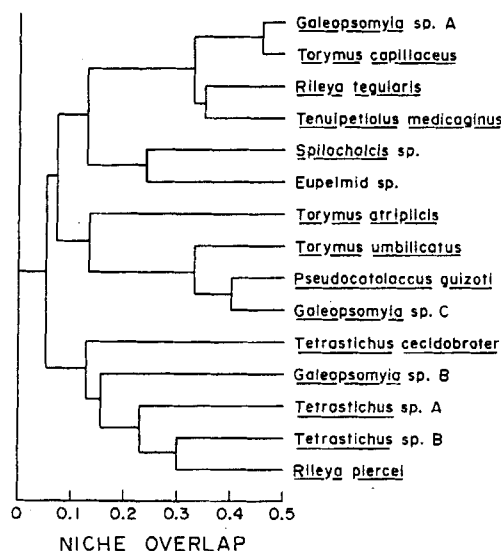


FIG. 4. Parasitoid community dendrogram based on simultaneous analysis of gall type, site and season niche dimensions.

round). Therefore, although the parasitoids are formed into three fairly distinct host guilds, extensive overlap between the generalist and woolly stem gall specialist guilds in the woolly stem galls (Fig. 3B) suggests that the gall community is partitioned into two subcommunities, the tumour stem and blister leaf gall (TS + BL) sub-community and the RARE and woolly stem gall (RARE + WS) sub-community.

Structure of the TS + BL sub-community

Of the fourteen chalcidoid species reared from tumour stem galls at Palm Desert, *Tetrastichus oecidobroter* clearly predominated (Fig. 5A), accounting for 63.2% 'parasitism' over the season. Because *T. oecidobroter* is gregarious, per cent 'parasitism' was estimated by counting the apparent number of attacked larval cavities in dissected

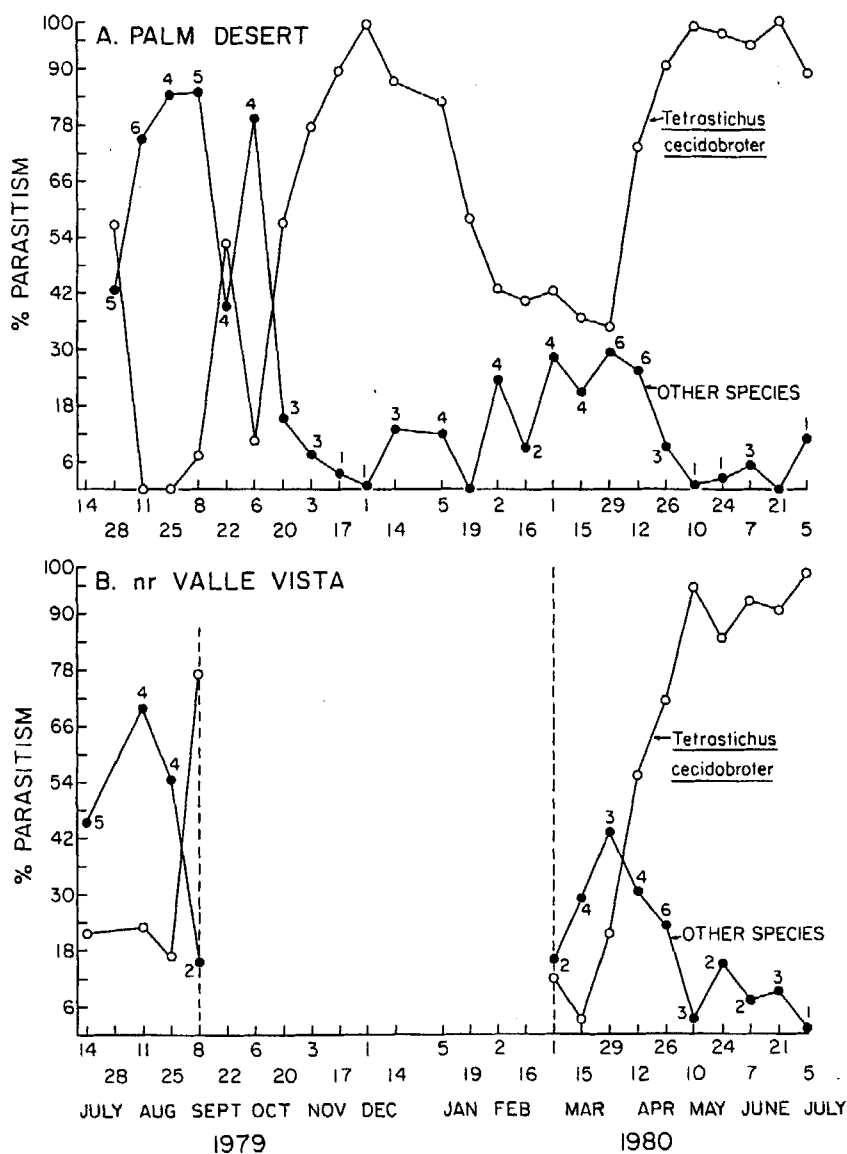


FIG. 5. Patterns of parasitism in the tumour stem gall, expressed at per cent 'parasitism' by *Tetrastichus oecidobroter* and per cent parasitism by all other species. Numbers above points are the number of co-occurring species. (A) At Palm Desert (Colorado Desert). (B) Near Valle Vista (chaparral).

galls, or by dividing the number of emerged adults by 4 (see below). The complementarity between *T.cecidobroter* and all other species was striking, and negative correlations of per cent 'parasitism' by *T.cecidobroter* and other species were highly significant in terms of either per cent parasitism ($r = -0.838$, $P < 0.01$, arcsine transformed) or the number of other species found in a sample ($r = -0.689$, $P < 0.01$).

Tumour stem galls in the chaparral showed a similar pattern (Fig. 5B), although gall densities were too low from September to February to obtain adequately sized samples for analysis. *Tetrastichus cecidobroter* was also less important in the chaparral, accounting for 51.3% 'parasitism' over the year. For the periods when data are available, per cent 'parasitism' by *T.cecidobroter* was negatively correlated with parasitism by all other species ($r = -0.757$, $P < 0.01$). The relationship with the number of other species was marginally non-significant ($r = -0.462$, $0.05 < P < 0.10$).

Tetrastichus cecidobroter is an important determinant of community structure in the tumour stem galls. The reason for this overwhelming dominance is based on the developmental biology of this wasp. The novel biology of *T.cecidobroter* was described elsewhere (Hawkins & Goeden, 1982), but

briefly is as follows. A female lays one to nine eggs ($\bar{x} = 4.33$, $SD = 2.28$, $n = 55$) in the wall of a gall midge larval cavity. The gall parenchyma surrounding each egg proliferates mitotically, resulting in a cluster of spheroid endogalls within the *Asphondylia* gall. The outer margins of each endogall sclerify, becoming hard and brittle. The developing wasp larvae feed on the endogall tissue, eventually consuming all non-sclerified cells. After ecdysis, the adult wasp chews through the endogall and the enveloping stem gall and emerges. The gall midge larva is not fed upon by the wasps. However, only rarely does a midge larva survive attack by *T.cecidobroter*, because during endogall development the midge larval cavity is usually obliterated and the midge is physically crushed, as is any parasitoid larva associated with the midge. Therefore, although not a true parasitoid, the effect on midge populations is identical to that of a parasitoid, and the effect on populations of other wasp species is the same as that of an unbeatable competitor. *Tetrastichus cecidobroter* acts as an organizer species (Price, 1970) in these galls, in that the presence and abundance of all parasitoids depends directly on the abundance of *T. cecidobroter*.

The levels of 'parasitism' by *T.cecido-*

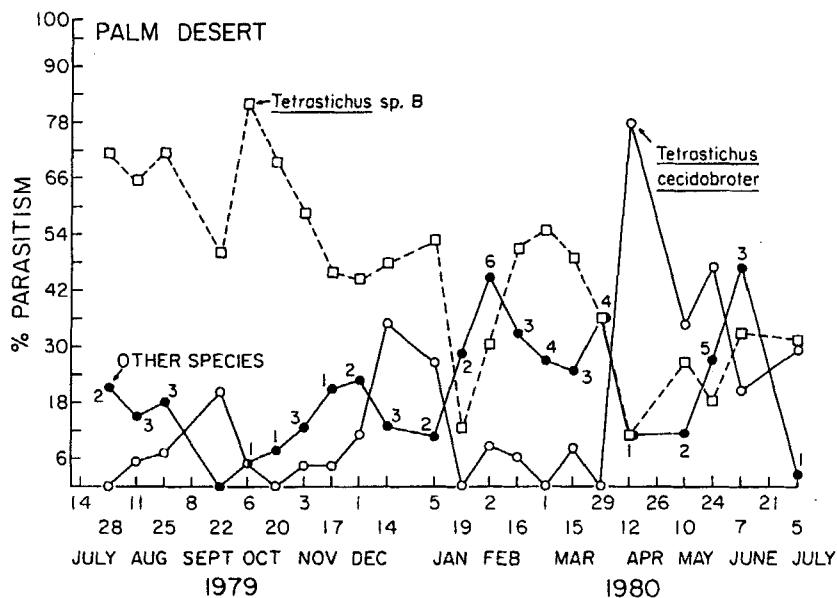


FIG. 6. Patterns of parasitism in the blister leaf gall at Palm Desert. Numbers above points are the number of co-occurring species.

broter depend primarily on gall density. The *Asphondylia* sp. forming the tumour stem gall undergoes population increases in the autumn and spring, resulting in an apparent decrease in the number of galls attacked by *T.cecidobroter* (Fig. 5). However, the wasps rapidly multiply, and as gall densities decline, 'parasitism' approaches 100%. These high levels are maintained until the next gall midge seasonal population increase.

Patterns of parasitism in the blister leaf galls differed from those found in the tumour stem gall (Fig. 6). *Tetrastichus cecidobroter* was dominant only in April and May 1980, with most of the remaining samples dominated by the internal, larval-pupal parasitoid, *Tetrastichus* sp. B. The remaining eight species were relatively rare.

As in the tumour stem gall, per cent 'parasitism' by *T.cecidobroter* in the blister leaf gall was negatively correlated with that of all other species ($r = -0.547$, $P < 0.01$). When the effect of *T.cecidobroter* was removed using partial correlation, the relationship between *Tetrastichus* sp. B and other species was significant ($r = -0.583$, $P < 0.01$). Lastly, these two dominant species had a combined effect on the number of other species in a sample ($r = -0.409$, $P < 0.05$).

Thus, although differing somewhat in the nature of the species involved, both tumour

stem and blister leaf galls are characterized by the presence of organizer species whose abundances determine both the number of other parasitoid species and their abundances. The mechanism for the success of *T.cecidobroter* is clear, but the traits that account for the dominance of *Tetrastichus* sp. B are not known.

Structure of the RARE + WS sub-community

Parasitoid populations in the RARE and woolly stem galls did not show clear patterns. Species interactions in these galls were examined using correlations to detect density compensation. For each of the twelve species that occurred in at least eight RARE and woolly stem gall samples (five generalists, four woolly stem gall specialists and three *canescens*-specialists), per cent parasitism by a species was tested against total per cent parasitism by all co-occurring species. This represented a test of diffuse competition (MacArthur, 1972) rather than potential competition between pairs of species. All data were arc-sine transformed for analysis. The tumour stem and blister leaf galls were also tested so that the results of the RARE and woolly stem gall analysis could be compared with a system known to be structured around the abundances of dominant species.

TABLE 2. Correlation coefficients for tests between per cent parasitism by one species and per cent parasitism by all co-occurring species in the RARE + woolly stem gall sub-community (RARE + WS) and the tumour stem + blister leaf gall sub-community (TS + BL).

Species	TS + BL		RARE + WS	
	No. of samples	<i>r</i>	No. of samples	<i>r</i>
<i>Eupelmid</i> sp.	—		20	— 0.343 ^{ns}
<i>Galeopsomyia</i> sp. A	14	— 0.050 ^{ns}	19	— 0.294 ^{ns}
<i>Pseudocatolaccus gulzoti</i>	10	— 0.705*	19	0.001 ^{ns}
<i>Rileya piercei</i>	11	— 0.638*	9	— 0.490 ^{ns}
<i>Rileya regularis</i>	34	— 0.692**	48	— 0.352*
<i>Spilochalcis</i> sp.	—		27	— 0.355 ^{ns}
<i>Tenuipetolus medicagnus</i>	36	— 0.643**	40	— 0.224 ^{ns}
<i>Tetrastichus cecidobroter</i>	76	— 0.853**	16	— 0.709**
<i>Tetrastichus</i> sp. B	43	— 0.905**	33	— 0.338 ^{ns}
<i>Torymus atriplicis</i>	8	— 0.786*	22	— 0.348 ^{ns}
<i>Torymus capillaceus</i>	52	— 0.632**	72	— 0.283*
<i>Torymus umbilicatus</i>	12	— 0.364 ^{ns}	19	— 0.292 ^{ns}
All species pooled	298	— 0.826	344	— 0.448

* $P < 0.05$; ** $P < 0.01$; ^{ns} = non-significant.

In the tumour stem and blister leaf galls, eight of the ten species were significantly negatively correlated with their competitors (Table 2). When the data were pooled and all species tested simultaneously, the correlation was very strong ($r = -0.826$), although the significance of this value could not be tested because of a partial loss of independence among the data when species were pooled. Therefore, density compensation appears to be widespread in these galls, with most species responding to the population levels of *Tetrastichus cecidobroter* and *Tetrastichus* sp. B.

In the RARE + WS sub-community, only three of the twelve correlations were significant, although there was a negative trend in all others save one. These results suggest that parasitoids might be responding to the levels of co-occurring species to some extent, but the abundances of many species fluctuate independently.

Despite the absence of strong population-level interactions among the species utilizing the RARE and woolly stem galls, the parasitoids do not necessarily represent random assemblages of species (Fig. 7) (see Table 1 for site codes and Fig. 1 for gall codes). In five of the seven cases in the Colorado Desert and chaparral, *Torymus capillaceus* was the dominant parasitoid, followed

in each case by *Rileya tegularis*. The oval bud galls differed from the others by supporting a large number of *Tetrastichus cecidobroter*, the only case where a RARE gall was heavily attacked by a *canescens*-specialist. However, *T. capillaceus* was the dominant parasitoid attacking this gall type. The club stem gall did not support *T. capillaceus*, and *R. tegularis* was the most abundant parasitoid. Therefore, although abundance patterns for the less common parasitoids varied from site to site and gall to gall, a fairly stable dominance hierarchy was apparent in the galls of the Colorado Desert and chaparral. In the Mojave Desert, on the other hand, no pattern was discernible (Fig. 7), and a different species dominated each site.

Host phenology and community structure

The gall-forming *Asphondylia* spp. require c. 8 weeks for development, and the species range from univoltine to multivoltine with overlapping generations. These differences in phenology were associated with differences in the relative abundances of the associated parasitoids. Dominance of the major parasitoid species significantly increased with lengthening duration of gall availability at each site (Fig. 8). Most para-

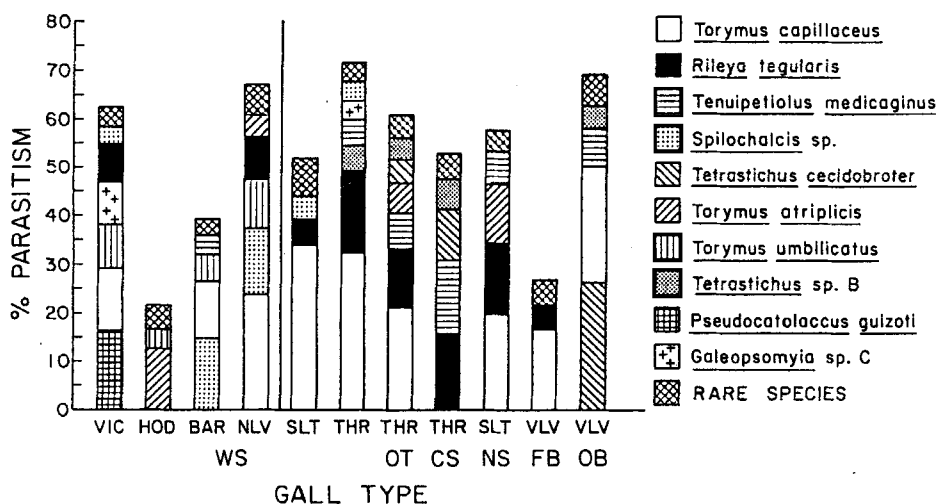


FIG. 7. Relative abundances of parasitoids in the RARE and woolly stem galls at each site during 1979–80. Within each data set, species are ranked from most abundant (bottom) to rarest (top). Rare species accounting for less than 4% total parasitism over the year were pooled. The four sites to the left of the vertical line are in the Mojave Desert, and those to the right are in the Colorado Desert and chaparral.

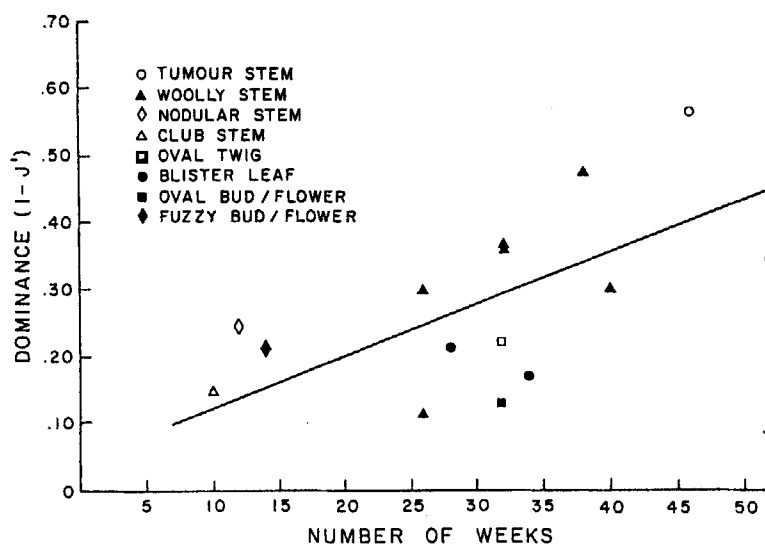


FIG. 8. Relationship between dominance in the parasitoids reared from each *Atriplex* gall and the number of weeks galls occurred. ($y = 0.004 + 0.008x$; $r = 0.679$ ($P < 0.01$).)

sitoids had several generations in multivoltine galls. When galls first appeared in the field, initial parasitoid populations were low, species colonized galls more or less equally and, consequently, dominance was low. However, as hosts remained available for longer periods, parasitoid populations increased, and some species became relatively more abundant. This dominance was expressed most strongly in tumour stem galls by the gall-forming *T. cecidobroter*. Dominance in the blister leaf gall was relatively low, because two species dominated the fauna rather than a single species. (This analysis was repeated using Simpson's (1949) λ to ensure that the result was not 'index dependent'. The correlation remained significant ($r = 0.554$, $P < 0.05$), although the relationship was curvilinear rather than linear).

The association of dominance by parasitoids with seasonality suggests that the intensity of competition between parasitoid species ranges from low in highly ephemeral galls to high in galls that are continuously available to parasitoids. This is also indicated by the large number of significant negative correlations in parasitism levels among the parasitoids in the tumour stem and blister leaf galls compared to those in the RARE and woolly stem galls (Table 3).

Host seasonality is also believed to be

TABLE 3. *Atriplex* gall distributions in 1980–81.

Gall	Area (km ²)
Woolly stem	421
Oval twig	190
Tumour stem	150
Blister leaf	107
Oval bud	15
Fuzzy bud	15
Nodular stem	5
Club stem	5–50

primarily responsible for parasitoid guild structure. Fig. 9 illustrates the phenologies of each of the gall types in 1979–80. These phenologies are summarized over all areas within the range of this study, thereby representing overall phenologies in contrast to those at specific sites as in Fig. 8. The phenological patterns of 1979–80 were consistent with additional observations during 1980–82, although exact dates of appearance and disappearance varied from year to year.

The tumour stem and blister leaf galls are the only galls available year round and are the major resources for the *canescens*-specialist parasitoid guild. All other galls are seasonal and are dominated by generalist species. This suggests that some parasitoids have specialized on hosts which allow for con-

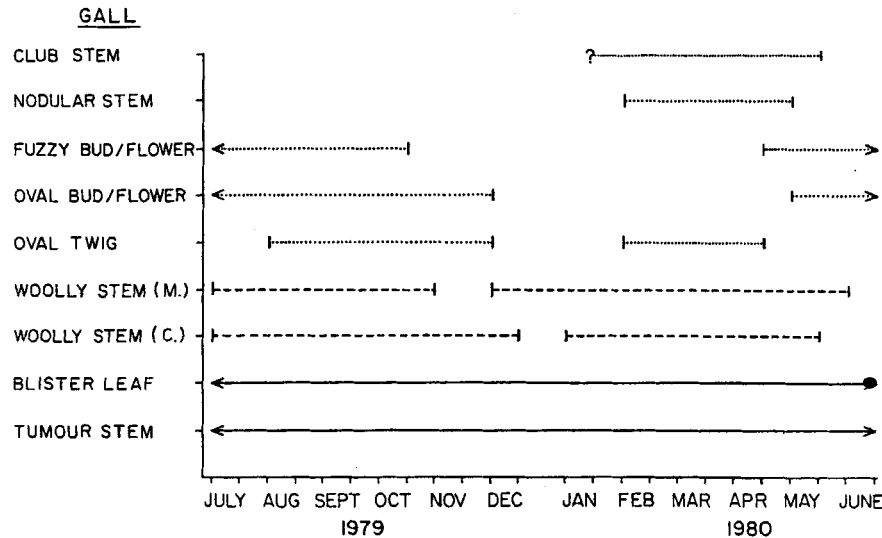


FIG. 9. Generalized phenologies of *Atriplex* galls in 1979-80. (M = Mojave Desert, C = Colorado Desert.)

tinuous utilization, while others maintain wider host ranges and utilize ephemeral hosts.

The woolly stem gall represents an intermediate case between the more ephemeral RARE galls and the continuous tumour stem and blister leaf galls. These galls are available for 9-10 months at some sites, and support a specialist guild which in terms of abundance is sub-dominant to the generalist guild also attacking these galls.

The basic assumption of the hypothesis that the parasitoids have specialized on continuously available hosts but will behave as generalists on ephemeral hosts is that parasitoids are maximizing the period of time that they are able to reproduce. If a parasitoid species occurs only part of the year, the presence of its host during periods when parasitoids are not present is irrelevant, and host seasonality cannot be the driving force behind host utilization patterns. Therefore, if *canescens*-specialists are seasonal, it is unlikely that they utilize tumour stem and blister leaf galls because of their continuous availability. Furthermore, if generalists avoid disruption of their reproduction on seasonal hosts by shifting hosts, they should also occur the year round. Lastly, if woolly stem gall specialists utilize this gall primarily because of its availability, parasitoid phenologies should be coupled with the phenology of the

gall. Parasitoid guild structure was determined on the basis of emergence patterns without regard to phenologies; the relative abundances of species was determined solely from the total number of individuals reared over the year. Therefore, a comparison of host and parasitoid phenologies provides a partially independent test of the hypothesis.

Fig. 10 gives the rearing patterns for each of the species in the three guilds, expressed as the proportion of the total number of individuals of the species reared each month. Among the *canescens*-specialists (Fig. 10A), the two dominant species, *Tetrastichus cecidobroter* and *Tetrastichus* sp. B, were reared every month. The three uncommon species were reared sporadically and were absent in some months. Only *Tetrastichus* sp. A was absent two months in a row. However, in no cases were these parasitoids highly seasonal. Four of the five generalists were also collected throughout the year (Fig. 10B) (the bimodal distributions in their numbers reflected the seasonal availability of most of the galls). Only *Torymus atriplicis* was highly seasonal, having a single generation in the spring. Therefore, of the ten species in these two guilds, nine maintained essentially continuous populations in the field. This pattern at least does not contradict the resource stability hypothesis.

Woolly stem gall specialists (Fig. 10C)

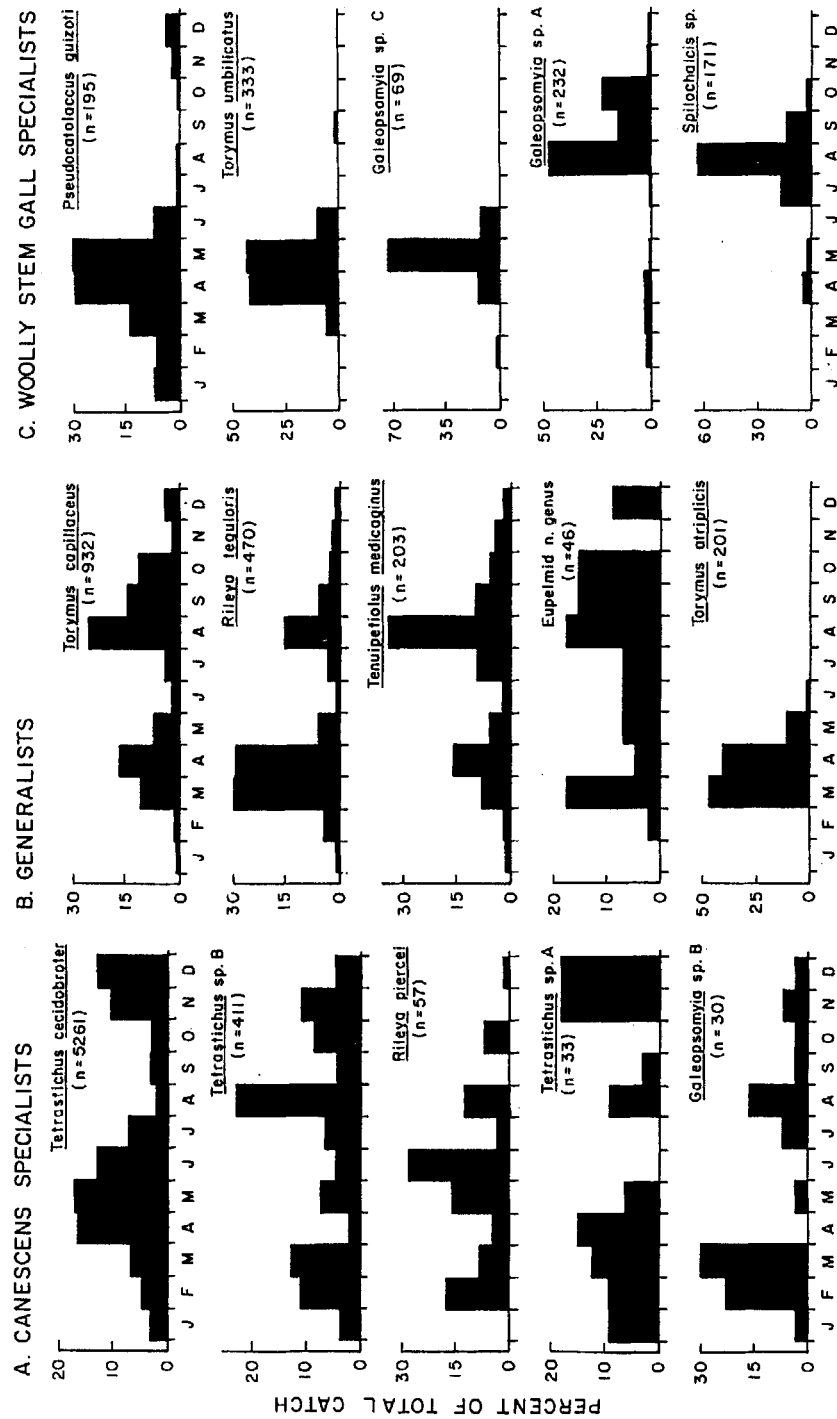


FIG. 10. Phenologies of gall parasitoids, expressed as the proportion of the total number of individuals reared each month.

showed a mixed pattern of seasonality. Only two species, *Pseudocatolaccus quizoti* and *Galeopsomyia* sp. A, display a degree of non-seasonality. Unlike the species in the other guilds, all five of these species had unimodal distributions, occurring primarily in either the spring or autumn. Most of these species did not utilize the woolly stem galls for as long as the galls were available, suggesting that the resource stability hypothesis does not apply to this guild.

The woolly stem gall specialists may represent a competitively inferior, fugitive guild of parasitoids. These specialists were more common at sites where woolly stem galls occurred alone (Fig. 11). At the two Colorado Desert sites that supported several RARE galls (and blister leaf galls at one site), woolly stem gall specialists accounted for 13–15% of the total parasitoid complex. At the four Mojave Desert sites where RARE galls were absent, woolly stem gall specialists accounted for 28–60% of all parasitoids. These differences were significant ($t = 3.33$, $P < 0.05$, arcsine transformed). Sites supporting many gall types, all of which were dominated by generalists, provided reservoirs for generalist populations. When the woolly stem galls

appeared at these sites, generalists attacked these galls rapidly, perhaps preventing specialists from achieving high population levels. At sites where woolly stem galls occurred alone, local reservoirs for parasitoids did not exist and colonization was variable (see Fig. 7). Presumably, the absence of resident generalist populations afforded specialists the opportunity to attain higher abundances.

If woolly stem gall specialists are competitively inferior to generalists and can be successful only at sites where they can escape from generalists, the woolly stem gall may represent the only resource available to these species. Distribution maps of *Atriplex* galls for 1981 and 1982 indicated that the woolly stem gall was the most widely distributed gall type (Table 3), primarily on the Mojave Desert. Also, the woolly stem gall was the only gall that occurred alone. All other galls were sympatric with at least one other gall type. Therefore the woolly stem gall specialists may utilize the woolly stem gall opportunistically, not because of any special adaptations to these galls.

Discussion

The success of dominant wasp species attacking *Atriplex* galls may be largely due to two biological attributes, mode of feeding (phytophagy and facultative hyperparasitism) and voltinism. Inquilines are important components of many gall communities, and can cause most of the mortality of the gall former (Caltagirone, 1964; Evans, 1967; Shorthouse, 1973; Washburn & Cornell, 1981; Ito & Hattori, 1982). Three of the seven inquilines known in *Atriplex* galls have a significant impact on *Asphyondylia* populations. The gelechiid species occurring in the fuzzy bud gall tunnels through the gall feeding on gall tissue. Although the midge larva is usually not killed directly, it frequently dies because the gall deteriorates. The two wasps, *Galeopsomyia* sp. A and *T. cecidobroter*, on the other hand, cause almost complete midge mortality in attacked galls. Both species of wasps oviposit in midge larval cavities. The phytophagous *Galeopsomyia* sp. A kills the midge by crowding it out of its larval cavity, while with *T. cecidobroter* the

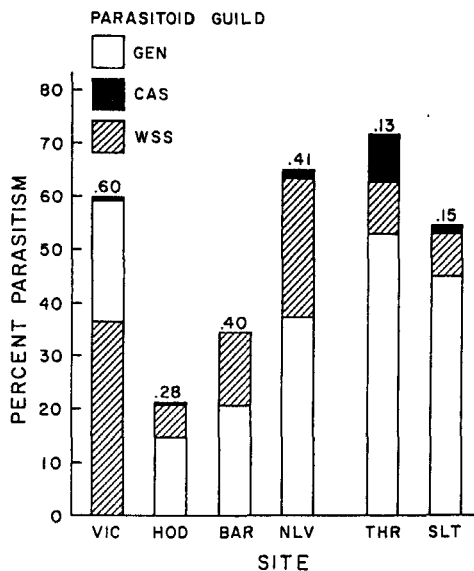


FIG. 11. Per cent parasitism by parasitoid guild in the woolly stem galls at six sites. Numbers above bars are the proportion of the total parasitoid complex belonging to the woolly stem gall specialist guild.

midge larva is crushed by the developing endogall (Hawkins & Goeden, 1982).

Gahan (1922) has made a strong case that phytophagous and cecidogenic species of Chalcidoidea have arisen secondarily from parasitoids of endophytic hosts, and both of the inquiline wasps in *Atriplex* are probably derived from parasitic forms. Of the c. 700 species of *Tetrastichus*, three are known to be phytophagous, and only one other species forms galls (Ishii, 1931). An outgroup comparison (Watrous & Wheeler, 1981) of the other nineteen, almost exclusively parasitic genera (including *Galeopsomyia*) comprising the sub-family Tetrastichinae provides strong evidence that cecidogenesis in *Tetrastichus* is a derived characteristic. Furthermore, it is unlikely that a gall-forming wasp would become obligatorily associated with midges not required for wasp development. Although avoidance of competition with other gall-inhabiting wasps cannot be proven to be the selective force responsible for the evolution of this highly unusual mode of development, the result is that *T. cecidobroter* populations can increase unrestrained by the actions of other members of the gall community.

Galeopsomyia is poorly known, but both described species from North America are parasitic (Burks, 1979a). Of the five *Galeopsomyia* spp. associated with *Atriplex* galls, only *Galeopsomyia* sp. A is phytophagous.

Phytophagy also increases the amount of food available to wasp larvae. Both inquilines are gregarious; up to nine *T. cecidobroter* and seven *Galeopsomyia* sp. A develop in each midge larval cavity. All of the parasitic wasps in *Atriplex* galls are solitary.

A mixed entomophagous-phytophagous feeding habit may also be an important component of parasitoid success. *Torymus capillaceus* and *Rileya tegularis*, the most abundant generalists, completely consume the midge larvae and complete their development by feeding on gall tissue. *Torymus capillaceus* larvae feed externally and rapidly kill the host midges (early second instars to pupae). *Rileya tegularis* attacks first to early second instar midges. The parasitoid larvae initially develop internally and slowly, not killing the host until it has reached the late third instar. The parasitoids then develop

rapidly, completely consume the internal tissues, burst the host integument (which is also consumed) and complete development as a phytophage.

As with the inquilines, phytophagy provides a parasitoid larva with more food than is available to a strict parasitoid. Consequently, the larvae of *T. capillaceus* and *R. tegularis* larvae grow much larger than do those of the other generalists. Larval size is important in cases of intraspecific competition, as larger larvae usually kill smaller conspecifics (Salt, 1961). Although the morphological and behavioural adaptations conferring competitive abilities on parasitoids are complex, the large larval sizes attained by *T. capillaceus* and *R. tegularis* may partly explain their success in most of the galls in 1979–80. The relative abundances of these two species remained high through 1982. Samples of woolly stem, oval twig and nodular stem galls collected for dissection from the Coachella Valley in 1981 and 1982 were consistently dominated by either *T. capillaceus* or *R. tegularis*. Oval twig galls taken at Mecca and near Thermal (11.6 km apart) in October 1982 and held for adult emergence showed patterns similar to those seen in 1980. *Torymus capillaceus* and *R. tegularis* accounted for 90.4% of the total parasitoid sample ($n = 397$) at Mecca and 91.7% ($n = 205$) near Thermal. Furthermore, total per cent parasitism at Mecca and near Thermal were similar (49.0% and 40.9%, respectively). The relative abundances of the eight parasitoid species reared from these galls were also virtually identical, with per cent parasitism by each species highly correlated between the sites ($r = 0.987$, $P < 0.01$). In March 1981, *T. capillaceus* and *R. tegularis* accounted for 61.2% of the parasitoids ($n = 212$) in nodular stem galls at Torres Martinez Indian Reservation, with 52.4% total parasitism.

The relative abundances of the two dominant generalists typically reverse as gall midge populations age. Because *R. tegularis* attacks first instars, this parasitoid often dominates early in the gall midges' development (Fig. 12). However, *T. capillaceus* rapidly accumulates, with a concomitant decrease in the abundance of *R. tegularis*. This pattern was probably responsible for the significant

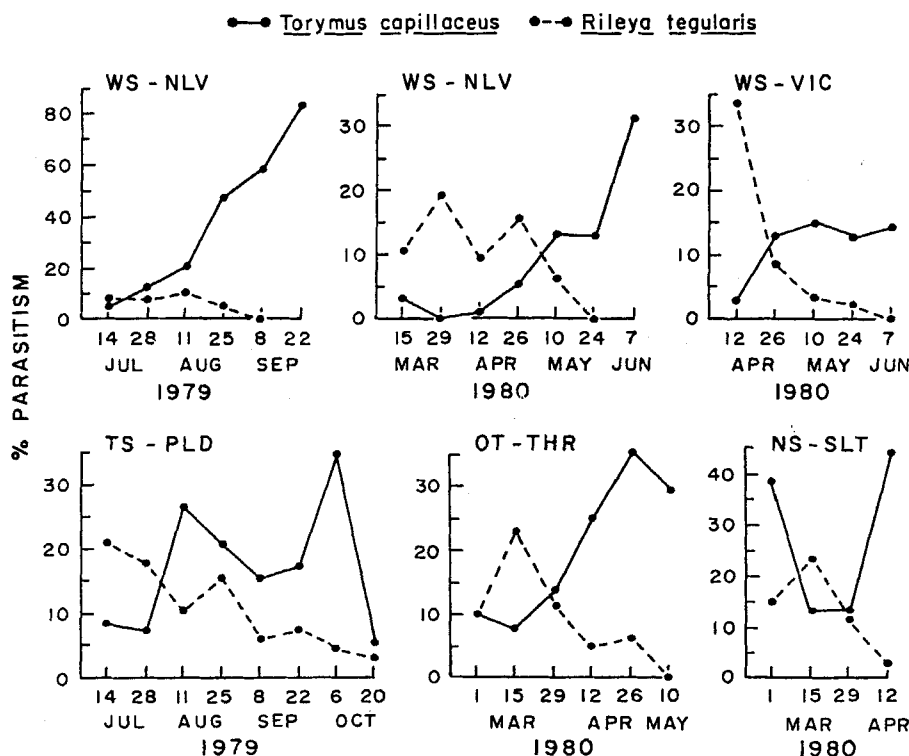


FIG. 12. Bi-weekly abundances of *Torymus capillaceus* and *Rileya tegularis* in four gall types at five sites in 1979 and 1980. (WS = woolly stem gall; TS = tumour stem gall; OT = oval twig gall; NS = nodular stem gall.) See Table 1 for sites.

negative correlations between the levels of parasitism by these species against parasitism by all co-occurring species in the RARE and woolly stem galls (Table 2). A shift in the abundances of *R. tegularis* and *T. capillaceus* was also observed in the tumour stem galls from July to October 1979 (Fig. 12) until 20 October, when parasitoid populations were reduced by the actions of *T. cecidobroter*. The consistent dominance of *T. capillaceus* over *R. tegularis* in all galls where they co-occurred (see Fig. 7) reflects the advantage of facultative hyperparasitism. *Torymus capillaceus* larvae feed on early instar midges in which *R. tegularis* larvae are developing and directly on *R. tegularis* larvae that have consumed their midge host. This characteristic gives *T. capillaceus* larvae an unambiguous competitive advantage.

Voltinism may also play a major role in determining parasitoid success. Five of the six univoltine parasitoids were clustered in the woolly stem gall specialist guild. There are

few *a priori* reasons why a seasonal parasitoid would be unable to compete with non-seasonal species. However, if competition for hosts is frequent and strong enough to select for traits conferring competitive success, multivoltine species should have an advantage over univoltine species which cannot respond to selection as rapidly. Also, unless the breaking of diapause in univoltine parasitoids is closely synchronized with the appearance of their hosts, females of non-seasonal species would have a greater chance of colonizing the new galls first. This advantage to non-seasonal parasitoids would be greatest when they are already at a site utilizing alternate hosts.

Washburn & Cornell (1979, 1981) reported that host-shifting from alternate hosts was a major organizing force of the parasitoid communities associated with the cynipids on *Quercus prinus* L. and *Q. stellata* Wang. and suggested that this might be the general pattern in cynipid galls. This pattern is also

evident in the *Atriplex* gall complex. Parasitoids occurring at sites supporting several RARE and woolly stem galls or RARE and blister leaf or tumour stem galls have some hosts available essentially the year round. As the seasons progress and each gall type appears and disappears, generalist parasitoid populations already established can shift from one host to the next. Once a dominance hierarchy is established on one host, this hierarchy may be maintained when new galls are colonized. However, at sites supporting only seasonal hosts, parasitoid populations become locally extinct when hosts diapause, because the *Asphondylia* spp. diapause as eggs, which none of the parasitoids can utilize. Furthermore, with the exception of *T. cecidobroter*, *Atriplex* gall parasitoids do not diapause inside old galls. Recolonization varies from site to site depending on the distance colonizing females have to travel, on local host densities and perhaps on the availability of non-*Atriplex* hosts. The unpredictable parasitoid complexes found at the Mojave Desert sites (Fig. 7) suggest that the presence of several hosts is required to stabilize the parasitoid community.

Gall structure is an important organizing force on parasitoids attacking cynipid galls on oaks (Askew, 1961), and the diversity of cynipid galls may be an evolutionary response by gall-formers to escape attack by portions of their parasitoid complex. This acquisition of enemy-free space allows the co-existence of many cynipid galls in spite of high rates of parasitism (Askew, 1980). However, the morphological characteristics of galls on *Atriplex* do not appear to affect the host utilization patterns of most of the parasitoids. The three major generalist species, *Torymus capillaceus*, *Rileya tegularis* and *Tenuipetiolus medicaginus*, occur in seven of the eight *Asphondylia* galls and do about equally well, at least in the Colorado Desert and chaparral (Fig. 7). Therefore the idea that a diversity of gall morphologies circumvents parasite searching patterns by appearing different from other sympatric potential hosts (Price, 1980) does not appear applicable to this gall system.

Although gall morphology apparently does not affect the host spectrum of most of the

parasitoids, the structure of the fuzzy bud gall (thick gall walls covered by a dense mat of trichomes) may exclude some parasitoids. This gall type supported only five species of midge parasitoids in 1979, the least of any gall type. Fuzzy bud gall structure may also limit the efficiencies of species that attack that gall. In 1979 the level of parasitism was the lowest (28.0%) of any gall in the chaparral. Samples taken in 1982 revealed a parasitism rate of 16.8%, indicating that the fuzzy bud gall may be consistently parasitized less than any other gall on *Atriplex*. However, the characteristics that deter parasitoids seem to attract inquilines. In September 1979, fifty-five of 189 galls (29.1%) were infested with gelechiid sp. B. In the final 1982 sample, the midges in twenty-three of seventy-nine fuzzy bud galls (29.1%) had apparently been killed by the inquiline.

In general, gall structure does not appear to be a major organizing force of the *Atriplex* gall parasitoid community. That the structure of galls formed by Cecidomyiidae does not strongly influence the associated parasitoids has also been observed in leaf galls on birch (Askew & Ruse, 1974).

The difference between 'specialist' and 'generalist' parasitoids is a matter of degree rather than kind. Few of these species can be considered specialists in the strict sense (see Price, 1984). The distinction between generalist and specialist guilds is not necessarily indicative of the absolute number of gall types that the parasitoids attack. Generalists occurred in a mean (± 1 SD) of 5.8 (± 2.17) gall types, while *canescens* specialists occurred in 5.4 (± 1.10) gall types. Only woolly stem gall specialists showed any degree of absolute host restriction ($\bar{x} = 3.2$, SD = 0.84). Instead, guild structure reflects that specialists were successful in only a few galls while generalists were successful in many galls.

There is indirect evidence that the generalist versus specialist strategies we recognize within the *Atriplex* gall complex may be applicable to these parasitoids in general, at least for the non-fugitive species. The galls of *Atriplex* constitute a fraction of the potential hosts of these parasitoids. If those species which act as generalists in *Atriplex* are true generalists, they should also occur

TABLE 4. Known alternate hosts of *Atriplex* gall chalcidoids.

Species	Host (with associated plant)	Source
GENERALISTS		
<i>Torymus capillaceus</i>	<i>Asphondylia</i> spp. (<i>Larrea divaricata</i> Cav. (Zygophyllaceae))	Grissell, 1976
	<i>Asphondylia</i> sp. (<i>Hymenoclea salsola</i> T. & G. (Asteraceae))	Hawkins, unpubl.
	Cecidomyiid sp. (<i>Artemisia</i> sp. (Asteraceae))	Huber, 1927
	Cecidomyiid sp. (<i>Rhus copallina</i> L. (Anacardiaceae))	Grissell, 1976
	<i>Procidochares</i> sp. (<i>Ambrosia dumosa</i> (Gray) Payne (Asteraceae))	Silverman & Goeden, 1980
	In seed pods (<i>Prosopis</i> sp. (Fabaceae))	Grissell, 1976
<i>Rileyia regularis</i>	<i>Asphondylia illicicola</i> (<i>Ilex opaca</i> Alton (Aquifoliaceae))	Highland, 1964
	<i>Asphondylia</i> spp. (<i>Larrea divaricata</i>)	Waring, unpubl.
	<i>Asphondylia</i> sp. (<i>Hymenoclea salsola</i>)	Hawkins, unpubl.
<i>Tenuipetiolus medicaginus</i>	<i>Asphondylia mentzeliae</i> Ckll. (<i>Mentzelia</i> sp. (Loasaceae))	Burks, 1979b
	<i>Asphondylia websteri</i> Felt (<i>Medicago sativa</i> L. (Fabaceae))	Gahan, 1919
<i>Torymus atriplicis</i>	<i>Asphondylia</i> sp. (<i>Hymenoclea salsola</i>)	Hawkins, unpubl.
<i>Eupelmid</i> sp.	Cecidomyiid sp. (<i>Ambrosia dumosa</i>)	Goeden, unpubl.
	Lepidopterous leaf miner (<i>Eriodictyon</i> sp. (Hydrophyllaceae))	Gibson, pers. comm.
	Mantid egg case	Gibson, pers. comm.
CANESCENS-SPECIALISTS		
<i>Tetrastichus cecidobroter</i>	None	
<i>Tetrastichus</i> sp. B *	None	
<i>Rileyia piercei</i>	None	
<i>Tetrastichus</i> sp. A *	None	
<i>Galeopsomyia</i> sp. B *	None	
WOOLLY STEM GALL SPECIALISTS		
<i>Torymus umbilicatus</i>	<i>Asphondylia</i> sp. (<i>Clematis drummondii</i> T. & G. (Ranunculaceae))	Grissell, 1976
	<i>Asphondylia</i> sp. (<i>Hymenoclea salsola</i>)	Hawkins, unpubl.
	<i>Asphondylia</i> spp. (<i>Larrea divaricata</i>)	Grissell, 1976
	Cecidomyiid sp. (<i>Ambrosia</i> sp.)	Grissell, 1976
	Cecidomyiid sp. (<i>Amsinckia douglasiana</i> A. DC. (Boraginaceae))	Grissell, 1976
	Cecidomyiid sp. (<i>Mimulus</i> sp. (Scrophulariaceae))	Grissell, 1976
	Cecidomyiid sp. (<i>Suaeda</i> sp. (Chenopodiaceae))	Grissell, 1976
	In flower heads (<i>Senecio douglasii</i> DC. (Asteraceae))	Grissell, 1976
	In flower heads (<i>Viguiera deltoidea</i> Gray (Asteraceae))	Grissell, 1976
	<i>Lasiopoda</i> sp. (<i>Aster spinosus</i> Benth. (Asteraceae))	Grissell, 1976
	Tephritid sp. (<i>Eupatorium adenophorum</i> Spreng. (Asteraceae))	Grissell, 1976
<i>Spilochaetis</i> sp.	<i>Asphondylia</i> sp. (<i>Hymenoclea salsola</i>)	Hawkins, unpubl.
<i>Pseudocatolaccus guizoti</i>	<i>Asphondylia</i> spp. (<i>Larrea divaricata</i>)	Waring, unpubl.
<i>Galeopsomyia</i> sp. A *	None	
<i>Galeopsomyia</i> sp. C *	None	

* Undescribed species.

in other hosts. Alternatively, if *canescens*-specialists are known from many alternative hosts, it is unlikely that any special adaptations for the galls of *A. canescens* account for their success.

Table 4 lists the known hosts of each of the fifteen parasitoids. All five generalists are known from at least one non-*Atriplex* host, and four species have at least two alternate hosts. The five *canescens*-specialists, on the other hand, have no known alternate hosts. Host lists are not available for undescribed species, but that three species are undescribed suggests that they are not widespread on non-*Atriplex* hosts. *Tetrastichus cecidobroter* was described during the course of this study (Gordh & Hawkins, 1982). *Rileyia piercei* Crawford is known from a single, non-reared specimen from Arizona (Crawford, 1919).

The woolly stem gall specialists are inconsistent in their use of alternate hosts. *Torymus umbilicatus* has the broadest known host range of any *Atriplex* gall parasitoid. Two species have no known alternative hosts, suggesting that this guild may include species restricted to *Atriplex* as well as opportunists. Within each guild, the most abundant species in 1979–80 also has the broadest known host range (*T. cecidobroter* had the broadest within-*Atriplex* host range in 1979–80, being the only specialist found in seven gall types), a commonly observed pattern (McNaughton & Wolf, 1970).

Parasitoid communities often show little evidence of internal structure (Force, 1970; Legner & Olton, 1971; Ables & Shepard, 1976), perhaps because parasitoid communities are usually organized around ephemeral hosts (Washburn & Cornell, 1979, 1981). Because of the presence of some non-ephemeral hosts, the *Atriplex* gall complex offers a unique system for evaluating the effects of resource stability on parasitoids. Ephemeral hosts are dominated by parasitoids which tend to be general in host associations and feeding habits. Woolly stem galls may offer a refuge for opportunists and more specialized species unable to compete with aggressive generalists, because these galls are widely distributed and are available to parasitoids most of the year. The most obvious difference between these two guilds

of parasitoids is that the specialists are primarily univoltine, while generalists are primarily multivoltine. The domination of univoltine, host-specific parasitoids by multivoltine, non-specific species attacking seasonal hosts duplicates the pattern found in cynipid galls on oaks (Askew, 1975).

Force (1974) has suggested that community structure in parasitoid assemblages is the haphazard result of competitive jostling as some species carve their niches from broader niches occupied by more 'r-selected' species. The results of this study support this idea. The *Atriplex* gall community is dominated by aggressive generalist parasitoids. At least some parasitoids occupy a portion of the generalists' niches in the tumour stem and blister leaf galls. Others apparently depend on the chance colonization of woolly stem galls to avoid the generalists. Competition appears to be the driving force behind these patterns, although the intensity of competition that currently exists can range from low to very high, depending on the situation.

Acknowledgments

We thank E. E. Grissell for identification of the chalcidoids. D. C. Force, P. W. Price and T. R. Unruh made valuable comments on drafts of this manuscript.

References

- Ables, J.R. & Shepard, M. (1976) Seasonal abundance and activity of indigenous hymenopterous parasitoids attacking the house fly (Diptera: Muscidae). *Canadian Entomologist*, 108, 841–844.
- Askew, R.R. (1961) On the biology of the inhabitants of oak galls of Cynipidae (Hymenoptera) in Britain. *Transactions of the Society for British Entomology*, 14, 237–268.
- Askew, R.R. (1975) The organization of chalcid-dominated parasitoid communities centred upon endophytic hosts. *Evolutionary Strategies of Parasitic Insects and Mites* (ed. by P. W. Price), pp. 130–153. Plenum Press, New York.
- Askew, R.R. (1980) The diversity of insect communities in leaf-mines and plant galls. *Journal of Animal Ecology*, 49, 817–829.
- Askew, R.R. & Ruse, J.M. (1974) The biology of some Cecidomyiidae (Diptera) galling the leaves

- of birch (*Betula*) with special reference to their chalcidoid (Hymenoptera) parasites. *Transactions of the Royal Entomological Society of London*, 126, 129–167.
- Bouton, C.E., McPherson, B.A. & Weis, A.E. (1980) Parasitoids and competition. *American Naturalist*, 116, 876–881.
- Brower, J.E. & Zar, J.H. (1977) *Field and Laboratory Methods for General Ecology*. W. C. Brown Co., Dubuque.
- Burks, B.D. (1979a) Family Eulophidae, *Catalog of Hymenoptera in America North of Mexico* (ed. by K. V. Krombein *et al.*), pp. 967–1022. Smithsonian Institution Press, Washington, D.C.
- Burks, B.D. (1979b) Family Eurytomidae, *Catalog of Hymenoptera in America North of Mexico* (ed. by K. V. Krombein *et al.*), pp. 835–860. Smithsonian Institution Press, Washington, D.C.
- Caltagirone, L.E. (1964) Notes on the biology, parasites, and inquilines of *Pontania pacifica* (Hymenoptera: Tenthredinidae), a leaf-gall incitant on *Salix lasiolepis*. *Annals of the Entomological Society of America*, 57, 279–291.
- Cody, M.L. (1974) *Competition and the Structure of Bird Communities*. Princeton University Press.
- Crawford, J.C. (1919) Two new parasitic Hymenoptera from Arizona. *Proceedings of the Entomological Society of Washington*, 16, 29.
- Dean, J.M. & Ricklefs, R.E. (1979) Do parasites of Lepidoptera larvae compete for hosts? *Nol American Naturalist*, 113, 302–306.
- Dean, J.M. & Ricklefs, R.E. (1980) Do parasites of Lepidoptera larvae compete for hosts? No evidence. *American Naturalist*, 116, 882–884.
- DeBach, P. & Sundby, R.A. (1963) Competitive displacement between ecological homologues. *Hilgardia*, 34, 105–166.
- Ehler, L.E. (1978) Competition between two natural enemies of Mediterranean black scale on olive. *Environmental Entomology*, 7, 521–523.
- Ehler, L.E. (1979) Assessing competitive interactions in parasitic guilds prior to introduction. *Environmental Entomology*, 8, 558–560.
- Evans, D. (1967) The bisexual and agamic generations of *Besbicus mirabilis* (Hymenoptera: Cynipidae), and their associated insects. *Canadian Entomologist*, 99, 187–196.
- Force, D.C. (1970) Competition among four hymenopterous parasites of an endemic insect host. *Annals of the Entomological Society of America*, 63, 1675–1688.
- Force, D.C. (1972) *r*- and *K*-strategists in endemic host-parasitoid communities. *Bulletin of the Entomological Society of America*, 18, 135–137.
- Force, D.C. (1974) Ecology of insect host-parasitoid communities. *Science*, 184, 624–632.
- Force, D.C. (1980) Do parasitoids of Lepidoptera larvae compete for hosts? Probably! *American Naturalist*, 116, 873–875.
- Foster, D.E. (1981) A new species of *Phyllobaenus* (Coleoptera: Cleridae). *Journal of the Kansas Entomological Society*, 54, 661–664.
- Gagné, R.J. & Hawkins, B.A. (1982) Biosystematics of the Lasiopterini (Diptera: Cecidomyiidae: Cecidomyiinae) associated with *Atriplex* spp. (Chenopodiaceae) in southern California. *Annals of the Entomological Society of America*, 76, 379–383.
- Gahan, A.B. (1919) Some chalcid-wasps reared from cecidomyid galls. *Annals of the Entomological Society of America*, 12, 159–170.
- Gahan, A.B. (1922) A list of phytophagous Chalcidoidea with descriptions of two new species. *Proceedings of the Entomological Society of Washington*, 24, 33–58.
- Gordh, G. & Hawkins, B.A. (1982) *Tetrastichus cecidobroter* (Hymenoptera: Eulophidae), a new phytophagous species developing within the galls of *Asphondylia* (Diptera: Cecidomyiidae) on *Atriplex* (Chenopodiaceae) in southern California. *Proceedings of the Entomological Society of Washington*, 84, 426–429.
- Grissell, E.E. (1976) A revision of western nearctic species of *Torymus* Dalman (Hymenoptera: Torymidae). *University of California Publications in Entomology*, Vol. 79.
- Hawkins, B.A. & Goeden, R.D. (1982) Biology of a gall-forming *Tetrastichus* (Hymenoptera: Eulophidae) associated with gall midges on saltbush in southern California. *Annals of the Entomological Society of America*, 75, 444–447.
- Highland, H.A. (1964) Life history of *Asphondylia illeicola* (Diptera: Cecidomyiidae), a pest of American holly. *Journal of Economic Entomology*, 57, 81–83.
- Huber, L.L. (1927) A taxonomic and ecological review of the North American chalcid-flies of the genus *Callimone*. *Proceedings of the United States Natural History Museum*, 70, 1–114.
- Ishii, T. (1931) Notes on the phytophagous habits of some chalcidoids, with descriptions of two new species. *Kontyu*, 5, 132–138.
- Ito, Y. & Hattori, I. (1982) A kleptoparasitic moth, *Nola innocua*, attacking aphid galls. *Ecological Entomology*, 7, 475–478.
- Legner, E.F. & Olton, G.S. (1971) Distribution and relative abundance of dipterous pupae and their parasitoids in accumulations of domestic animal manure in the southwestern United States. *Hilgardia*, 40, 505–535.
- Luck, R.F. (1976) Bionomics and parasites of a needle miner, *Coleotechnites* sp., infesting Jeffrey pine in southern California. *Environmental Entomology*, 5, 937–942.
- MacArthur, R.H. (1972) *Geographical Ecology*. Harper & Row, New York.
- McNaughton, S.J. & Wolf, L.L. (1970) Dominance and the niche in ecological systems. *Science*, 167, 131–139.
- Osmond, C.B., Björkman, O. & Anderson, D.J. (1980) *Physiological Processes in Plant Ecology. Toward a Synthesis with Atriplex*. Springer, Berlin.
- Parnell, J.R. (1964) Investigations on the biology and larval morphology of the insects associated with the galls of *Asphondylia sarothamni* H. Loew. (Diptera: Cecidomyiidae) on broom

- (*Sarothamnus scoparius* (L.) Wimmer.). *Transactions of the Royal Entomological Society of London*, 116, 255–273.
- Pianka, E.R. (1973) The structure of lizard communities. *Annual Review of Ecology and Systematics*, 4, 53–74.
- Pielou, E.C. (1966) The measurement of diversity in different biological collections. *Journal of Theoretical Biology*, 13, 131–144.
- Price, P.W. (1970) Characteristics permitting coexistence among parasitoids of a sawfly in Quebec. *Ecology*, 51, 445–454.
- Price, P.W. (1971) Niche breadth and dominance of parasitic insects sharing the same host species. *Ecology*, 52, 587–596.
- Price, P.W. (1980) *Evolutionary Biology of Parasites*. Princeton University Press.
- Price, P.W. (1984) Communities of specialists: vacant niches in ecological and evolutionary time. In: *Ecological Communities: Conceptual Issues and the Evidence* (ed. by D. Strong, D. Simberloff and L. Abele). Princeton University Press.
- Salt, G. (1961) Competition among insect parasitoids. *Symposium of the Society for Experimental Biology*, 15, 96–119.
- Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science*, 185, 27–39.
- Schoener, T.W. (1982) The controversy over interspecific competition. *American Scientist*, 70, 586–595.
- Shannon, C.E. & Weaver, W. (1949) *The Mathematical Theory of Communication*. University of Illinois Press, Urbana.
- Shorthouse, J.D. (1973) The insect community associated with rose galls of *Diptolepis polita* (Cynipidae, Hymenoptera). *Quaestiones Entomologicae*, 9, 55–98.
- Silverman, J. & Goeden, R.D. (1980) Life history of a fruit fly, *Procecidochares* sp., on the ragweed, *Ambrosia dumosa* (Gray) Payne, in southern California (Diptera: Tephritidae). *Pan-Pacific Entomologist*, 56, 283–288.
- Simpson, E.H. (1949) Measurement of diversity. *Nature*, 163, 688.
- Sneath, P.H.A. & Sokal, R.R. (1973) *Numerical Taxonomy*. H. F. Freeman, San Francisco.
- Strong, D.R., Jr (1980) Null hypotheses in ecology. *Synthese*, 43, 211–285.
- Washburn, J.O. & Cornell, H.V. (1979) Chalcid parasitoid attack on a gall wasp population (*Acraspis hirta* (Hymenoptera: Cynipidae)) on *Quercus prinus* (Fagaceae). *Canadian Entomologist*, 111, 391–400.
- Washburn, J.O. & Cornell, H.V. (1981) Parasitoids, patches, and phenology, their possible role in the local extinction of a cynipid gall wasp population. *Ecology*, 62, 1597–1607.
- Watrous, L.E. & Wheeler, Q.D. (1981) The out-group comparison method of character analysis. *Systematic Zoology*, 30, 1–11.
- Zwölfer, H. (1979) Strategies and counterstrategies in insect population systems competing for space and food in flower heads and plant galls. *Fortschritte der Zoologie*, 25, 331–353.

Accepted 18 December 1983