EFFECTS OF PRIOR DEFOLIATION ON THE TIMING OF LIFE CYCLE EVENTS AND SUSCEPTIBILITY TO NATURAL ENEMIES OF A

HOST SPECIFIC GALL-FORMER

THESIS

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by

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ABSTRACT

EFFECTS OF PRIOR DEFOLIATION ON THE TIMING OF LIFE CYCLE EVENTS AND SUSCEPTABILITY TO NATURAL ENEMIES OF A HOST SPECIFIC GALL-FORMER

by

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In short lived phytophagous insects specialized to exploit specific plant tissues, phenological synchronization between plant and insect life cycle events is crucial and likely under selection. Here I report on past (1995–2001) and recent (2006–2007) patterns of emergence phenology and survivorship of the asexual generation of the host specific gall-former, *Belonocnema treatae* (Hymenoptera: Cynipidae) that develops within and emerges from leaf galls on *Quercus fusiformis*, a live oak endemic to the Edwards Plateau region of central Texas. Comparisons of these patterns document an apparent shift in the timing of *B. treatae* emergence (Past: Oct.–Dec., Recent: Dec.–Mar.)

and survivorship (Past: 0–50%, Recent: 0–13%) in the presence of natural enemies. These shifts in conjunction with past and recent defoliation of live oaks by oak leaf rollers (which alter the timing of tissue formation coinciding with *B. treatae* oviposition) motivated a defoliation experiment inducing variation in the timing of leaf flush, thus altering the timing of oviposition to test the following hypothesis: variation in the timing of leaf formation, induced by defoliation, creates temporal variation in the timing of oviposition, affecting subsequent gall maturation schedules, and *B. treatae* emergence phenology and survivorship. Galls induced by early and delayed oviposition mature at the same time and produce adult *B. treatae* that have similar emergence phenologies and levels of survivorship in the presence and absence of natural enemies. Thus B. treatae development is a plastic trait. However, survivorship, when exposed to natural enemies, differed significantly between early (mean \pm SE = 1.37% \pm 1.29%) and delayed (mean \pm $SE = 20.99\% \pm 1.43\%$) oviposition events. These results indicate that defoliation, as manipulated herein, created variation in oviposition timing but is not responsible for observed shifts between past and recent emergence phenologies. However, variation in oviposition timing, driven by defoliation can explain differences in survivorship in the presence of natural enemies. These results highlight the effects that common but patchy outbreaks of defoliators can have on the timing of life cycle events and survivorship of phytophagous insects.

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INTRODUCTION

In short-lived phytophagous insects specialized to exploit specific plant tissues, phenological synchronization between insect and plant life cycle events is critical for insect population maintenance and likely under selection (Clancy and Price 1986, Potter and Redmond 1989, Eliason and Potter 2000, Yukawa and Akimoto 2006, Forkner et al. 2006). Reviews by Yukawa (2000), Mopper (2005), and Asch and Visser (2007) link the synchronization of plant resource availability to phytophagous insect life cycle events, life history patterns, and ecological dynamics. If variation in host plant tissue availability is induced (by high levels of prior herbivory, for example), alteration of the timing of life cycle events for those insects that subsequently use the plant may be necessary to complete their life cycle (Abe 1991, Kaitaniemi et al. 1997). Life cycle events closely tied to host plant phenology and likely altered during insect-host plant resynchronization can include the timing of oviposition (Potter and Redmond 1989, Ohgushi 1991, Kaitaniemi and Ruohomaki 1999, Wang 2006), the rate of larval development (Krause and Raffa 1995, Kaitaniemi et al. 1997, Hicks et al. 2007), eclosion (Komatsu and Akimoto 1995, Van Dongen et al. 1997, Kaitaniemi and Ruohomaki 1999, Rehill and Hatch 2002, Ivashov et al. 2002) and mating (Cushman et al. 1994, Mopper 1996). When host plants exhibit consistent local/regional variation in the timing of resource availability, selection within insect populations to shift life-cycle events to match their

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host plant can promote adaptive radiation via allochronic shifts among insect populations (Horner et al. 1999, Blair et al. 2005, Joy and Crespi 2007).

Asynchrony in herbivorous insect and plant life cycle events related to the timing of plant tissue formation can also directly affect mortality due to natural enemies through changes in enemy abundance (Yukawa and Akimoto 2006), attack timing (Briggs and Latto 1996, Kaitaniemi and Ruohomaki 1999, Parry et al. 2003, Van Houhuys and Lei 2004), and community structure (Kaitaniemi and Ruohomaki 1999, Yukawa and Akimoto 2006). When changes in the timing of insect life cycle events creates enemy free space (Clancy and Price 1986, Berdegue et al. 1996, Murphy 2004), continued selection limiting gene flow can lead to divergence in the timing of those life cycle events and provide the template for divergence among host affiliated phytophagous insect populations (Ohgushi 1991, Mopper 1996, Eubanks et al. 2003, Blair et al. 2005, Santos et al. 2007).

Prior herbivory from other insects (Rossiter et al. 1988, Kaitaniemi 1997, Parry et al. 2003) can induce variation in the timing of plant tissue formation and/or availability. This may lead to phenological shifts in life cycle events of host-specific insect populations. Insect herbivores can induce temporal variation in plant resources particularly during outbreaks that produce partial to complete defoliation of host plants (Crawley and Akhteruzzaman 1988, Krause and Raffa 1994, Parry et al. 2003). This variation might exist within and among plants or even among plant populations creating heterogeneity in plant resource availability. Patchiness can induce changes in insect distribution (Doak 2000, Hassell 2008), abundance (Potter and Redmond 1989, Cushman et al. 1994, Mopper and Simberloff 1995, Doak 2000, Hassell 2008), performance

(Rossiter 1988, Roslin et al. 2006), fecundity (Roland and Myers 1987, Ohgushi 1991, Van Dongen 1997, Rehill and Schultz 2002, Tikkanen and Julkunen-Titto 2003), and mortality from natural enemies (Hassell et al. 2008).

Defoliation by insect herbivores can have cascading effects for insect species that use defoliated hosts before and/or after defoliation (Barbosa and Schultz 1987). Consumption of leaf tissue, particularly at outbreak densities, can eliminate previously deposited eggs or larvae of other insects dependent on the plant for essential resources (Barbosa and Schultz 1987, Potter and Redmond 1989, Mopper and Simberloff 1995), as well as potential sites for feeding, mating and oviposition and refuge from natural enemies (Barbosa and Schultz 1987). However, some plant species respond to defoliation by refoliation at a later date (Potter and Redmond 1989). Refoliation creates time lags in the availability of resources, and can induce variation in the realized timing of life cycle events. Partial to complete defoliation can also alter host plant chemistry (Karban and Baldwin 1997) with either positive (Potter and Redmond 1989, Rieske and Raffa 1998, Wallin and Raffa 2001) or negative (Tikkanen and Julkunen-Tiitto 2003) affects on associated host-specific phytophagous insect populations (Potter and Redmond 1989, Rieske and Raffa 1998, Wallin and Raffa 2001).

For gall-forming insects, the timing of host plant tissue availability is particularly important because gall formers are typically host- and tissue-specific, restricted to ovipositing into newly formed tissue, sessile during development, and short-lived during the oviposition phase of the life cycle (Stone et al. 2002). As a consequence, gall formers are characterized by tightly synchronized phenological schedules with their host plants (Stone et al. 2000, Yakuwa 2000, Hayward and Stone 2005). Thus, temporal variation in tissue formation can alter the timing of, or even prevent, gall-former oviposition and/or subsequent development (Kaitaniemi and Ruohomaki 1999, Eliason and Potter 2000, Stone et al. 2002). Because gall formers are associated with diverse communities of natural enemies (Askew 1971, Stone et al. 2002, Hayward and Stone 2005) and exhibit windows of vulnerability to portions of their associated natural enemy community (Clancy and Price 1986, Craig et al. 1990, Briggs and Latto 1996, Stone et al. 2002), a change in the timing of resource availability leading to variation in oviposition timing and gall-former development potentially alters the affects of natural enemies synchronized to attack gall-formers at specific developmental stages (Krause and Raffa 1995, Crawley and Akheruzzaman 1998, Kaitaniemi and Ruohomaki 1999, Parry et al. 2003). While available evidence suggests the importance of changes in the timing of tissue availability for gall formers, it is not clear at present, for any gall-former system, what the effects of prior defoliation are on gall former life cycle events and subsequent susceptibility to natural enemies.

In the analysis presented herein, I document patterns of defoliation of host plants used by a gall-forming leaf specialist, and the phenology of oviposition into those same defoliated plants. I then estimate subsequent emergence phenology and survivorship when exposed to natural enemies of this gall-former. I then use these results to justify a manipulative experiment aimed at understanding the effects of variation in the timing of oviposition, induced by defoliation, on leaf gall maturation schedules, emergence phenology and survivorship of the gall former in both the presence and absence of natural enemies. I mimicked natural defoliation to create temporal variation in tissue formation and used an enclosure experiment to allow insects to oviposit into two temporally segregated leaf flush events to compare the timing of life cycle events and survivorship between oviposition events. By examining the effects of oviposition timing on gall maturation, emergence phenology and survivorship I was able to assess the potential impact that patchy but common defoliation events of this gall-former's host plant have on the life cycle events and population ecology of this host-specific phytophagous insect.

METHODS

STUDY SYSTEM

Belonocnema treatae (Hymenoptera: Cynipidae) is a host-specific gall-former, that in Edwards Plateau region of central Texas, USA, develops on a single plant species, live oak, Ouercus fusiformis (Fagaceae; Lund et al. 1998, Egan and Ott 2007). B. treatae exhibits heterogony wherein an asexual generation developing within unilocular leaf galls alternates with a sexual generation that develops within multilocular root galls (Lund et al. 1998). Coinciding with spring leaf flush, sexual females emerge from root galls, mate, fly to the canopy, and oviposit into the lateral veins on the underside of newly flushed leaves (Lund et al. 1998). Each ovipositor insertion results in a permanent "oviposition scar" documenting potential oviposition (Egan and Ott 2007). On trees possessing high leaf gall densities, up to 100% of leaves can show oviposition scars (Lund 1998). Asexuals develop within leaf galls through the summer and typically emerge from October to December. Following emergence, the short-lived asexual females, which live two to six days in laboratory settings (G. Hood personal observation) descend to the ground and oviposit into oak rootlets (Lund et al. 1998). Trees possessing high leaf gall densities equate to high quality host plants, and are both patchy and rare. The leaf gall generation of *B. treatae* exhibits spatially structured populations that show demic adaptation to individual trees (Egan and Ott 2007).

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During growth, leaf galls are characterized by changes in consistency and color representing different stages of development. Immature leaf galls are fleshy and yellow. As galls mature, they lignify, becoming brown. Harvesting galls at earlier stages of development halts growth and can result in gall-former death (Lund 1998). The state of gall maturity (mature or immature) was used to assess gall maturation schedules, and only mature leaf galls were used to monitor emergence and survivorship in the studies described herein.

B. treatae larvae in leaf galls are attacked throughout development by a diversity of parasitoids and the galls themselves are attacked by inquilines (23 different species; Lund et al. 1998, Hall 2001). However, as *B. treatae* do not emerge from galls following inquiline attack both parasitoids and inqulines act as, and are collectively considered to be, natural enemies (Hall 2001). For a fuller description of the life cycle and biology of *B. treatae*, see Egan and Ott (2007).

Plateau live oaks, *Quercus fusiformis*, Small (Mueller 1961) are deciduous trees, and flush new leaves in early spring. In central Texas live oaks can experience defoliation during outbreaks of caterpillars of two species of oak leaf rollers, *Archips semtferana* and *Sparganothis pettitana* (Lepidoptera: Tortricidae; Stewart and Bailey 1993, Drees 2004). Defoliation events are often patchy, and the severity of leaf consumption varies among adjacent trees, and live oak populations (Steward and Bailey 1993, Drees 2004). However, severe outbreaks appear to occur in successive two to four year periods (Stewart and Bailey report outbreak numbers from 1988 through 1990) positioned between longer periods of less severe herbivory (G. Hood and J. Ott, personal observation). Because caterpillar feeding coincides with leaf flush and *B treatae* oviposition, these defoliators also consume *B. treatae* eggs and eliminate oviposition sites. (G. Hood and J. Ott, personal observation). However, partial to complete defoliation by caterpillars induces a second leaf flush six to eight weeks later that can be used for oviposition by later-emerging sexual *B. treatae* females (G. Hood and J. Ott, personal observation). Thus, *B. treatae* leaf galls developing on partially defoliated trees likely represent both "pre- and post-defoliation" oviposition events while *B. treatae* developing on completely defoliated trees likely represent delayed "post-defoliation" oviposition events.

PAST EMERGENCE PHENOLOGY AND SURVIVORSHIP

Herein I first summarize previous studies of *B. treatae*'s asexual generation emergence phenology from populations in Hays County in 1996, 1998 and 1999, Comal County in 1998, and Travis County in 2001. These studies collectively estimated "past" *B. treatae* emergence phenologies. For studies conducted in 1996, 1998, and 1999, leaf galls were haphazardly sampled from high gall density trees in the lower and middle strata in each cardinal direction once in late October at the onset of gall maturity. Gall occupants were then reared individually in gelatin capsules in the lab (following the methods in Lund 1998, Galusky 2000, and Reynolds 2000). In 2001, an aberrant population at one site in Travis County was observed from which *B. treatae* were emerging in mid-December. For this population, galls were sampled from four trees in each cardinal direction once in mid-December. In 2001, gall occupants were bulk reared in collection traps (mason jars fitted with a vented funnel top with a collection vial) and stored outdoors. Emergence phenologies of *B. treatae* were monitored for both gelatin capsule and collection trap techniques in weekly intervals until emergence ceased. The total number of emerged *B. treatae* was counted and emergence phenologies were estimated per tree for all studies.

Independent studies from Hays County in 1995–1998 and 2000, Comal County in 1997 and Travis County in 2000 were also conducted to estimate "past" *B treatae* survivorship in the presence of natural enemies. Galls were sampled from the same populations used to estimate emergence phenology and were stored and monitored using the methods outlined above. Survivorship was estimated per tree within each region (county) by counting the total number of *B treatae* that emerged/the total number of galls sampled. Henceforth, these patterns will be referred to as "past" *B treatae* emergence phenology and survivorship.

RECENT EMERGENCE PHENOLOGY AND SURVIVORSHIP

The above studies show spatial and temporal asynchrony in asexual *B treatae* emergence phenology among populations sampled in Hays, Comal and Travis Counties, with average emergence in Travis County being 10 weeks later than in Hays and Comal Counties. To assess the consistency of past patterns observed in Hays and Travis counties in winter of 2007, and to correlate these patterns with estimates of levels of defoliation monitored prior to gall-former emergence in the spring of 2007, I sampled leaf galls from the following trees: eight and 22 high-gall-density trees in 2006 and six and 17 trees in 2007 from Hays (one site) and Travis (six sites) counties respectively. Sample sizes were reduced in the second year because many trees did not have high

enough gall densities to provide sufficient sample sizes. For both 2006 and 2007, galls were haphazardly sampled from lower and middle strata of each tree in all cardinal directions and in 2006 galls were collected monthly from November through February, while in 2007, galls were collected once at the onset of gall maturity in early November. For each tree, galls were removed from leaves, sorted as immature or mature, and placed in collection traps outside at the Texas State University-San Marcos greenhouse. Gallformer emergence phenology was monitored by weekly surveys conducted from November till March 15th in each year. *B treatae* survivorship per tree per population was calculated following the methods used in previous years. Henceforth, these *B treatae* patterns of emergence phenology and survivorship in 2006 and 2007 will be referred to as "recent" patterns.

HOST PLANT DEFOLIATION AND GALL-FORMER OVIPOSITION PHENOLOGY

In the spring of 2007, which represented the third consecutive year of severe, widespread defoliation throughout parts of central Texas, I monitored both the level of naturally occurring defoliation by caterpillars and the oviposition phenology of the sexual generation into oak leaves for the same eight and 22 trees in Hays and Travis Counties previously monitored for emergence phenology and survivorship. This allowed me to test the prediction that among-tree variation in defoliation in spring 2007, creating variation in the timing of leaf tissue could control the timing of oviposition, and hence drive natural variation in gall maturation schedules, and *B. treatae* emergence timing and survivorship during the fall of 2007.

Beginning in late March, each tree was examined for caterpillar-induced damage (see Bailey and Dress 1993 for detection details). At three-week intervals from April through July, defoliation was visually estimated. Estimated defoliation/tree was categorized as 0, 25, 50, 75, and > 95% defoliation (corresponding to none, light, moderate, heavy, and near-complete defoliation).

The percentage of leaves with oviposition scars was surveyed for six of the eight and 17 of the 22 trees in Hays and Travis Counties monitored for defoliation that had high enough oviposition scar densities to quantify. Beginning in early April, and continuing in three-week intervals through the conclusion of *B. treatae* oviposition (late July), eight branches per tree were randomly chosen and all leaves per branch were scored for the presence/absence of ≥ 1 oviposition scar. An average of 603 leaves \pm 162 (range 162 to 990) were scored for oviposition scars at each monitoring interval. Cumulative oviposition intensity, defined as the percent of leaves with scars/the total number of leaves sampled summed over the season, was computed and compared to past oviposition phenology records from Hays County in 1998, captured by a previous study using the same methods (Lund 1998).

EXPERIMENTAL DEFOLIATION

Observational differences in past and recent *B. treatae* oviposition phenologies and observations of wide spread defoliation provided the justification for conducting a manipulative defoliation experiment to test the following hypotheses: variation in the timing of leaf flush, driven by defoliation, dictates variation in *B. treatae* oviposition timing observed in nature that subsequently drives *B. treatae* leaf gall maturation

schedules, emergence timing, and survivorship. Six live oak trees each possessing both suitably high root and leaf gall densities were chosen at Texas State's Freeman Ranch in Hays County, Texas, USA (29°55' N, 98°00' W). Each tree was used as a source population for sexual *B. treatae* and as rearing sites for the experiment described herein. In the early spring of 2008, root galls housing sexual generation B. treatae were collected from each tree. One half of galls were stored in an incubator at seasonally adjusted light and temperature regimes and the other half were stored in an incubator at 48°C. This storage method had been previously shown to delay sexual *B. treatae* emergence from root galls (Hood, unpublished data). On each tree, 48 Nytex screen (BioDesign, Carmel, New York, USA) enclosures (replicates) measuring 30 cm x 46 cm, were secured around branches prior to leaf flush to exclude natural enemies. Following leaf flush, 24 enclosures/tree were opened and those branches were manually stripped of their leaves to mimic defoliation and stimulate a second leaf flush. Manual methods of defoliation were used because natural defoliation was monitored but not detected for any of the six trees in the spring of 2007. Furthermore, defoliation (above 25%) was not observed, for any tree, at the 4000 acre research site in 2008 where high levels of defoliation has been observed in the three pervious years (G. Hood, personal observation). Therefore, manual defoliation was used to induce the second flush to standardize the timing and magnitude of defoliation. As observed with natural defoliation, artificial defoliation induced a second leaf flush six to eight weeks later. This manipulation created two temporally segregated leaf flush events: (1) a natural early spring leaf flush and (2) a second artificially stimulated late spring reflushing event (n = 24/tree). Immediately following natural leaf flush that occurred during the week of March 31, 2008, B. treatae reared

from root galls, were allowed to mate in the lab, and three to five mated females were placed inside each of the 24 early flush enclosures/tree and allowed to oviposit for five days (Egan and Ott 2007). The procedure was repeated six to eight weeks later (dependent on the flush of manually stimulated leaves) using the cohort of *B treatae* whose development was delayed by cold storage. Oviposition scars were verified in all enclosures five days after stocking. For each leaf flush, 12 of the 24 enclosures/tree were then opened after the five-day oviposition period to allow natural enemy attack to occur during leaf-galler development. One tree subsequently failed to produce sufficient number of leaves after manual defoliation and was dropped from the study. Thus each of five trees consisted of two temporally distinct oviposition events composed of 24 replicates/leaf flush event (early and delayed), with a subset of 12 replicates/leaf flush exposed to natural enemies. Throughout the spring the Lepidoptera-specific pesticide, *Bacillus thuringiensis kurstaki* (Btk) was applied, as needed, to branches to guard against defoliation by caterpillars (van Frankenhuyzen 1990). For all treatments, galls were allowed to develop through the fall of 2008.

The schedule of *B. treatae* gall maturation/tree, indexed by the state of gall maturity, was monitored by observing the percent of galls/color class at two-week intervals from early October through December (by which time all galls were mature) to test the prediction that galls initiated from early oviposition reach maturity earlier than those induced by delayed oviposition. All galls from each of 12 random replicates/tree that were protected from natural enemies were scored as either mature or immature (based on color) for both the early (n = 6 replicates/tree) and delayed (n = 6 replicates/tree) oviposition events. Also, all galls from six random branches/tree with

sufficient gall densities from wild oviposition (control) were indexed using the same methods.

To test the hypothesis that experimental defoliation delaying oviposition timing, controls the timing of B treatae emergence and survivorship, leaf galls were collected once a month beginning in December 2008 and continuing through February 2009, from a subset of sixteen enclosures/tree, four exposed and four protected from natural enemies for each of the early and delayed leaf flush events. Galls were initially to be collected once a month beginning in November (coinciding with past emergence records) through February (coinciding with recent emergence records), however monitoring in early November 2008 showed that galls developing from both early and delayed oviposition events were still immature. Galls were collected monthly as opposed to one time at the onset of past gall-former emergence to eliminated potential death of gall formers that were not mature at the time of the first collection date from delayed oviposition (see Table 1 for a representation of the study design and sampling methods). For each tree, galls were sorted by oviposition timing and exposure to natural enemies. All galls/replicate from the two treatments protected from natural enemies were scored at the time of their collection for the presence/absence of an emergence hole to verify the number of *B. treatae*/treatment that emerged prior to the date of collection. Those galls from which B. treatae had not yet emerged (those without holes) were then placed outdoors in collection traps at the Texas State greenhouse. The rearing of gall contents revealed that one out of 81 enclosures yielded one emerged insect from a gall that was not a *B. treatae* (> 98% exclusion of natural enemies in all enclosures), thus I conclude that enclosures excluded natural enemies across the study. B treatae emergence

phenology as a function of oviposition timing and collection interval was then monitored by weekly surveys of collection traps. *B. treatae* survivorship/tree from early and delayed oviposition were evaluated at the end of the emergence season by determining the total number of *B. treatae* that emerged/total number of galls for each replicate. This protocol tested the following null hypotheses: galls produced from early and delayed oviposition have similar (1) maturation schedules, (2) emergence phenologies and (3) levels of survivorship when exposed to and protected from natural enemies.

ANALYSIS

OBSERVATIONAL STUDIES

Gall-former Emergence Phenologies

Life history phenology attributes include the average timing or peak occurrence of a life history event. *B. treatae* emergence phenology curves on a per tree basis however are not typically unimodal and are not normally distributed and so no single transformation of typical measures of life history phenology can mitigate non-normality across all emergence phenology curves. Therefore, I used three attributes as independent variables in observational analyses of determinants and patterns of emergence phenology: the length of the emergence window (the number of days between the first and last emergence), and the interval, measured in weeks, to the 50% and 95% emergence percentiles. The initial emergence date/tree was standardized relative to the earliest day of emergence observed among all trees in each year.

I performed a one-way ANOVA (between sites) using each of the three phenological variables for the four sites with replication monitored in Travis County to determine whether phenologies of the 22 trees surveyed in 2006 could be pooled to provide one estimate of regional phenology. There was not enough replication at the site level in 2007 to perform an ANOVA for both sampling years because sample sizes (gall densities) were reduced the second year. Therefore, I pooled all trees in Hays and Travis Counties in 2007 for this analysis. I then assessed potential differences in regions (Hays and Travis Counties) by performing a two-way ANOVA (region and year each set as random factors) for each of the three phenological variables.

Effects of Natural Defoliation on Emergence Phenology

To assess whether the level of naturally occurring defoliation observed in the spring of 2007 influenced the phenology of gall-former emergence in the fall of 2007, a series of six one-way ANOVA's were performed using each of the three phenology variables and the two following measures of defoliation: (1) the maximum level of defoliation observed during the four monitoring dates and (2) the monitoring period (ranging from 1-4) in which the highest level of defoliation was observed. This analysis was performed by combining trees from Hays (n = 4) and Travis (n = 11) counties from which *B. treatae* emerged.

Effect of Natural Defoliation on Survivorship

To assess whether the level of naturally occurring defoliation influenced *B*. *treatae* survivorship, two one-way ANOVA's were performed using the maximum level of defoliation observed and the time at which the maximum level of defoliation was observed as the independent variables. This analysis was performed using trees from Hays (n = 6 trees) and Travis (n = 14 trees) counties respectively.

Comparing Past and Recent Oviposition Phenologies

The timing of peak oviposition density in 2007 was compared between Hays and Travis Counties. A students t-test was used to test the null hypothesis of no difference in peak oviposition density (measured in weeks) between regions. Of the trees surveyed, only those trees at each location that contained an accumulation of high densities of oviposition scars at the end of the oviposition monitoring period were used in the analysis (n = 6 for Hays County; n = 17 for Travis County). Recent oviposition phenology in 2007 was then graphically compared to past records from Hays County in 1998.

EXPERIMENTAL STUDY

Influence of Collection Date on Emergence Phenology and Survivorship

To rule out the possibility that the date of collection influenced the timing of emergence and survivorship of *B treatae*, a series of four ANOVA's were used with the following factors: the timing of oviposition, and the collection date (1-3 corresponding to Dec., Jan., and Fed.) with collection date nested within tree. The response variables used in the analysis were the time to 50% and 95% emergence for replicates protected from natural enemies and survivorship for replicates protected from and exposed to natural enemies. This analysis revealed that the time at which galls were sampled had no effect on *B. treatae* emergence phenology and survivorship when protected from natural enemies because the presence of an emergence hole from later collections indicated *B. treatae* emergence. However, when exposed to natural enemies, later collections had underestimated survivorship because *B. treatae* had already emerged. Therefore, we estimated survivorship in those replicates exposed to natural enemies collected at a later date (see the section title "Effects of oviposition timing on survivorship" for survivorship estimation methods). This allowed us to pool data across collection dates/tree to estimate emergence phenologies and survivorship for each treatment.

Effects of Oviposition Timing on Gall Maturation Schedules

To test the null hypothesis that gall maturation schedules do not differ between early, delayed and wild (control) oviposition, a one-way ANOVA was conducted to compare gall-former maturation schedules among trees between oviposition events with the time to 50% and 95% gall maturity used as response variables.

Effects of Oviposition Timing on Emergence Phenology

I compared the phenology of emergence of *B. treatae* from leaf galls from early and delayed ovipositon treatments using the 50% and 95% emergence. The length of the emergence period was not assessed because collections from later sampling dates (i.e. Jan. and Feb.) excluded earlier portions of the emergence window. Also only January and February collections were used to estimate the time to 50% emergence as after this sampling date the 50% emergence had already occurred. However, because the time to 90% percent emergence did not occur till after the final February collection date, data from all collection intervals were used to compare the time to the 95% emergence. A two-way ANOVA with tree and the timing of oviposition, set as fixed factors, was used to assess differences in emergence phenologies between early and delayed oviposition in the treatments that were protected from natural enemies.

Effects of Oviposition Timing on Survivorship

A two-way ANOVA was performed, with tree and the timing of oviposition set as fixed factors, to assess potential differences in *B. treatae* survivorship among the five

trees when protected from natural enemies. In treatments that were exposed to natural enemies and sampled at a later date (Jan. and Feb.), the presence of an emergence hole indicates either a gall former or natural enemy emerged. To account for inflated estimates of survivorship from later collections that possibly had B treatae emergence, a weighted average of survivorship for early and delayed oviposition treatment exposed to natural enemies from the first December collection was calculated (this collection date preceded gall former emergence in nature as indicated by the absence of galls with holes protected from natural enemies). I multiplied this weighted average by the number of galls exposed to natural enemies with holes sampled in January and February for each of two treatments to estimate survivorship from those galls that had emergence holes at the date of collection. This number gives a conservative estimate of *B. treatae* survivorship given that weighted averages were calculated from survivorship across the entire emergence period, when I am only estimating prior emergence in nature from a portion of the emergence period (just the December collection date) for a percentage of gall with holes for which a B. treatae did not emerge. Without the weighted average correction, the difference between replicates protected from and exposed to natural enemies would have been even greater. All statistical analyses were performed in the R project for statistical computing (R Development Core Team 2007).

RESULTS

OBJECTIVE 1

Temporal and Spatial Variation in Emergence Phenology

Average emergence in Hays and Comal Counties in mid November was about 10 weeks earlier than the estimates of mid February for Travis County (Figure 1a, Table 2). This difference in emergence timing was estimated from more than 26,000 galls that yielded over 3,200 emerged *B. treatae* sampled from multiple trees from multiple sites in three counties (Figure 1a). However, additional sampling of more than 92,000 galls yielding over 5,100 B. treatae from multiple trees from multiple sites in Hays and Travis Counties revealed emergence from leaf galls has recently shifted from early December to early March (Figure 1b). This roughly matches the emergence timing of historical Travis County records (Figure 1a/1b, Table 2). No differences existed among trees within sites for any of the three phenological variables measured within Travis County in 2006. These individual emergence phenologies/tree were pooled across sites and years to produce a recent composite regional emergence phenology (Figure 1b). When comparing regions (Hays and Travis Counties), year and region x year interactions for each of the three variables analyzed to compare emergence phenology, only one significant effect was found: the length of the emergence interval differed between years ($F_{1,1} = 7.46$, P < 0.05). See Table 2 for the number of trees per site, and galls per tree and emerged Btreatae per site used to estimate past and recent emergence phenologies.

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Temporal and Spatial Variation in Survivorship in the Presence of Natural Enemies

Survivorship estimated from Hays and Comal Counties was < 1 to 9% per tree (Figure 2a, Table 3). This estimate was based on a sample of more than 37,000 galls yielding over 850 *B. treatae* from multiple trees at multiple sites. In the past, *B. treatae* from Travis County exhibited 32 to 50% survivorship/ per tree and on average, had 24 times higher survivorship when compared to Hays and Comal Counties (Figure 2a, Table 3). A total of 2658 *B. treatae* emerged from a sample of 5029 galls in 2001 in Travis County collected from four trees at one site were used to estimate the apparent temporally isolated population of "atypical" *B. treatae* (Figure 2a, Table 3). Recent survivorship, ranging from 0 to 17% per tree, did not differ between Hays and Travis Counties in 2006 and 2007 measured from over 95,000 galls producing over 5,100 *B treatae* (Figure 2b, Table 3). Given low rates of survivorship in the presence of natural enemies, exceedingly large sample sizes in 2007-2008 were still not large enough to detect a single emerged *B treatae* in eight of 23 trees monitored.

Patterns of Natural Defoliation

Defoliation was visible, in varying intensities, on all of the eight and 22 trees monitored in both Hays and Travis Counties respectively in 2007. Evidence of defoliation was apparent on only a subset of trees in April but by May all trees exhibited some level of defoliation. Beginning in June, and increasing into July however, defoliation levels/tree dropped to 0%, indicating trees had reflushed their leaves. The level of defoliation by caterpillars during four monitoring periods within and among trees, and the highest level observed within each monitoring period varied between trees in each county (Figure 3). Peak levels of defoliation occurred in Hays County in May and in Travis County in June. In total 12 of 30 trees (40%) had near complete defoliation at some point in the spring.

Relationships Between Natural Levels of Defoliation and Emergence Phenology and Survivorship

Gall formers emerged from only four of the six and 11 of the 17 trees monitored from Hays and Travis Counties respectively due to the high mortality from natural enemies, so all subsequent analyses of the relationship between levels of defoliation and emergence are based on these trees. The two indices of defoliation, the maximum level of defoliation and the time of the maximum level of defoliation, and the three measures of emergence phenology were positively correlated in two out of six cases. Defoliation in the spring of 2007, measured as the maximum level/tree over the entire monitoring period, did not affect the length ($F_{14} = 1.16$, P > 0.1), or the time to 50% emergence, (F_{14} = 0.52; P > 0.5) of B. treatae from leaf galls in the fall of 2007. The time to 95% emergence was moderately but positively correlated to defoliation intensity ($F_{14} = 3.83$, P < 0.05; Figure 4a). The timing of maximum level of defoliation did not effect the time to 50% ($F_{14} = 0.18$, P > 0.5) or 95% emergence ($F_{14} = 3.37$, P > 0.05). However, the timing of maximum level of defoliation did moderately but positively affect the length of emergence ($F_{14} = 4.69$, P < 0.05; Figure 4b). The length of the fall emergence period of asexuals when the maximum level of defoliation occurred in April was 39 days, compared to 71 days in June when maximum levels of defoliation were observed, a difference of 32 days (Figure 4b).

The maximum amount of defoliation affected survivorship in the presence of natural enemies ($F_{19} = 6.57$, P < 0.005; Figure 4c). Only at the > 95% defoliation level was average survivorship greater (about 8%) from survivorship at lower defoliation levels (Figure 4c). However, survivorship at the > 95% defoliation level ranged from 0 to 14% (the lowest and highest survivorships). The timing of the maximum amount of defoliation had no affect on survivorship ($F_{15} = 0.95$, P > 0.1).

Temporal Variation in Oviposition Phenology

Current oviposition phenologies, based on six and 17 trees in Hays and Travis counties in 2007 did not differ between counties (t = 0.32, P > 0.5), and occurred from mid-April to early July. Therefore, all trees within Hays and Travis Counties were pooled for one composite oviposition phenology curve (Figure 5). A difference of about 10 weeks in the timing of attainment of peak oviposition density exists between past and recent oviposition phenologies.

OBJECTIVE 2

Manual defoliation affectively created a delay in the timing of leaf flush of six to eight weeks, and oviposition occurred in all of the 240 replicates across five trees. An average of 97 ± 24 (range = 47–145) galls were scored from early, late and wild oviposition events at each sampling interval on a per tree basis to assess gall maturation schedules. Galls were established in 75 of the 120 replicates (63%) protected from natural enemies and 87 of the120 replicates (73%) exposed to natural enemies. All analyses of emergence phenology as a function of oviposition timing were performed using replicates protected from natural enemies because natural enemies greatly reduce *B treatae* survivorship which reduces sample size and incorporates uncertainty in estimates of emergence phenologies.

Effects of the Timing of Oviposition on Gall Maturation Schedules

Gall maturation schedules from delayed and wild oviposition did not differ as galls reached 50% and 95% maturity at the same time across all five trees (Figure 6). The frequency of mature galls began to asymptote in early December. Therefore, the six to eight week delay in oviposition did not translate into a difference in the maturation schedules of *B. treatae* leaf galls.

Effects of the Timing of Oviposition on Emergence Phenology

B treatae emergence phenology did not differ between early and delayed oviposition across all five trees for both measures of the timing of emergence (Figure 7). The emergence window occurred from early December to late February, with two peaks of emergence occurring in early January and February for both oviposition events. The average time to 50% emergence did not differ between early and delayed oviposition ($F_{4, 1} = 0.40$, P = 0.53; 6.7 weeks for both treatments), between trees ($F_{4, 1} = 0.28$, P = 0.89), and there was no interaction between tree and the timing of oviposition ($F_{4, 1} = 1.53$, P = 0.21). Similarly the average time to the 95% emergence did not differ between early and late oviposition ($F_{4, 1} = 0.002$, P > 0.5, 10.8 weeks for both treatments), between tree ($F_{4, 1} = 0.08$, P > 0.5), and no significant interactions was seen between tree and the timing of oviposition ($F_{4, 1} = 0.11$, P > 0.5).

Effects of the Timing of Oviposition on Survivorship

Gall former survivorship, when protected from natural enemies, induced by early and delayed oviposition differed moderately among trees, ranging from 51% to 73% and ranged from 40% to 95% in individual replicates across the study (Table 4, Figure 8a). However, there was no difference in survivorship, across treatments (early and delayed oviposition; 67.0 and 67.6 respectively). Survivorship did not differ between early and delayed oviposition on the same tree ($F_{4,1} = 0.17$, P > 0.5), and only moderately differed between trees ($F_{4,1} = 3.31$, P < 0.05), with no significant interaction between the timing of oviposition and tree ($F_{4,1} = 0.08$, P > 0.5).

B. treatae survivorship from individual trees for early and delayed oviposition exposed to natural enemies differed significantly (Table 4, Figure 8b). Although survivorship did not differ between trees ($F_{4,1} = 0.32$, P > 0.5), a highly significant effect was detected between early and delayed oviposition ($F_{4,1} = 161.61 P < 0.0001$), and no significant interaction was seen between trees and treatment ($F_{4,1} = 0.23$, P > 0.5). Survivorship did not differ between wild and exposed early oviposition treatments (Figure 8b). Survivorship ranged from 0 to 39% in individual replicates across the study, with average survivorship/oviposition event across trees ranging from 0.80 (early oviposition) to 22.41% (delayed oviposition) respectively (> 27 times increase in survivorship in late ovipositing *B. treatae*; Figure 8b, Table 4). Average survivorship from wild oviposition ranged from 0.51 to 2.27%. See Table 4 for the number of replicates/treatment, the number of galls and emerged *B. treatae* used to estimate *B. treatae* survivorship. (

DISCUSSION

This experimental study convincingly demonstrates that variation in the timing of oviposition, driven by host plant defoliation, as manipulated herein, does not dictate the schedule of gall maturation, and is not responsible for a shift in the pattern of *B. treatae* emergence phenology. Also, in the absence of natural enemies, oviposition timing does not influence gall former survivorship. However, in the presence of natural enemies oviposition timing does affect gall former survivorship, and could dictate spatial and temporal patterns observed in survivorship in the past and more recently. While host plant defoliation by herbivores is common (see Roland and Myers 1987, Rossiter et al. 1988, Potter and Redmond 1989, Watt el al. 1991, Krause and Rappa 1995, Mopper and Simberloff 1995, Kaitaniemi et al. 1997, Parry et al. 2003, Tikkanen and Julkunen-Tiito 2003 for examples), little is known about the effects that defoliation could have on gallformer life cycle events that are dependent on plant susceptibity to defoliation prior to gall former use. By manipulating the timing of oviposition via manual defoliation, I was able to assess the phenology of different life cycle events and survivorship throughout the life cycle of *B* treatae, in both the presence and absence of natural enemies that can be used to better understand ecological drivers that could influence the timing of *B* treatae life cycle events and survivorship.

The Effects of Defoliation on Life Cycle Phenologies and Survivorshi

A number of hypotheses can be formulated to explain the effects of defoliation on the timing of asexual B. treatae emergence: (1) If sexual B. treatae exclusively oviposit before defoliation, and defoliation is not tree wide, then it is predicted that no relationship will exist between defoliation and delayed emergence, (2) If an entire tree experiences less than complete defoliation, and *B. treatae* oviposit both before and after defoliation, then it is predicted that there will be a relationship between percent defoliation and the percent of *B. treatae* that emerge later (due to delayed oviposition into a second leaf flush), or (3) If B. treatae exclusively oviposit after defoliation, it is predicted that there is no relationship between defoliation and later emergence. I observed a moderate but positive correlation between the maximum level of defoliation and the time to 95% emergence (Figure 4a), and the timing of the maximum level of defoliation and the length of the emergence period (Figure 4b). Because observed patterns of defoliation are patchy within individual trees (Figure 3), it would seem likely that oviposition is taking place both pre- and post-defoliation (hypothesis 2). However, experimental manipulation showed that variation in oviposition timing, driven by manual defoliation, does not affect the timing of emergence. Also, the moderately significant positive relationship between the maximum level of defoliation and *B. treatae* survivorship (Figure 4c) could indicate that the greater percentage of leaf tissue consumed by defoliators, the greater the percentage of *B* treatae escaping attack by a portion of the natural enemy community. However, this is also contingent on existing variation in the timing of natural oviposition that was not observed. Observational results of a lack of natural variation in the timing of oviposition coupled with our experimental results of synchrony in the timing of

emergence imply that defoliation has no mechanistic relationship with the timing of emergence. However, because observational results estimating both oviposition timing and defoliation consist of a relatively few trees and the methods for estimating defoliation are rather arbitrary, relationships between natural levels of defoliation and the timing of *B. treatae* emergence and survivorship should be interpreted with caution. Broader sampling on more trees, and more rigorous methods to accurately estimate the amount of defoliation are needed to assess defoliation-emergence phenology and defoliationsurvivorship relationships under natural conditions.

At the time of delayed oviposition, galls were not yet visible from early oviposition events. This indicates that during early oviposition there is a latent period before gall growth begins when eggs and/or larvae are more vulnerable to natural enemy attack. This could help explain why survivorship is greatly reduced in the presence of natural enemies from the first oviposition event; *B. treatae* developing from early oviposition could simply be exposed to natural enemies for a greater length of time during the most vulnerable stage of their life cycle. Given that *B. treatae* from both early and delayed oviposition events emerge in synchrony, gall formers developing from delayed oviposition are exposed to natural enemies six to eight weeks less. The most vulnerable stage of gall former development is most likely the time right after eggs are deposited into host plant tissue when eggs and/or larvae are exposed (Hayward and Stone 2005), continuing through early gall development because gall tissue is soft and gall walls are relatively thin (Price 1972, Askew 1975, Weis et al. 1985, Craig et al. 1990). It has been documented in this (Hall 2001) and many other gall-forming systems (Askew 1975, Wiebes-Rijks 1982, Jones 1983, Clancy and Price 1986, Craig et al. 1990, Schronrogge et al. 1996) that a subset of natural enemies that attack during or after the timing of typical oviposition are partially or completely absent during later development. Exposing asexual *B. treatae* leaf galls to natural enemy attack at different times during development via exclusion experiments, Hall (2001) showed that *B. treatae* ovipositing early into leaf tissue are attacked by 18 out of the 24 different species of natural enemies during the first two months following the timing of early oviposition (pre-defoliation), and of these 18 species, three species only attack during the first two months of gallformer development. Therefore, *B. treatae* developing from delayed oviposition are not exposed to as many species of natural enemies as those induced by early oviposition.

Experimental results presented herein for *B. treatae* developing within leaf galls parallels a similar study manipulating the timing of oviposition of asexual *B. treatae* inducing root galls. Assessing the effects of variation in asexual *B. treatae* oviposition timing on sexual root gall development and survivorship, Cryer (2003) showed that later oviposition translates into slower rate of gall development and a greater chance of survivorship when exposed to natural enemies. However, despite variation in the rate of gall development, root galls formed from multiple, temporally segregated oviposition events produced *B. treatae* that emerge synchronously, similar to results from asexual *B. treatae* emerging from leaf galls. Experimental results herein contradict those found by Ivanshow et al. (2002) who found that the larvae of the oak leafroller moth that oviposit into leaves that vary in natural flush, hatch earlier from earlier oviposition.

Given that leaf galls formed from delayed oviposition reach maturity at the same time as galls induced by early oviposition, and *B. treatae* emerge synchronously, it is likely that that the timing of *B. treatae* development, or more specifically the latent

period before gall growth is initiated, is a plastic trait. According to reviews by Nylin and Gotthard (1998) and Danks (2006) plasticity in arthropod development, induced by adverse conditions or short-term seasonal variation in habitat patterns, can influence adult size and/or growth rates that can have consequences for fitness. In this (Reynolds 2000) and other gall forming systems average gall size is negatively influenced by natural enemies, and the probability of gall former emergence exponentially increases with an increase in gall size (Weis et al. 1985, Weis and Abrahamson 1986, Price and Clancy 1986, Price 1988, Zwolfer and Arnold-Rinehart 1994). Also in this system, previous research has shown that larger galls give rise to larger *B. treatae* that are more fecund (Hood and Ott unpublished). One might predict that *B. treatae* developing from earlier oviposition events would emerge from mature galls that, on average, are larger than those formed from delayed oviposition because they have a longer time to gather and use resources for development. In this scenario, those gall formers developing from early oviposition would experience decreased survivorship when exposed to natural enemies but these galls would give rise to larger individuals that are more fecund. Alternatively, one might predict that increased quality and/or amounts of resources provided by the second leaf flush could induce rapid gall growth (plasticity in development timing due to resource alteration), resulting in larger galls. Therefore, delayed oviposition could positively affect survivorship in the presence of natural enemies by producing more fecund individuals. Rehill and Schultz (2002), studying gall forming aphids, and Roland and Myers (1987), studying winter moths, showed that insects that feed on a second flush of leaves have increased weight and fecundity, which appeared to be contradictory to typical patterns of insects that feed on a first flush of leaves. Also, because survivorship

is positively influenced as gall size increases, an increase in gall size from delayed oviposition could explain *B* treatae survivorship differences in the presence of natural enemies documented herein. In each of the two scenarios outlined above, plasticity in the timing of *B* treatae development creates tradeoffs between survivorship in the presence of natural enemies and potential fecundity. Future behavioral studies directly aimed at understanding the relationship between oviposition strategies, nutritional differences that are important for gall growth between leaf flush events, and potential and realized fecundity proceeding oviposition would help to better understand the costs and benefits of developmental plasticity as its adaptive significance.

Although the timing of sexual *B. treatae* emergence from root galls varies within and between trees (Cryer 2003), the timing of past sexual gall former emergence monitored in a number of studies in this system coincides with initial leaf flush, but does not extend to coincide with the timing of the second reflush (Lund 1998, Cryer 2003). Due to shifts in emergence phenology of the asexual generation from leaf galls documented herein, the timing of asexual generation oviposition into oak rootlets has likely shifted as well. As a result, subsequent sexual *B treatae* life cycle events such as the timing of emergence from root galls could also shift from previous emergence records. This hypothesis could explain providing observations of delayed sexual oviposition into leaves (coinciding with the timing of the second reflush) across all trees monitored in the spring of 2007.

It many short-lived, host-specific, non-migratory phytophagous insects, fine scale genetic adaptation to individual host plants is the likely mechanism for controlling the timing of life cycle events. For example, Komatsu and Akimoto (1995), working with a

galling aphid, showed that variation between the timing of individual host plant budburst acts as a selective agent on the timing of egg hatching. While previous research has indicated that B. treatae are adapted to individual host plants (Egan and Ott 2007) and natural variation in the timing of leaf tissue formation exists (G. Hood, personal observation), and because experimental emergence phenology is synchronous among oviposition events, it is likely that emergence is controlled by environmental variables/cues. Although cynipid galls act as sinks for photoassimilates (see a review by Weis et al. 1988, and Larson and Whitham 1997 and Dorchin et al. 2006 for more recent examples), and gall tissue is thought to shelter the developing gall former from the outside environment (Price et al. 1987), environmental cues, in particular a change in day length or temperature can be received from the host plant and sent to the developing gall former, or received by the gall former itself. In many gall-forming insects such as horned oak gall wasp, Callirhytis cornigera (Eliason and Potter 2000) and the oriental chestnut gall wasp, Dryocosmus kuriphilus (Cooper and Rieskie 2007) emergence is dependent upon the accumulation of degree days. However, because the timing of oviposition does not dictate the timing of *B. treatae* emergence, it is likely that environmental factors, regulated through the host plant, or received by the gall former itself control emergence phenology (Danks 2006).

Because delayed oviposition into leaves was observed on all trees monitored, even in the absence of complete defoliation, selection could favor delayed oviposition as a strategy to overcome defoliation on the level of the tree, and/or perhaps the population (although the number of trees used in this study is not large enough to unequivocally pick up such an effect). Life cycle phenologies have been shown to have adaptive

significance and a genetic basis in herbivorous insects. Ohgushi (1991) studying herbivorous lady beetles suggested that there is a genetic basis for oviposition schedules based on differences in oviposition phenologies and the timing of reproduction. Abe (1991) found that genetic changes of ovipositional preference, due to different host plant phenologies, were evident in host race formation of a gall forming cynipid. Only eight years prior to current monitoring efforts were early oviposition phenologies in central Texas observed (including some of the same trees, and trees within the same general areas as the experiment conducted herein). However, because high levels of defoliation (complete to near complete on all observed trees throughout parts of central Texas) were witnessed between 2004 and 2007 (G. Hood and J. Ott, personal observation), selection could have acted rapidly to favor delayed oviposition strategies, on a large spatial scale, as a bet hedging strategy in response to potential resource limitations. In this scenario, selection would further reinforce delayed oviposition strategies that lead to the creation of enemy free space. Although the population dynamics of defoliators on live oaks in central Texas are understudied, it appears that typical cyclic population dynamics often associated with outbreaks of herbivorous insects (successive years of intense defoliation, followed by longer periods of less intense to completely absent defoliation) are at work in this system (Barbosa and Schultz 1987). If the dynamics are truly cyclical in nature, the behavioral and/or developmental plasticity exhibited is to counteract regularly timed defoliation events. Here, selection could rapidly alter these plastic characteristics dependent on environmental conditions (Nylin and Gotthard 1998, Danks 2006).

Also, selection for later oviposition could have other unknown advantages for *B treatae*. Mopper and Simberloff (1995) suggest that, while performance does not differ

between leaf flush events, oviposition preference of a leaf mining moth into delayed spring leaf production on defoliated host plants in the genus *Quercus*, could have a selective advantage. For example, Yukawa and Akimoto (2006) and Forkner et al. (2008) directly link the degree of plant-insect phenological synchrony to population densities in the next generation. Population densities of *B treatae* vary on the level of the individual host plant (Egan and Ott 2007). Selection for delayed oviposition, resulting in increased survivorship in the presence of natural enemies could contribute to the varied *B. treatae* densities across host plants.

Although gall maturation schedules do not differ between oviposition events, the rate of gall maturation was only indexed by assessing the maturity of surveyed galls by color. More thorough tests of gall former developmental rate would have included gall hardness, gall growth, and larval development via gall dissection across time. Also, fine scale differences in emergence phenology in both the observational and experimental studies could have been observed had the monitoring periods been shorter apart, but given the number of galls that were being monitored across all studies, time did not allow for such efforts. A change in the phenology of emergence is not a likely explanation for the survivorship differences between *B. treatae* induced by early and delayed oviposition. To guard against the possibility that a relationship exist between late emergence and increased survivorship and that I did not over estimate the effects of oviposition timing on survivorship in the presence of natural enemies, I compared survivorship in both the presence and absence of natural enemies in just the 54 replicates that were sampled on the first collection date in December. When protected from natural enemies, for just the December collection, survivorship does not differ between oviposition events. When

exposed to natural enemies, for just the December collection, survivorship is still greatly increased in the delayed oviposition replicates, therefore I conclude that pooling data from all the collection dates was appropriate.

A conservative estimate of the total amount of leaf tissue manually stripped from each tree during experimental defoliation is less than 5%. Defoliation events that eliminate the majority of leaf tissue on a host plant, have been known to effect chemical processes within the defoliated plant (Rossiter 1988, Potter and Redmond 1989, Watt et al. 1991) and could have cascading affects that could be the driver behind observed differences in emergence phenology. For example, defoliation could send signals to developing or already mature *B. treatae* within root galls to forego pending emergence until the production of new leaf tissue (Nylin and Gotthard 1998, Danks 2006). Therefore, it is important to note that this experimental design does not directly test the effect that tree wide defoliation has on the gall former through changes in tree chemistry, and/or natural enemy community composition. This experiment also did not test the effect of a larger delay (> 8 weeks) in oviposition that could influence gall maturation schedules, and *B. treatae* emergence phenology and survivorship. It is also important to note that abiotic factors such as climate variation (Potter and Redmond 1989, Dewar and Watt 1992, Watt and Woiwood 1999, Yukawa 2000) can also affect host plant tissue formation. At a minimum, this experiment tests the affect of a change in the timing of resource availability on life cycle events and survivorship of *B. treatae* with defoliation as a naturally occurring mechanism. The experimental design, however, does alter the immediate local region from which most gall formers directly receive nutrients (Weis et al. 1988, Dorchin et al. 2006). Following Parry et al. (2003), lab reared defoliators could have been released in the field to more accurately stimulate natural defoliation in the field. More research in the area of the timing of *B treatae* life cycle events of the sexual generation would corroborate and strengthen evidence of the recent shifts from early to delayed oviposition into leaves and leaf gall emergence phenology. To more fully understand the effect of defoliation on gall former life cycle phenologies and survivorship a comparison of the affects of low to complete defoliation between trees would need to be performed.

Table 1. Experimental design of treatment creation including the number of realized replicates that had galls produced/the number of total replicates for each treatment summed across collection dates and treatments for all 5 trees. Wild galls were collected from multiple branches containing high gall densities at each collection date for each tree. Across the study, galls were established in 162/240 replicates (68%).

Т	reatments	Co	llection D		
Timing of Oviposition	Exposure to Natural Enemies	Dec. 1st	Jan. 1st	Feb. 1st	Tota Reps/Tree
Wild (Control)	+	5	5		15
E-d.	-	12/20	14/20	12/20	38/60
Early	+	15/20	14/20	14/20	43/60
Lata	-	12/20	12/20	13/20	37/60
Late	+	15/20	15/20	14/20	44/60
	Experimental Totals	54/80	55/80	53/80	1.62/240

Site	Year	# of Trees	# of Galls	B. treatae Emerged	Rearing Method *	Researcher
Freeman	1996	2	3116	9 8	G	Lund (1998)
Honey Creek	1998	5	2579	23	G '	Reynolds (2000)
Devils Backbone	1998	5	6590	144	G	Reynolds (2000)
Freeman	1998	5	5516	51	G	Reynolds (2000)
Freeman	1999	6	4122	301	G, T	Reynolds (2000)
Emma Long	2001	4	5029	2658	Т	Reynolds (unpublished)
Past Total		23	26952	3275		
Freeman	2006	8	22570	2208	Т	This Study
Camp Mabry	2006	8	25731	374	Т	60
Canyon Creek	2006	5	14236	1652	Т	11
Balcones	2006	3	7385	141	Т	F8
Walnut Creek	2006	2	2888	25	Т	11
Emma Long	2006	3	2409	54	Т	н
Rutherford	2006	1	2948	26	Т	м
Freeman	2007	4	3147	233	Т	11
Camp Mabry	2007	5	2347	85	Т	n
Canyon Creek	2007	1	862	31	т	n
Balcones	2007	1	1432	4	Т	п
Walnut Creek	2007	2	1415	8	т	11
Emma Long	2007	1	3290	108	Т	11
Rutherford	2007	1	1718	241	Т	ri
Recent Total		45	92378	5190		
	Site Freeman Honey Creek Devils Backbone Freeman Emma Long Past Total Freeman Camp Mabry Canyon Creek Balcones Walnut Creek Emma Long Rutherford Freeman Camp Mabry Canyon Creek Balcones Walnut Creek Balcones Walnut Creek Balcones Walnut Creek Emma Long Rutherford Recent Total	SiteYearFreeman1996Honey Creek1998Devils Backbone1998Freeman1999Emma Long2001Past Total2006Camp Mabry2006Canyon Creek2006Balcones2006Walnut Creek2006Freeman2006Freeman2006Camp Mabry2006Canyon Creek2006Balcones2006Freeman2007Camp Mabry2007Canyon Creek2007Balcones2007Balcones2007Walnut Creek2007Balcones2007Walnut Creek2007Balcones2007Walnut Creek2007Emma Long2007Rutherford2007Rutherford2007	Site Year # of frees Freeman 1996 2 Honey Creek 1998 5 Devils Backbone 1998 5 Freeman 1998 5 Freeman 1999 6 Emma Long 2001 4 Past Total 23 Freeman 2006 8 Camp Mabry 2006 8 Canyon Creek 2006 3 Walnut Creek 2006 3 Rutherford 2007 1 Freeman 2007 1 Balcones 2007 1 Walnut Creek 2007 1 Walnut Creek 2007 1 Walnut Creek 2007 1 Rutherford 2	Site Year # of Trees # of Galls Freeman 1996 2 3116 Honey Creek 1998 5 2579 Devils Backbone 1998 5 6590 Freeman 1998 5 5516 Freeman 1999 6 4122 Emma Long 2001 4 5029 Past Total 23 26952 Freeman 2006 8 25731 Camp Mabry 2006 3 7385 Walnut Creek 2006 3 2409 Rutherford 2006 3 2409 Rutherford 2007 1 2948 Freeman 2007 5 2347 Canyon Creek 2007 1 862 Balcones 2007 1 432 Walnut Creek 2007 1 1432 Walnut Creek 2007 1 3290 Balcones 2007 1	Site Year # of Trees # of Gails B. treatae Emerged Freeman 1996 2 3116 98 Honey Creek 1998 5 2579 23 Devils Backbone 1998 5 6590 144 Freeman 1998 5 5516 51 Freeman 1999 6 4122 301 Emma Long 2001 4 5029 2658 Past Total 23 26952 3275 Freeman 2006 8 25731 374 Canyon Creek 2006 5 14236 1652 Balcones 2006 3 7385 141 Walnut Creek 2006 2 2888 25 Emma Long 2006 1 2948 26 Freeman 2007 4 3147 233 Canyon Creek 2007 1 862 31 Balcones 2007 1	Site Year # of Trees # of Galls B. treatae Emerged Rearing Method * Freeman 1996 2 3116 98 G Devils Backbone 1998 5 6590 144 G Freeman 1998 5 5516 51 G Freeman 1999 6 4122 301 G, T Emma Long 2001 4 5029 2658 T Past Total 23 26952 3275 T G Freeman 2006 8 25731 374 T G Camp Mabry 2006 5 14236 1652 T Balcones 2006 3 7385 141 T Walnut Creek 2006 2 2888 25 T Emma Long 2006 1 2948 26 T Rutherford 2007 1 2347 85 T G Gamp Mabry 2007

Table 2. Number of trees/site and the total number of galls/tree and the number of emerged *B. treatae*/site used to estimate emergence phenologies shown in Figure 1. Data is partitioned between past and recent sampling efforts for the year of fall emergence and is pooled across region (county), site and year. In total, 119,690 galls were sampled yielding 8,465 *B. treatae*.

* Rearing Method: G = Gelatin Capsule, T = Collection Traps

Region	Site	Year	Avg. Survivorship (%)	Range (%)	# of Trees	# of Galls	# B. treatae	Rearing Method *	Researcher
Past									
Hays	Freeman	1995	0.52	0 - 0.62	3	2658	12	G	Lund (1998)
Hays	Freeman	1996	2.69	0 - 3 15	13	5081	115	G	l unc (1998)
Comal	Honey Creek	1997	2.09	0.08 - 3.29	5	2579	23	G	Reynolds (2000)
Hays	Freeman	1997	1.12	0.70 - 2.84	5	5516	51	G	Reynolds (2000)
Cornal	Devils Backbone	1997	5.55	1.20 - 8 42	5	4873	144	G	Reynolds (2000)
Hays	Freeman	1998	7.3	2.60 - 9.32	6	4122	301	G	Reynolds (2000)
Hays	Freeman	2000	1.97	0.81 - 2.98	6	12590	204	G	Hall (2001)
Travis	Emma Long	2001	41.93	32 86 - 50.87	4	5029	2658	Т	Reynolds (unpublished)
			Past Total		47	42448	3508		
Recent									
Hays	Freeman	2006	13.51	1.80 - 17.56	8	22162	2208	Т	This Study
Travis	Camp Mabry	2006	2.18	0.56 - 4.37	8	25731	374	Т	11
Travis	Rutherford	2006	0.88	-	1	2948	26	Т	tt
Travis	Emma Long	2006	7.74	0.87 - 9.53	3	2409	64	Т	14
Travis	Walnut Creek	2006	0.86	0.68 - 0.89	2	2918	25	Т	ec.
Travis	Canyon Creek	2006	11.87	8.63 - 13.46	5	14236	1652	Т	n
Travis	Balcones	2006	2.51	0.32 - 3.41	3	7385	141	Т	at.
Hays	Freeman	2007	10.42	0 - 12.50	6	3903	233	Т	*1
Travis	Camp Mabry	2007	2.88	0 - 3.54	6	3546	85	Т	41
Travis	Rutherford	2007	14.03	-	1	1718	241	Т	41
Travis	Emma Long	2007	3.28	-	1	3290	108	Т	51
Travis	Walnut Creek	2007	2.01	0.24 - 3.07	2	1415	8	Т	15
Travis	Canyon Creek	2007	0.72	0 - 3.60	5 -	1919	31	Т	8
Travis	Balcones	2007	0.09	0 - 0 28	3	2154	4	т	11
			Recent Total		54	95734	5196		

Table 3. The number of trees/site and the number of galls/tree and the number of emerged *B. treatae*/site used to estimate survivorship (total number of emerged *B. treatae*/total number of galls) shown in Figure 2. Data is partitioned by past and recent sampling efforts for the year galls were induced and are pooled by region (county), site and year. Ranges of survivorship are given if more than one tree was sampled at that site. In total 138,182 galls were sampled that yielded 8,704 *B. treatae*.

* Rearing Method: G = Gelatin Capsule, T = Collection Trap

Table 4. *B. treatae* survivorship (mean and range) for early and delayed oviposition exposed and protected from natural enemies and wild oviposition (control). The total number of galls established/treatment/tree and the total number of emerged *B. treatae*/treatment/tree that were used to estimate survivorship are also shown. C = control (wild oviposition), E = early oviposition, D = delayed oviposition, -NE = in the absence of natural enemies, +NE = in the presence of natural enemies.

Tree	Treatment	Avg. Survivorship (%)	Range	# of Galls	# B. treatae
FRT1	С	2.13	1.38-3.61	300	6
11	E - NE	61.98	30.43-89.66	273	131
Ħ	E + NE	0.92	0-6.02	165	2
17	D - NE	64.23	39.53-82.05	367	181
11	D + NE	22.41	2.38-35.64	281	55
FRT2	С	1.33	0.72-1.80	705	9
11	E - NE	54.49	36.22-71.68	880	305
31	E + NE	1.10	0.00-2.54	1141	13
34	D - NE	52.82	44.38-74.42	1209	460
11	D + NE	20.47	7.19-28.31	673	113
FRT3	С	1.58	1.34-2.00	666	10
11	E - NE	60.97	38.67-77.78	848	373
H	E + NE	3.34	0.00-14.08	517	15
n	D - NE	60.69	48.17-69.84	719	314
n	D + NE	21.47	7.49-38.97	718	111
FRT4	С	0.51	0.00-0.99	432	3
11	E - NE	61,74	45.98-70.37	616	256
11	E + NE	0.80	0.00-1.96	455	4
Ħ	D - NE	61.11	44.64-68.33	374	149
u	D + NE	18.77	6.64-30.16	426	81
FRT5	С	2.27	1.29-4.08	716	11
a	E - NE	52.33	42.19-55.65	619	237
8	E + NE	0.47	0.00-1.59	457	2
11	D - NE	48.78	42.65-54.40	889	294
**	D + NE	21.85	9.25-33.33	594	97
		Total		14740	3226



Figure 1. Composite emergence phenologies of adult *B. treatae* from leaf galls for (a) past and (b) recent monitoring efforts. Past emergence phenologies include Hays and Counties monitored in 1996, 1998, and 1999 (shaded circles), and Travis County in 2001 (open circles, undashed line). Recent emergence phenologies include Hays (open circles, dashed line) and Travis (shaded circles, dashed line) Counties. Emergence phenologies were pooled by region, site and year except for Travis County in 2000.



Figure 2. Survivorship, when exposed to natural enemies for (a) past and (b) recent monitoring efforts. Past survivorship estimates include Hays and Comal Counties monitored from 1995–2000. Recent survivorship estimates include Hays and Travis Counties monitored in 2006–2007. Survivorship is averaged across years, sites and trees except in Travis County in 2001. On average, Travis County in 2000 had a 24 times increase in survivorship when compared to Hays and Comal Counties from 1995–2000.



Figure 3. Phenology and level of defoliation for 8 trees in Hays and 22 trees in Travis counties in 2007. HY = Hays County; TR = Travis County. Color codes indicate percent of trees/county in each defoliation category/month. The highest frequency of > 95% defoliation for each county is indicated by an asterisk (*).



Figure 4. The 3 of 8 significant relationships between 2 measures of defoliation and the timing of emergence and survivorship (in the presence of natural enemies): (a) the maximum level of defoliation and the time to 95% emergence, (b) the timing of maximum level of defoliation and the length of the emergence period, and (c) the maximum level of defoliation and survivorship.



Figure 5. Composite phenology of oviposition for both past and recent monitoring efforts. Oviposition phenology is pooled for three trees in Hays County in spring 1998 (shaded circles, undashed line) and 17 trees in Travis (open circles, dashed line) and 6 trees in Hays counties (shaded circles, dashed line) in 2007.



Figure 6. Gall maturation schedules (mean \pm SE), as indexed by the percent of mature galls across time for early (shaded circles, undashed line), delayed (open circles, undashed line) and wild (control; open circles, dashed line) oviposition. The percent of mature galls for each oviposition event were pooled across 5 trees.



Figure 7. Composite *B. treatae* emergence phenologies from leaf galls resulting from early (shaded circles, dashed line) and delayed (open circles, undashed line) oviposition in the absence of natural enemies. Emergence phenologies were pooled across replicates for all 5 trees.



Figure 8. *B. treatae* survivorship/tree (mean \pm SE) for (a) early and delayed ovipositing in the absence of natural enemies and (b) early, delayed and wild (control) ovipositing in the presence of natural enemies. An average of 27 times increase in survivorship exists between *B. treatae* induced by delayed compared to early oviposition when exposed to natural enemies.

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