

**COMMUNITY STRUCTURE OF PARASITIDS ATTACKING LEAF GALLS
OF *BELONOCNEMA TREATAE* ON *QUERCUS FUSIFORMIS***

THESIS

Presented to the Graduate Council of
Southwest Texas State University
in Partial Fulfillment of
the Requirements

For the Degree

Master of Science

By

Myra Carmen Hall

San Marcos, Texas
August, 2001

ACKNOWLEDGEMENTS

I would like to thank Jim Ott for his guidance, support, and enduring pep talks. I would like to extend special thanks to Lezlie Jones who enthusiastically volunteered her time and energy in even the most difficult and tedious portions of the work. Thanks to my committee Dr. Jim Ott, Dr. Paul Barnes, and Dr. Caitlin Gabor. I would also like to thank my friends and colleagues, Richard Reynolds, Preston Galusky, Scott Egan, David Smith, James Russell, Mike Mcfadden, and Carrie Hess for their assistance in the field and laboratory. Financial support for this project was provide by the Southwest Texas State University Department of Biology, Sigma Xi Grants in Aid of Research, and the National Science Foundation.

Submitted on May 30, 2001

TABLE OF CONTENTS

	Page
LIST OF TABLES.....	v
LIST OF FIGURES.....	vii
ABSTRACT.....	ix
INTRODUCTION.....	1
METHODS.....	9
ANALYSIS.....	13
RESULTS.....	18
DISCUSSION.....	26
LITERATURE CITED.....	38

LIST OF TABLES

	Page
Table 1. Study Design: Windows of accessibility of parasitoids to leaf galls of <i>B. treatae</i> for exclusion study 2000. Each window runs from the 1 st to the last day of the month (Exception November from 1 st to 15 th) C = Bags in place, galls inaccessible to parasitoids. Open = Bags removed, galls accessible to parasitoids.....	43
Table 2. Study Design: Distribution of sampling effort (number of branches bagged) across trees (replicates) and windows. Six trees (labeled as FR10-H9) were each assigned four or five bags per window April (Control) - November. Each tree had a total of 35 bags. Each window had a total of 24 or 30 bags. Overall 210 bags were utilized in the study.....	44
Table 3. Study Design: Collection schedule and number of collected of bags for each window Control (April) - November and the dates they were collected (July 1- November 15). Column heading "Wild" refers to galls that were exposed to natural levels of parasitism throughout the study period. Fifty wild galls were collected from each of the six study trees on each of the collection dates.....	45
Table 4. Timing of attack and subsequent emergence of the <i>B. treatae</i> leaf gall community as determined by the exclusion study and rearing of gall occupants in the laboratory.....	46
Table 5. Levins's "B", a measure of microhabitat niche breadth standardized by the number of resource classes available for the 13 most common parasitoids ($n \geq 10$ emergences) of the <i>B. treatae</i> leaf gall community. A low niche breadth indicates that the species occurs in a restricted subset of resource classes. A niche breadth of 1.0 indicates that the species occurs in all resource classes equally. Species are listed in order of their occurrence in temporal windows and by the number of temporal windows in which they appear.....	47

- Table 6. Niche overlap for the niche dimension "Gall Size" among parasitoid species of the *B. treatae* leaf gall community. Horn's index of niche overlap (R_o) is presented for the 13 most common parasitoid species ($n \geq 10$ emergences) using 18 gall size classes. Gall sizes ranged in size from ≥ 0.5 to 9.0 mm; classes were .05 mm width. Species are listed in order of increasing median gall class size from which they emerged. Median gall size from which parasitoids emerged was 0.80, $\bar{x} = 0.75$, $SE = 0.14$48
- Table 7. Niche overlap for the niche dimension "Timing of Attack" among parasitoid species of the *B. treatae* leaf gall community. Horn's index of niche overlap (R_o) is presented for the 13 most common parasitoid species ($n \geq 10$ emergences) and eight temporal windows. Species are listed in order of temporal occurrence and number of windows in which they appear. Median gall size from which parasitoids emerged was 0.61, 62, $SE = 0.18$49
- Table 8. Summary of frequencies of outcomes of intraspecific and interspecific interactions within galls for both the gall former and parasitoid species of the *B. treatae* leaf gall community. Left to right: Total indicates the number of individuals reared from leaf galls for each species summed across all windows and all types of interactions; Single indicates the number of galls for each species that produced only one individual; Intra 2 - Intra 7 are the number of galls that produced two to seven individuals of the same species; Inter 1 - Inter 3 are the number of galls that produced one to three additional species along with the species listed to the left in column one; for example *Synergus* sp. 20 galls produces *Synergus* sp. plus one parasitoid, four *Synergus* sp. plus four additional species. Species listed in order of abundance.....50
- Table 9. Matrix of outcomes of intraspecific and pairwise interspecific interactions among community members within individual *B. treatae* leaf galls. Species listed exhibited ≥ 1 co-emergence from an individual gall with either the gall-former (row 1), their own species (diagonal), or another parasitoid species (off-diagonals). For interspecific contests the presence of an "X" in a cell indicates that the species listed can coexist (complete development) within individual galls. For intraspecific contests an "X" indicates that multiple individuals of the same species can coexist. Blank cells represent patterns of co-emergence not recorded. The total number of different species each species is capable of coexisting with is given in the right hand column.....51

LIST OF FIGURES

	Page
Figure 1. The relative frequency of parasitoid species of the <i>B. treatae</i> leaf gall community.	52
Figure 2. The rate of accumulation of species in the <i>B. treatae</i> leaf gall community against the cumulative total of individuals reared from individual leaf galls collected during the exclusion study. The relationship illustrated suggests most species present in the community were represented in the galls assayed (21,000) and 957 individual parasitoids reared from galls.....	53
Figure 3. Whittaker plots of species-abundance data for parasitoids of the <i>B. treatae</i> leaf gall community. (a) Theoretical plots. The logarithmic series produces a nearly straight line, while the lognormal distribution predicts a slightly hollow curve for the more abundant species. (b) Observed data. The relative abundance for the 27 species of parasitoids is best described by the lognormal distribution...	54
Figure 4. Diversity of the <i>B. treatae</i> community showing Evenness = E (filled circles) and Diversity = H' (unfilled circles) in each temporal window. An evenness index value of 1 indicates all species present in the community occur the window. An evenness index of 0 indicates no two species occur in the same window. A diversity index of 0 indicates no diversity. A diversity index of 5 is the highest value obtainable by a community. The overall diversity index for the entire community across the full season of parasitoid activity (April-November) is 3.48 with an evenness of 0.73.	55
Figure 5. The number of parasitoid species present in each window. The wild treatment consisted of galls exposed to parasitism for the entire study. The control treatment was exposed only during the oviposition period of <i>B. treatae</i> (April). The other windows indicate the month the galls were exposed to parasitism.....	56
Figure 6. A plot of the number of overall parasitoid species recovered versus the number of galls examined ($r = 0.72$). The number of gall required to produce the next species is shown.....	57

Figure 7.	Diversity of hymenopteran parasitoids of the <i>B. treatae</i> leaf gall community showing E (filled circles) and H' (unfilled circles) in each temporal window. An evenness index of 1 indicates all species present in the community occur in a windows. An evenness index of 0 indicates no two species occur in the same window. A diversity index of 0 indicates no diversity. A diversity index of 5 is the highest value obtainable by a community. The overall diversity index for hymenopteran parasitoids regardless of window is 3.32 with an evenness of 0.72.	58
Figure 8.	The number of hymenopteran species present in each window as determined by rearing occupants of galls exposed during each window.....	59
Figure 9.	The distribution of gall sizes at maturity at the study site for galls exposed to parasitism (April - November) (top left panel) and the distribution of gall sizes from which each of the 13 most common parasitoid species of the <i>B. treatae</i> leaf gall community emerged (all other panels). Chi-square and P values for test of the Ho: the gall size distribution used by each species is random (i.e. follows the observed distribution of gall sizes available).....	60
Figure 10.	The mean gall size and standard error for the 13 most commonly occurring parasitoid species. Error bars not visible were subsumed by the symbol.....	61
Figure 11.	The percent of <i>B. treatae</i> emergences from galls for each window is shown on the Y-axis (n = gall sample size). Percentages were calculated using only galls from samples capable of producing viable larvae (i.e. bags harvested during the collection periods: October, November, and November 15). The number of parasitoid species present is shown on the right axis. The wild window yielded 0.73% <i>B. treatae</i> and two parasitoid species.....	62

ABSTRACT

COMMUNITY STRUCTURE OF PARASITIDS ATTACKING LEAF GALLS OF *BELONOCNEMA TREATAE* ON *QUERCUS FUSIFORMIS*

By

Myra Carmen Hall, B.S.
Southwest Texas State University
August 2001

Supervising Professor: James R. Ott

The research presented herein addresses the structure of the parasitoid community centered on the asexual generation of the host-specific phytophage, *Belonocnema treatae* (Hymenoptera: Cynipidae) which induces leaf galls on *Quercus fusiformis*. Four specific objectives are examined: 1) determining the diversity and relative abundance of the parasitoid community members, 2) defining the specific niche dimensions of each parasitoid species in relation to size of gall attacked and timing of attack, 3) elucidating the nature of interactions among parasitoid species, and 4) determining the cumulative effect of parasitoids on *B. treatae* survivorship. The objectives were addressed using an exclosure study which limited access of parasitoids to leaf galls to a series of discrete 30 day window of opportunity. Following *B. treatae* oviposition (April) but before initiation of gall development, exclosure bags were placed on 210 branches distributed across six

of the gall formers host trees. Eight windows (May through November) were established by removing a subset of bags for a one month period to allow active parasitoids access to developing galls. Beginning in July, and monthly thereafter a subsample of galls previously exposed to parasitoids were collected. Just prior to emergence of the gall former (end of November window) all remaining galls were collected. All galls were returned to the lab, measured, stored individually in gelatin capsules, and incubated at seasonally adjusted temperatures and lighting conditions. Emergent parasitoid species were collected daily and identified. The relative frequency, abundance, niche breadth, niche overlap and within gall interactions were determined for each species. A total of 957 individual parasitoids were recovered from 21,690 galls sampled in the study. Four orders of insects (Hymenoptera, Coleoptera, Lepidoptera, and Diptera) and 27 species were represented in the parasitoid community. The relative abundance of species was lognormally distributed with most species being relatively rare and three species making up 49% of all individuals in the community. Diversity for both the overall parasitoid community and the hymenopteran component of the community (24 species) was high ($H' = 3.48$ out of a theoretical maximum of 4.76 and $H = 3.32$ out of 4.58 respectively). Diversity varied seasonally across windows though not significantly. Seven species were able to parasitize the gall former prior to gall development. Most parasitoid species attacked the gall early in the season with a peak in July while few species attacked late with only two species attacking in November. Parasitoid use of galls was not random with respect to gall size as the distribution of gall sizes used by the 10 commonest parasitoid species differed significantly from the distribution of gall sizes available. Niche breadth for time of attack had a broader range among the 13 commonest

parasitoid species (BA = 0.14 to 0.58) than niche breadth for gall size (BZ = 0.34 to 0.63). Niche overlap for gall size among species (n = 13) range RO = 0.42 to 0.95, was greater than niche overlap for time range RO = 0.07 to 0.088. The most frequent intraspecific interaction was the production of two individuals of the same species from a single gall. For eight of the 13 most common species multiple individuals were capable of emerging from a single gall. The most common interspecific interaction was the emergence of two different species from a single gall. There were 26 different pairwise co-emergences among the 27 parasitoid species (7.4% of the possible number of co-emergence interactions). *Belonocnema treatae* did not exhibit intraspecific interactions and in virtually all instances of co-occupation (99%) with any parasitoid species *B. treatae* did not emerge. This indicates that all species attacking the gall former, *B. treatae*, function as parasitoids in spite of their trophic level. *Belonocnema treatae* emergence was highest in the May and November windows at the time the number of parasitoid species present were lowest. For the July window which had the highest number of parasitoid species, *B. treatae* emergence success was lowest.

INTRODUCTION

Gall forming insects are specialized herbivores whereby the host plant is the habitat of the immobile, immature feeding stage. Gall formers are typically host-specific and thus subject to selection by the defensive mechanisms of their respective host plants as well as attack by natural enemies (Askew 1984). Currently little is known of the biology of most gall forming insects and even less is known about their associated parasitoid communities (Hawkins and Sheehan 1994, Hoffmeister and Vidal 1994; Sheehan 1994). Nevertheless, two elements of the biology of gall wasps and their parasitoids emerge from the relatively few systems that have been rigorously studied. First, high mortality via diverse groups of parasitoids is prevalent in gall forming communities (Askew 1984, Sitch et al. 1988; Ronquist 1994). Gall former vulnerability to parasitism may be affected by parasitoid aggregative response at high host densities, the availability of host refuges, or timing differences/similarities between the host and parasitoids (May and Hassell 1981). Second, the number of parasitoid species within a community (i.e., exploiting a particular gall former species), although highly variable with 1-20 species most commonly occurring, is quite high with some communities consisting of more than 50 parasitoid species (Hawkins 1988, Hawkins and Gangn 1989; Hawkins and Sheehan 1994). Fundamental to understanding the structure of parasitoid communities centered on gall former species is 1) determining the

diversity and relative abundance of the parasitoid community members, 2) determining niche dimensions of component species (temporal timing of attack / stage of gall attacked) and degree of niche partitioning among species, and 3) understanding the nature of interactions among the parasitoids within individual galls (Hawkins and Sheehan 1994, Hoffmeister and Vidal 1994; Sheehan 1994).

Diversity and Relative Abundance: Parasitoids comprise nearly 20% of all insect species; thus establishing the mechanisms that drive parasitoid species richness represents a major step in understanding the diversity of terrestrial communities (Hochberg and Hawkins 1992, Tschamntke 1992, Godfray 1994; Begon et al. 1995). Parasitoid communities of insects constitute some of the most diverse animal communities with assemblages, commonly comprising 10 or more species per host species, and sometimes attaining more than 30 (Askew 1984, Hochberg and Hawkins 1992, Godfray 1994; Begon et al. 1995). Understanding why some parasitoid species assemblages are more diverse than others is an important step toward the comprehension of community-wide and global patterns of biodiversity (Hochberg and Hawkins 1992, Godfray 1994; Begon et al. 1995).

Parasitoids can be a primary cause of host mortality. The impacts on host populations are correlated with the diversity and abundance of their parasitoid communities with communities containing high numbers of parasitoid species often being more suppressed than those with fewer parasitoids (Hawkins 1993).

While individual gall former species typically support a large number of parasitoid insect species, as in many other types of communities however, gall parasitoid communities typically contain both rare and common species (Hawkins 1988). Diversity

within communities may be influenced by several means. A community may have a large range of available resources thus allowing more species to utilize the community, the component species of the community may have very narrow niche breadths which increases the possibility of more species, or the component species may differ in the degree of niche overlap again increasing the possibility of more species (Pianka 1994).

Diversity can be represented in various ways: cataloging the total number of species, the number of individuals of each species, the location where each species is found, and the location where each individual is found. When species diversity is high, it is difficult to predict the species of a randomly chosen individual organism and low when an accurate prediction can be made. Indices of diversity are used to define community composition (Askew 1980; Hawkins and Sheehan 1994). Understanding species diversity within a community requires analysis of niche structure and interactions of the component species within the community. Total species diversity can be divided into three major niche dimensions: spatial, temporal, and trophic.

Niche Parameters: Niche overlap can occur when two or more species utilize the same resource(s). The degree of niche overlap determines the intensity of competition when the resources are limiting. It is assumed that when a community is fully saturated it cannot tolerate niche overlap for long periods (Briggs 1993; Schowalter 2000). Under these conditions, competition is assumed to be intense and results in the survival of only a single species in contested niche space (Abrams 1980, Briggs 1993, Pianka 1994; Schowalter 2000) Niche overlap is predicted to result in competitive exclusion between the overlapping species (Briggs 1993; Schowalter 2000). Niches often do overlap, however, without competitive exclusion taking place (Briggs 1993; Schowalter 2000).

The overlap of habitats may indicate that competitors have diversified in other ways or that the operative resource may not be in short supply (Briggs 1993; Schowalter 2000).

The mechanisms by which available resources are divided among members of a community must be known before determinants of species diversity and community structure can be fully understood.

Insights into the structure of parasitoid communities centered on gall formers can be gained by analyzing parasitoid guilds (Price 1970, Hoffmeister 1994, Hawkins and Sheehan, 1994; Mills 1994). Parasitoid guilds can be delineated according to specific niche criteria such as host stage(s) attacked (differences between species lead to temporal niche partitioning) and trophic level.

The different stages of host development attacked by individual parasitoid species serve to separate parasitoids temporally. Insect host development includes egg, larvae, and pupae stages. A form of temporal partitioning unique to insect gall communities consists of the temporal pattern of attack of parasitoid species relative to one another and relative to the timing and stage of gall development. The number of stages of the host insect attacked by parasitoid species, in the community determines in part, the intensity of interactions with other community members. Constraints on parasitoids, which may translate into temporal niche partitioning of the gall resource, include the relationship between gall size and parasitoid ovipositor length and gall toughness (Price 1970, Price 1971, Askew 1984, Weis and Abrahamson 1985, Craig et al. 1990, Briggs 1993, Hawkins and Sheehan 1994, Mills 1994, Briggs and Latto 1996; Schönrogge et al. 1996). It has been demonstrated that small galls often produce more parasitoid species (Jones 1983, Weis, Abrahamson 1985, Weis et al. 1985; Price and Clancy 1986). It is not clear.

however, if attack by parasitoids and the subsequent death of the gall former causes gall growth to stop, or if inherently smaller galls are more vulnerable to attack (Weis and Abrahamson, 1985, Craig et al. 1990; Plantard et al. 1996). The phenology of gall size-dependent parasitism depends on the niche width of each parasitoid and the degree of niche overlap among parasitoids (Takehashi et al. 1984).

The trophic levels of parasitoids are complex. Parasitoid communities centered on gall formers are comprised of species that feed at multiple trophic levels. There are several categories of parasitism. Inquilines are primarily phytophagous and feed on the gall tissue. The inquiline may cause the death of the host gall-former by depriving the host of nutrients or by opportunistically feeding on the host. Parasitism occurs when the parasitoid oviposits on (ectoparasitism) or in (endoparasitism) the developing host and the developing parasitoid larvae feeds directly on the gall former. Hyperparasitism occurs when the developing parasitoid larvae feed in or on an associated parasitoid. Superparasitism results when more than one individual of a parasitoid species occurs on a single host. Multiparasitism may occur when more than one parasitoid species feeds on a single host individual. Typically, in cases of superparasitism and multiparasitism, only a single individual will survive to maturity (Askew 1984). By definition, parasitoid attack results in the death of the gall former, while attack by inquilines may or may not result in the death of the gall former. The term parasitoid is used to encompass all trophic levels since almost all invariably kill their host whether directly or indirectly (Bouton et al. 1980).

Competitive Interactions: A third dimension of community structure is the outcome of competitive interactions among parasitoid species in gall communities. There

is little information concerning competitive relationships within parasitoid communities, therefore it is difficult to determine how many parasitoids should be able to coexist within any particular community (Hawkins and Mills 1996). There may be intense competitive interactions as multiple parasitoid species typically coexist within the same host population, multiple parasitoids typically use the same stage of gall former development, and each individual host can often support only one parasitoid (Askew 1984; Hawkins and Sheehan 1994). It is possible to have multiple trophic levels within the same gall whereby inquilines, parasitoids, or hyperparasitoids may be present at the same time. The outcome of interactions within and between guilds, degree of temporal overlap, and degree of overlap in the size or developmental stage of galls exploited by each species at large will determine the intensity of competition within individual galls and within the community of parasitoids.

The research presented herein is aimed at understanding the structure of the parasitoid community centered on the asexual generation of the host-specific Cynipid, *Belonocnema treatae* Mayr. The asexual generations develops exclusively within galls that develop on the leaves of the Plateau Live Oak (*Quercus fusiformis* Small). Four specific objectives are addressed: 1) determination of the diversity and relative abundance of the parasitoid community associated with *B. treatae*, 2) defining niche criteria of parasitoid species associated with *B. treatae* in relation to gall size attacked and the seasonal timing of attack, 3) elucidation of the nature of interactions among parasitoids associated with *B. treatae*, and 4) determination of the effect of parasitoids on *B. treatae* success within leaf galls.

Natural History of Study System: The Cynipid wasps are a diverse group of gall formers confined primarily to the Fagaceae. Within the family Cynipidae (Order Hymenoptera), there are approximately 2,000 species with 805 recorded for North America (Dreger-Jauffret and Shorthouse 1992). The majority of cynipid wasps occur on species of oaks (*Quercus* spp.) and are typically both host and tissue specific (Askew 1984; Ronquist 1994). The species, *B. treatae* is no exception as asexual generations induce galls only on the leaves of Coastal Live Oak, *Quercus virginiana* (Southeastern United States) and Plateau Live Oak, *Quercus fusiformis*, formerly *Q. virginiana* variety *fusiformis* (Central Texas). The Live Oak trees are semi-evergreen with leaf drop occurring from February to March, coinciding with bud break and development of a new cohort of leaves.

Belonocnema treatae exhibits heterogony, whereby a unisexual female generation develops within unilocular leaf galls and a bisexual generation develops within multilocular root galls of its host plant (Lund et al. 1998). The bisexual generation emerges from root galls from mid February through mid April coincident with the production of new leaves and females oviposit on lateral veins on the underside of leaves. Following oviposition, galls remain minute for 2 months and first become visible in early to mid May. Previous research (Lund et al 1998) has documented that *B. treatae* larvae within leaf galls are attacked by numerous species of parasitoids during their development (egg to maturity). Thirteen hymenopteran species have been identified in association with *B. treatae* leaf galls including three species of parasitoids, four species of inquiline, and one hyperparasitoid. The remaining eight species have not been characterized with respect to their trophic level. Additionally, numerous unidentified

hymenopteran and some nonhymenopteran species have been found (Lund et al. 1998, Reynolds 2000; Hall unpublished data).

Parasitism plays a crucial role in the mortality of the gall former (Lund 1998). Parasitism rates gathered from multiple sites and years exceeds 95% (Unpublished data). For example, in one study, approximately 30% of galls produced no insect, < 10% produced the gall-former, and the remaining 60% produced a parasitoid. At maturity (November) *B. treatae* leaf galls ranged in size from < 1 mm to 9 mm in diameter; $\bar{x} =$, $SE =$; $n =$; 199_ field data (Unpublished data). However, the mean gall size from which *B. treatae* successfully emerged was 6.94 mm ($\pm$ 0.06 mm) with 95% of emerging from galls greater than 6.1 mm (Lund et al. 1998). The size distribution of galls from which *B. treatae* emerged indicates that gall size is related to the probability of emergence. The size distribution of galls from which any hymenopteran parasitoids emerged ranged from 2.5 mm to 8.5 mm, indicating that parasitoids are capable of completing development in a wide range of gall development stages and sizes. Consequently, the composition of the parasitoid community that develops within individual *B. treatae* galls may be effected by gall size. The nature and complexity of competition among parasitoid species may differ between gall size classes. It is possible that strong interspecific competition exists among parasites foraging for small galls and reduced competition for large galls. The attacking parasitoid species identified thus far differ in ovipositor length, thus for a fixed gall size, parasitoid species may differ in their ability to parasitize *B. treatae*. The success of *B. treatae* in larger galls may be a function of gall size serving as a host refuge from parasitism or the presence of a parasitoid may determine the development of the gall (Lund 1998; Reynolds 2000).

METHODS

A study designed to manipulate parasitoid access to *B. treatae* developing within leaf galls was conducted (from April 2000 to November 2000) at Southwest Texas State University's Freeman Ranch located in Hays County, Texas. Located with the Edwards Plateau of central Texas the ranch is composed of four distinct habitats, live oak savanna, juniper woodlands, mesquite flats, and agarita / persimmon shrubland. The study area consisted of live oak savanna with solitary live oaks and oak mottes. The study design partitioned the growth and development period of the leaf galler and hence the concomitant attack period of parasitoids into eight discrete time intervals. This design allowed me to determine on a monthly basis from April – November the identity of each parasitoid species associated with the community and the relative abundance of each species (Objective 1), the temporal and gall size niche dimension of each parasitoid species (Objective 2), outcomes of interactions among the community members (Objective 3), and the effect of parasitoids on *B. treatae* success within leaf galls (Objective 4).

Study Design: In March 2000, several hundred live oak trees were surveyed for *B. treatae* leaf galls on the 1999 leaf cohort. In April of 2000, following cessation of oviposition into the newly developed cohort of leaves, the 13 trees that had exhibited the highest gall densities in 1999 were revisited and examined for evidence of *B. treatae* oviposition on new leaves (i.e., ovipuncture scars which are diagnostic of ovipositor insertion and which

remain as permanent features of the leaves). Six trees that exhibited both high leaf gall densities in 1999 and high ovipuncture density in 2000 were selected in an attempt to include trees in the study which exhibited a well developed parasitoid community and presented sufficient numbers of galls to adequately sample the community. Spatially the six trees were distributed from 100 meters to 1 km apart in order to provide a general assessment of the parasitoid community structure across a local scale. When developing galls became visible (May 1st), 35 branches exhibiting high density of oviposition scars were chosen on each of the six trees (210 overall) and exclosure bags (2' X 3' in size and constructed of fine mesh Nytex screen) were placed on these branches to protect the galls from parasitoid attack except during predetermined windows of accessibility. The exclosure bags shown in previous studies to successfully exclude parasitism of the leaf gall (Reynolds 2000) and were large enough to include 200-400 leaves per bag.

Windows: The design partitioned the temporal pattern of parasitism of *B. treatae* leaf galls on *Quercus fusiformis* into eight intervals or windows. Parasitoids subsequently reared from galls (see below) from each window provided a snapshot of the composition of the parasitoid community during each window of accessibility that coincides with a particular stage of gall development. Subsets of bags placed on trees (May 1st) were allowed to remain in place for the duration. These restricted parasitoid access to the month of April and allowed me to determine which species were able to successfully attack the gall former prior to gall development (egg parasitoid). Beginning May 1st and on the 1st of each month (May-November) thereafter, a subset of bags for each window of accessibility (selected at random) were removed from each of the six trees and parasitoids were allowed access to developing leaf galls for 30 days except for

the last window, which ran from November 1 until November 15. The last treatment window was truncated in order to capture emergence data on *B. treatae*, which begins emergence in mid November. All bags were replaced at the end of each thirty-day window and remained closed for the duration of the study. A second "open" control was also utilized and consisted of 50 galls . collected at the beginning of each window beginning May 1, from each of the six trees that had been exposed to natural levels of parasitism throughout the study. The open galls (total of 300 / window) provided information of gall size in the natural community throughout the season, presence of species that may not be captured in the exclosure bags, times of parasitoid emergences, and natural levels of parasitism for each window and cumulatively across the season. The study design is summarized in Tables 1 and 2, which illustrate the open, and closed intervals and the number of bags for each window respectively.

Sampling: Previous observations (corroborated by the current study) have shown that adult parasitoids begin to emerge from *B. treatae* leaf galls in July (Lund 1998; Hall unpublished data). Thus, to capture parasitoid community members whose development period is completed prior to that of *B. treatae* (November - final bag retrieval) sampling of galls in exclosure bags began at the end of the June window. Subsequently at one-month intervals, a subset of bags from all previous windows were collected, galls were returned to the lab and occupants reared. Table 3 lists the number of bags sampled for each window and collection date. By taking a subsample of galls from each window throughout the study, I was able to determine the identity of parasitoids that emerged throughout the study. The final collection of all remaining bags occurred at the close of the November window.

When bags were collected galls were removed and stored individually in labeled gelatin capsules. Galls were kept in incubators set to the mean monthly temperature and light cycles and were checked daily for emergences from July 2000 to March 15, 2001. The majority of insects emerge during this time though from previous studies a small percentage of insects may emerge for up to one year following gall maturation (Lund 1998; Hall unpublished data). Emerging insects were captured, stored in 1-dram vials of 70% ethanol, and identified to species using a key developed by the author with help from the USDA Systematics Entomology Laboratory. Any species without a confirmed identification was given an identification of morphotype and a number.

All galls were examined for the presence of exit holes. The presence of an exit hole indicates that at least one individual had emerged from the gall prior to collection. This value may be negatively biased due to multiple individuals using the same exit hole. There were no exit holes present in the July 1 sample indicating that parasitoid emergences did not occur prior to July 1. The number of exit holes combined with the number of parasitoid emergences offers an estimate of gall production. A total of 957 individual parasitoids emerged from the 21,690 galls individually incubated in the lab. A large number of parasitoids emerged prior to galls being collected. There were 3,127 emergence holes in sampled galls at the time galls were removed from their respective bags and returned to the lab. The sum total parasitoid emergence was 4,084 thus 23% of parasitoid emergences were captured.

ANALYSIS

Diversity and Relative Abundance: The relative frequency of each parasitoid species across all windows and collections dates was determined. The resulting species abundance curves for summation across the entire season were transformed into logarithmic and lognormal species abundance curves which were then compared to Theoretical Whittaker Plots using Krebs Ecological Methodology Software (1999) to determine whether the observed pattern of relative abundance of parasitoid species reflect the patterns of community structure implicit in the logarithmic or lognormal models. The diversity of the parasitoid community associated with *B. treatae* leaf galls was evaluated for the entire parasitoid community (four orders : 27 species) and the hymenopteran component of the parasitoid community (24 species). The Shannon-Wiener (Weaver) information index (H')

$$H' = - \sum_{i=1}^N p_i \log_2 p_i$$

where N = number of individuals and p_i is the proportion $\left(\frac{n_i}{N}\right)$ of the i^{th} species in a sample, was applied to the entire community and the hymenopteran subset using Krebs Ecological Methodology software (1999). The Shannon-Wiener index measures the level of certainty in predicting the identification of randomly chosen individuals and assumes that individuals are randomly sampled from an effectively infinite population and that all

species are represented in the sample. H' increases as the number of species increase and could theoretically be a very large number, in natural systems however, H' does not exceed a value of 5.0 (Krebs 1999). When the assumption of a random sample is violated, the estimates of H' are biased so that the observed H' is lower than the actual H' .

The index E , which is a measure of evenness of species representation adjusted to s (s = number of species), was examined across all windows and collections dates for the overall parasitoid community and the hymenopteran subset using Krebs Ecological Methodology Software (1999). Evenness is given by:

$$E = \frac{H'}{H'_{\max}} = \frac{H'}{\log_e s}$$

The evenness index ranges from 0 to 1 where 1 indicates all species present occur in equal numbers.

In addition, the diversity (H') and evenness (E) were calculated for both the overall parasitoid community and the subset of hymenoptera for each of the eight temporal windows. A regression analysis of H' against temporal window was conducted for both the overall and hymenopteran parasitoid communities to test whether diversity varied systematically with the temporal windows (across the season).

The rate of accumulations of the parasitoid species plotted against the cumulative total of individuals and serves as a predictor of community totality.

Niche Parameters: The time of attack (window) and the gall size from which each individual parasitoid emerged was recorded. Gall size at emergence was used as an index of gall size used by parasitoids. These two niche parameters were estimated only for

those parasitoid species ($n = 13$) for which ≥ 10 individuals emerged from galls. The distribution of gall sizes in nature (unbagged - galls exposed to natural levels of parasitism) at maturity (following lignification) was determined using the wild-control galls collected from the study trees during the September, October, and November samples ($n = 1,336$) in combination with mature galls collected from the same trees by a concurrent study ($n = 2,177$; $n = 3513$ overall). The distribution of gall sizes used by each parasitoid species was determined and compared to the distribution of mature gall size classes to test whether gall size use was random. A chi-square test was used in each case to test for goodness of fit. If gall sizes used by parasitoids was significantly different than the natural distribution of mature galls then gall size use was not random.

Niche breadth for 1) timing of attack and 2) gall size used was calculated for each parasitoid species using Levins' standardized measure of niche breadth (B_A)

$$B_A = \frac{\left(\frac{1}{\sum p_j^2} \right) - 1}{n - 1}$$

where p_j = Proportion of individuals found using resource state j (i.e., gall size class j or window j) and n = number of possible resource states ($n = 18$ for size and $n = 8$ for temporal windows April - November). Gall size classes were 0.5 mm in width and ranged from 0.5 mm to 9.0 mm. This metric assumes all resource categories are equally available in the community. The uniform intensity of sampling effort per temporal window illustrated in Table 2 was implemented to satisfy this assumption for the niche parameter. The distribution of gall sizes available were not uniform. The frequencies of

gall size classes while not uniform were roughly equivalent (see Figure 9, upper left panel).

To access the degree of overlap between species for the niche parameters gall size and timing of attack. Horn's index of niche overlap (R_o)

$$R_o = \frac{\sum (p_{ij} + p_{ik}) \log(p_{ij} + p_{ik}) - \sum p_{ij} \log p_{ij} - \sum p_{ik} \log p_{ik}}{2 \log 2}$$

where for species j and k

p_{ij} = Proportion resource i of the total resources utilized by species j

p_{ik} = Proportion resource i of the total resources utilized by species k

was calculated for all pairs of parasitoid species. Horn's index of niche overlap ranges from 0 to 1 where a value of 1.0 indicates complete overlap.

Species Interactions Within Galls: The frequency and outcomes of both intro and interspecific interactions within and among parasitoid species within galls as well as outcomes of interactions with the gall-former were determined from the patterns of insect emergences from individually incubated galls of known window, sampling date, and size. Subsequent inspection of the patterns of co-emergence for all pairwise combinations of species allowed me to determine a) which pairs of parasitoid species could co-develop within galls, b) the number of different parasitoid species each species could coexist with and, c) which species could successfully co-develop with the gall-former.

Effect of parasitoids on *B. treatae*: While the primary intent of the exclosure study was to investigate parasitoid community structure, the sampling design employed also provides an estimate of the effect of parasitoids on *B. treatae* survivorship. Samples of galls collected through August effectively prevent the completion of *B. treatae*

development and hence cannot be used to estimate *B. treatae* survivorship. However, later samples (September – November 15th) provide mature galls capable of producing *B. treatae*. Galls from these later samples were used to determine the percent emergent success of *B. treatae* (number of *B. treatae* / number of galls) during each window. Comparison to the number of parasitoids and number of species present produced in each window allows comparison of *B. treatae* success versus intensity of parasitism and parasitoid community diversity by window. Coupled with the analysis of gall-former co-emergence patterns (above) these analyses provides a first insight into roles individual species may play in impacting *B. treatae* emergence success.

RESULTS

Diversity and Relative Abundance: Four orders of insects were represented in the overall parasitoid community centered on leaf galls induced by *B. treatae* on *Quercus fusiformis*: Hymenoptera, Coleoptera, Lepidoptera, and Diptera. The orders, Coleoptera, Lepidoptera, and Diptera were represented by a single species each. Ninety one percent (872 / 957) of all parasitoids collected were hymenopterans. Seven families and 24 species in the parasitoid community were represented by Hymenoptera: Cynipidae (n = 5), Eurytomidae (n = 5), Ormyridae (n = 1), Torymidae (n = 2), Pteromalidae (n = 6), Braconidae (n = 1), and Eulophidae (n = 4). Twenty-seven species functioned as parasitoids of which three were keyed to order, 11 were keyed to family and designated as "Morphotypes" pending taxonomic resolution, eight were keyed to genus, and five were keyed to species.

For the overall parasitoid community of 27 species (summed emergences across all windows and collection dates), most species were relatively rare while a few species were abundant with three species, *Synergus sp.*, *Brasema sp.* 3, and *Allorhogas sp.*, making up 49% of all individuals in the community (Figure 1). The rate of accumulation of parasitoid species plotted against the number of individual examined indicated that the parasitoid community identified herein offered a reasonably complete picture of the community (Figure 2). Comparison of the relative abundance of species of the parasitoid community to logarithmic and lognormal Theoretical Whittaker Plots (Figure 3) showed

best fit to the predicted lognormal curve indicating the community to be either opportunistic or equilibrium in nature.

Diversity (H') for the overall parasitoid community was 3.48 out of a theoretical possible maximum of 4.76 and evenness (E) was 0.73. Diversity for the overall parasitoid community varied slightly across the temporal windows, April to October, from 1.73 to 2.87. Only in November did H' drop substantially (Figure 4). In contrast, evenness values ranged from 0.52 to 0.87 from April through November indicating that most of the species present during each window were roughly equally abundant (Figure 4). Regression analysis showed no relationship between temporal window and diversity for the overall parasitoid community ($F = 1.52$ and $P = 0.26$).

While 27 species of parasitoids were present in the community, in no windows were all 27 present. The number of species present in each window ranged from a high of 17 in July to a low of two in November (Figure 5). The number of species present in the community increased from April ($n = 7$) to July ($n = 17$) (period of gall induction and rapid gall growth) and then declined from August ($n = 7$) to November ($n = 2$) (period of gall maturation) (Figure 5).

The number of species recovered / window was correlated with the number of galls examined ($r = 0.72$), however, variation in sample size / window did not explain seasonal variation in the number of parasitoid species present in the community. Examination of the number of galls required to produce the next species in each window followed the seasonal pattern of number of species present (Figure 6). For example approximately 3,500 galls were examined for both the May and July windows, however, the July window ($n = 17$ species) required only 197 galls / species while the May window

($n = 10$ species) required 352 galls / species. Thus on a per gall basis species diversity was highest in July and followed the pattern depicted in Figure 5.

Diversity for the hymenopteran parasitoid community ($n = 24$ species) across all windows was 3.24 (Theoretical Maximum = 4.59) varied slightly across temporal windows, from 1.64 to 2.69 (Figure 7). Only in November did H' drop substantially. Evenness across all windows was 0.72 and values ranged from 0.52 to 0.87 from April through October indicating that most species present occurred roughly equally. Regression analysis indicated that there was no linear relationship between diversity and temporal window for the hymenopteran parasitoid community ($F = 1.50$ and $P = 0.27$).

In no windows were all 24 hymenopteran parasitoids present. The number of hymenopteran species present in each window ranged from a high of 15 in July to a low of one in November. Across the season, the number of species present in the hymenopteran community in each window followed the pattern for the overall parasitoid community (Figure 8). Only one species, *Sycophila sp.*, appeared in all windows. As for the entire parasitoid community the number of hymenopteran species recovered per window was correlated to sample size ($r = 0.60$), however on a per gall basis. species diversity and the number of species present followed the patterns depicted in figures 7 and 8 respectively.

Niche Parameters. Temporal Pattern of Parasitoid Attack. Seven species of parasitoids (six hymenoptera, one coleoptera) were reared from the galls that developed from the April window indicating that these species were able to parasitize the gall former prior to gall development. Thus, these species appear to be idiobionts and delay growth and development until the gall former makes the gall. However, all parasitoids

that were active in April occurred in low numbers and each exhibited maximum attack levels in windows later in the season indicating flexibility in timing and stage of gall attacked. In context of guild membership, these seven species were members of egg and larvae guilds. Six species (Coleoptera sp., *Synergus* sp., *Sycophila flava*, *O. labotus*, *Brasema* sp. (3), and *Allorhogas* sp.) maximally attacked during July (period of active growth) (Table 4). Four species, *Sycophila* sp., *Eurytoma bugbeeii*, *Brasema* sp. (1), and *Brasema* sp. (2), attacked primarily in September at which point gall growth has nearly ceased and most galls have reached their maximum size (Table 4). *Torymus tubicola* has a maximum attack in October after the galls are mature. *E. bugbeeii*'s development period is unclear as it appears in one-month intervals, yet, the maximum emergence occurs in March, which is six months after the last recorded attack date (Table 4). Only two species *Brasema* sp. (3) and *Allorhogas* sp. exhibited discrete windows of attack (Table 4).

Niche Parameters: Patterns of Gall Size Use: Leaf galls induced by *B. treatae* following cessation of growth and lignification, "mature galls," range from 0.5 mm to 9.0 mm in size and the distribution of mature gall size is decidedly skewed to the left (Figure 9). The distribution of galls sizes from which each of the 13 most common parasitoid species emerged was compared to the distribution of mature gall sizes to test size distribution from which the species emerged differed from the size distribution of mature galls (Figure 9). For all ten species with sufficient sample size to test the hypothesis the distribution of gall sizes from which each species emerged differed significantly from the distribution of gall sizes available. Thus, galls used by these parasitoids were not random with respect to size (Figure 9). The mean gall size used by parasitoid species ranged

from 3.38 mm to 5.54 mm (Figure 10). No attempt was made to statistically compare the mean gall size used between species, instead niche breadth for gall size was established for each species.

Niche Parameters: Niche Breadth: Niche breadth for gall size ranged from $B_A = 0.34$ to 0.63 among species and was less variable than niche breadth for time of attack (range $B_A = 0.14$ to 0.58) (Table 5). Within species niche breadth for gall size was greater than breadth for timing of attack for ten of 13 species examined (Table 5). Niche breadths for gall size and time were uncorrelated ($r = 0.03$ and $P < .0001$). Among parasitoid species *Allorhogas* sp. had the narrowest niche breadth for both time of attack ($B_A = 0.14$) and gall size ($B_A = 0.34$). *Sycophila* sp. had the largest niche breadth for time of attack ($B_A = 0.58$) and *Synergus* sp. had the widest niche breadth for gall size ($B_A = 0.63$) (Table 5).

Niche Parameters: Niche Overlap: Niche overlap for gall size classes used among the 13 most common species ranged from $R_O = 0.42$ to 0.95 (Table 6). In comparison with all parasitoid species except *Allorhogas* sp. and *S. flava*, *Galeopsomyia* sp. had the smallest niche overlap for ($R_O = 0.42$ to $R_O = 0.71$) (Table 6). Morphotype (07) had the smallest niche overlap with *Allorhogas* sp. ($R_O = 0.46$) and *S. flava* ($R_O = 0.45$). Twelve pairs of species had gall size niche overlap ≥ 0.90 . *T. tubicola* had the greatest gall size niche overlap with *Sycophila* sp. ($R_O = 0.95$). Five of the 13 parasitoid species had a gall size niche overlap ≥ 0.90 with Coleoptera sp. (Table 6).

As expected from Table 5, the niche overlap for time of attack was much lower than that for gall size ranging from $R_O = 0.07$ to 0.88 (Table 7). The highest niche overlap for time was $R_O = 0.88$ for *S. flava* and *Allorhogas*, *S. flava* and *Ormyrus labotus*,

and *O. labotus* and *Allorhogas*. The smallest niche overlap observed was between *Allorhogas* and *Galeopsomyia* ($R_o = 0.07$) (Table 7).

Competitive Interactions Within Galls: Multiple emergences of individual parasitoids of the same or different species from single galls were recorded and provided insight into the frequency and outcomes of both intra and interspecific interactions within galls. Thirty four percent (627 / 957) of all parasitoids reared during the study emerged from galls from which two or more parasitoids of either the same or another species emerged indicating that interactions within individual uni-locular galls of the host *B. treatae* are a common feature of the community dynamic. Among the 13 common parasitoid species three species, *Sycophila* sp., *Coleoptera* sp., and *Galeopsomyia* sp, emerged exclusively as one individual per gall while ten of 13 species were capable of co-emerging with other species (Table 8). Two of these ten species (*E. bugbeei*, and *Brasema* sp. (2)), emerged either singly or with other species while eight of these ten species were capable of emerging singly and multiply per gall as well as co-emerging with other species. Additionally three of the 14 rare species showed evidence of the capability of co-emerging with other species in spite of small sample size. The remaining 11 rare species provide no information on intra or interspecific interactions.

Competitive Interactions: Intraspecific Outcomes: Eight of 13 common parasitoid species (30%) had instances of intraspecific occurrences within galls: *Allorhogas* sp., *Brasema* sp. (1), *Brasema* sp. (3), *O. labotus*, *S. flava*, *Synergus* sp., *T. tubicola*, and Morphotype (07) (Table 8, 9). The most frequent observed outcome of interactions in galls was the production of two individuals of the same species (Table 8). Five species (*Synergus* sp., *Brasema* sp. (3), *Allorhogas* sp., *O. labotus*, and *T. tubicola*) were capable

of emerging three to a gall and two species (*Synergus* sp. and *S. flava*) emerged four individuals to a gall. *Allorhogas* sp. had one instance where five individuals emerged from a single gall and *O. labotus* had one instance where seven individuals emerged from a single gall (Table 8).

Competitive Interactions: Interspecific Outcomes: There were 351 unique 2 x 2 interspecific co-emergences possible between the pairs of the 27 parasitoid species. However, only 26 (7.4%) unique interactions were recorded (Table 9). The most common observed outcome of interspecific interaction in galls was the production of two different species (n = 13 species) (Table 8). Four species were produced from galls producing three species (Table 8). One gall produced four different species, *Brasema* sp. (2), *Brasema* sp. (3), *T. tubicola*, and Morphotype (06) (Table 8). The number of different species each species was capable of co-emerging with ranged from one to nine: (*Brasema* sp. (3) co-occurred with nine different species) (Table 9).

Parasitoid effects on *Belonocnema treatae*: *Belonocnema treatae* does not exhibit any intraspecific interactions (Table 8.9). In addition, of the 214 individual *B. treatae* reared from galls only two individuals emerged from galls that also produced *Brasema* sp. (1) (Table 8,9), thus in virtually all instances of co-occupation with another species within the leaf gall, *B. treatae* was precluded from completing development and emergence. This indicates that all species are shown to act as parasitoids in spite of trophic level. *Belonocnema treatae* success per window (number *B. treatae* emerged / number galls exposed to parasitoids / window) ranged from 0.67% to 3.00%.

Belonocnema treatae success was greatest in the May and November windows at the time the number of parasitoid species were the least abundant. In the July window when

parasitoid species were most abundant *B. treatae* success was at its lowest rate (Figure 11).

DISCUSSION

Diversity and Relative Abundance: Although insect induced galls are highly visible and easy to locate, the protection afforded by gall structure and chemical defenses are thought to limit the number of parasitoid species within a community (Hawkins 1988). For those cynipid gall former systems studied, the number of parasitoid species ranged from 2 to 20 with a mean of 8.6 (Hawkins 1988). The *B. treatae* community with 27 species of parasitoids has a high number of species present when compared to these other cynipid systems. The majority of the parasitoid species in the *B. treatae* community, however, are not very abundant: most in fact are rare to very rare relative to the entire community. I hypothesize that rare species have little or no impact upon the dynamics of *B. treatae* and are non-interactive with other parasitoids in the community. The rarity of these parasitoid species may be due to host defense whereas the galls are too large or tough to exploit and thus are food limited (Southwood 1973; Hawkins 1988).

A previous study also conducted at Freeman Ranch made an initial identification of the hymenopteran parasitoid community associated with *B. treatae*. Leaves with galls were collected bimonthly from mid-July until March for two seasons (1995-1996 and 1996-1997). Galls were placed in emergence traps and emergent gall-associated hymenoptera were fixed in 70% ETOH and sent to the USDA SEL for identification (Lund 1998). Thirteen hymenopteran parasitoid species were identified in contrast to the

27 species identified in the current study a difference of nearly 50% in the number of species identified. The earlier study recovered 804 hymenopteran parasitoids in 1995 - 1996 and 741 hymenopteran parasitoids in 1996-1997 whereas the current study recovered 957 individuals. The previous study found for both seasons that *Synergus* sp. was the most abundant hymenopteran parasitoid species present making up 65% of the 95/96 season and 48% of the 96/97 season. The second most abundant species were *S. flava* (8%) 95/96 and *Galeopsomyia* (15%) 96/97. The third most abundant species were *Brasema* sp. (1) and *Acaenacis lausus* both making up 7% of the community in 95/96 and *Brasema* sp. (1) and *T. tubicola* both making up 7% of the community in 96/97 (Lund 1998). The current study found that *Synergus* sp. was also the most abundant parasitoid species in the community making up 23% of the population. The second and third most abundant species however were not the same as the previous study. *Brasema* sp. (3) and *Allorhogas* sp. were the second and third most abundant (~13%) parasitoid species in the community. Previous work by the author (unpublished data) recorded *Galeopsomyia* sp. as the most abundant species in the parasitoid community making up 43% of the community with *Synergus* sp. making up a much smaller proportion (11%) of the community. *Galeopsomyia* sp. made up 1% of the community in this study. Typically, the most abundant parasitoid species are thought to have the most impact on the host as well as on other parasitoids in the community. *Synergus* sp. appears in the *B. treatae* community consistently and in high numbers suggesting that this species may have high impact on *B. treatae* and associated parasitoids. The inconsistency of the next three species ranks indicates that these species are capable of profound effects on *B. treatae* and the parasitoid community, however, this is not consistent. The relative abundance in

these species appears to fluctuate from season to season. Of note, the current study considers *Sycophila* sp. and *S. flava* to be two separate species originally due to minor taxonomic differences and corroborated during the study with differing attack patterns, emergence patterns, and intraspecific / interspecific interaction, whereas all the previously mentioned studies did not separate the two species.

The abundance relationships are a reflection of the underlying distributions. The logarithmic distribution is similar to a geometric series whereby a species occupies a fraction (k) of a habitat, another species occupies the same fraction of the remainder of the habitat continuing until all species accounted for in the community. In the logarithmic series, it is assumed that all species arrive in the community randomly. The lognormal distribution series assumes a normal distribution of individuals between species and that population growth is geometric. The lognormal series is typically seen in opportunistic communities or communities in which the species are at equilibrium (Southwood 1978).

The community elucidated in the current study had a high H' of 3.5 when compared to the diversity indices of other cynipid gall systems that have a typical H' of 1.22 to 1.62 (Askew 1984; Hawkins 1988). Species were ranked according to abundance. The distribution of relative abundance was compared to theoretical Whittaker Plots. The Shannon-Wiener diversity index predicted H_{max} for the community was 4.8 suggesting that 73% of the community had been described. This could mean that not all community members have been collected or that the community is not saturated. The estimated number of species in the community per lognormal distribution is 34, which suggests that 79% of the community have been described. The number of species

recovered was correlated to the sample size, however, on closer examination it was apparent that the number of galls required to produce the next species was not correlated to sample size. The April and May windows (early season) had large sample sizes but produced less than ten species requiring 412 and 352 galls respectively per species. On the other hand, the July and September window (late season) had comparable sample sizes and both produced over ten species per window and required fewer galls per species. The November and April window (temporal extremes) both produced a low number of species, though November was very low, and had very different sample sizes ($n = 832$ - November and $n = 2887$ - April), yet required the same number of galls for each species recovered.

The entire parasitoid community and the hymenopteran parasitoid community were examined to determine if there was a difference in diversity through time. Regression analysis indicated that diversity did not differ through time for the entire community nor the subset of hymenopteran species. Though the number of different species did not differ, the composition of species did differ. The number of species present in each window increased from early to mid-season and then declined in numbers in the later half of the season. July contained the most species, which is not surprising, since July is the period of rapid gall growth. November, which is the period when *B. treatae* has reached maturity and is reaching maximum emergence, had the fewest parasitoid species present, therefore the galls are effectively no longer viable to the parasitoid. There was no window that included all 27 parasitoid species. It was assumed that the wild-control would contain all possible species since galls would be exposed to all parasitoids throughout the seasons. This was not the case however.

Though the wild-control contained the most species there were only 18 species recovered. This could be due to lower sample sizes for the wild-control or to the intensity of interactions among the parasitoids. Since all parasitoids could theoretically be present in the wild-control galls, then it is possible that some species were not able to successfully develop in the wild-control galls. The hymenopteran subset had less community members in the wild-control ($n = 14$) than in the July window ($n = 15$), which could be due to the reasons listed above for the entire parasitoid community.

Six of the seventeen species present in the July window (35%) were also present in the Control (April) bags. Five of which were present in every treatment from April to July, suggesting they have several generations and effectively reparasitize galls within enclosure bags or that they are koinobionts exhibiting premature or late emergences with maximum emergences in July. *Sycophila* sp. was the only parasitoid species present in every treatment window from April to November. Coleoptera sp. was present in every window except October. The majority of Coleoptera sp. attacked in July, and at much lower densities during the later windows thus it is presumable that Coleoptera sp. is also present in the October window, but in such low numbers that its presence was not detected. The majority of *Allorhogas* sp. attacked the galls in July and was the only parasitoid species found only in windows that had enclosure bags in place. There were no *Allorhogas* sp. recorded collected from the wild-control. This suggests that the enclosure bags protected *Allorhogas* sp. from competition or parasitism from the other parasitoids present in the leaf gall community. More species were present in July than in any other window however, so determination of which possible parasitoids may affect *Allorhogas* sp. is unclear.

Niche Parameters: All galls were examined for the presence of exit holes when sampled. For the July 1 sample there were no exit holes present indicating that parasitoid emergences do not occur prior to July 1. The first emergences were recorded in mid July; therefore sampling of the *B. treatae* parasitoid community should begin in July to recover the community members. Thirteen species with $n > 10$ and the distribution of gall size classes were examined. The size of galls at emergence was significantly different from the mature gall size distribution in the community. This indicates that gall use is not random. The gall sizes were determined using the size of galls from which each species emerged. Gall size classes that successfully produce each species are an index of gall size use and may not reflect the size of galls attacked. *T. tubicola* had the largest mean gall size at time of emergence and also attacked *B. treatae* galls late in the season (October) after galls were mature which is a good indication that *T. tubicola* utilizes larger galls. Morphotype (07) had the smallest mean gall size at time of emergence and attacked galls prior to the period of rapid gall growth indicating that Morphotype (07) attacked smaller galls. It cannot be determined if Morphotype (07) cannot utilize larger galls since gall size may be an artifact of the time Morphotype (07) is present. Mean gall size use by parasitoids ranged from 3.2 mm to 5.6 mm.

Seven species were present prior to gall formation (April) indicating they are capable of locating and parasitizing *B. treatae* eggs. However, all parasitoids attacking in April occur in low numbers and have maximum attack windows later in the season. The majority of *T. tubicola* attacked late in the season (October) after galls are fully mature. Although present in April, the low numbers of *T. tubicola* present in the control (1.9%) indicates that although capable of parasitizing eggs they predominantly attacked galls. *T.*

tubicola has a long, robust ovipositor relative to the other parasitoids in the community and may be more capable of successfully attacking mature, lignified galls. *T. tubicola* occurs in relatively high numbers throughout the season suggesting that *T. tubicola* has multiple generations. *T. tubicola* is the only recorded parasitoid of the sexual root gall generation and exhibits maximum emergence in November, which coincides with the maximum emergence of *B. treatae* in time with *B. treatae* oviposition on rootlets. Only two species *Brasema* sp. (3) and *Allorhogas* sp. have definitively discrete windows of attack.

Niche breadth for the parasitoid community was broad for time and narrow for gall size classes. There was no correlation between niche breadth for time and gall size classes. Therefore, the amount of niche overlap was greater for gall size class than for time. As expected those species with similar gall size class usage had a higher degree of niche overlap than those with gall size class usages at the extremes. Niche overlap for temporal windows was lower on average than that for gall size classes and the gradation of overlap was less distinct. *Allorhogas* sp. had the smallest niche breadth for both the window of attack and the gall size class utilized. *Allorhogas* sp. is one of two species that has definitively discrete times of attack where 95% of all *Allorhogas* sp. attacked in July. The other species with a definitive attack window was *Brasema* sp. (3), which attacked in July and September. *Brasema* sp. (3) had a low niche breadth for time of 0.30 and a moderate niche breadth for gall size class of 0.47. None of the 27 parasitoid species demonstrated complete niche overlap with any other species. The greatest amount of niche overlap occurred in the gall size classes with *T. tubicola* and *Sycophila* sp. (0.95) and a relatively high niche overlap for time of 0.77. Those species with

corresponding high overlap in both gall size class and time may have more opportunities for interaction and therefore competition.

Competitive Interactions: Specific parasitoids within a community would be in competition since they depend entirely on the host species. Typically, such communities support only one specific parasitoid (Askew 1980). Generalist parasitoid species, however, can be supported at higher numbers. It is always advantageous for either party in a competitive interaction to avoid the other whenever possible. Competition presumably promotes the use of different resources and hence generates ecological diversity. The mechanisms by which members of a community of organisms partition resources among themselves and reduce interspecific competition shapes community structure and may often influence species diversity profoundly. The results of this study show patterns of coexistence within the parasitoid community. Six species maximally attacked the *B. treatae* leaf galls in July suggesting considerable temporal overlap. The numerous multiple emergences of species and individuals of the same species from a single gall suggest interspecific and intraspecific competition is taking place at an individual gall level. Of the 27 parasitoid species, there were 351 possible pairwise interactions. Only 26 unique pairwise interactions occurred (7.4%). The low percentage of occurring interactions may be due to several reasons. First the low occurrences may reflect that such interactions are rare and simply do not occur. Secondly, it could mean that interactions are taking place but the outcome cannot be defined since interactions are recorded based on emergence data and some interactions may result in the death of one or more participating parasitoids. Third, it could be that the sample of species recovered (14 of the 27 species were represented by less than ten individuals) was not large enough to

record an occurrence. The interactions within galls may be used to hypothesize trophic relationships. It is rare for multiple parasitoids to utilize a single host individual (Askew 1980). *T. tubicola* and *O. labotus* are defined as parasitoids but occurred multiple times with other species as well as themselves within galls. Two possibilities arise: these species may be functioning as inquilines within the *B. treatae* community or they are capable of exploiting any species within the gall, thus multiple individuals within the gall (host + inquilines) can produce multiple parasitoids. *Brasema* sp. (1) emerged in conjunction with the host *B. treatae* and numerous other parasitoid species, which suggests that *Brasema* sp. (1) is functioning as an inquiline. *Coleoptera* sp. does not emerge with any other species and is an inquiline, but effectively functions as a parasitoid since no other species can survive in a gall that contains a *Coleoptera* sp.

Two species in this study were previously defined as a single species, *S. flava* and *Sycophila* sp. These two species were originally separated due to morphological differences. *Sycophila* sp. had a darker pigmentation on the head, thorax, and abdomen. *S. flava* and *Sycophila* sp. have similar niche breadths for gall size (0.40 and 0.42 respectively), however, niche breadth for the temporal window is much different (0.23 and 0.58 respectively). *Sycophila* sp. attacked galls in every temporal window from April to November with maximum attacks (39%) occurring in September. *S. flava*, on the other hand, attacked from April to September with maximum attacks (71%) occurring in July. Horn's index of overlap for these two species for gall size class is 0.89 and for temporal windows, 0.63 both of which are lower than niche overlap indices for distinctly different species. It is possible with the overlap data that two generations are being examined and therefore producing artificial niche overlap indices, however this does not

appear to be the case. Examination of within gall interactions also reveals that *S. flava* emerges with multiple other species (*Allorhogas* sp., *Brasema* sp. (3), *O. labotus*, *Synergus* sp., and *T. tubicola*). In addition, *S. flava* demonstrates intraspecific interactions. *Sycophila* sp. did not emerge with any other species or demonstrate intraspecific emergences even though there were over 2.5 times more individuals recovered than *S. flava*. Therefore, it appears that *S. flava* and *Sycophila* sp. are distinct species with different life habits and possibly different trophic levels. It is possible *Sycophila* sp. is functioning as a parasitoid or hyperparasitoid and *S. flava* appears to function as an inquiline. This differentiation has not been confirmed.

Effects of Parasitoids on *B. treatae*: Although the exclosure study was not expressly designed to examine *B. treatae* success, it is possible to extrapolate the effect of parasitoids on *B. treatae*. The early samples (July – August) effectively prevent the completion of *B. treatae* development, however, later samples (September – November 15th) provide mature galls capable of producing *B. treatae*. The low and high emergences of *B. treatae* correspond inversely with the high and low emergences of parasitoid both with the number of species present and the number of individuals present. This supports previous findings that parasitism affects *B. treatae* success. Unexpectedly the success of *B. treatae* emergences from the control bags (April) is less than one percent. I would expect that the control bags would be more protected from parasitism throughout the season and produce more *B. treatae*. The number of parasitoid species present in the control bags was moderate ($n = 7$) and the number of individuals was low ($n = 16$) so it does not appear that the low percentage of *B. treatae* present in the control bags was due to parasitism unless the parasitoids were unable to reach maturity for some reason. The

wild-control had the lowest percent of *B. treatae* success (0.73) as expected since the galls from the wild-control were exposed to parasitoids continuously throughout the season. *Belonocnema treatae* exhibit the low emergence rates that have been typical to the system. Only the May and November treatments resulted in a higher percentage of *B. treatae* emergences to parasitoid emergences. At the peak of parasitoid, attack (July) the emergences of *B. treatae* decreased. Less than one percent of *B. treatae* emerged with *Brasema* sp. (1). *Belonocnema treatae* does not emerge with any other species, which indicates the presence of parasitoids is fatal regardless if they are inquiline or parasitoids.

There are several ways to approach studies of parasitoid communities of gall formers. The structure of the parasitoid community may be examined by following the emergence sequences and thereby determining the presence of species and interactions among species, but does not relay any information about the time of attack or host stage of development. The parasitoids may be correlated with their corresponding gall sizes by dissecting galls of various sizes throughout the development period. This method focuses on the gall sizes utilized. Visual observations of the presence of parasitoids in the field allows information to be gathered on the species present and abundance, however, the presence of a species is not indicative that it actually utilizes the specific gall former. Enclosure studies allow determination of the presence of parasitoids during specific intervals, emergence sequences, gall sizes that successfully produce parasitoids, and competitive interactions. It is not able to determine the size of galls attacked or for resolution of competitive interactions that result in the death of parasitoids. Enclosure

studies in which specific parasitoids are added to bags would allow distinction of the specific gall sizes utilized as well as the outcome of interspecific interactions .

LITERATURE CITED

- Abrams, P. 1980. Some comments on measuring niche overlap. *Ecology*. 61(1):44-49.
- 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. 1984. *The Biology of Gall Insects*. T.N. Ananthakrishnan ed. Oxford and IBH Publishing Co. 66 Janpath, New Delhi 110001.
- Begon M., S.M Sait, and D.J. Thompson. 1995. Persistence of a parasitoid–host system: refuges and generation cycles? *Proc. R. Soc. Lond.* 260:131-137.
- Bouton, C.E., B.A. McPheron, and A.E. Weis. 1980. Parasitoids and competition. *The American Naturalist*. 116:876-881.
- Briggs, C.J. 1993. Competition among parasitoid species on a stage-structured host and its effect on host suppression. *The American Naturalist*. 141(3): 372-397.
- Briggs, C.J. and J. Latto. 1996. The window of vulnerability and its effect on relative parasitoid abundance. *Ecological Entomology*. 21:128-140.
- Craig, T.P., J.K. Itami, and P.W. Price. 1990. The window of vulnerability of a shoot-galling sawfly to attack by a parasitoid. *Ecology*. 71(4):1471-1482.
- Dreger-Jauffret F. and J.D. Shorthouse. 1992. Diversity of gall-inducing insects and their galls, pp. 8-33. In J.D. Shorthouse and O. Rohfritsch, eds., *Biology of Insect-Induced Galls*. Oxford University Press, New York.
- Godfray, H.C.J. 1994. *Parasitoids: behavioral and evolutionary ecology*. Princeton: Princeton University Press.

- Hawkins, B.A. 1988. Species diversity in the third and fourth trophic levels: patterns and mechanisms. *Journal of Animal Ecology*. 57:137-162.
- Hawkins, B.A. and R.J. Gangné. 1989. Determinants of assemblage size for the parasitoids of Cecidomyiidae (Diptera). *Oecologia*. 81:75-88.
- Hawkins, B.A. 1993. Parasitoid species richness, host mortality, and biological control. *The American Naturalist*. 141(4):634-641.
- Hawkins, B.A., and N.J. Mills. 1996. Variability in parasitoid community structure. *Journal of Animal Ecology*. 65:501-516.
- Hawkins, B.A. and W. Sheehan. 1994. *Parasitoid Community Ecology*. Oxford University Press, Oxford. 516.
- Hawkins, C.P. and J.A. MacMahon. 1989. Guilds: the multiple meanings of a concept. *Annual Review of Entomology*. 34:423-451.
- Hochberg, M.E. and B.A. Hawkins. 1992. Refuges as a predictor of parasitoid diversity. *Science*. 255:973-976.
- Hoffmeister, T.S. and S. Vidal. 1994. The diversity of fruit fly (Diptera: Tephritidae) parasitoids. *Parasitoid Community Ecology*, B.A. Hawkins, W. Sheehan, Eds. Oxford University Press, New York, NY. 47-76.
- Jones, D. 1983. The influence of host density and gall shape on the survivorship of *Diastrophus kincaidii* Gill. (Hymenoptera: Cynipidae). *Canadian Journal of Zoology*. 61:2138-2142.
- Kakehashi, N., Y. Suzuki, and Y. Iwasa. 1984. Niche overlap of parasitoids in host-parasitoid systems: its consequence to single versus multiple introduction controversy in biological control. *Journal of Applied Ecology*. 21:115-131.

- Krebs, C. J. 1999. *Ecological Methodology*. Benjamin Cummings. New York, NY. 620.
- Lund, J.N., J.R. Ott, and R.J. Lyon. 1998. Heterogony in *Belonocnema treatae* Mayr (Hymenoptera: Cynipidae). *Proceedings of the Entomological Society of Washington*. 100(4):755-763.
- Lund, J. N. 1998. Thesis: The biology and ecology of *Belonocnema treatae* (Hymenoptera:Cynipidae) on its host plant, *Quercus fusiformis*. Southwest Texas State University. P. 73.
- May, R.M. and M.P. Hassell. 1981. The dynamics of multiparasitoid-host interactions. *The American Naturalist*. 117(3):234-261.
- Mills, N.J. 1994. Parasitoid guilds: a comparative analysis of the parasitoid communities of tortricids and weevils. *Parasitoid Community Ecology*, B.A. Hawkins, W. Sheehan, Eds. Oxford University Press, New York, NY. 30-46.
- Pianka, E.R. 1994. *Evolutionary Ecology*. HarperCollins College Publishers. New York, N.Y. 486.
- Plantard, O., J. Rasplus, and M.E. Hochberg. 1996. Resource partitioning in the parasitoid assemblage of the oak galler *Neuroterus quercusbaccarum* L. (Hymenoptera: Cynipidae) *Ecologica* 19(1):1-15.
- Plantard, O., J. Rasplus, and M.E. Hochberg. 1998. Factors affection parasitism in the oak-galler *Neuroterus quercusbaccarum* (Hymenoptera: Cynipidae). *Oikos*. 81:289-298.
- Price, P.W. 1986. Interactions among three trophic levels: gall size and parasitoid attack. *Ecology*. 67:1593-1600.

- Price, P.W. 1971. Niche breadth and dominance of parasitic insects sharing the same host species. *Ecology* 52(4):587-596.
- Price, P.W. 1970. Characteristics permitting coexistence among parasitoids of a sawfly in Quebec. *Ecology* 51(3):445-454.
- Price, P.W. and K.M. Clancy. 1986. Interactions among three trophic levels: gall size and parasitoid attack. *Ecology*. 67(6):1593-1600.
- Reynolds, R.J. 2000. Thesis: The role of natural enemies in determining the relationship between gall size and emergence success of a host-specific cynipid. Southwest Texas State University. P. 35.
- Ronquist, F. 1994. Evolution of parasitism among closely related species: phylogenetic relationships and the origin of inquilinism in gall wasps (Hymenoptera, Cynipidae). *Evolution*. 48(2):241-266.
- Schönrogge, K., G.N. Stone, and M.J. Crawley. 1996. Abundance patterns and species richness of the parasitoids and inquilines of the alien gall-former *Andricus quercuscalicis* (Hymenoptera: Cynipidae). *Oikos*. 77:507-518.
- Schowalter, T.D. 2000. *Insect Ecology: An Ecosystem Approach*. Academic Press. New York, N.Y. 483.
- Sheehan, W. 1994. Parasitoid Community structure: effects of host abundance, phylogeny, and ecology. *Parasitoid Community Ecology*, B.A. Hawkins, W. Sheehan, Eds. Oxford University Press, New York, NY. 90-102.
- Sitch, T.A., D.A. Grewcock, and F.S. Gilbert. 1988. Factors affecting components of fitness in a gall-making wasp (*Cynips divisa* Hartig). *Oecologia*. 76:3721-375.

- Southwood, T.R.E. 1973. The insect/plant relationship – an evolutionary perspective. Symp. Roy. Ent. Soc. Lond., 6:3-30.
- Tasharntke, T. 1992. Coexistence, tritrophic interactions and density dependence in a species-rich parasitoid community. Journal of Animal Ecology. 61:59-67.
- Weis A.E., W.G. Abrahamson, and K.D. McCrea. 1985. Host gall size and oviposition success by the parasitoid *Eurytoma gigantea*. Ecological Entomology. 10:341-348.
- Weis, A.E. and G. W.G. Abrahamson. 1985. Potential selective pressures by parasitoids on a plant-herbivore interaction. Ecology 66(4):1261-1269.

Table 1. Study Design: Windows of accessibility of parasitoids to leaf galls of *B. treatae* for exclusion study 2000. Each window runs from the 1st to the last day of the month (Exception November from 1st to 15th) C = Bags in place, galls inaccessible to parasitoids. Open = Bags removed, galls accessible to parasitoids.

April	May	June	July	August	September	October	November
Open	C	C	C	C	C	C	C
Open	Open	C	C	C	C	C	C
Open	C	Open	C	C	C	C	C
Open	C	C	Open	C	C	C	C
Open	C	C	C	Open	C	C	C
Open	C	C	C	C	Open	C	C
Open	C	C	C	C	C	Open	C
Open	C	C	C	C	C	C	Open

Table 2. Study Design: Distribution of sampling effort (number of branches bagged) across trees (replicates) and windows. Six trees (labeled as FR10-H9) were each assigned four or five bags per window April (Control) - November. Each tree had a total of 35 bags. Each window had a total of 24 or 30 bags. Overall 210 bags were utilized in the study.

Window	Tree						Total per window
	FR10	H3	H6	H7	H8	H9	
Control (April)	6	6	6	6	6	6	36
May	5	5	5	5	5	5	30
June	4	4	4	4	4	4	24
July	5	5	5	5	5	5	30
August	4	4	4	4	4	4	24
September	5	5	5	5	5	5	30
October	4	4	4	4	4	4	24
November	2	2	2	2	2	2	12
Total per tree	35	35	35	35	35	35	210

Table 3. Study Design: Collection schedule and number of collected of bags for each window Control (April) - November and the dates they were collected (July 1- November 15). Column heading "Wild" refers to galls that were exposed to natural levels of parasitism throughout the study period. Fifty wild galls were collected from each of the six study trees on each of the collection dates.

Collection Date	Window								Wild
	Control	May	June	July	Aug	Sept	Oct	Nov	
July 1	6	4	3	0	0	0	0	0	6
Aug 1	6	4	3	6	0	0	0	0	6
Sept 1	6	5	3	6	6	0	0	0	6
Oct 1	6	5	3	6	6	18	0	0	6
Nov 1	6	12	12	12	12	12	24	0	6
Nov 15	6	0	0	0	0	0	0	12	6
Total	36	30	24	30	24	30	24	12	36

Table 4. Timing of attack and subsequent emergence of the *B. treatae* leaf gall community as determined by the exclusion study and rearing of gall occupants in the laboratory.

	Control (April)	May	June	July	August	September	October	November	December	January	February	March
<i>Sycophila</i> sp.	6	8	5	10	3	31	12	4				
						1	1	4	24	36	3	14
Coleoptera sp.	1	1	3	39	18	2		1				
						7	10	22	8	3	2	
<i>Synergus</i> sp.	3	41	27	83	5							
				23	31	93	22	39	5			
<i>Sycophila flava</i>	3	2	2	25		3						
				1	25	1	1	3	3			1
Morphotype (07)	1	1	3	2								
				3		6	1	1				
<i>Torymus tubicola</i>	1			15		12	24					
				1		3	5	24	15	1	1	
<i>Galeopsomyia</i> sp.	1	3	2		18	1	2					
								4		3	1	2
<i>Eurytoma bugbeeii</i>		1	4	1		8	1					
				1	4	1	3	3	2			5
<i>Brasema</i> sp. (1)		1		4	1	38	12					
					11	7	7	19	14	9		2
<i>Brasema</i> sp. (2)		1		2		5						
					4	2	1	5	1			1
<i>Ormyrus labotus</i>			4	21	1	2	1					
				8	33	20	6	3				
<i>Brasema</i> sp. (3)			4	37		35	4					
				10	48	17	12	26	11	4		
<i>Allorhogas</i> sp.				118		6						
					84	34	3		2	1		

The blue line indicates the window (month) during which each parasitoid species attacked galls. The green line indicates the time each parasitoid species emerged from galls. The numbers indicate the number of individuals that attacked or emerged during each interval. Attack and emergence numbers may not be equal as emergence data included individuals reared from the wild-control falls for each window, for which a time of attack could not be extrapolated. The control also listed above is the period of time before gall formation (April). Timing of attack and emergences are shown for the 13 most common species ($n \geq 10$).

Table 5. Levins's "B", a measure of microhabitat niche breadth standardized by the number of resource classes available for the 13 most common parasitoids ($n \geq 10$ emergences) of the *B. treatae* leaf gall community. A low niche breadth indicates that the species occurs in a restricted subset of resource classes. A niche breadth of 1.0 indicates that the species occurs in all resource classes equally. Species are listed in order of their occurrence in temporal windows and by the number of temporal windows in which they appear.

Species	Temporal Window		Gall Size	
	Standardized Levins's B	Sample size (n)	Standardized Levins's B	Sample size (n)
<i>Sycophila</i> sp.	0.58	80	0.42	83
Coleoptera sp.	0.28	65	0.46	78
<i>Synergus</i> sp.	0.34	159	0.63	213
<i>Sycophila flava</i>	0.23	35	0.40	35
Morphotype (07)	0.41	7	0.35	11
<i>Torymus tubicola</i>	0.36	52	0.44	67
<i>Galeopsomyia</i> sp.	0.53	9	0.35	10
<i>Eurytoma bugbeeii</i>	0.34	15	0.43	20
<i>Brasema</i> sp. (1)	0.24	56	0.35	69
<i>Brasema</i> sp. (2)	0.27	8	0.39	14
<i>Ormyrus labotus</i>	0.23	29	0.44	69
<i>Brasema</i> sp. (3)	0.30	80	0.47	129
<i>Allorhogas</i> sp.	0.14	124	0.34	124

Table 6. Niche overlap for the niche dimension "Gall Size" among parasitoid species of the *B. treatae* leaf gall community. Horn's index of niche overlap (R_o) is presented for the 13 most common parasitoid species ($n \geq 10$ emergences) using 18 gall size classes. Gall sizes ranged in size from ≥ 0.5 to 9.0 mm; classes were .05 mm width. Species are listed in order of increasing median gall class size from which they emerged. Median gall size from which parasitoids emerged was 0.80, $\bar{r} = 0.75$, $SE = 0.14$

	<i>Brasema</i> sp. (3)	Morphotype (07)	<i>Brasema</i> sp. (2)	<i>Synergus</i> sp.	<i>Ormyrus labotus</i>	<i>Eurytoma bugbee</i>	<i>Brasema</i> sp. (1)	<i>Galeopsomyia</i> sp.	<i>Coleoptera</i> sp.	<i>Sycophila</i> sp.	<i>Torymus tubicola</i>	<i>Allorhogas</i> sp.	<i>Sycophila flava</i>
<i>Brasema</i> sp. (3)	1	.78	.88	.90	.81	.81	.67	.64	.79	.67	.70	.68	.69
Morphotype (07)		1	.80	.71	.61	.59	.48	.42	.54	.48	.45	.46	.45
<i>Brasema</i> sp. (2)			1	.82	.80	.84	.68	.52	.66	.61	.64	.59	.55
<i>Synergus</i> sp.				1	.87	.89	.86	.64	.89	.84	.87	.86	.82
<i>Ormyrus labotus</i>					1	.74	.80	.64	.91	.84	.83	.87	.83
<i>Eurytoma bugbee</i>						1	.86	.57	.83	.82	.88	.79	.75
<i>Brasema</i> sp. (1)							1	.61	.85	.93	.93	.88	.81
<i>Galeopsomyia</i> sp.								1	.71	.66	.65	.65	.72
<i>Coleoptera</i> sp.									1	.94	.92	.92	.91
<i>Sycophila</i> sp.										1	.95	.92	.91
<i>Torymus tubicola</i>											1	.92	.89
<i>Allorhogas</i> sp.												1	.94
<i>Sycophila flava</i>													1

Table 7. Niche overlap for the niche dimension "Timing of Attack" among parasitoid species of the *B. treatae* leaf gall community. Horn's index of niche overlap (Ro) is presented for the 13 most common parasitoid species ($n \geq 10$ emergences) and eight temporal windows. Species are listed in order of temporal occurrence and number of windows in which they appear. Median gall size from which parasitoids emerged was 0.61, 62, SE = 0.18

	<i>Sycophila</i> sp.	<i>Coleoptera</i> sp.	<i>Synergus</i> sp.	<i>Sycophila flava</i>	Morphotype (07)	<i>Torymus tubicola</i>	<i>Galeopsomyia</i> sp.	<i>Eurytoma bugbee</i>	<i>Brasema</i> sp. (1)	<i>Brasema</i> sp. (2)	<i>Ormyrus labotus</i>	<i>Brasema</i> sp. (3)	<i>Allorhogas</i> sp.
<i>Sycophila</i> sp.	1	.55	.55	.63	.54	.77	.77	.82	.86	.77	.59	.77	.39
<i>Coleoptera</i> sp.		1	.78	.81	.59	.48	.29	.37	.36	.50	.86	.66	.78
<i>Synergus</i> sp.			1	.84	.87	.39	.52	.48	.26	.53	.80	.58	.69
<i>Sycophila flava</i>				1	.75	.59	.41	.51	.42	.67	.88	.79	.88
Morphotype (07)					1	.32	.64	.57	.81	.40	.66	.47	.48
<i>Torymus tubicola</i>						1	.51	.59	.85	.63	.63	.78	.56
<i>Galeopsomyia</i> sp.							1	.70	.52	.42	.33	.77	.07
<i>Eurytoma bugbee</i>								1	.77	.76	.56	.77	.29
<i>Brasema</i> sp. (1)									1	.80	.46	.79	.34
<i>Brasema</i> sp. (2)										1	.56	.85	.57
<i>Ormyrus labotus</i>											1	.84	.88
<i>Brasema</i> sp. (3)												1	.76
<i>Allorhogas</i> sp.													1

Table 8 Summary of frequencies of outcomes of intraspecific and interspecific interactions within galls for both the gall former and parasitoid species of the *B. treatae* leaf gall community Left to right Total indicates the number of individuals reared from leaf galls for each species summed across all windows and all types of interactions, Single indicates the number of galls for each species that produced only one individual, Intra 2 - Intra 7 are the number of galls that produced two to seven individuals of the same species, Inter 1 - Inter 3 are the number of galls that produced one to three additional species along with the species listed to the left in column one, for example *Synergus* sp 20 galls produces *Synergus* sp plus one parasitoid, four *Synergus* sp plus four additional species. Species listed in order of abundance

Species	Total	Single	Intra 2	Intra 3	Intra 4	Intra 5	Intra 6	Intra 7	Inter 1	Inter 2	Inter 3
<i>Belonocnema treatae</i>	214	212	0	0	0	0	0	0	2	0	0
<i>Synergus</i> sp	213	112	26	5	2	0	0	0	20	4	0
<i>Brasema</i> sp (3)	128	77	12	1	0	0	0	0	19	3	1
<i>Illorhogas</i> sp	124	42	19	6	0	1	0	0	13	5	0
<i>Sycophila</i> sp	83	83	0	0	0	0	0	0	0	0	0
Coleoptera sp	81	81	0	0	0	0	0	0	0	0	0
<i>Brasema</i> sp (1)	69	52	2	0	0	0	0	0	13	0	0
<i>Ormyrus labotus</i>	69	31	10	1	0	0	0	1	8	0	0
<i>Torymus tubicola</i>	68	58	0	1	0	0	0	0	3	0	1
<i>Sycophila flava</i>	35	18	3	0	1	0	0	0	8	2	0
<i>Eurytoma bugbei</i>	19	17	0	0	0	0	0	0	2	0	0
<i>Brasema</i> sp (2)	14	11	0	0	0	0	0	0	3	0	1
Morphotype (7)	11	6	2	0	0	0	0	0	1	0	0
<i>Galeopsomyia</i> sp	10	10	0	0	0	0	0	0	0	0	0
Morphotype (02)	8	8	0	0	0	0	0	0	0	0	0
Morphotype (01)	4	4	0	0	0	0	0	0	0	0	0
<i>Eurytoma</i> sp	3	2	0	0	0	0	0	0	1	0	0
Lepidoptera sp	3	2	0	0	0	0	0	0	1	0	0
Morphotype (05)	3	3	0	0	0	0	0	0	0	0	0
Morphotype (06)	3	1	0	0	0	0	0	0	0	0	1
Morphotype (08)	2	2	0	0	0	0	0	0	0	0	0
<i>Acaenacis lausus</i>	1	1	0	0	0	0	0	0	0	0	0
Diptera sp	1	1	0	0	0	0	0	0	0	0	0
Morphotype (03)	1	1	0	0	0	0	0	0	0	0	0
Morphotype(04)	1	1	0	0	0	0	0	0	0	0	0
Morphotype (09)	1	1	0	0	0	0	0	0	0	0	0
Morphotype (10)	1	1	0	0	0	0	0	0	0	0	0
Morphotype (11)	1	1	0	0	0	0	0	0	0	0	0

Table 9. Matrix of outcomes of intraspecific and pairwise interspecific interactions among community members within individual *B. treatae* leaf galls. Species listed exhibited ≥ 1 co-emergence from an individual gall with either the gall-former (row 1), their own species (diagonal), or another parasitoid species (off-diagonals). For interspecific contests the presence of an "X" in a cell indicates that the species listed can coexist (complete development) within individual galls. For intraspecific contests an "X" indicates that multiple individuals of the same species can coexist. Blank cells represent patterns of co-emergence not recorded. The total number of different species each species is capable of coexisting with is given in the right hand column.

	<i>Belonocnema treatae</i>	<i>Allorhogas</i> sp.	<i>Brasema</i> sp. (1)	<i>Brasema</i> sp. (2)	<i>Brasema</i> sp. (3)	<i>Eurytoma bugbee</i>	<i>Eurytoma</i> sp.	Lepidoptera sp.	<i>Ormyrus labotus</i>	<i>Sycophila flava</i>	<i>Synergus</i> sp.	<i>Torymus tubicola</i>	Morphotype (06)	Morphotype (07)	Total
<i>Belonocnema treatae</i>			X												1
<i>Allorhogas</i> sp.		X	X	X	X					X	X	X			6
<i>Brasema</i> sp. (1)	X	X	X		X	X	X				X	X			7
<i>Brasema</i> sp. (2)		X			X							X	X		4
<i>Brasema</i> sp. (3)		X	X	X	X			X	X	X	X	X	X		9
<i>Eurytoma bugbee</i>			X												1
<i>Eurytoma</i> sp.			X												1
Lepidoptera sp.					X										1
<i>Ormyrus labotus</i>					X				X	X	X				3
<i>Sycophila flava</i>					X				X	X	X	X			4
<i>Synergus</i> sp.		X	X		X				X	X	X			X	6
<i>Torymus tubicola</i>		X	X	X	X					X		X	X		6
Morphotype (06)				X	X							X			3
Morphotype (07)											X			X	1

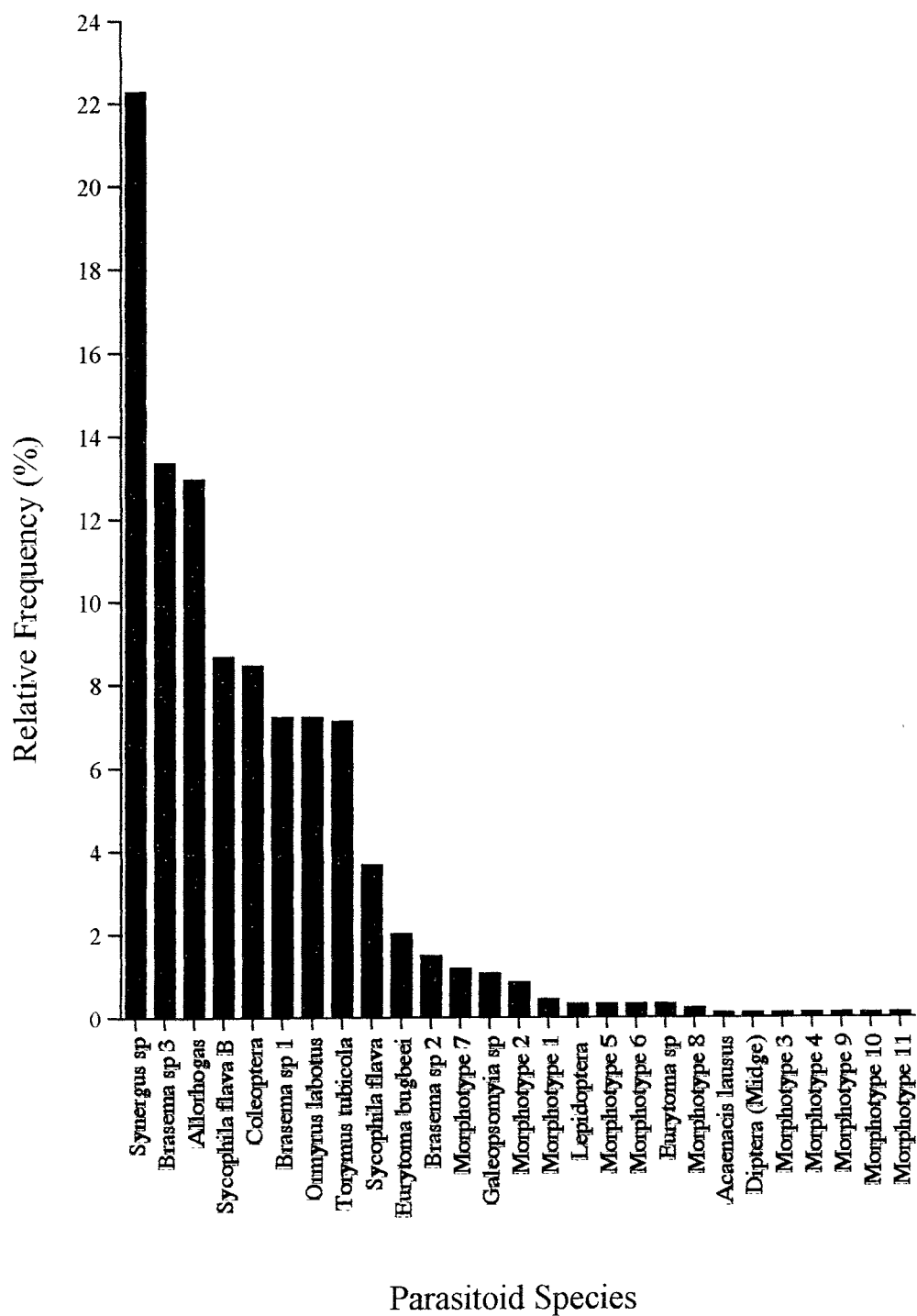


Figure 1. The relative frequency of parasitoid species of the *B. treatae* leaf gall community

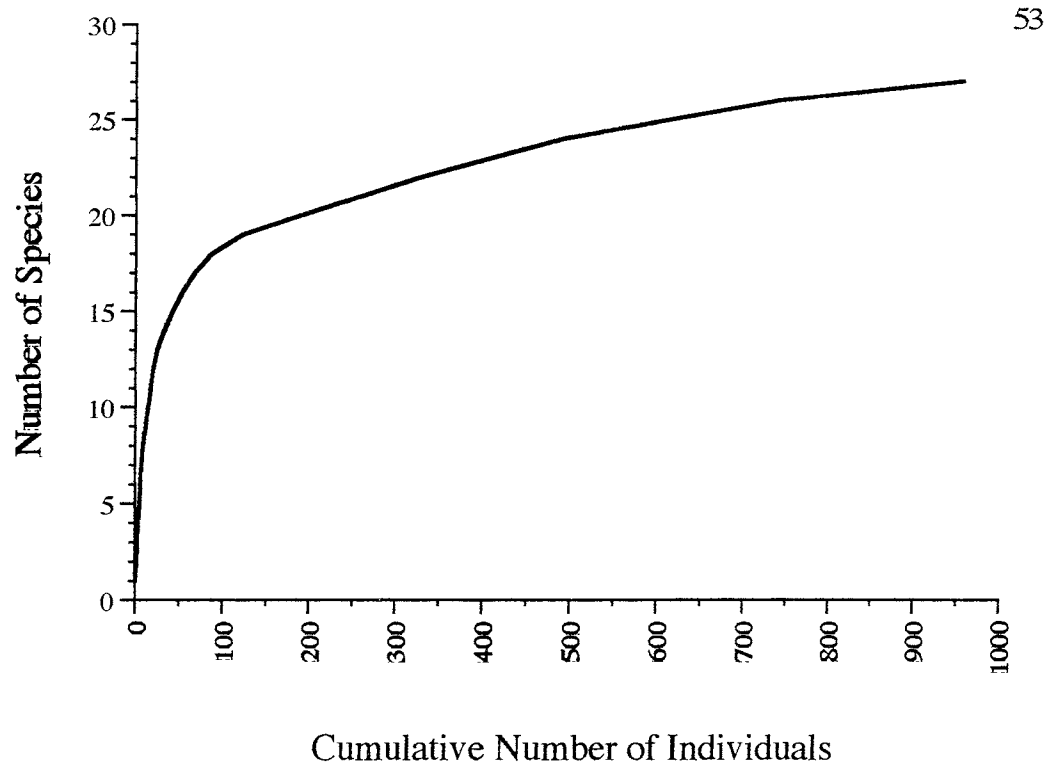


Figure 2. The rate of accumulation of species in the *B. treatae* leaf gall community against the cumulative total of individuals reared from individual leaf galls collected during the exclusion study. The relationship illustrated suggests most species present in the community were represented in the galls assayed (21,000) and 957 individual parasitoids reared from galls.

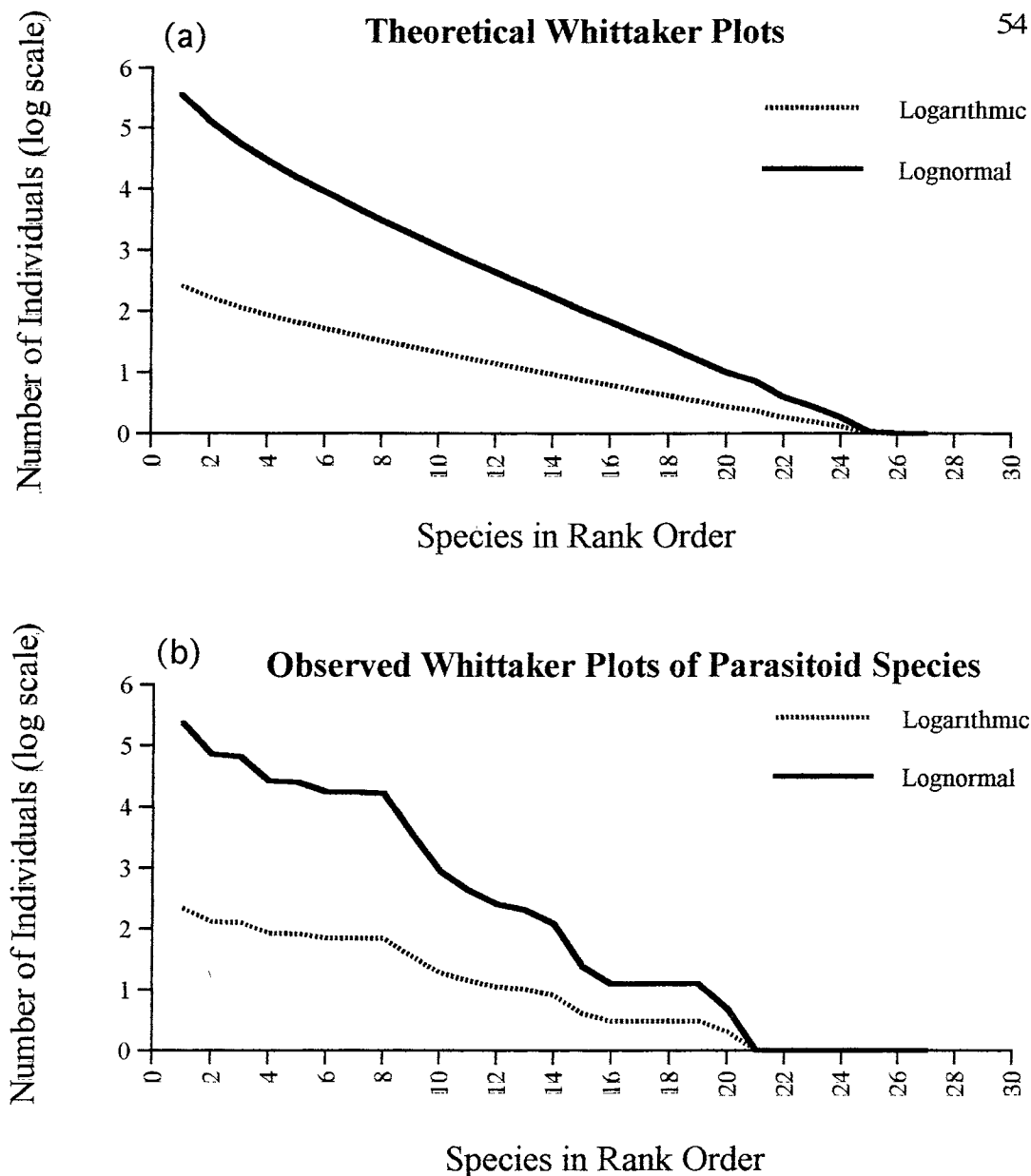


Figure 3. Whittaker plots of species-abundance data for parasitoids of the *B. treatae* leaf gall community. (a) Theoretical plots. The logarithmic series produces a nearly straight line, while the lognormal distribution predicts a slightly hollow curve for the more abundant species (b) Observed data. The relative abundance for the 27 species of parasitoids is best described by the lognormal distribution.

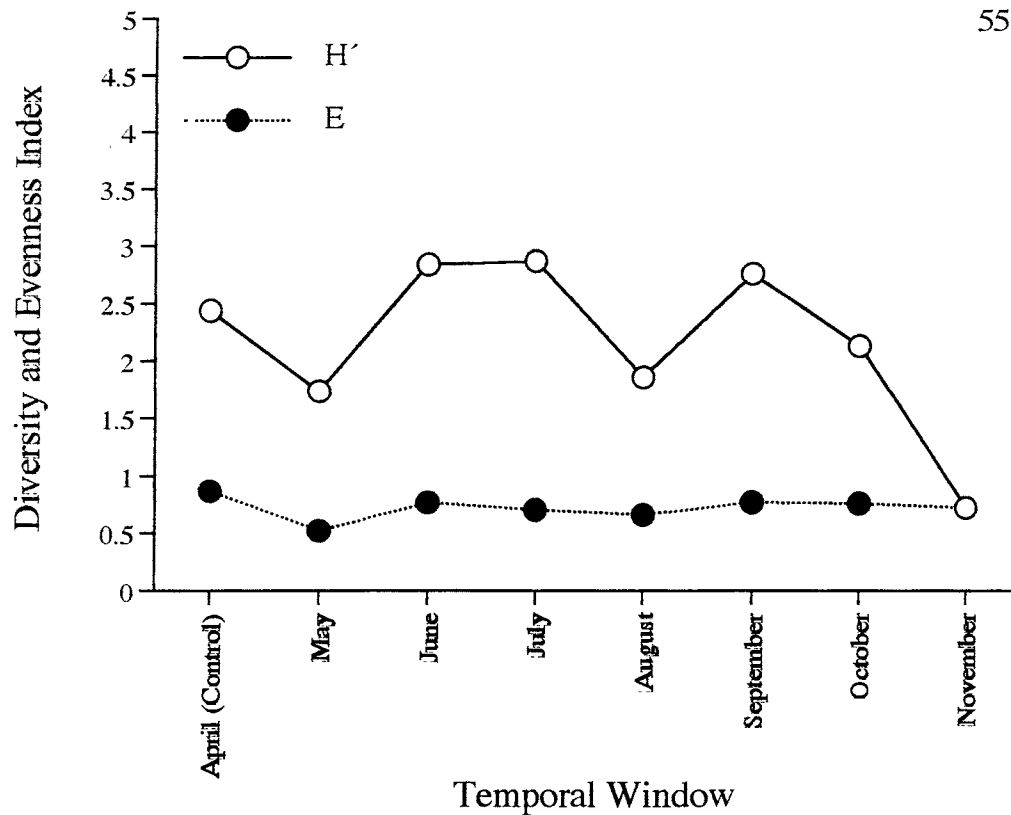


Figure 4. Diversity of the *B. treatae* community showing Evenness = E (filled circles) and Diversity = H' (unfilled circles) in each temporal window. An evenness index value of 1 indicates all species present in the community occur the window. An evenness index of 0 indicates no two species occur in the same window. A diversity index of 0 indicates no diversity. A diversity index of 5 is the highest value obtainable by a community. The overall diversity index for the entire community across the full season of parasitoid activity (April-November) is 3.48 with an evenness of 0.73.

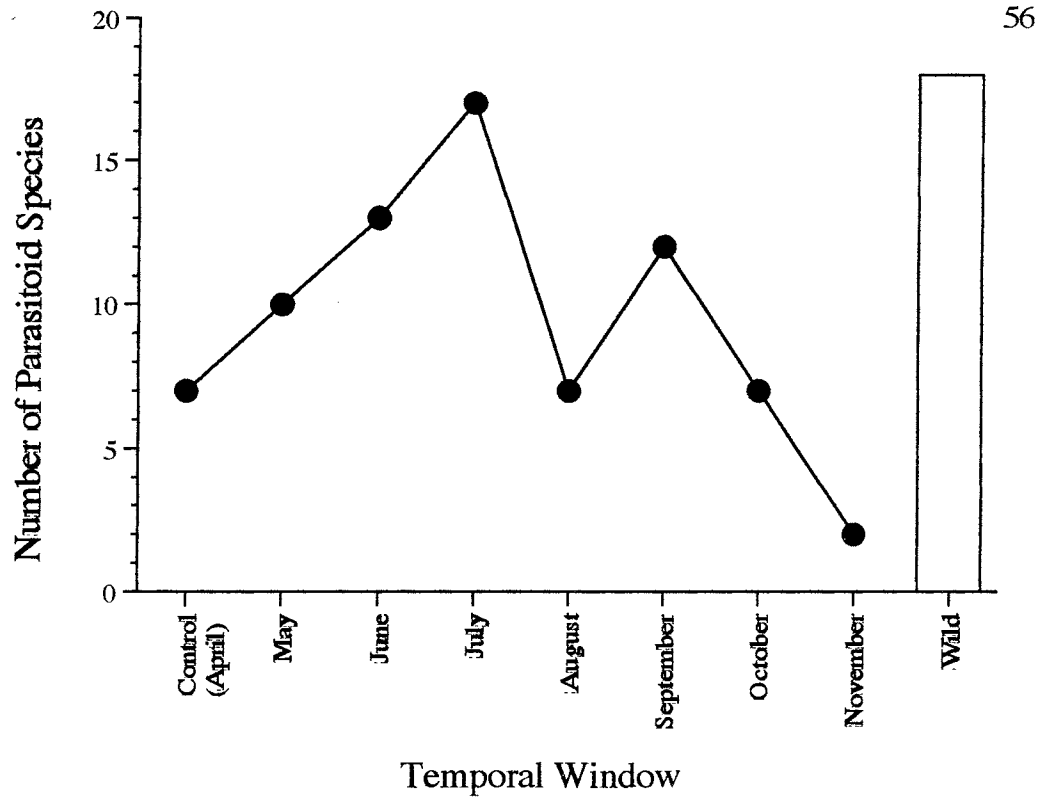


Figure 5. The number of parasitoid species present in each window. The wild treatment consisted of galls exposed to parasitism for the entire study. The control treatment was exposed only during the oviposition period of *B. treatae* (April). The other windows indicate the month the galls were exposed to parasitism.

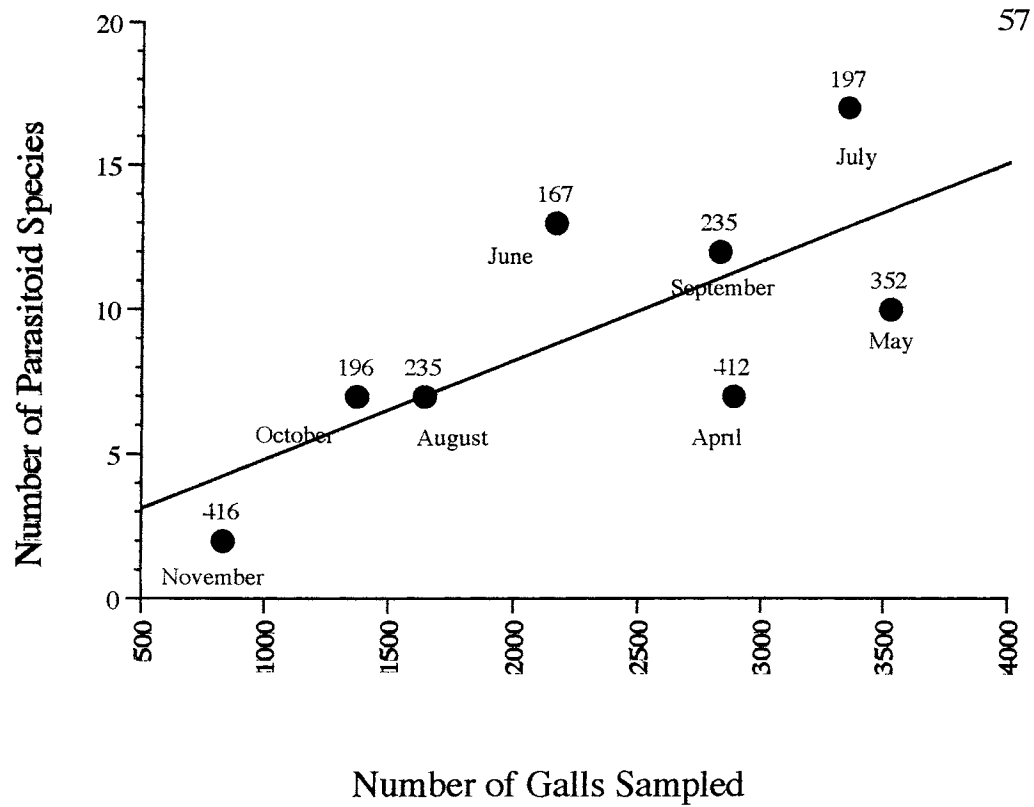


Figure 6. A plot of the number of overall parasitoid species recovered versus the number of galls examined ($r = 0.72$). The number of galls required to produce the next species is shown.

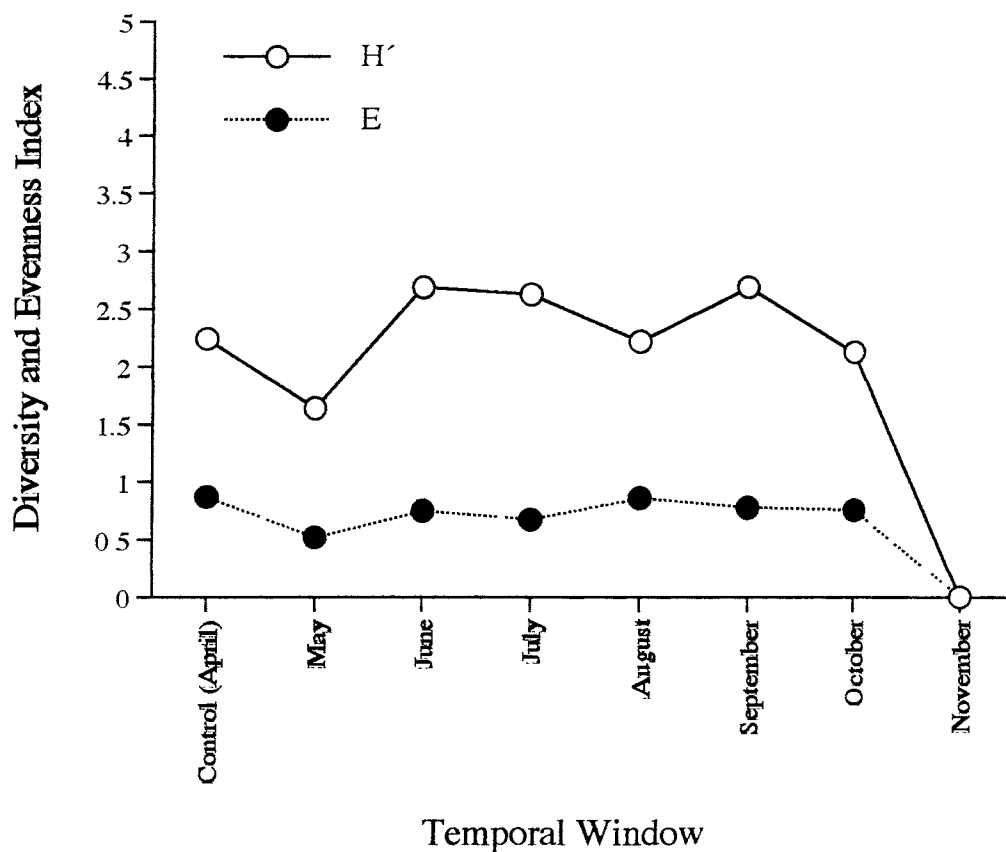


Figure 7. Diversity of hymenopteran parasitoids of the *B. treatae* leaf gall community showing E (filled circles) and H' (unfilled circles) in each temporal window. An evenness index of 1 indicates all species present in the community occur in a windows. An evenness index of 0 indicates no two species occur in the same window. A diversity index of 0 indicates no diversity. A diversity index of 5 is the highest value obtainable by a community. The overall diversity index for hymenopteran parasitoids regardless of window is 3.32 with an evenness of 0.72.

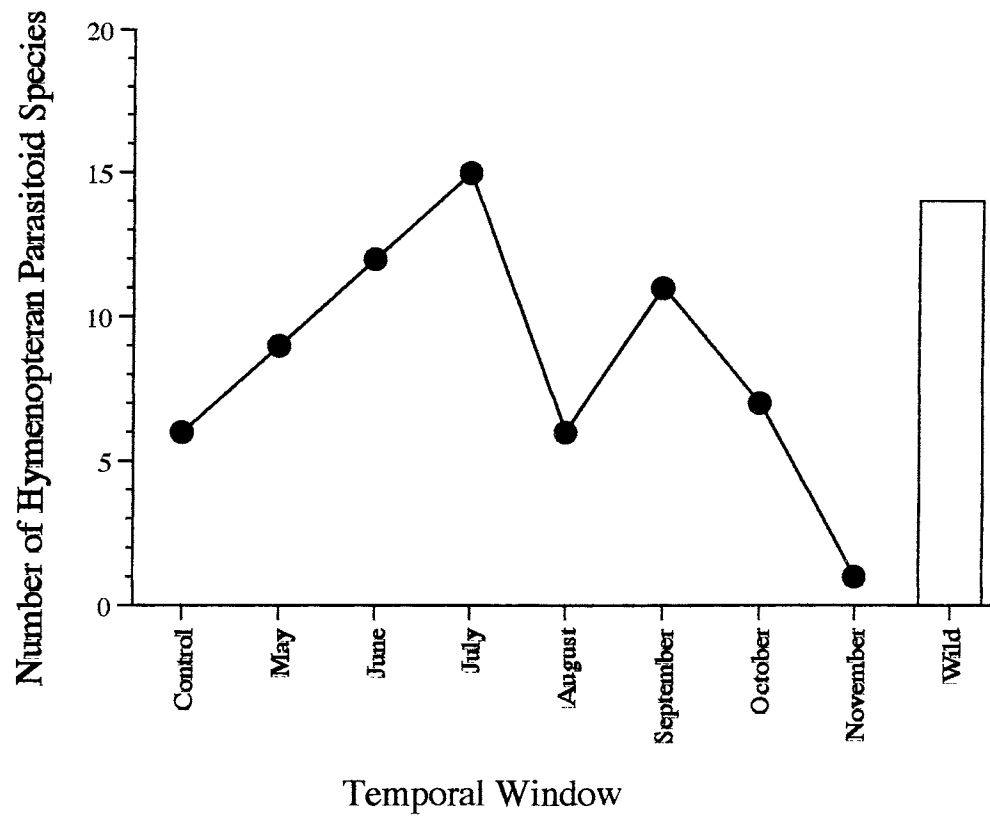


Figure 8. The number of hymenopteran species present in each window as determined by rearing occupants of galls exposed during each window.

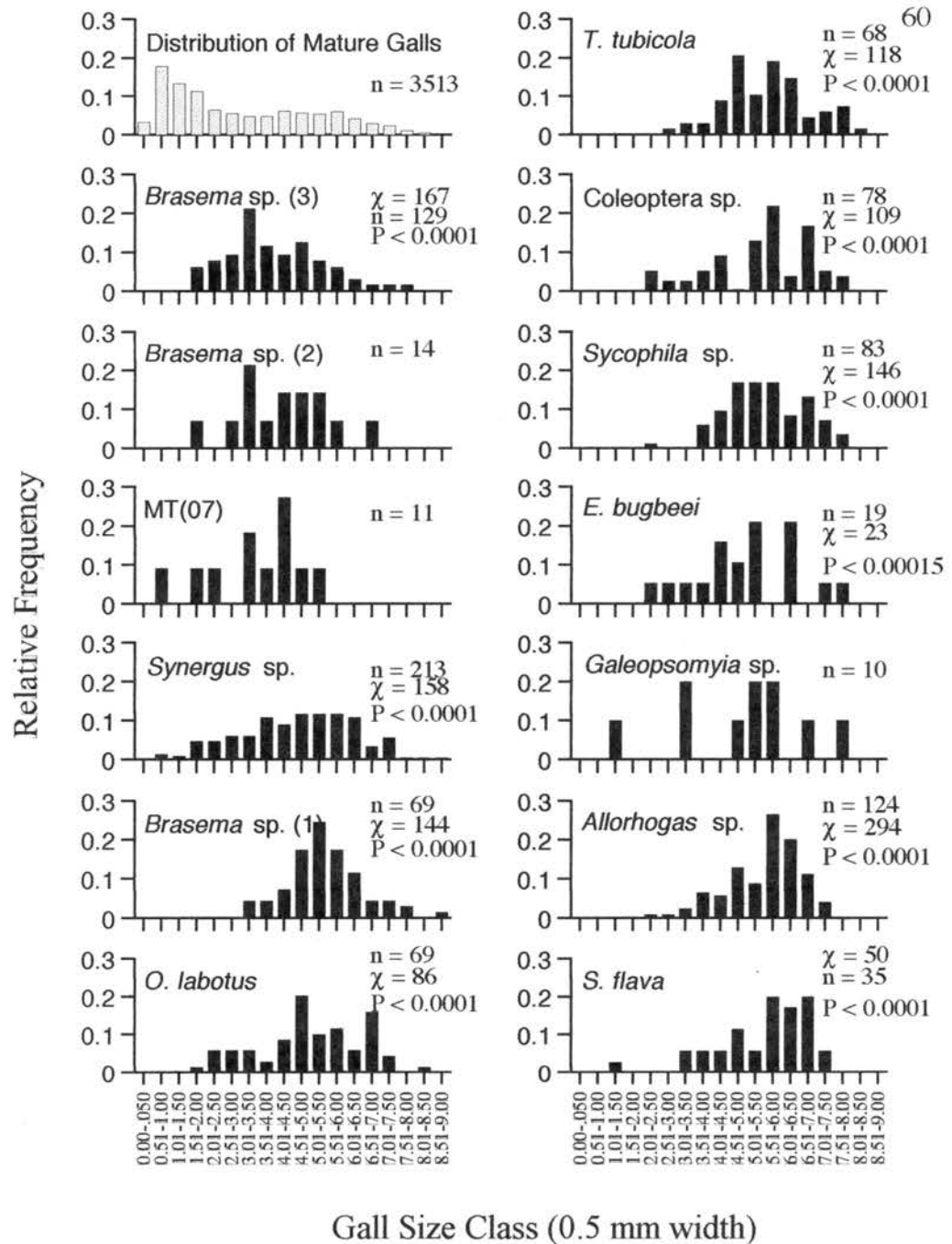


Figure 9. The distribution of gall sizes at maturity at the study site for galls exposed to parasitism (April - November) (top left panel) and the distribution of gall sizes from which each of the 13 most common parasitoid species of the *B. treatae* leaf gall community emerged (all other panels). Chi-square and P values for the test of the H_0 : the gall size distribution used by each species is random (i.e. follows the observed distribution of gall sizes available).

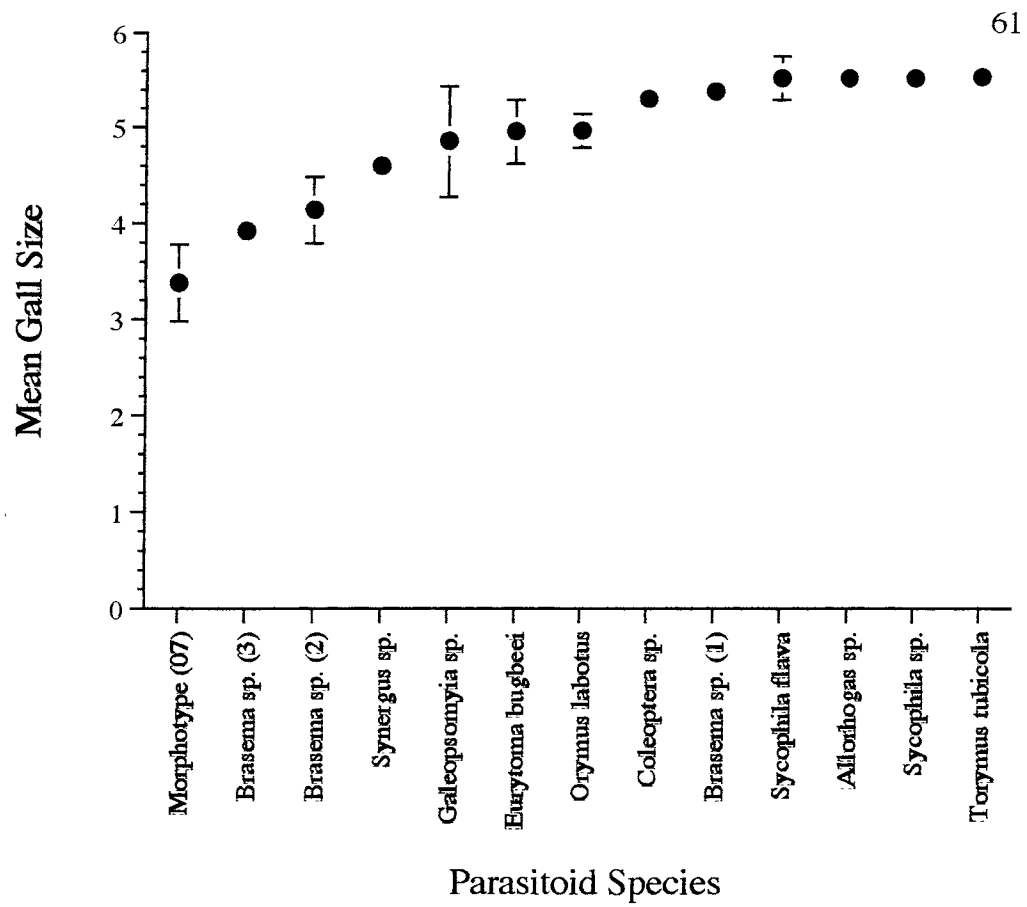


Figure 10. The mean gall size and standard error for the 13 most commonly occurring parasitoid species. Error bars not visible were subsumed by the symbol.

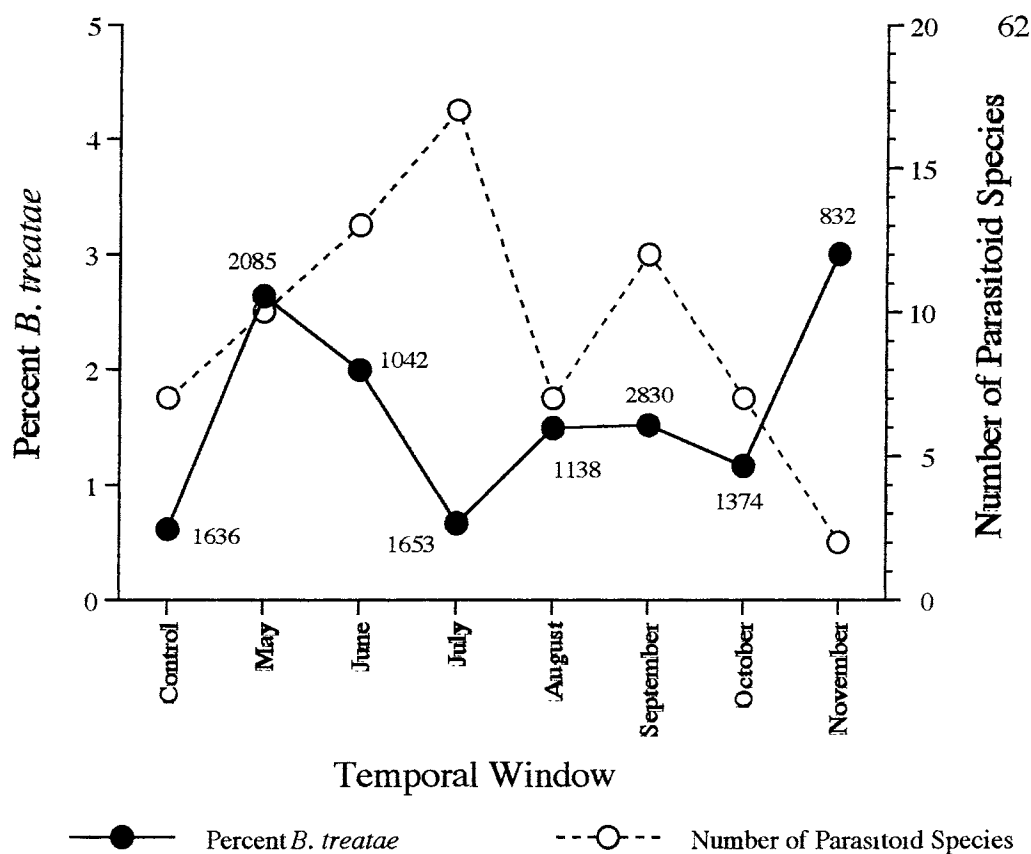


Figure 11. The percent of *B. treatae* emergences from galls for each window is shown on the Y axis (n = gall sample size). Percentages were calculated using only galls from samples capable of producing viable larvae (i.e. bags harvested during the collection periods: October, November, and November 15). The number of parasitoid species present is shown on the right axis. The wild window yielded 0.73 % *B. treatae* and two parasitoid species.

VITA

Myra Carmen Hall was born in Shelbyville, Kentucky, on May 18, 1966, the daughter of Willena Cook Hall and Raymond Lee Hall. She joined the United States Army in 1989 and served for four years. She received a Bachelor of Science in Biology in December, 1997 from Southwest Texas State University. In August 1998, she entered the Graduate School of Southwest Texas State University, San Marcos, Texas.

Thesis manuscript typed by Myra Carmen Hall