TEMPORAL AND SPATIAL PATTERNS OF PARASITOID ATTACK ON A ROOT-GALLING CYNIPID

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ABSTRACT

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Here in I assess for the host-specific gall former *Belonocnema treatae* (1) the effects of temporal variation in oviposition timing on (a) gall growth, and (b) parasitism; (2) the effects of spatial variation in gall-former densities on (a) gall discovery, and (b) gall parasitism; (3) ecological parameters related to (a) host-tree selection, (b) gall growth, (c) gall occupancy, (d) parasitism, and (e) sex.

(1) To assess the effects of variation in oviposition timing on gall growth and parasitism rates, I created three *B. treatae* cohorts, and exposed them to parasitoid attack during each of four intervals. Oviposition timing significantly affected developmental gall sizes ($p < 0.001$), but not the sizes of galls at maturity ($p > 0.10$). Both host-tree selection ($p < 0.001$) and oviposition timing ($p < 0.05$) significantly affected the rates at which parasitoids discovered galls, and an interaction between these two variables had a significant effect on gall parasitism rates ($p < 0.05$). Gall discovery ($p > 0.90$) and parasitism rates ($p > 0.10$) were not size dependent. Analyses of

temporal patterns of parasitoid attack suggest that parasitoids were attacking eggs and not mature galls.

(2) To test for density dependent parasitism, I collected four 1/8-m^2 samples of galls from unmanipulated root regions of 10 host-trees and lab reared their occupants. Gall densities were significantly different among host-trees ($P < 0.005$), yet these differences did not correlate with gall discovery ($R^2 = 0.003$), or gall parasitism rates ($R^2 = 0.003$). Coefficient estimates of both gall discovery and parasitism rates suggest that the probability of each increase by only 1% for every 50 galls/m^2 increase. Density independent patterns of parasitoid attack are explained by visual limitations and high travel costs associated with searching for prey in a subterranean environment, or by small sample sizes that were possibly insufficient for detecting subtle patterns of density dependant foraging.

(3) To describe root-galling *B. treatae* ecological parameters, I collected and lab reared the occupants of 771 galls taken from unmanipulated root regions of 10 host-trees. Analyses of these galls showed that significantly more females emerged from root galls than did males ($p < 0.001$), yet the number of female and male producing galls did not differ within ($p > 0.50$) or among ($p > 0.10$) trees. Analysis of gall sizes between the sexes showed that on average females emerged from larger galls than did males ($p < 0.05$), yet their mean gall occupancy levels did not differ ($p > 0.60$). Neither gall discovery ($p > 0.05$) nor gall parasitism rates ($p > 0.20$) differed between the sexes. Analysis of host tree regulated fitness parameters suggests that host-trees exert a major selective force on root-galling *B. treatae*. These analyses show that host-tree selection influences everything from gall size ($p < 0.01$) and gall occupancy levels ($p < 0.0001$) to gall discovery ($p < 0.0001$) and gall parasitism rates ($p < 0.00001$). When considered together, my results provide evidence that root-gall parasitism rates are both temporally and spatially influenced, and that bottom-up and top-down regulatory processes are experienced similarly between the sexes.

INTRODUCTION

Encompassing over 25% of all named insect species and 10% of all animals, parasitoids are an extremely diverse and abundant group of organisms (Askew 1971; Tscharntke 1992). Representing such a significant portion of the global biota, it is clear why many ecologists view the analyses of host-parasitoid assemblages as vital to understanding the interactions that influence the structure of terrestrial communities (Zwolfer 1971; Hawkins and Lawton 1987; Hawkins 1990; Tscharntke 1992). Although great emphasis has been placed on the analyses of the interactions governing these assemblages (Mills 1984; Weis and Abrahamson 1985; Price 1986; Hochberg and Hawkins 1992; Hawkins and Mills 1996; Ronquist 1994), comparatively few studies have addressed below-ground host-parasitoid assemblages (Shaw and Askew 1979; Hawkins and Goeden 1984; Hawkins 1988).

Additionally, little research has been conducted contrasting top-down selective pressures experienced by separate generations of bivoltine herbivores, such as found in Cynipidae. Representing the second largest radiation of gall-forming insects, Cynipidae are characterized by their predominantly bivoltine life cycles (Cornell 1983). Askew (1961) suggested that the evolution of bivoltine life cycles within this group is the result of intense top-down selection, yet empirical research showing how the addition of a second generation might reduce parasitism in this group is lacking (Askew1980). If it can be shown that one generation of a bivoltine cynipid experiences a marked reduction in parasitoid related mortality, relative to the other, than this would support the hypothesis

that predator avoidance was the driving mechanism behind the evolution of bivoltine life cycles.

The interactions governing below ground host-parasitoid assemblages and selective pressures experienced by separate generations of a bivoltine herbivore are addressed by this study. By comparing the top-down selective pressures experienced by the root-galling generation of the bivoltine cynipid, *Belonocnema treatae*, to previous studies that assessed the selective pressures experienced by its leaf-galling counterparts, this research completes the description of the top-down selective pressures experienced by this bivoltine herbivore across its complete life cycle. The information derived from this study advances the understanding of mechanisms that govern below-ground host-parasitoid assemblages (Hochberg and Hawkins 1992), as well as those that drive the evolution of bivoltine life cycles (Askew 1971; Cook et al. 1998).

Study Objectives

The objectives of this study of the root-gall former, *Belonocnema treatae*, were (1) to determine the effects of temporal variation in oviposition timing on gall growth, and parasitism, (2) measure the effects of spatial variation in gall-former densities on gall discovery, and gall parasitism, and (3) assess ecological parameters related to host-tree selection, gall growth, gall occupancy, parasitism, sex, and emergence.

Objective 1: Temporal Study

Size is a structural attribute of galls considered to function as a defense against natural enemies (Price et al. 1980; Cornell 1983; Abrahamson and Weis 1997; Stone et

al. 2002). In many systems gall size varies greatly within and among host plants (Washburn and Cornell 1981; Weis and Abrahamson 1985; Weibs-Rijks and Shorthouse 1992; Reynolds 2000). In these systems, gall-formers generally show increased probability of emergence from large galls, and small galls experience higher levels of parasitism (Jones 1983; Weis and Abrahamson 1985; Price and Clancy 1986; Zwolfer and Arnold-Rinehart 1994; Lund 1998; Reynolds 2000). This discrepancy between the parasitism rates of large and small galls is typically attributed to the inability of parasitoids to successfully parasitize large galls due to insufficient ovipositor lengths (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; Reynolds 2000). Thus, as galls develop in size over time, fewer parasitoids are physically able to attack them. Therefore, I predict that root-galls experiencing more lengthy durations of development before being attacked by parasitoids will be larger, and less vulnerable to parasitism than galls that experience less lengthy periods of development before being attacked.

I tested the above hypotheses by creating three *B. treatae* cohorts (***A***, ***B***, ***C***), each oviposited at one of three time periods (*A*-Oct22-Nov5; *B*-Nov11–Nov25; *C*-Dec1–Dec15), and exposed them to four parasitoid attack windows (*AW1*–Dec20-Jan19; *AW2*-Jan19-Feb7; *AW3*-Feb17-Mar20; *AW4*-Mar20-Apr19). By measuring galls from each cohort on four separate dates, I was able to compare, across the full duration of their development, the mean sizes of galls initiated early (Cohort A), mid-way (Cohort B), and late (Cohort C) in the root-gall oviposition season. By exposing each cohort to parasitism,

I was able to determine the relationship between timing of oviposition and subsequent vulnerability to parasitism.

Objective 2: Spatial Study

Spatially density dependent attack of above-ground gall-formers has been intensely investigated for many years, yet no clear trends in the frequency or direction of parasitoid attack patterns have emerged (Hassell 1966; Washburn and Cornell 1982; Weis 1983; Stilling 1987; Price 1988; Walde and Murdoch 1988; Bernstein et al. 1991; Tscharntke 1992; Hails and Crawley 1992; Weis and Kapelinski 1994). In 1966 Hassell coined the term "aggregative response" to describe the behavioral phenomenon of predators allocating greater amounts of time searching in areas abundant with prey. Intuitively, it seems reasonable to expect that parasitoid behavior might follow this simple rule of foraging, yet literature reviews show that this type of direct density dependence is not frequently detected in nature (Stilling 1987; Walde and Murdoch 1988; Hails and Crawley 1992; Tscharntke 1992). In fact, negative density dependence has been reported to occur almost as frequently as positive density dependence (Lessells 1985; Stilling 1987; Walde and Murdoch 1988). Some proposed mechanisms for these inversely dependent foraging trends are high travel costs to parasitoids in areas of patchy host distributions, and parasitoid egg limitations (Lessells 1985; Bernstein et al.1991; Hails and Crawley 1992). Regardless of the direction of the density dependent attack, most ecologists agree that density dependent foraging has a regulatory effect on host population dynamics (Washburn and Cornell 1982; Weis 1983; Hassell 1985; Price 1988; Cornell 1990; Hails and Crawley 1992).

Gall-forming wasps make ideal subjects for studies of spatial density dependence. Because they are sessile, their densities can be easily and accurately assessed. Also, because their parasitoids complete development within galls, causes of mortality can be determined from a single sampling at the end of the growing season (Lewis and Taylor 1967; Cornell 1990). Because galls themselves are discrete units of gall former occupation, the spatial density of multilocular gall-formers should be considered at two levels, galls per unit area and wasp per unit area. When assessing parasitism rates as a function of gall density, one must only consider the number of galls within a given area that have at least one chamber parasitized (gall discovery). But when assessing parasitism rates as a function of wasp density, it is necessary to also consider the number of occupants per gall and the percentage of those occupants that have been parasitized at each gall density (percent parasitism).

Previous studies have shown that *B. treatae's* root-gall densities (galls/m^2) vary greatly among host-trees (Egan 2003; Cryer unpub. data); effectively creating islands of high density host-trees surrounded by a sea of low and no density host-trees. This patchy distribution provides the template for investigating density dependent parasitism.

To test for density dependent parasitoid attack, I collected samples of galls from the unmaniputated root regions of 10 host-trees to estimate each tree's mean gall density. To estimate mean levels of gall discovery and the percent parasitism for each tree, I lab reared wasps from these galls, and galls collected in an end of the season mass harvest.

Objective 3: Ecology Study

Because all herbivore communities are composed of at least three interacting tropic levels, plants, herbivores, and natural enemies of herbivores, it is important to assess the selective pressures exerted by both host-plants and natural (Price et al. 1980; Price and Clancy 1986; Roininen et al. 1990). To elucidate the bottom-up and top-down selective pressures experienced by the below ground generation of this bivoltine herbivore, I mass harvested galls from the unmanipulated root regions of 10 host-trees. Sizes were measured, chambers were counted, and gall occupants were reared and identified by sex and species. By measuring each gall, and counting each galls chambers, I was able to determine (1) the distribution of gall sizes within and among trees, and (2) the distribution of gall occupancies within and among trees. By lab rearing gall occupants, and identifying them by sex and species, I was able to determine (3) the rates of gall discovery and parasitism within and among trees, (4) the gall and overall *B. treatae* sex ratios, and (5) the *B. treatae* and parasitoid emergence phenologies. By analyzing these factors together I was able to assess the selective pressures exerted by host-trees and parasitoids on both male and female *B. treatae*. Overall, these analyses allowed me to estimate the intensity of both the bottom-up and top-down selection experienced by the below ground generation of this bivoltine herbivore.

MATERIALS AND METHODS

Study System

B. treatae (Hymenoptera: Cynipidae) is a host-specific, gall-former on the leaf and root tissue of plateau live oak, *Quercus fusiformis* (Fagacae). Like most cynipids *B. treatae* exhibits a heterogonous life cycle, whereby an asexual generation alternates with a sexual generation (Figure 1.A). Also like most cynipids, each *B. treatae* generation is tissue specific. The sexual generation develops in multilocular galls on live oak roots, while the asexual generation develops in unilocular galls on live oak leafs.

Study Site

Texas State University's Freeman Ranch (FR) (Hays Co, 98° 00' W. Long, 29° 55' N. lat) is a 3,500 acre ranch located in the eastern portion of the Edwards Plateau region of Central Texas. It has an abundance of live oak, gall formers, and parasitoids, making it ideal for examining parasite/ parasitoid interactions. The landscape of Freeman Ranch is typical of that across the Edwards Plateau, and therefore trends elucidated here, should be representative of trends occurring throughout the region.

Host Tree

The host plant *of B. treatae* is Plateau Live Oak. Plateau live oak is a wintergreen tree, retaining annual leaves in the Texas Hill Country until late February to early April.

Although native to southwestern Oklahoma, central Texas, and northern Mexico, its greatest aggregations are on the Edwards Plateau region of central Texas. Considered a late seral stage tree, live oaks may reach heights of over 25m, but are more typically found in clonal clusters of less than 10m in height. Despite its abundance throughout this region, relatively few trees actually harbor root galls (Egan 2003). Only those phenotypes expressing carpets of immature clonal shoots have been found to support root gall development. Each shoot extends from root regions and typically produces one to ten leaves. Although each shoot might potentially develop into a mature oak, they appear to be short lived; only growing to heights of 10 – 20 cm before dropping their leaves. Despite the relatively high turnover of individual rootlets, the clonal carpets themselves appear to be relatively long lived; possibly providing long-term stable habitats for root gall development.

Study Organism

Coincident with *Q. fusiformis* bud break, parthenogenetic *B. treatae* are oviposited into the lateral veins of immature leaves by sexual generation females. Although oviposition occurs from early in leaf development (March - May), gall growth does not commence until the leaves fully mature in mid-May through mid-June. Unilocular galls grow until the onset of gall lignification in mid-August through late-September. Emergence of the asexual generation occurs in mid-October through mid-December (Lund 1998; Reynolds 2000). Following their emergence, asexual *B. treatae* oviposit either all male or all female egg clusters into the root regions of their hosts.

Leaf galls are attacked by a diverse community of parasitoid, inquilines and herbivores throughout their development. To date, 23 parasitoid and inquiline species have been shown to be associated with the asexual *B. treatae* generation, twenty of which belong to the order Hymenoptera (Cynipidae, Eurytomidae, Ormyridae, Torymidae, Pteromalidae, Braconidae, and Eulophidae). In addition, one Diptera, one Lepidoptera, and one Coleoptera species have also been shown to develop within leaf-galls. Given the large community of natural enemies, it is not surprising that parasitism plays a major role in the mortality of this generation. Parasitoid related mortality rates for the *B. treatae* leaf-galling generation may exceed 99% (Lund 1998; Reynolds 2000; Hall 2001). Of the < 1% of gall formers that do emerge successfully, greater than 90% do so from relatively large galls, suggesting that leaf-gall size is related to emergence success (Lund 1998; Reynolds 2000). However, the size distribution of galls from which parasitoid species emerge indicates that parasitoids are capable of completing development in a wide range of gall sizes, including those associated with the greatest rates of emergence success (Lund 1998; Reynolds 2000).

Asexual females are typically androphores (male producing) or gynophores (female producing), thus it is rare that both male and female wasps occur in the same root-gall. Oviposition of this generation is coincident with asexual emergence in mid-October through mid-December. Previous studies have shown that root-galls are highly variable in size and occupant number; with gall sizes ranging from 5 to 28 mm in length and occupants/gall ranging from 1 to 28 (Lund 1998). Emergence of sexual *B. treatae* lasts from early-March through mid-May, and is followed by the subsequent oviposition of the asexual generation onto leaf tissues of their hosts.

In contrast to the leaf-galling generation, very little is known about the community of natural enemies associated with *B. treatae's* root-galling generation. Thus far, pilot studies have yielded evidence that three natural enemies inflict up to 40% mortality on root-galling *B. treatae* generations (Ott unpub. data). Of the three, only the most abundant has been identified to species, *Torymus tubicola* (Torymidae). A second hymenopteran species occurring at low frequencies and a relatively rare lepidopteran species have also been found to be associated with this generation (Egan unpub data; Ott unpub data). Of the three species, only *T. tubicola* is known to bridge the generational gap, parasitizing both the sexual and asexual generations. Neither the attack interval, nor the emergence phenology is known for any of these species.

Cohort Creation

Before the onset of asexual *B. treatae* emergence (Oct. 15th), access of gall formers to the root regions of 15 experimental trees, chosen for their high rootlet densities and observed histories of leaf-gall infestation, was restricted with 16 haphazardly placed exclusion chambers/tree (Figure 1.B). Fifteen of each trees sixteen exclusion chambers were used to create three distinct *B. treatae* cohorts (*A*, *B*, *C*) with which to test for variation in gall size (n = 5 trees), and parasitism (n = 10 trees) as a function of oviposition timing (Table 1.A). Each cohort was created by opening a subset of exclusion chambers (n = 5/ tree) during one of three oviposition access periods (*A* = Oct. 22 – Nov 5, *B* = Nov. 11 –Nov. 25, *C* = Dec. 1 – Dec. 15). With the exclusion chambers opened, *B. treatae* was allowed to oviposit in the experimental areas at natural frequencies. At the end of each access period, chambers were closed, and access of

ovipositing *B. treatae* to these areas was again restricted. The remaining exclusion chamber/tree, used to test the effectiveness of the cambers to exclude ovipositing *B. treatae*, was left closed for the duration of the study.

Gall Development Study

Five of the 15 experimental trees were randomly selected to test for variation in the sizes of galls produced by the three cohorts (A, B, C). On each of four sample dates (February 1, February 26, March 24, April 19), one of each tree's three cohorts were destructively sampled (Table 2.A). Destructive sampling consisted of the complete removal of all root-galls from the 1/4 m^2 experimental areas. After removal, galls were returned to the lab and measured. Because two of the five trees failed to produce sample sizes sufficient for analysis (>10 galls), only galls from three trees were used to estimate gall sizes for each of the cohorts across the four sample dates.

Parasitism Study

Ten of the fifteen experimental trees were randomly selected to test for variation in parasitism rates as a function of oviposition timing. For each of these trees, 12 of the 15 chambers used to create the tree cohorts were opened to parasitism over four attack intervals (*AW1* – Dec. 20 – Jan. 19; *AW2* – Jan. 19 – Feb. 7; *AW3* – Feb. 17 – Mar. 20; *AW4* – Mar. 20 – Apr. 19). The three remaining cohort chambers/tree were left closed for the duration of the study; hence they provided a measure of parasitism during each of the three-oviposition time intervals. Parasitoid attack windows were created by opening one of each cohort's exclusion chambers/tree during each of the four 30-day parasitoid access

periods (Table 1.B). At the end of each attack interval, access of parasitoids to the experimental areas was again restricted. Chambers remained closed until just prior to the onset of *B. treatae* emergence, at which time galls were harvested according to their relative maturity. Because one of the nine trees failed to produce sample sizes sufficient for analysis (>10 galls), only galls from nine were used to estimate the parasitism rates of each cohort.

Gall Density Estimations

To estimate the mean density of galls/m^2 for each of the ten host trees used in the analyses of density dependent parasitoid attack, I collected one 1/8 m^2 samples of galls from haphazardly selected unmanipulated root regions of each tree on each of four sample dates (February 1, February 26, March 24, and April 19). Sample dates were partitioned across the gall development season so that gall densities and gall development could be simultaneously estimated. Because one of the nine trees failed to produce sample sizes sufficient for analysis (>10 galls), only galls from nine trees were used to estimate density dependent parasitoid attack.

Gall Harvesting

Galls were harvested from the cohort exclusion chambers used to estimate parasitism on two separated sample dates, March 27 and April 19. The first round of harvesting on March 27 was undertaken to ensure that harvested galls were maximally informative, i.e., all or most occupants could be accounted for. Only those exclusion chambers that had completed their parasitoid access windows were harvested at this time. Because the galls

contained within these exclusion chambers were not all at the same stage of development, only mature galls, those with deeper reddish hues and more pronounced chambers, were harvested on this date. Immature galls were left in the exclusion chambers to be sampled on the second sampling date of April 19. They, and the galls from the chambers that had not yet completed their parasitoid access window by March 27, were harvested on April 19.

Galls used to estimate the parasitism rates of the 10 trees used in the analyses of density dependent attack, were harvested in two manners. First, galls were collected from the four 1/8 m^2 density estimations. Because galls collected during the first two samples were not mature enough to lab rear their occupants, only galls from the last two samples contributed to the parasitism estimates of each tree. Second, galls were sampled in an end of the season mass harvest. Mass harvesting consisted of the complete removal of all galls from each tree's remaining unmanipulated root regions on April 19. These galls were combined with the galls harvested during the density harvests to achieve a more robust estimation of parasitism for each of the 10 host-trees.

Lab Rearing

After being returned to the lab, galls were measured for size and occupancy levels. Because root galls are amorphic in shape, linear measurements of length and width are not appropriate. Therefore, gall size measurements were determined by submerging galls in water filled graduated cylinders, and recording the amounts of displaced water. Volumetric measurements were then converted to linear measurements (1mm = $1cm^3$) to make gall sizes comparable to previous studies (Egan unpub data; Ott unpub data) using

measurements of length and width. After being measured, galls were individually housed and incubated in moistened vermiculite filled vials. Insects were allowed to emerge naturally from the incubated galls for one month, and then all galls, and any non emergent insects contained within, were preserved in 70% ethanol. Gall occupancy assessments, and occupant identification was achieved at a later date through gall dissection.

Objective 1: Temporal Study

To test the effectiveness of the exclusion chambers to prevent uncontrolled oviposition, I performed two analyses comparing the frequency and intensity of *B. treatae* oviposition in the experimental chambers to that of the control chambers that were closed for the duration of the study. To test for differences in the frequency of oviposition between the two, I used a chi-square analysis that compared the ratios of cohort and control chambers that did and did not produced galls. To test for differences in oviposition intensity between the two, I performed a t-test comparing the mean number of galls produced per square meter in the experimental and control chambers.

To test for differences in gall sizes among the three cohorts over the four sampling dates, I performed a fully crossed 2-Factor ANOVA, with the factors cohort and date designated as fixed. For this analysis and all analyses that follow, I designate the gall as my unit of replication. To meet the ANOVA assumption of homoscedastcity in this analysis and the ones described below, the response variable, size, was log transformed.

In addition to testing for variation in gall sizes over time among each cohort, I was also interested in testing for differences in the sizes of mature galls of each. To test for differences in sizes of mature galls among the three cohorts, I used only lab reared galls that had either partial field emergence at their time of collection, or that produced wasps within the first 10 days of lab incubation. This selection process was used to insure that only those galls that had reached full maturity, i.e., galls producing fully mature adult insects, would be used to test for differences in final gall sizes. To test for differences in the sizes of mature galls among the three cohorts, I performed a single-factor ANOVA, with cohort designated as fixed.

To test for differences in the gall discovery rates among each tree's three cohorts across the four attack windows, I performed a fully crossed 3-Factor ANOVA, with the factors cohort, tree, and window designated as fixed. To test for differences in the parasitism rates among each tree's three cohorts across the four attack windows, I performed a fully crossed 3-Factor ANOVA, with the factors cohort, tree, and window designated as fixed.

To explicitly test whether variation in discovery and parasitism rates were due to variation in gall sizes, I performed linear regression analyses. For each analysis I used fully matured galls (n = 400) collected from unmanipulated root regions. For the gall discovery analysis, I averaged the gall discovery rates of each of 35 observed gall size classes. Gall discovery rates were averaged to insure a conservative estimate of gall discovery rates as a function of gall size. Also, parasitism rates were assessed for only those galls that were discovered (n = 83). This step was taken to insure that the gall discovery did not influence the estimated relationship between gall size and parasitism.

Also, by excluding non-discovered galls from the analysis, a clearer picture of parasitoid attack behavior as determined by gall size is discerned.

Objective 2: Spatial Study

Before testing for density dependent attack patterns among host-trees, I first had to establish that their mean gall densities differed. To test for differences in gall densities among host-trees, I performed a single-factor ANOVA comparing the mean gall densities of each. To test for density dependent gall discovery and parasitism under these naturally occurring ranges of root-gall densities, I used linear regression analyses.

Objective 3: Ecology Study

Ecology of the Sexes

Here I analyze the relative selective pressures experienced by female and male *B. treatae*. Analyses of sexually mediated selective pressures are of importance within this system because of the fact that root-galls typically harbor either all female or all male wasps. Because female and male *B. treatae* spend all but their last moments isolated from one another, it is reasonable to expect that selective pressures experienced by each might differ. To test for differences in the selective pressures experienced by female and male *B. treatae*, I analyze (a) the overall *B. treatae* sex ratio, (b) the ratio of female to male producing galls, (c) within tree sex ratios, (d) mean sizes of female and male galls, (e) mean occupancy levels of female and male galls, (f) mean discovery rates of female and male producing galls, and (g) the mean discovery rates of female and male producing galls.

The overall sex ratio, and the ratio of female to male producing root-galls among all trees, were estimated using wasps (n = 3,844) collected from 559 wild galls. Both, lab reared wasps and wasps collected during lab dissection were used in these analyses. To test for skewness in the overall *B. treatae* sex ratio, I performed a chi-square analysis comparing the total number of observed female (2,084) and male (1,760) wasps to the number of each that would be expected if they were equally present (1,922). To test for skewness in the number of male and female producing galls among all host-trees, I performed a chi-square analysis comparing the observed number of female (284) and male (249) producing galls to the number of each that would be expected if they were equally present (266.5). To test for differences in sex ratios among trees, I performed a chi-square analysis comparing the ratio of females to males for each tree to that of the overall ratio of females to males among all trees (1.18).

To determine the mean gall size of male and female producing galls, I used 436 fully matured galls, for which knowledge of occupancy and sex were complete. I used only mature galls to eliminate the possibility of observing differences in gall size due to differences in developmental phenologies, which may differ as much as one to two weeks (Cryer unpublished). To test for differences in the mean size of mature female and male producing galls, I preformed a single-factor ANOVA, with the factor sex designated as fixed.

To determine the mean gall occupancy levels of male and female producing galls, I used 533 wild collected galls for which knowledge of occupancy and sex were complete. To test for differences in the mean level of gall occupancy by sex, I performed a single-factor ANOVA, with the factor sex designated as fixed.

To determine the gall discovery and parasitism rates of male and female producing galls, I used 533 galls for which knowledge of sex and parasitism rates were complete. But because it is not possible to determine the sex of the wasps that produced galls experiencing complete parasitism, percent parasitism and gall discovery rates of female and male producing galls are lower than those of the overall rates of parasitism and discovery. To test for differences in the mean rates of gall discovery and parasitism between female and male galls, I performed single-factor ANOVAs for each variable, with the factor sex designated as fixed for both.

Host-Tree Selection

Here I analyze the role of host-tree selection in regulating root-gall former fitness parameters. Because host-trees provide the foundations for all gall-former interactions, the selective pressures they exert can often have major effects on gall former fitness. To explore the fitness consequences associated with host-trees selection I analyze (a) the distribution of gall size within and among trees, (b) the distribution of gall occupancy levels within and among trees, (c) the rates of gall discovery among trees, and (d) the rates of gall parasitism among trees.

The distribution of root-gall sizes across all trees was elucidated with a frequency distribution of gall sizes. The test for differences in gall sizes among trees, I used only galls (n = 400) that had either partial field emergence at their time of collection, or galls that produced wasps within the first 10 days of lab incubation. Again, this selection process was used to insure that only those galls that had reached full maturity, i.e., galls producing fully mature adult insects, would be used to test for differences in gall sizes.

To test for differences in the sizes of mature galls among trees, I performed a single-factor ANOVA, with the factor tree designated as fixed.

To describe the distribution of chambers per gall across trees and to test for differences in the number of chambers per gall between trees, I used galls (n=870) who's chamber counts were accurately assessed through dissection. Because gall development does not affect occupancy levels, galls of various sizes and developmental stages could be used to assess the distribution of chambers per gall. To test for differences in the mean number of chambers per gall among trees, I performed a single-Factor ANOVA, with the factor tree designated as fixed.

To test weather gall sizes and gall occupancies co-varied among trees, I performed a single-factor ANOVA comparing the mean standardized gall sizes (size/chambers) of each host-tree. By standardizing gall sizes, I was able to determine the average amount of area that each gall occupant contributed to the ultimate size of the gall. By comparing these sizes among trees, I was able to determine weather gall resources were equally experienced among individual wasps across all hosts.

The test for differences in the gall discovery and parasitism rates among trees, I used only galls (n=470) for which knowledge of parasitism was complete. Complete knowledge of parasitism was achieved through lab rearing and gall dissection. To test for differences in the mean rates of gall discovery and parasitism among trees, I performed two single-factor ANOVAs, with the factor tree designated as fixed for both.

Parasitoid Community

Here I describe (a) diversity and (b) impact of the parasitoid community on *B. treatae* root-galler survival. To determine the diversity and impact of the root-galler parasitoid community, I collected, preserved, and identified to their lowest taxonomic levels, parasitoids retrieved from 913 galls during the lab rearing and gall dissection phases of this study. Only those specimens that could be positively identified to species were used in this analysis. Therefore, those parasitoids that were in the initial stages of their development were not considered. The realized effect of each parasitoid species on *B. treatae* survival was determined by dividing the number of each parasitoid species by the total number of parasitoids.

Emergence Phenologies

Here I describe the emergence phenologies of the (a) *B. treatae* root-galling generation, and (b) that of their parasitoid community. To determine the *B. treatae* and parasitoid emergence phenologies, I lab reared insects from 913 galls from March 27 to May 11, 2003. Additionally, I then dissected each gall to extract any non emergent insects in order to determine the total numbers of *B. treatae* and parasitoids likely to have emerged after the final census date of May 11.

RESULTS

Objective 1: Temporal Study

Chi-square analysis comparison of the ratios of exclusion chambers producing and not producing root-galls among the cohorts and controls, showed that significantly fewer control chambers produced galls ($X^2_{df=1} = 8.21$; $p < 0.05$). Comparisons of the number of galls produced in experimental and control chambers indicated that the control chambers produced significantly fewer galls on average than did the experimental chambers ($T_{1,163} = 2.09$; $p < 0.05$). A total of 369 galls were produced by 84 of the 150 experimental chambers. A total of eight galls were produced by three of the 15 control chambers.

Comparisons of mean gall sizes produced by the three cohorts over four sample dates indicated that there as not an interaction between gall initiation date and time, yet gall initiation date did have a significant effect on gall size ($F_{2,144} = 4.29$; $p < 0.001$; Figure 2.A). Fisher's LSD post hoc test show that galls initiated during the cohort A oviposition interval were significantly larger than galls initiated during the cohorts B and C oviposition intervals, which did not differ from each other.

Comparisons of the mean sizes of mature galls across the three cohorts showed that at maturity, gall size did not differ ($F_{2,212} = 2.05$; $p > 0.10$; Figure 2.B). However, chi-square analysis showed that the percentage of galls reaching full maturity by the

April 19 collection date did differ among cohorts ($X^2_{df=2} = 12.73$; $p < 0.01$). The percentage of galls for cohorts A, B, and C that reached full maturity by April 19 were 72.8, 55.8, and 53.1 respectively.

Comparisons of mean percents of galls discovered by parasitoids among the three cohorts indicates that both host-tree selection ($F_{8,187} = 3.18$; $p < 0.001$; Figure 3.A) and oviposition timing ($F_{2,187} = 0.62$; $p < 0.05$; Figure 3.B) influenced discovery rates. Fisher's LSD post hoc tests showed that the discovery rates of galls initiated during the cohort B oviposition interval were significantly greater than the discovery rates of galls initiated during the cohort A and C oviposition intervals, which did not differ. Mean discovery rates did not differ among the attack windows ($F_{4,187} = 0.58$; $p > 0.20$).

Comparisons of mean parasitism rates among the three cohorts indicates that host-tree selection and oviposition timing had an interactive effect on gall parasitism rates ($F_{16,187} = 1.62$; $p < 0.05$; Figure 4), with each cohort being most heavily parasitized on different hosts. Cohorts A, B, and C experienced the greatest rates of parasitism on 11, 67, and 22 percent of the host-trees respectively. Similar to gall discovery rates, gall parasitism rates did not differ among the attack windows ($F_{4,187} = 0.28$; $p > 0.25$).

Regression analysis of the mean gall discovery rates for 35 gall size classes (range, 0.05 – 4.0 cm^3) indicates that there is not a relationship between gall size and gall discovery rates ($R^2 = 0.0002$; $F_{1,34} = 0.006$; $p > 0.90$; Figure 5.A). Regression analysis for 81 discovered galls (range, 0.05 – 4.0 cm^3) indicates that there is not relationship between gall size and parasitism rates ($R^2 = 0.027$; $F_{1,80} = 2.25$; $p > 0.10$; Figure 5.B).

Objective 2: Spatial Study

Examination of the gall densities among the nine trees showed that some trees had gall densities that were many times that of others (mean ± SE, 83.6 ± 1.14cm^3; range, 34 – 194 galls/m^2). ANOVA comparisons showed that these differences in gall densities were significant ($F_{9,30} = 4.09$; $p < 0.005$).

Analysis of gall densities and gall discovery showed that there was not a relationship between the two ($R^2 = 0.003$; $F_{1,7} = 0.02$; $p > 0.85$; Figure 6.A). In fact, coefficient estimates of gall discovery suggest that the probability of discovery increases only 1% for every 50 galls/m^2 increase. Parasitism rates were also density independent ($R^2 = 0.003$; $F_{1,7} = 0.02$; $p > 0.85$; Figure 6.B). Similar to coefficient estimates of gall discovery, coefficient estimates of parasitism rates suggest that parasitism also increase by only 1% for every additional 50 gall/m^2.

Objective 3: Ecology Study

Ecology of the Sexes

Of the 3,844 *B. treatae* reared from 559 wild collected galls, 2,084 (54.2 %) were females and 1,760 (45.8 %) were males (Figure 7.A). The overall *B. treatae* sex ratio was 1.18 females to every 1 male. Chi-square analysis showed that the overall sex ratio was significantly different than that of the expected 1:1 ratio ($X^2_{df=1} = 13.68$; $p < 0.001$). Of the 559 wild collected galls used to determine overall sex ratios, 284 (50.8 %) were female producing, 249 (44.8 %) were male producing and 26 (4.65 %) produced a mixture of females and males (Figure 7.B). The ratio of female to male producing galls is 1.14 female producing galls to every 1 male producing gall. Chi-square analysis showed

that the overall sex ratio of male and female producing galls was not significantly different than that of the expected 1:1 ratio ($X^2_{df=1} = 1.15$; $p > 0.10$). The overall ratio of female to male wasps for nine host-trees ranged from 0.53 – 1.32. Chi-square analysis showed that the sex ratios of the nine host-trees did not differ from that of the overall *B. treatae* sex ratio of 1.18 ($X^2_{df=8} = 0.03$; $p > 0.50$).

Both female (range 0.10 – 5.0 cm^3) and male (range, 0.05 - 3.6 cm^3) root-galls varied greatly in size. Mean sizes of female galls were significantly larger than male galls ($F_{1,435} = 4.66$; $p < 0.05$; Figure 8.A). Analysis of occupancy levels for female and male producing galls showed that the number of chambers for female (range 1 – 34 chambers/gall) and male (range, 1 – 42 chambers/galls) galls were quite variable. Yet, comparisons of gall occupancy levels for female and male galls indicated that there was not a difference in the mean number of chambers per female and male galls ($F_{1,531} = 0.27$; $p > 0.60$; Figure 8.B).

Comparisons between female and male producing galls suggest that female producing galls were no more likely to be discovered by parasitoids than were male producing galls ($F_{1,531} = 2.99$; $p > 0.05$; Figure 9.A). Also, the percent of occupants parasitized in females and male producing galls did not differ ($F_{1,531} = 1.60$; $p > 0.20$; Figure 9.B).

Host-Tree Selection

Analysis of the distribution of fully mature galls among host-trees showed that the sizes of mature galls were quite variable, and that most galls were relatively small compared to those at the high end of the size distribution (mean ± SE, 0.66 ± 0.03cm^3;

range, 0.05 – 5.0 cm^3; Figure 10.A). Ninety percent of all of wild galls were 1.4 cm^3 or less. Analysis of the sizes of mature galls among host-trees was similarly variable (range, 0.42 – 1.19 cm^3). Comparisons of the mean sizes of mature galls indicated that mature gall sizes differed between trees ($F_{8,390} = 2.63$; $p < 0.01$; Figure 10.B).

Analysis of the distribution of the number of chambers per gall across all host-trees showed that gall occupancy levels were quite variable, and that most galls had relatively few chambers compared to those at the high end of the distribution (mean ± SE, 6.98 ± 0.18 chambers/gall; range, 1 – 41 chambers/gall; Figure 11.A). Ninety percent of all wild galls had 14 chambers or less. Analysis of distribution of chambers per gall among host-trees showed similar variability in gall occupancy levels (range, 5.53 – 10.11 chambers/gall). Comparisons of the mean number of chambers per gall indicated that gall occupancy levels differed between trees ($F_{8,861} = 4.29$; $p < 0.0001$; Figure 11.B).

Although chamber number and size both varied significantly among trees, the analysis of standardized gall sizes (size/chambers) indicates that the former was not the result of the latter. Comparisons of standardized gall sizes among trees showed that the mean volume occupied by individual wasps per gall differed significantly among trees ($F_{9,390} = 5.47$; $p < .0001$).

Analysis of gall discovery rates by tree showed that gall discovery rates were quite variable (range, 10.2 – 68.8 % galls discovered/tree), differing significantly among trees ($F_{8,461} = 5.14$; $p < 0.0001$; Figure 12.A). Analysis of the average percent of occupants within individual galls being parasitized showed that galls varied in their vulnerability to parasitism from tree to tree (range, 2.8 – 68.8 % parasitism/gall).

Comparisons of the mean percent of occupants per gall being parasitized indicated that parasitism percentages differed among trees ($F_{8,461} = 5.83$; $p < 0.00001$; Figure 12.B).

Parasitoid Community

Analysis of realized effect of each parasitoid species on *B. treatae* survival showed that the vast majority of parasitism was done by *T. tubicola*. Of the 668 parasitoids collected during the lab rearing and gall dissecting portions of this study, 659 were *T. tubicola*; making it responsible for 98.7% of all root gall parasitism. The other nine as of yet unidentified parasitoids include one hymenopteran species (n = 3), one coleopteran species (n = 3), and a lepidopteran species (n =3). The overall impact of each of these unidentified species is 0.45%; collectively composing only 1.3% of all root gall parasitism.

Emergence Phenologies

The analysis of *B. treatae* and parasitoid phenologies showed that on average parasitoids emerge from galls at a later date than did *B. treatae* (Figure 13). The majority of *B. treatae* emerged in the month of April, while the majority of parasitoids emerged in May. The *B. treatae* emergence percentages for March, April, and May were 10.4, 60.8, and 10.7 respectively. An additional 18.1% of *B. treatae,* detected through lab dissection, had not emerged (N.E.) by the May 11 census cessation. Parasitoid emergence phenologies for March, April, and May were 0.0, 5.9, and 23.1 respectively. An additional 71.0% of all parasitoids, detected through lab dissection, had not emerged (N.E.) by the May 11 census cessation.

DISCUSSION

Objective 1: Temporal Study

Comparisons of gall size among the three cohorts indicated that gall sizes differed significantly among the three over time. This suggests that on average, the earlier a gall is oviposited the larger that gall is at any given interval (Figure 2.A). Although analyses of mature gall sizes did not differ among the cohorts (Figure 2.B), the number of galls achieving maturity by the time of their harvest did. This suggests that some galls oviposited late in the oviposition season matured at a greater rate than did some galls oviposited early in the season, but on average the later the date of oviposition, the later the date of maturity, further suggesting that gall growth within this system is fairly constant regardless of oviposition timing.

In addition to oviposition timing influences, comparisons of gall size among nine trees showed that gall size was also significantly influenced by the quality of the substrate on which it grew (Figure 10.B). Analysis of standardized gall sizes (size/chambers) between trees showed that variation in gall size between trees is not the result of variation in occupancy levels. This indicates that some trees, on average, produce larger galls regardless of the number of occupants. These results are consistent with other gall former studies that show gall sizes to be significantly influenced by the quality of their hosts (Washburn and Cornell 1981; Weis and Abrahamson 1985; Weibs-Rijks and Shorthouse 1992). In this system, studies addressing the *B. treatae's* leaf-galling

generation produced similar patterns in host-tree regulation of gall size (Reynolds 2000; Egan 2003). Unpublished date taken by myself in 2001 for the same generation showed that gall size is highly correlated with female size ($r = 0.53$), which in turn is highly correlated with egg-load ($r = 0.93$). When considering these results together, it is clear that size is a structural attribute of galls that is under multiple controls, and that both temporal and spatial elements are interacting to influence gall-former fitness.

Comparisons of mean gall discovery rates among the three cohorts indicates that both host-tree selection and oviposition timing influenced gall discovery rates (Figures 3.A and 3.B). These results, along with the results of the comparison of gall discovery rates among nine host trees (Figure 12.A), suggest that some trees harbor significantly fewer parasitoids than do other trees, and that galls oviposited in the middle of the oviposition season are more likely to be discovered regardless of host-tree or parasitoid community associations. The fact that the intermediate sized cohort B galls were discovered significantly more often than the larger cohort A, and smaller cohort C galls, suggests that gall discovery is not size dependent within this system. This assertion is further supported by the analysis of gall discovery as a function of gall size, where gall size was shown not to be associated with gall discovery rates (Figure 5.A).

Similar to gall discovery rates, parasitism rates were also shown not to be associated with gall size (Figure 5.B). Instead, parasitism rates were influenced by an interaction between host-tree selection and oviposition timing, with each cohort being most heavily parasitized on different host-trees (Figure 4.A). These results suggest that first and second trophic levels interactions are regulating third trophic level resource (Price et al. 1980; Price and Clancy 1986; Roininen et al. 1990). Although the influence

of oviposition timing on parasitoid attack is shown to vary among host trees, the general trend is that galls oviposited in the middle of the oviposition season run a greater risk of being parasitized (Figure 4.B). Again, because the intermediate sized galls are most heavily parasitized, these results are consistent with the observation that parasitoid attack is not size dependent within this system.

Analysis of the gall discovery and parasitism rates among the parasitoid attack intervals may provide the clues for explaining why parasitoid attack is seemingly temporally dependent, but not structurally dependent within this system. In the analyses of gall discovery and gall parasitism rates among the parasitoid attack windows, neither gall discovery nor parasitism were shown to differ. Included in these analyses were galls collected from the cohort control chambers, which were only opened during the oviposition interval. The fact that gall discovery and gall parasitism rates were not different during the oviposition intervals than at any other time, suggests that the majority of parasitism observed in each attack window may have occurred during oviposition. If this is the case, than it would follow that that parasitoids were attacking eggs and not mature galls, which would explain why gall size provided little relief from parasitoids within this system.

Additional evidence for this pattern of attack is provided by previous research that shows that *Torymus tubicola*, the parasitoid responsible for 98% of root-gall parasitism, peaks in its emergence from leaf galls during the same November time interval that cohort B wasps are being oviposited (Hall 2001). It is likely that natural selection has fined tuned *T. tubicola* emergence so that their emergence from leaf galls corresponds perfectly with the median date of root-gall oviposition, assuring that *T. tubicola's*

potential for encountering gall-formers is maximized, and subsequently assuring that *B. treatae* oviposited in this middle interval are more heavily parasitized.

Objective 2: Spatial Study

The result of the density dependent gall discovery and parasitism analyses indicated that gall discovery and parasitism rates within this system were likely not under density dependent regulation (Figures 6.A and 6.B). Although gall densities varied significantly among host trees, gall former attack patterns did not vary accordingly. This suggests that parasitoids are not aggregatively responding to high gall-former densities, as would be expected in situations of direct density dependent regulation (Hassell 1966; Rothman and Darling 1991; Vanveen et al. 2002). Nor are they likely limited by their egg-loads, as would be expected in situations of negative density dependence (Lessells 1985; Bernstein et al.1991; Hails and Crawley 1992).

The lack of density dependent gall parasitism is more likely a consequence of the environment in which the galls develop than it is of any adaptive foraging strategy on the part of parasitoids. It is reasonable to assume that parasitoids searching for prey in a subterranean environment have an imperfect understanding of patch quality as it relates to host density. Lessells (1985) suggested that time and energy costs associated with extensive searches may outweigh the benefits of such searches, ultimately reducing the likelihood of aggregative foraging. This inability of parasitoids to quickly and accurately assess host densities is likely explained by the inherent visual limitations and travel costs associated with searching for subterranean prey (Shaw and Askew 1979; Hawkins 1988).

Although it is reasonable to expect that the observed density independent gall parasitism patterns are the result of imperfect parasitoid foraging strategies, it is also reasonable to expect that these patterns are the result of small sample sizes and limitations in the sampling methods. Because the same trees were used for both the temporal and spatial studies, much of the usable root area was occupied by the exclusion chambers used in the temporal study, leaving only a small area of gall former habitat for density sampling. This method of sampling resulted in small sample sizes that lacked the robustness likely required for detecting subtle patterns of density dependent attack. Also because galls collected for density estimations were also used to determine gall growth rates, collections were taken throughout the gall development season, precluding any direct analysis of parasitism rates as they pertained to each sample.

Future studies addressing density dependent attack should assure that multiple density samples are taken at the end of the gall growth season for a larger number of host-trees. By taking samples at the end of the gall growth season, parasitism rates can be directly linked to each gall density. Also, by taking multiple samples per tree the likelihood of detecting small-scale patterns of density dependent attack is increased.

Objective 3: Ecology Study

Ecology of the Sexes

Analyses of sexually relevant *B. treatae* root-galling ecological parameters suggest that there are not major differences in the ecology of female and male *B. treatae*. Analysis of sex ratios shows that significantly more females emerge from root galls than did males (Figure 7.A), yet the number of female and male producing galls did not differ

within or among trees (Figure 7.B). Analysis of gall sizes between the sexes showed that on average females emerged from larger galls than did males (Figure 8.A), yet their mean gall occupancy levels did not differ (Figure 8.B). Neither gall discovery rates (Figure 9.A) nor gall parasitism rates (Figure 9.B) differed between the sexes.

Overall, these results do not suggest major selective differences. Although overall sex ratios were marginally skewed, this skew did not come near to the 3:1 ratio found in other hymenopteran systems where strong selective difference exist (Trivers and Hare 1976; Breed and Gamboa 1977; Andrew and Burk 1992). Also, gall discovery and gall parasitism rates did not differ between the sexes, further suggesting that selective pressures do not differ greatly between female and male *B. treatae*. Additionally, the differences in gall sizes can be explained by the fact that larger wasps are associated with larger galls ($r = 0.53$), and that because of their enlarged abdomens, female *B. treatae* are on average larger than male *B. treatae*. The fact that wasps were not oviposited at different rates according to their sexes further suggests that differences in gall sizes were likely due to differences in occupant body sizes.

Although these results do not suggest major selective differences between the sexes, it must be cautioned that these interpretations are based on incomplete data. Because it is not possible to determine the sex of the wasps that formed galls experiencing complete parasitism, potentially important selective differences may have been missed due the exclusion of 48 completely parasitized galls. The forty-eight galls excluded from analyses represent nine percent of the total number of galls used in the analyses of gall discovery and gall parasitism rates. With such a large number of

potentially informative galls excluded from these analyses, it is impossible to make robust conclusions with regard to selective pressures associated with gall-former sex.

Future studies addressing sexually relevant gall former selection should involve the transplantation of individual wasps into controlled study areas. Because asexual *B. treatae* are typically gynophores (female producing) or androphores (male producing), galls that are completely parasitized can be assumed to be the same sex as the rest of the galls oviposited by these individual females. This type of experiment would allow for a more complete picture of the selective pressures experienced by female and male *B. treatae*.

Host-Tree Selection

Analysis of host tree regulated *B. treatae* ecological parameters suggests that host-trees exert a major selective force on root-galling *B. treatae*. These analyses showed that host-tree selection influences everything from gall size (Figure 10.b) and gall occupancy levels (Figure 11.B) to gall discovery rates (Figure 11.A) and gall parasitism rates (Figure 11.B). Taken together, these results indicate that trees vary in their quality as hosts, and that this variability in quality extends all the way to the third trophic level. This suggests that tritrophic interactions are occurring within this system, with the interactions between the first two trophic levels regulate the resource availability of the third, and with the interactions between the first and third trophic levels determine the survivorship of the second.

Emergence Phenologies

Additional evidence for tritrophic interactions within this system come from analyses of *B. treatae* and parasitoid emergence patterns (Figure 13). Analyses of *B. treatae* emergence phenologies show that the vast majority (60.8%) emerge in the month of April. This emergence pattern can be considered to be dependent on the timing of *Q. fusiformis* leaf initiation, which also peaks in April (Hall 2001; Egan 2003). This bottom-up regulation of *B. treatae* emergence is attributed to the fact that gall-formation in Cynipidae is dependent upon undifferentiated meristematic tissue (Cornell 1983), which in this system may be found in developing leaves. In turn, *Q. fusiformis* can also be considered to be indirectly regulating parasitoid emergence patterns. This indirect regulation of parasitoid emergence patterns is due to the fact that parasitoid development and subsequent emergence is contingent upon the timing of gall former development, which is in turn contingent upon host-tree development. Therefore, by regulating *B. treatae* emergence phenologies, *Q. fusiformis* also has an indirect impact on parasitoid emergence patterns.

Additional insight into the bottom-up regulation of parasitoid emergence patterns comes from analyses of parasitoid community structure. In these analyses, *T. tubicola* is found to be responsible for 98% of root-gall parasitism. This root-gall parasitoid is the only one of the four natural enemies confirmed to prey upon both root and leaf-gall generations. Analyses of *T. tubicola* emergence patterns show that the majority (71.0%) of lab reared *T. tubicola* had not matured enough to emerge from the incubated galls by the May 11 cessation to lab-rearing. Drawing from previous research showing that they begin to attack leaf galls in June (Hall 2001), it is likely that the immature *T. tubicola*

were on schedule to emerge in the later half of May, or in June. This would place their peak emergence in the period of leaf-gall development where galls are at their smallest and most vulnerable. This synchrony between second and third trophic levels is invariably driven by the first, to the benefit of both the first and third (Price et al. 1980; Price and Clancy 1986; Roininen et al. 1990).

Summary

When considered together, my results provide evidence that root-gall parasitism rates are temporally, and spatially influenced, and that bottom-up and top-down regulatory processes are experienced similarly between the *B. treatae* sexes. When compared to previous studies describing parallel processes in the leaf gall generation, it is evident that tritrophic interactions are a constant within this system. In both generations, parasitism rates appear to be regulated by first and second trophic level interactions, directly influencing gall size and gall former fitness, and indirectly influencing parasitism rates and parasitoid fitness.

Although both generations experience similar regulatory processes, the ultimate result of these processes is widely divergent. Multiple years of data collection for the leaf-galling generation have shown that a diverse community of 23 natural enemies are responsible for *B. treatae* mortality rates in excess of 99% (Lund 1998; Reynolds 2000; Hall 2001). In contrast, parasitism levels described by this study show that root galling generation experiences a comparably meager mortality rate of 18.5% meted out by a relatively non-diverse community of four natural enemies.

These great differences in parasitism rates and parasitoid community diversity between the separate *B. treatae* generations provide empirical evidence supporting the hypothesis that the evolution of bivoltine life cycles in Cynipidae is the result of shifts in host resource utilization due to top-down selective pressures (Askew 1961; Askew 1971; Askew1980; Jefferies and Lawton 1984). The greater implication of this evidence is that asexuality would necessarily be the ancestral state of Cynipidae, and sexuality the derived state (Cook et al. 1998). Although my work provides preliminary support that natural enemy avoidance drove the evolution of bivoltine life cycles in Cynipidae, this interpretations should be taken as tentative and contingent upon the fact that there are not differences in resource utilization between sexual and asexual generations that would mitigate any selective advantage in natural enemy avoidance.

To eliminate this as a possibility, future studies should address cross generational fitness differences due to resource utilization. These studies should compare the relative fitness of each *B. treatae* generation on the same host-trees, in both parasitoid free and parasitoid inclusive environments. Parasitoid free environments might offer a glimpse into evolutionary environments in which shifts in host resource utilization would carry a reduced penalties in top-down selection due to inherent lag times associated with parasitoid aggregation, while enemy inclusive environments would offer an ecological look at the consequences of such host utilization shifts. Taken together, cross generational fitness measurements of gall formers in enemy free and enemy inclusive environments should either strengthen or eliminate top down selection as the driving force behind the evolution of bivoltine life cycles within Cynipidae.

APPENDIX I:

TABLES

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Table 1.A. Manipulative cohort design for 15 trees. Three cohorts of galls (*A*, *B*, *C*) were created by removing 1/4 m^2 exclusion chambers (n = 5 chambers/ cohort/ tree) during three oviposition windows (*A*-Oct22-Nov5; *B*-Nov11–Nov25; *C*-Dec1–Dec15), thus allowing *B. treatae* to oviposit at natural levels during each window.

Cohort Treatment	Open	# Treatments	Total
A	Oct22 - Nov5	5/ tree	75
B	Nov11–Nov25	5/ tree	75
C	Dec1 – Dec15	5/ tree	75

Table 1.B. Parasitism exposure intervals for ten trees. One fourth of each cohort (*A*, *B*, *C*) was exposed to natural levels of parasitism starting on December 20th and lasting through April 19th. One exclusion chamber per cohort was opened on each of the four parasitoid attack windows (*AW1*–Dec20-Jan19; *AW2*-Jan19-Feb7; *AW3*-Feb17-Mar20; *AW4*-Mar20-Apr19). At the end of each attack interval, each chamber was closed until the end of the *B. treatae* developmental season, at which time the galls contained within were harvested and returned to lab.

Attack Window	Open	Closed	Cohorts A	Cohort B	Cohort C	Total/ Window
AW1	Dec20-Jan19	Jan19–Apr 19	1/tree	1/tree	1/tree	30
AW2	Jan19-Feb7	Feb 7–Apr 19	1/tree	1/tree	1/tree	30
AW3	Feb17-Mar20	Mar 20–Apr 19	1/tree	1/tree	1/tree	30
AW4	Mar20-Apr19	Apr 19	1/tree	1/tree	1/tree	30

Table 2.A. Gall size-sampling intervals for five trees. Galls were destructively sampled on four separate dates (Feb 1, Feb 26, Mar 24, and Apr 19). On each sample date, three exclusion chambers (1/cohort- A,B, and C) were sampled per tree (n= 5). A total of 15 exclusion chambers were sampled on each sample date (5/ cohort).

Sample	Date	# Trees	# Cohort A	# Cohort B	# Cohort C	Total
S1	Feb 1	5	5	5	5	15
S2	Feb 26	5	5	5	5	15
S3	Mar 24	5	5	5	5	15
S4	Apr 19	5	5	5	5	15

Table 2.B. Gall density-sampling intervals for 5 trees. Galls were destructively sampled on four separate dates (Feb 1, Feb 26, Mar 24, and Apr 19). On each sample date, one 1/2 m^2 sample was taken for each host tree. A total of 15 density samples were taken on each sample date, for an overall total of four estimated densities per tree.

Sample	Date	# Trees	1/2 m^2 Samples/Tree	Total
S1	Feb 1	5	1	15
S2	Feb 26	5	1	15
S3	Mar 24	5	1	15
S4	Apr 19	5	1	15

APPENDIX II:

FIGURES

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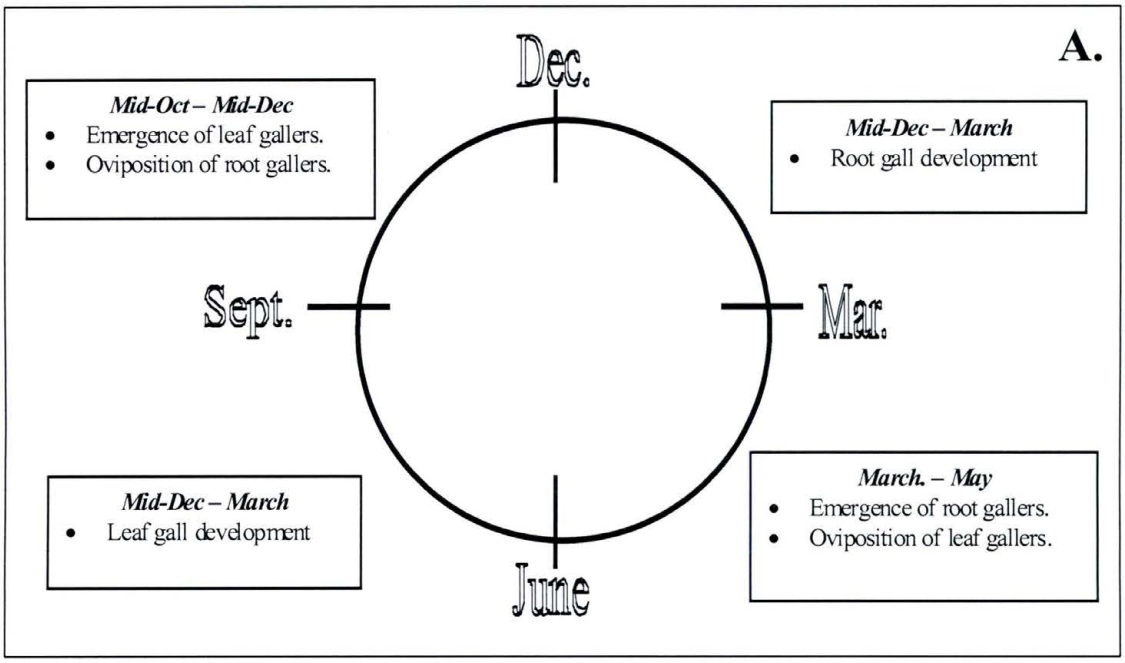

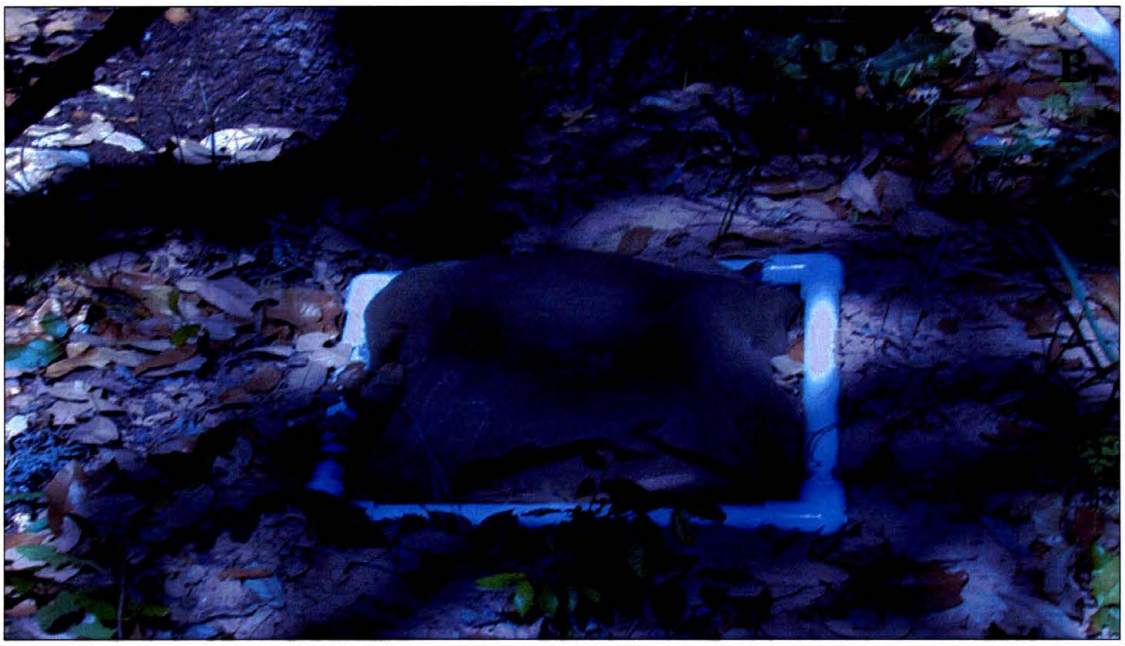

FIGURE 1. (A) *B treatae* life cycle. Oviposition of the root gall generation by the leaf galling generation occurs in mid- October and last through mid-December. These wasps develop through February, and begin emerging in March. Emergent root-gallers oviposit the leaf galling generation from March through May. Leaf gall wasps develop through September, and begin emerging in October. At this time, the leaf-gallers begin another cycle with the oviposition of the next root galling generation. (B) Exclusion chambers (1/4 m^2) used to restrict access of insects to root regions of study trees. Chambers were constructed of 1/2" sand filled PVC pipe and 1/4-mm nytex screening.

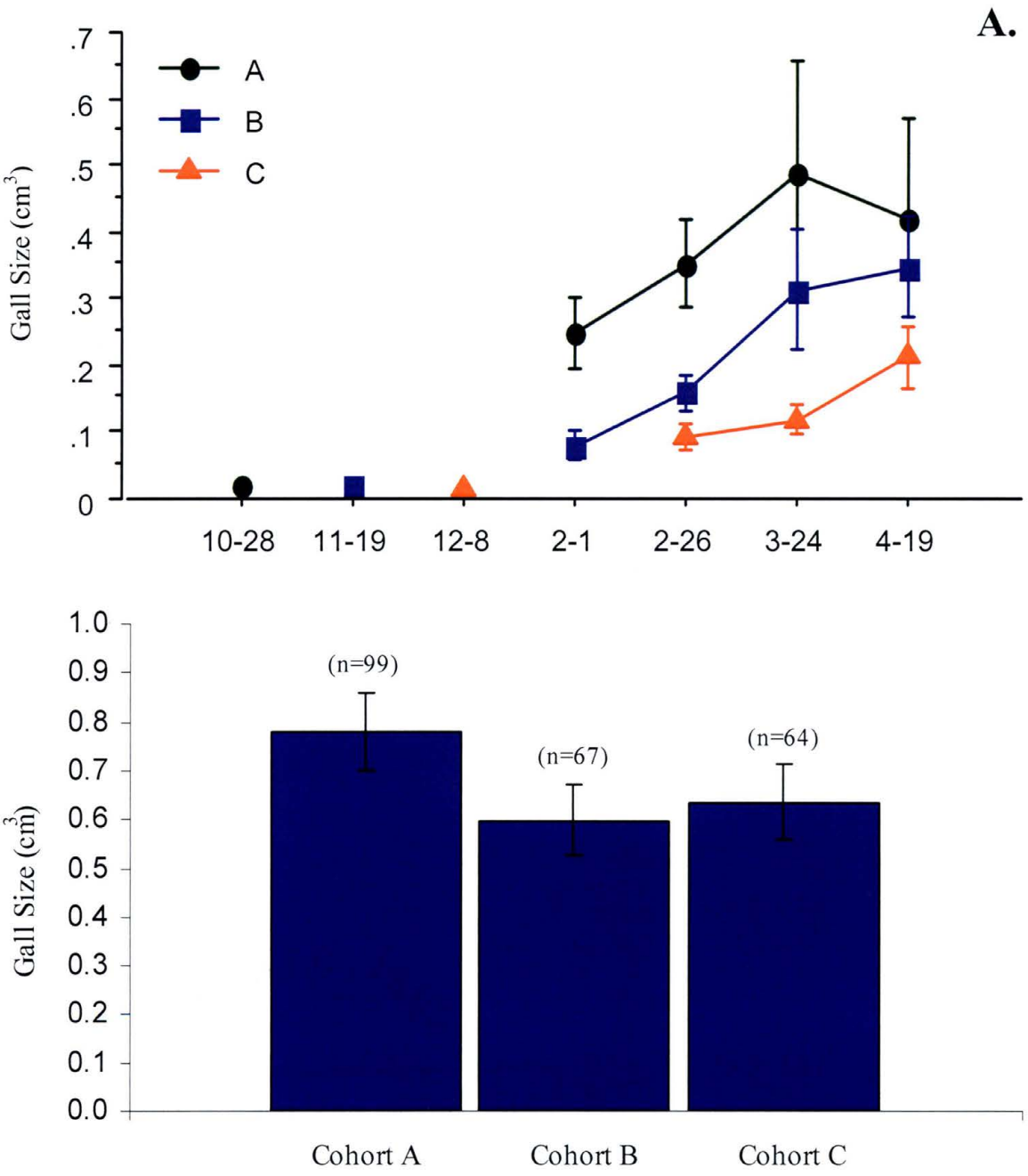

FIGURE 2. (A) Growth curve showing mean gall sizes (± 1 SE) for cohorts A, B, and C across four sample dates. Cohort A is represented by closed circle lines, cohort B by closed squares, and cohort C by closed triangles. Zero gall size values represent the median oviposition date for each cohort. Mean gall sizes are taken from 155 galls: A (n = 52), B (n = 68), and C (n = 35). Mean gall size differ significantly between the three cohorts ($p < 0.001$) during active growth periods. (B) Mean size (± 1 SE) of mature galls for cohorts A, B, and C. Mean final gall size were taken from 216 galls that had either partial field emergence at their time of collection, or galls that produced wasps within the first 10 days of lab incubation. Mean final gall size did not differ significantly between cohorts ($F_{2,212} = 2.05$; $p > 0.10$).

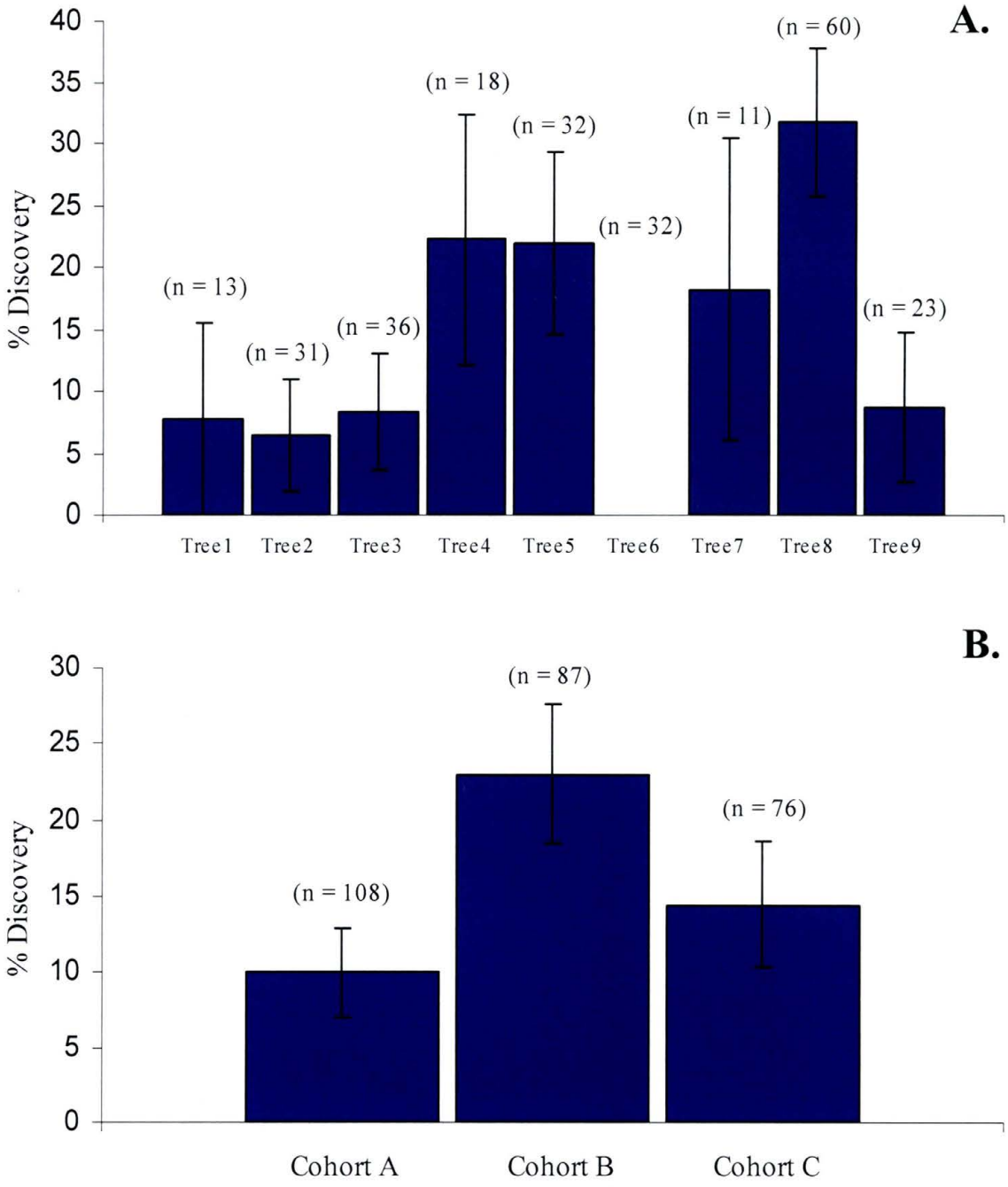

FIGURE 3. (A) Mean discovery rates (± 1 SE) for nine host trees taken from 271 galls. Mean discovery rates differ significantly among trees ($F_{8,187} = 3.18$; $p < 0.001$). (B) Mean discovery rates (± 1 SE) for cohorts A, B, and C. Discovery rates were taken from 271 galls. Mean discovery rates differ significantly among cohorts ($F_{2,268} = 3.09$; $p < 0.05$). Specifically, post hoc analysis shows that cohort B differs significantly from cohorts A and C.

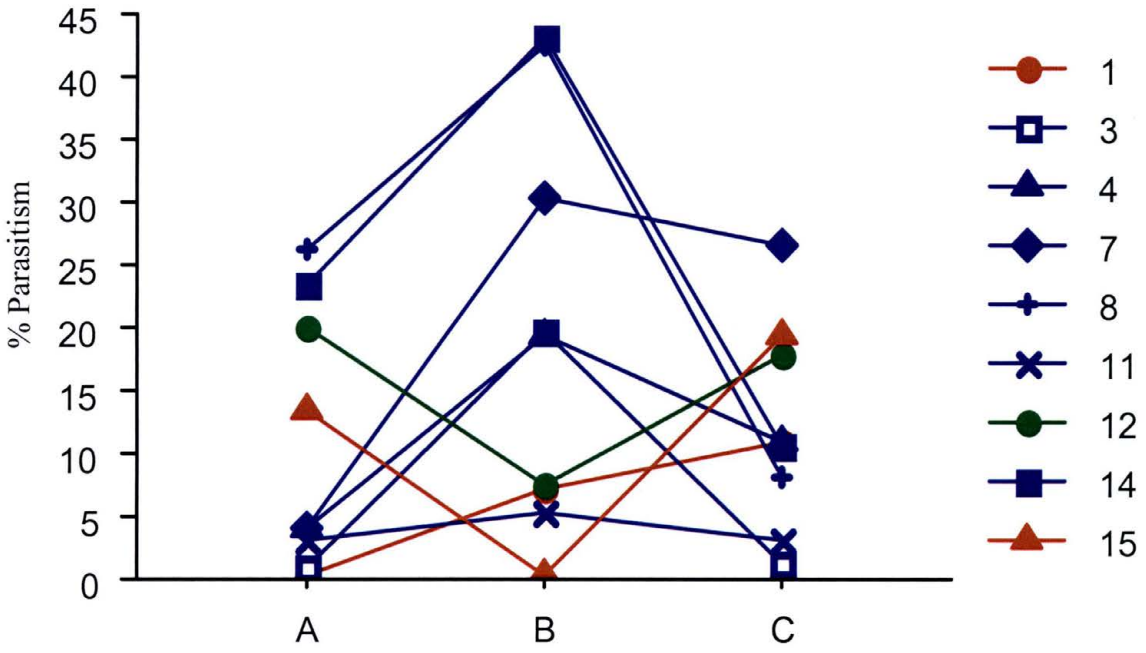

FIGURE 4. Mean Parasitism rates for cohorts A, B, and C across nine host-trees. Green lines represent trees where cohort A experienced the greatest rates of parasitism, blue line represent trees where cohort B experienced the greatest rates of parasitism, and red lines represent the trees where cohort C experienced the greatest rates of parasitism. Mean parasitism rates were significantly influenced by an interaction between oviposition timing and host-tree selection ($F_{16,187} = 1.62$; $p < 0.05$).

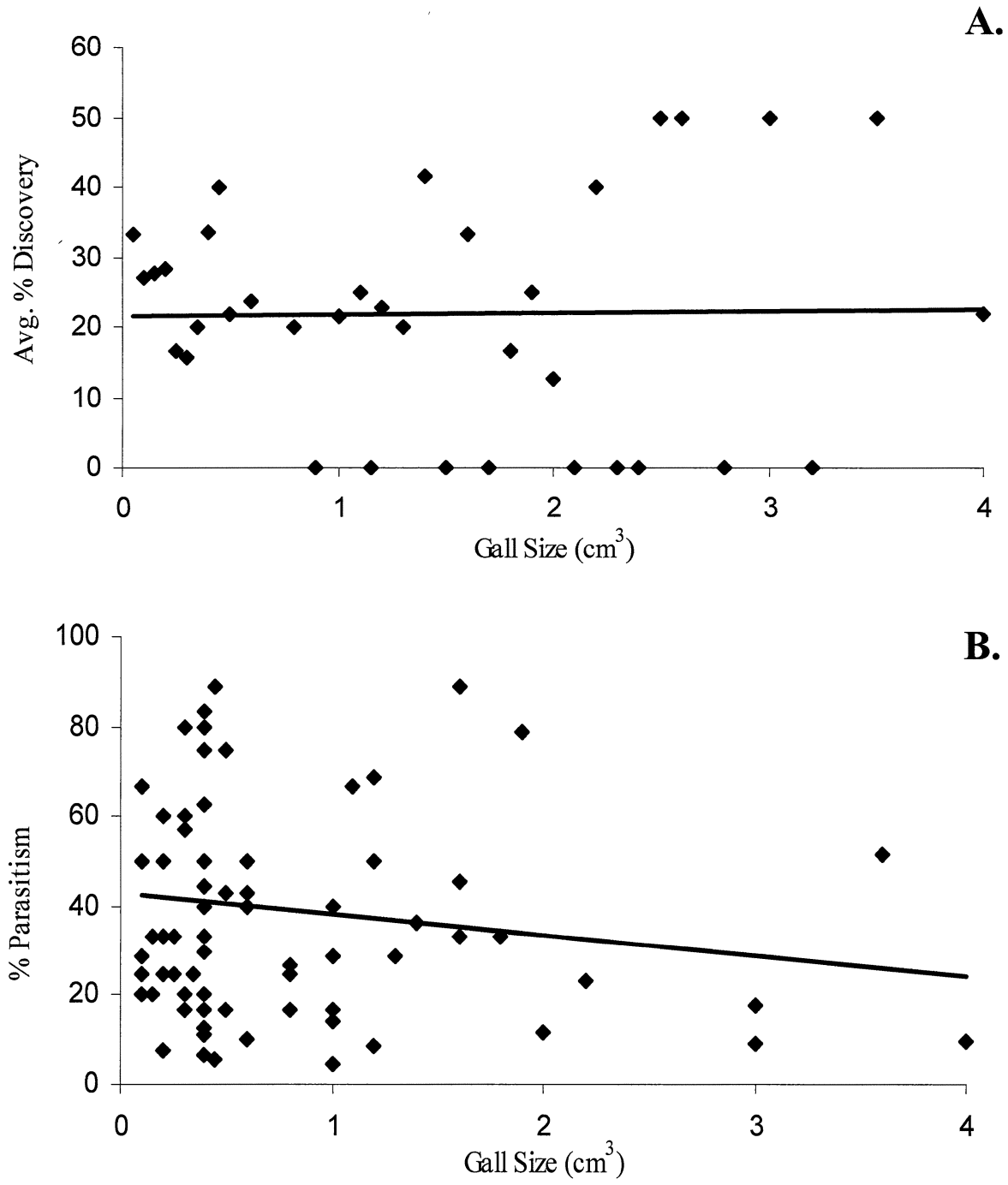

FIGURE 5. (A) Regression analysis of mean gall discovery rates for 35 gall size classes (range, 0.05 – 4.0 cm^3). Analysis indicate that there is not a relationship between gall size and gall discovery rates ($R^2 = 0.0002$; $F_{1,34} = 0.006$; $p > 0.90$). (B) Regression analysis for 81 discovered galls (range, 0.05 – 4.0 cm^3). Analysis indicate there is not relationship between gall size and parasitism rates ($R^2 = 0.027$; $F_{1,80} = 2.25$; $p > 0.10$).

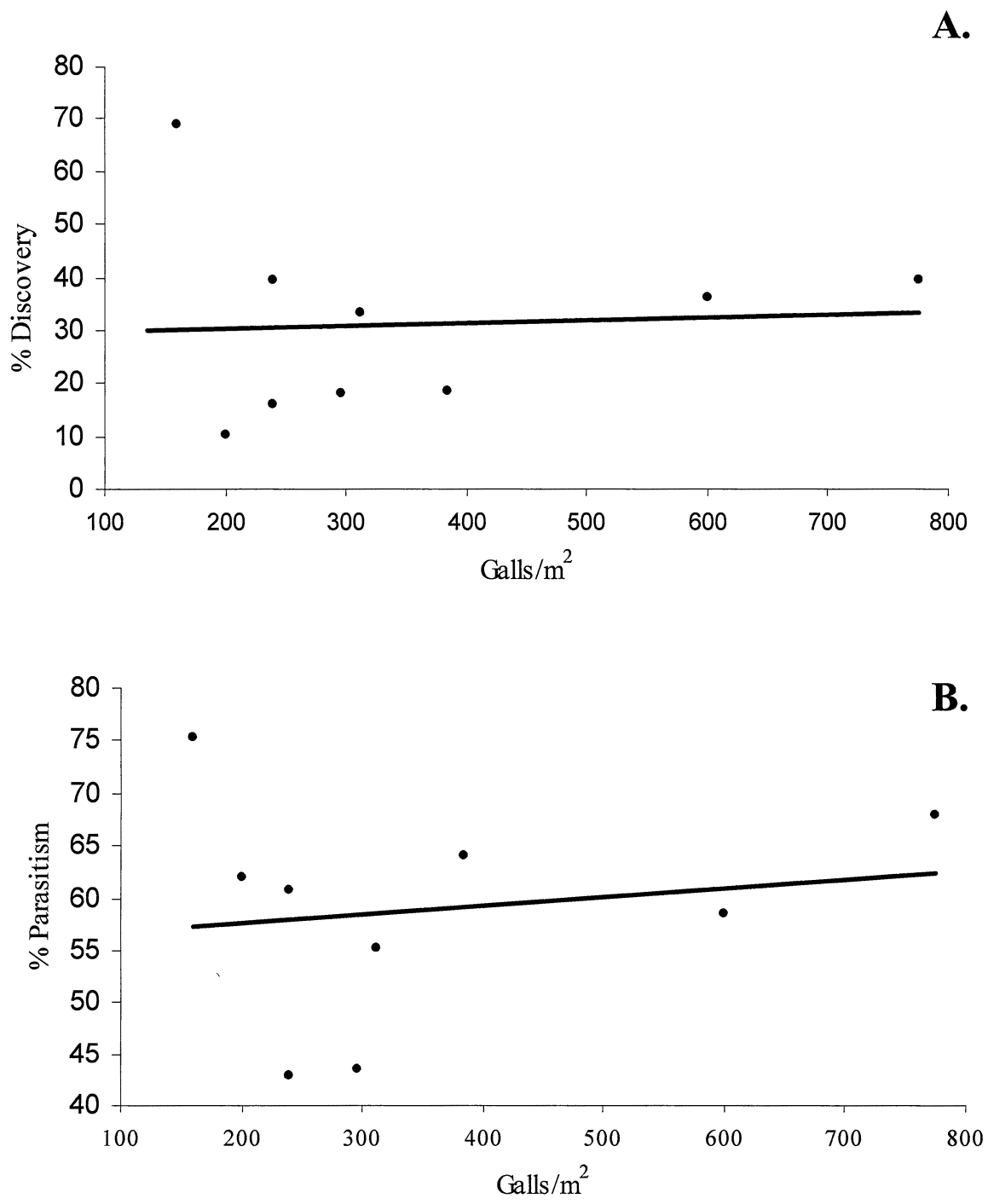

FIGURE 6. (A) Regression analysis of gall discovery rates for nine gall densities. Gall/m^2 represents the mean gall densities of four 1/8 m^2 samples taken for each of nine host-trees (range, 776 – 160 galls/m^2). Tests of spatially dependent gall discovery indicate that there is not relationship between gall densities and discovery ($R^2 = 0.003$; $F_{1,7} = 0.02$; $p > 0.85$). (B) Regression analysis of parasitism rates for nine gall densities. Gall/m^2 represents the mean gall densities of four 1/8 m^2 samples taken for each of nine host-trees (range, 776 – 160 galls/m^2). Tests of spatially dependent parasitism indicate there is no relationship between gall densities and parasitism rates ($R^2 = 0.003$; $F_{1,7} = 0.02$; $p > 0.85$).

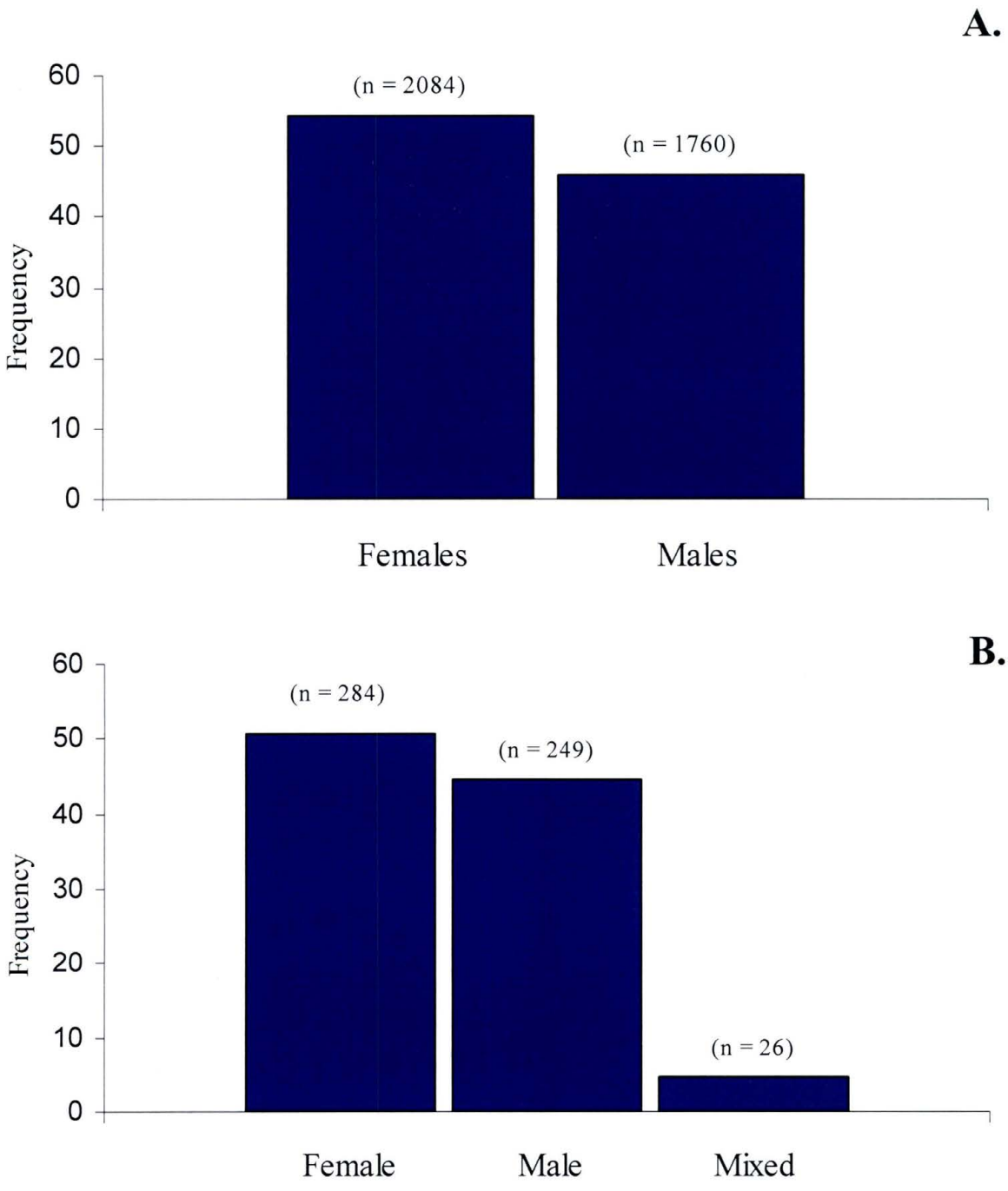

FIGURE 7. (A) Percent of female and male B. treatae collected from 559 wild collected galls. Percentages are taken from a sample of 3,844 wasps. (B) Percent of galls that produced only females, only males, and both males and females. Percentages are taken from 559 wild collected galls.

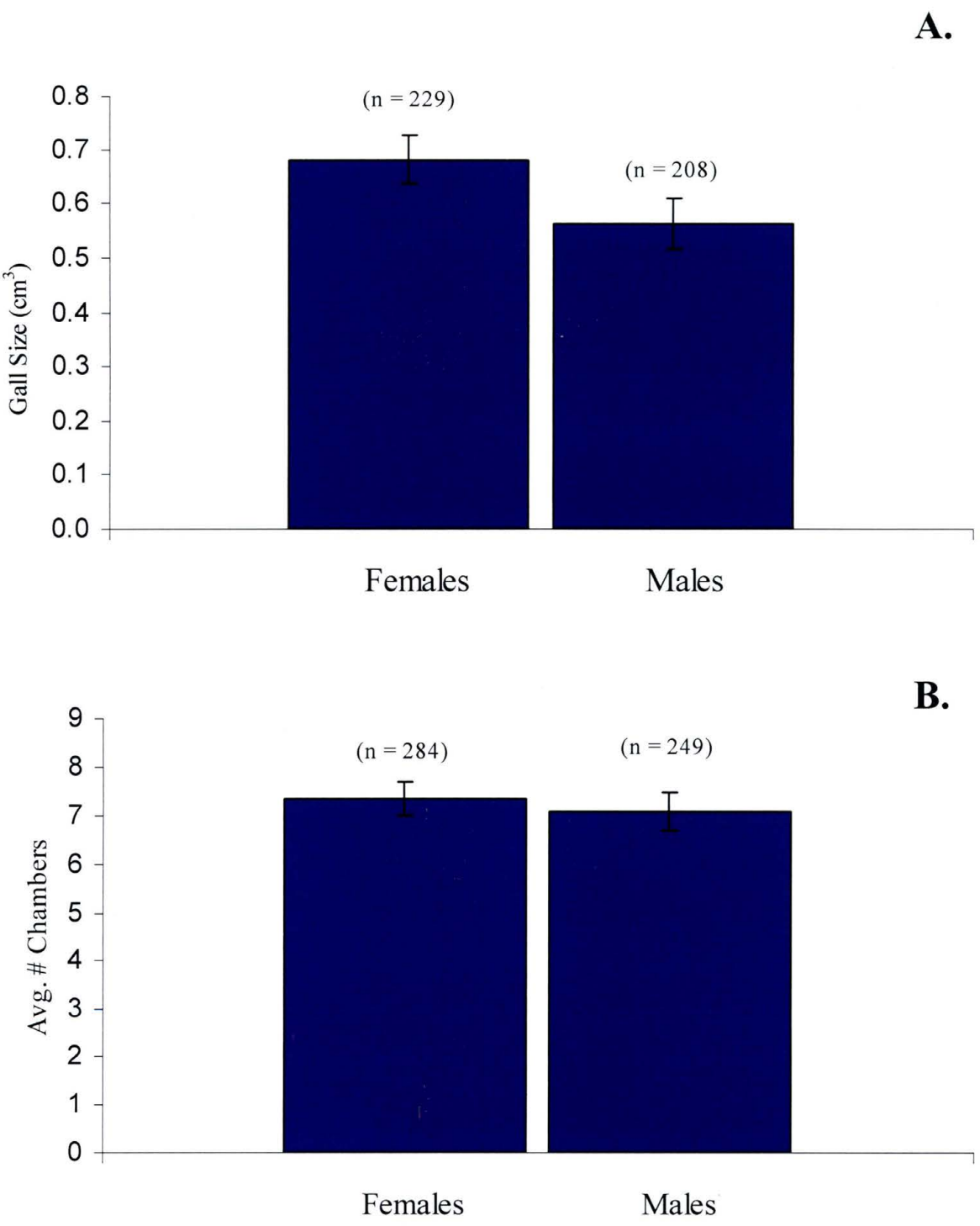

FIGURE 8. (A) Mean sizes of mature galls that produced female and male *B. treatae* (± 1 SE). Mean final sizes differ between male and female producing galls ($F_{1,435} = 4.66$; $p < 0.05$). (B) Mean number of chambers per gall for female and male producing galls (± 1 SE). Mean number of chambers per gall differ between female and male producing galls ($F_{1,531} = .27$; $p > 0.60$).

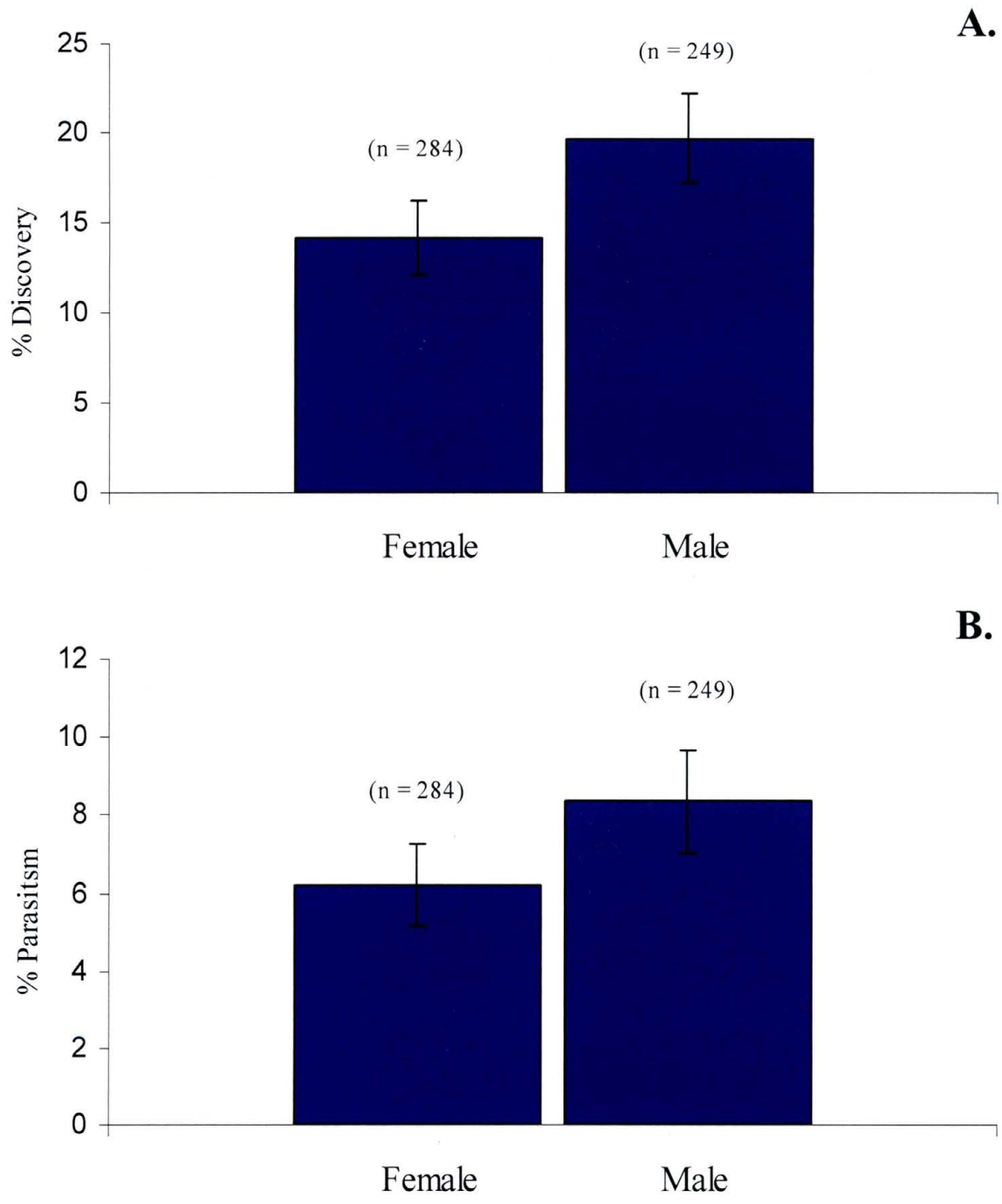

FIGURE 9. (A) Mean percent discovery of female and male producing galls (± 1 SE). Mean discovery percentages do not differ between female and male producing galls ($F_{1,531} = 2.99$; $p > 0.05$). (B) Mean percent of parasitism between female and male producing galls (± 1 SE). Mean parasitism percentages do not differ between male and female producing galls ($F_{1,531} = 1.60$; $p > 0.20$).

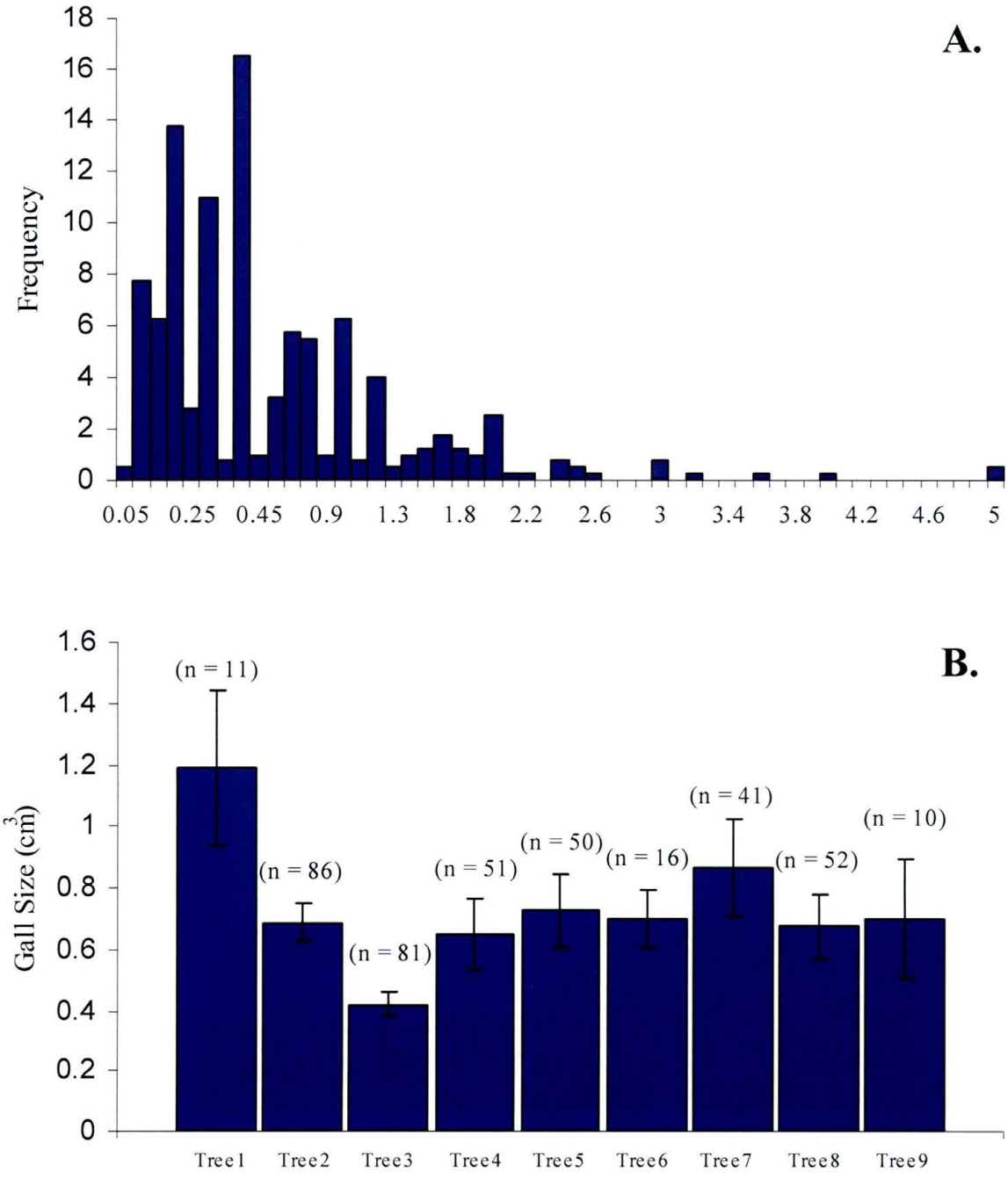

FIGURE 10. (A) Distribution of mature gall sizes among 9 host trees (mean ± SE, .66 ± 0.03cm^3; range, 0.05 – 5.0 cm^3). Final gall size were taken from 400 galls that had partial field emergence at their time of collection, or that produced wasps within the first 10 days of lab incubation. This selection process was used to insure that only those galls that had reached full maturity were used in the analysis of final gall size. Ninety percent of all galls had a size of ≤ 1.4 cm^3. (B) Mean size of mature galls (± 1 SE) for nine host-trees. Mean sizes of mature galls differed significantly among trees ($F_{9,390} = 2.63$; $p < 0.01$).

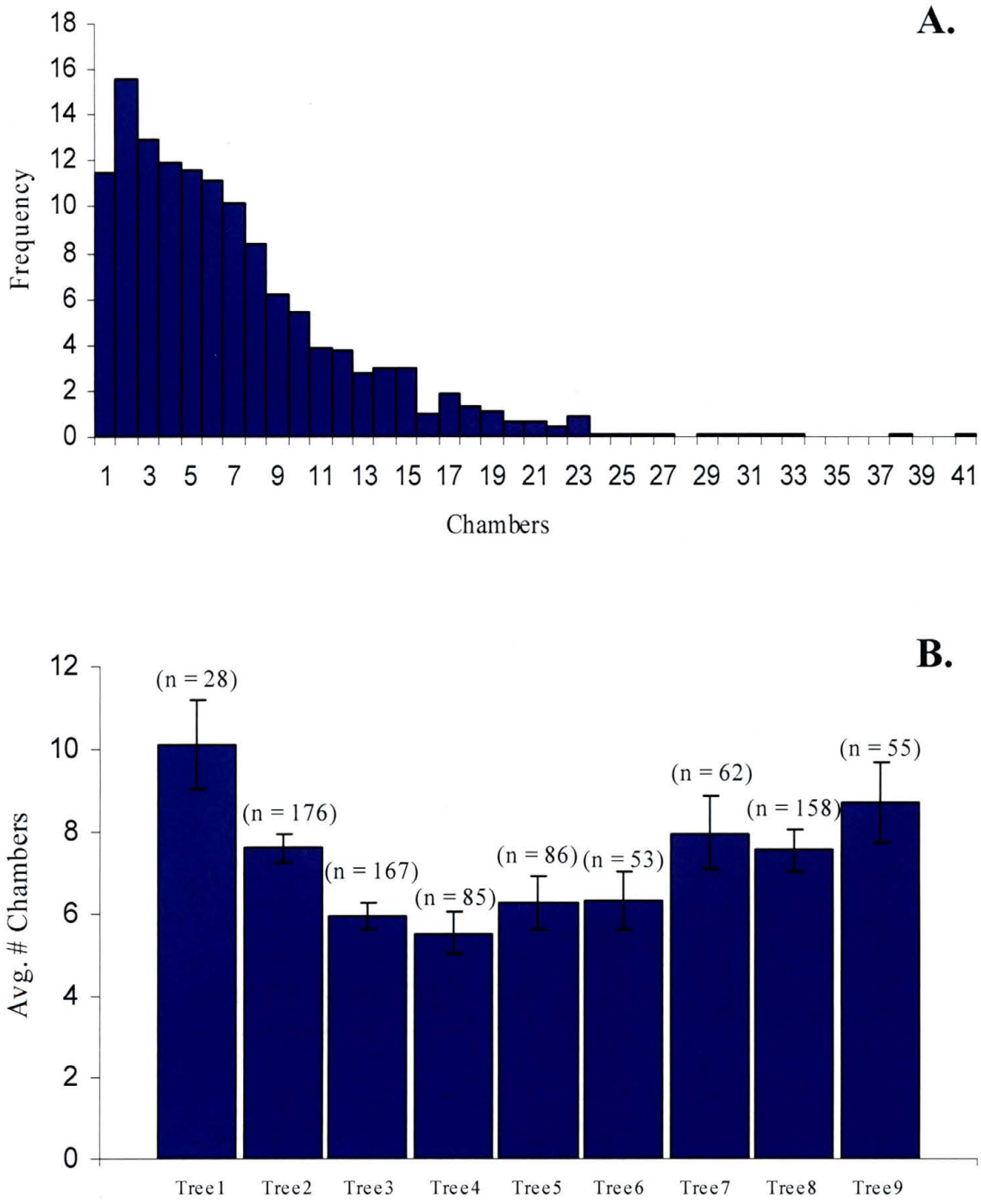

FIGURE 11. (A) Distribution of chambers per gall for 9 host-trees (mean ± SE, 6.98 ± 0.18 chambers/gall; range, 1 – 41 chambers/gall). Chambers per gall estimates were taken from 870 galls, ninety percent of which had ≤ 14 chambers per gall. (B) Mean number of chambers per gall (± 1 SE) for 9 host-trees. Mean number of chambers per gall differed significantly between trees ($(F_{8,861} = 4.29$; $p < 0.0001$).

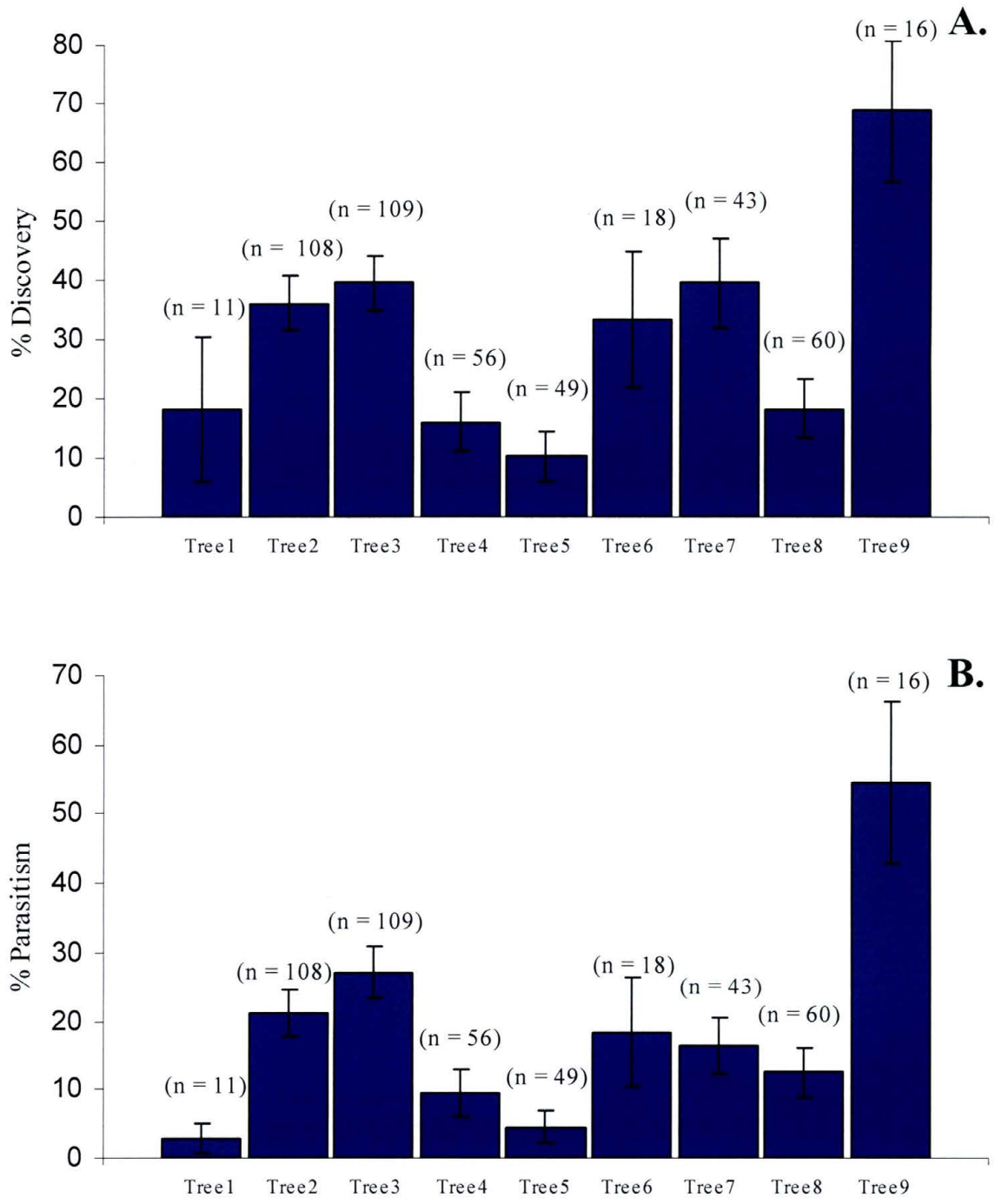

FIGURE 12. (A) Mean percent of galls per tree that were discovered by parasitoids (± 1 SE). Mean percent of galls discovered by tree indicates that percent gall discovery rates differed significantly among trees ($F_{8,461} = 5.14$; $p < 0.00001$). (B) Mean percent of occupants that were parasitized (± 1 SE) among nine host trees. Mean percent of occupants being parasitized differed significantly among trees ($F_{8,461} = 5.83$; $p < 0.00001$).

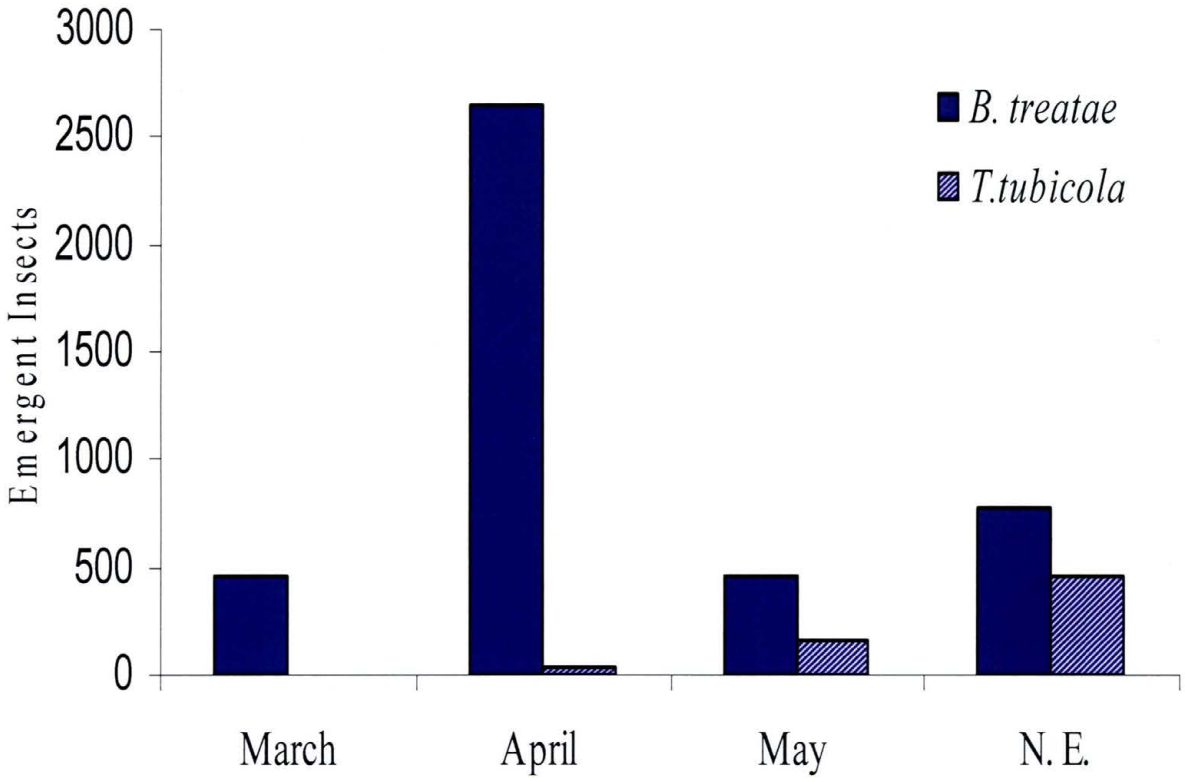

FIGURE 13. *B. treatae* and parasitoid emergence phenologies collected from 916 galls that were lab reared from March 27 through May 11, 2003. *B. treatae* emergence percentages for March, April, and May were 10.4, 60.8, and 10.7 respectively. An additional 18.1% of *B. treatae,* detected through lab dissection, had not emerged (N.E.) by May 11. Parasitoid emergence phenologies for March, April, and May were 0.0, 5.9, and 23.1 respectively. An additional 71.0% of all parasitoids, detected through lab dissection, had not emerged (N.E.) by May 11.

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