AN INVESTIGATION OF COMMUNAL GALL SHARING BY *TAMALIA COWENI* UNDER VARIABLE CONDITIONS OF POPULATION DENSITY ON *ARCTOSTAPHYLOS MANZANITA* (ERICACEAE)

A Thesis

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Master of Science

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Biological Sciences

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by

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APPROVED BY THE INTERIM DEAN OF GRADUATE STUDIES:

_____

Sharon Barrios, Ph.D.

APPROVED BY THE GRADUATE ADVISORY COMMITTEE:

_____

Donald G. Miller, Ph.D., Chair

_____

Colleen A. Hatfield, Ph.D.

_____

Christopher T. Ivey, Ph.D.

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ABSTRACT

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Tamalia coweni is unusual among gall-forming aphids in that it will often share its gall space with other members of its species, even as this has been shown to lower its fitness. Previous research utilizing manipulated densities of *T. coweni* on inflorescences of its host plant has indicated that population density is a strong predictor of gall-sharing rates, while kinship appears to be less predictive. The current study expands on this finding by investigating gall-sharing rates under natural population density conditions in leaf galls. In addition, it does an initial examination of whether gall-sharing correlates with preferential or optimal galling sites, and in line with the preference-performance aspect of the Plant Vigor Hypothesis (PVH). Cofounding rates were found to strongly align with those from studies using artificial aphid densities, and population density was shown to be a strong predictor of cofounding rates in a natural setting. Although strong patterns showing basal leaf positions were more frequently chosen as galling sites than distal ones, there was no evidence these sites were more likely to be cofounded. Over all, gall and cofounding distributions did not show a strong alignment with the PVH. Instead,

other factors, notably timing, may offer more promising explanations, and offer a rich set of questions for further examination.

CHAPTER I

INTRODUCTION

Understanding how and why herbivorous insects attack and distribute themselves on plants is a long-standing interest for a diverse number of fields, ranging from agriculture to behavioral ecology. For pest control and agriculture, a sophisticated understanding of how insects—both those that are desirable (such as pollinators) and detrimental (pests)—aggregate and propagate on plants can be highly consequential for crop yields and quality. For conservation work and community ecology, understanding these factors may be key to delimiting and predicting food webs and the complex interdependence of species in an ecosystem. In the field of behavioral ecology, these questions often revolve around building an understanding of patterns of social interaction, such as interspecific and intraspecific competition, and how these behaviors relate to factors such as resource availability, population density, and habitat quality.

Galling aphids provide a particularly good system for studying population density and habitat selection because of their inherent characteristics. The stationary nature of galls means galling insect populations are relatively fixed in space, facilitating spatial measures. Selection of gall sites has significant consequences for galling species, because the gall inducers will live out key developmental stages (and in some cases their entire lives) in this single location. In addition, because galling aphids encapsulate all of their young inside a gall, it is easy to connect an aphid with her offspring, facilitating measures of fitness consequences under varying conditions. This study uses the galling aphid *Tamalia coweni* to investigate patterns of habitat selection.

Biology of Galls and Galling Aphids

Galls are plant tumors, typically in the form of hypertrophy (an increase in the size of cells) or hyperplasia (an increase in the number of cells) that result from physical and chemical alteration of plant tissue (Hartley 1998; Gajek & Boczek 1999). This growth is induced by a variety of insects and other organisms (Rhomberg 1984; Shorthouse 1986), and can take place on most plant parts, including woody stems and branches, petioles, fruit, roots, and leaf margins and midribs (Bogran et al. 1999). A gall is typically indicative of the organism that induces it, and a given species will usually be associated with one kind of gall on a specific plant host (Hartley 1998; Stone et al. 2002). The exact mechanism used to induce most galls is unknown, but it is thought that both chemical and mechanical interactions between the gall-inducer and its host plant may play a role (Marin 1942; Leatherdale 1955; McCalla et al. 1962; Shorthouse 1986; Inbar et al. 2004).

A minority of aphids form galls, and these make up approximately 10% of all described aphid species (Wool 2004; Miller 2005). The aphids that do form galls are primarily found in a contained set of families and subfamilies: Adelgidae, Pemphigidae, Phylloxeridae, Tamaliinae, and Hormaphididae (Miller 2005).

There are three principal stages of gall induction: initiation, growth, and maturation (Bogran et al 1999). During initiation, the host plant and gall site are chosen—usually intimately timed to the emergence of new plant growth because galls typically require immature plant tissue for induction (Weis et al. 1988; Rohfritsch 1992; Santo et al. 2007). Early modifications to the tissue are made to form the gall and any chambers inside it. In the case of galls formed on the margins of leaves, this may involve a folding over of the leaf to create a pocket-like space. During the growth stage, the gall inhabitants actively feed on the gall tissue, which plays a role

in the sustained growth and maintenance of the gall (Lewis & Walton 1958; Rehill & Schultz 2001). During this time, the gall becomes a sink for mineral nutrients and products of photosynthesis (Larson & Whitham 1991; Fay et al. 1996; Compson et al. 2011). This is thought to occur through a number of means; galls may enhance photosynthetic rates of the leaves they occur on, and subsequently benefit from the increase in photosynthetic products (Stone et al. 2002). They may also mobilize resources from other areas of the host plant (Larson & Whitham 1991; Bagatto et al 1996; Paquette et al 1993). The maturation phase of a gall typically involves alterations that prepare the inhabitants to exit. It is often characterized by a decrease in cell division, and the gall ceasing to be a nutrient sink. These alterations may be influenced by changes in the feeding patterns of the gall inhabitants as well as external factors (Stone et al 2002). In the case of some cynipid wasp galls, the larval chamber of the maturing gall will lignify and the gall will be shed from the host plant. In many aphid galls, the walls of mature gall will harden and crack open, allowing aphids to exit.

There are a number of hypotheses regarding the adaptive significance of gall induction, many of which are described in detail by Price et al. 1987. The nutrition hypothesis suggests that gall inducers manipulate plant resources to their benefit through gall induction. This could be through increasing the quality or concentration of plant nutrients, or by extending the period of time immature plant tissue can be used for feeding. The microenvironment hypothesis proposes that galls protect their hosts from inhospitable external environmental conditions—which in particular might have a protective effect against dangers such as desiccation. Thirdly, the enemy hypothesis suggests that galls function as a protective barrier against the gall inducer's natural enemies, reducing its risk of predation and parasitism. All three hypotheses are mutually

compatible, and may have differing significance on patterns of gall induction in different systems (Price 1987; Stone et al. 2002).

Biology of *Tamalia* in the Study Area

The *Tamalia* aphids are a North American genus in the Aphididae subfamily Tamaliinae, and are a common feature of chaparral shrub lands. Despite their prominence in these ecosystems, relatively little research has been done on them, and many questions remain unanswered. At the time of writing, five *Tamalia* species have been described in publication, and another five have been identified and are awaiting publication (Miller & Sharkey 2000; Miller unpublished).

Tamalia coweni (originally published as *Phyllaphis coweni*) was first described by Theodore Dru Allison Cockerell on *Arctostaphylos* uva-ursi (Cockerell 1905). Like most aphids, *Tamalia* are cyclically parthenogenetic, meaning they alternate sexual and asexual generations and their clonal life history includes both sessile and mobile phases.

A number of features are unique to *Tamalia*, including the presence of winged mating females, a truncated life cycle, and the communal galling habit (Miller 1998b, Miller 2004). As a group, they are taxonomically removed from the majority of other galling aphids, and are one of the few galling aphid genera outside of the families and subfamilies Adelgidae, Pemphigidae, Phylloxeridae, and Hormaphididae (Miller 2005).

As a genus, *Tamalia* induce or occupy galls on shrubs across the genus *Arctostaphylos*, with two novel species reported on the closely related *Comarostaphylis* and *Arbutus*. (Miller & Crespi 2003). Some *Tamalia* species appear to show more host plant specificity than others (Miller & Crespi 2003). Due to differences in plant phenology, the life cycles of the aphids can vary notably depending on host species and bioregion (Miller 1998b, Miller & Crespi 2003).

Among *Tamalia*, *T. coweni* is the most wide-spread, and is known to utilize at least 25 species of *Arctostaphylos* as host plants (Miller 2005).

The population under study occurs at the Big Chico Creek Ecological Reserve (BCCER) in Butte County, CA. This site is at 300m elevation, and lies in a canyon near the edge of the Cascade Foothills region. The vegetation is a mixture of chaparral, mixed oak woodland, and grasslands. Two species of *Arctostaphylos* are found in this area: *A. manzanita*, and *A. viscida.* Both species regularly carry heavy populations of *T. coweni*. For the purposes of this study, galls were only taken from *A. manzanita*.

Arctostaphylos manzanita is a perennial shrub in the heath family, Ericaceae. It is widely found across Northern California chaparral and foothills woodlands, especially in xeric conditions on rocky slopes and canyons (Chesnut 1902; Adams 1940). The plant is endemic to the California region (Jepson 1923), and is well-adapted to the hot, dry summers and moderate wet winters of the region. It blooms in late winter to early spring before putting out new leaves (Eastwood 1934; Smith 1985). Its leaves are thick and oblong-ovate with simple margins, and are oriented in an alternate pattern along shoots, which emerge over an extended period in mid spring through early summer (Abrahamson 2014).

In the study area, the aphids emerge in early spring, around March. This coincides with budburst on their host plants—a timing that will allow them to exploit the newly growing foliage. The first generation are wingless female gall inducers known as foundresses (this first generation is also referred to as stem mothers). They hatch out of eggs that remained in a dormant diapause state at the base of their host plants throughout the winter. The foundresses crawl up the plant to the newly emerging leaves, and probe the tissue. When they have chosen a

site, they begin to induce a gall by inserting their mouthparts into the immature plant tissue (Miller 2004).

On *A. manzanita*, the vast majority of galls are formed on the leaf margin (out of 1,000 galls sampled in this study, only two were formed elsewhere, both on the leaf midrib). Early gall-induction involves the edge of the leaf folding over and enclosing the foundress—an asexual wingless female gall-inducer. A foundress may probe a leaf, starting and abandoning many galls before inducing one to completion. During its early stages, a gall is soft and exposed, and intruders can easily enter through the exposed edge before it seals in later growth—a process thought to take a matter of days (Miller 2004).

Each foundress feeds and matures in her developing gall, eventually completing four molts (Figure 1). She then gives birth to live offspring through parthenogenesis. These offspring are all female, and will be winged at maturity. They complete three molts in the gall, and then emerge to complete their fourth and final molt outside the gall. This emergence occurs in conjunction with the gall drying out and cracking open, allowing the aphids to exit (Miller 1998b).

After emerging, the winged morphs disperse and find new immature foliage, where they deposit a new generation of asexual wingless females, known as foundresses. This third generation quickly begins the process of inducing a new set of galls. Like the first generation of foundresses, they complete four molts inside their gall, and then give live birth to a fourth generation. The new generation consists of sexual males and females, who will become winged morphs at maturity. After completing three molts, they exit the gall, complete their fourth and final molts, and then disperse to mate. After mating, the sexual females deposit eggs at the base

of the host plants, which then diapause throughout winter and hatch into a new generation of foundresses the following spring (Miller 1998b).

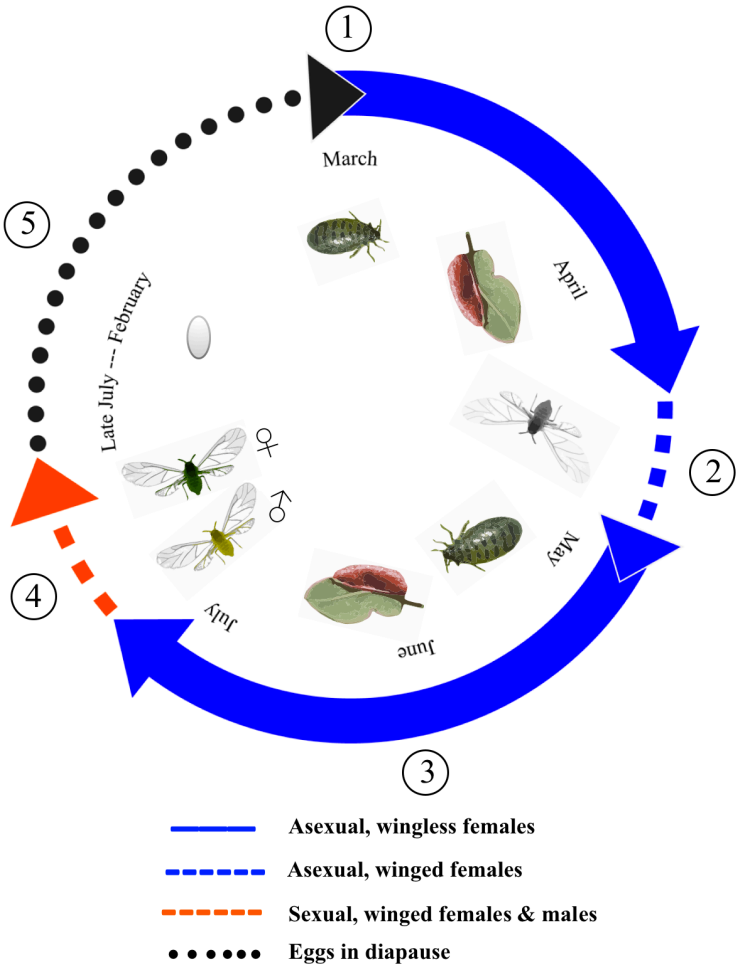

Figure 1. *Tamalia coweni* life cycle on *Arctostaphylos mazanita* in Butte County, CA

In early to mid-March, *Tamalia coweni* aphids emerge from eggs at the base of their host plants. This first generation is comprised of wingless, gall-inducing morphs known as foundresses, which induce galls on the margin of newly forming *A. manzanita* leaves. After completing four molts within their gall, the foundresses reproduce through parthenogenesis (1). Their offspring are asexual, winged daughters, who grow to maturity inside the gall, and emerge just before completing a fourth and final molt outside the gall. They then disperse and deposit live offspring—a second generation of wingless, asexual, gall-inducing foundresses, on new *A. manzanita* foliage (2). The second generation of wingless foundresses induce new galls, and complete four molts before reproducing. Their offspring are sexual, winged males and females, which grow to maturity inside the gall before emerging to complete their final molt (3). The sexual males and females then disperse and mate (4). After mating, the females deposit eggs at the base of *A. manzanita* host plants, which then remain in diapause throughout winter and hatch into a new generation of foundresses the following spring, completing the life history of the aphid clone (5).

Communal Gall-Sharing

The majority of galling aphids initiate their galls alone (Wertheim & Linder 1961; Wool & Bernstein 1991; Moran 1993); however, the *Tamalia* aphids are a noteworthy deviation from this pattern. While most *Tamalia* foundresses occupy their galls alone, frequently, multiple foundresses will reside in the same gall at once. This gall-sharing (also referred to as cohabiting, and sometimes as co-founding when the foundresses not only reside together but also initiate the gall together), which most commonly occurs as two or three foundresses, will sometimes result in as many as 10 foundresses in the same gall (Miller 1998b).

Gall-sharing behavior appears to be very rare among galling aphids, and the *Tamalia* species are some of the only aphids observed to co-found their galls (Miller 1998b). It is, however, consistently observed within the *Tamalia* genus, and seems to be widespread not only across *Tamalia* taxa, but across populations and host plants (Miller 2005). While shared galls are in the minority in *Tamalia* populations, they are far from rare. The recorded incidence rate of shared galls varies across host plants and galling sites (the highest known rates are on *A. patula* inflorescences), but can range as high as roughly 50% of galls (Miller 1998b). The apparent isolation of the behavior to this genus may be indicative of *Tamalia*'*s* evolution. The genus is morphologically and ecologically distinct such that it is often placed in its own sub-family, *Tamaliinae* (Remaudiere 1984, Nieto 1997). Gall-sharing behavior appears to be symplesiomorphic in this clade, and is likely to have been retained from a common ancestor (Miller, unpublished).

The reasons for the evolution and the persistence of communal gall-sharing are unknown. Among other galling aphids, gall space, as well optimal gall sites, are usually guarded and often fought over in territorial disputes (Whitham 1978, 1979). In contrast, territorial disputes over

galls or gall spaces have not been observed in *Tamalia* (Miller 1998a). This is particularly notable in light of the observation that there are measurable costs to sharing galls. As addressed previously, the number of offspring a gall foundress is able to produce is in part limited by the amount of space in her gall; foundresses that share galls produce on average fewer offspring per capita, although co-founded galls on average produce more collective offspring (Taylor & Miller 2014).

A number of explanations for why *Tamalia* would continue to exhibit gall-sharing behavior have been proposed. Genetic analysis demonstrated that *Tamalia* foundresses that share galls are more likely than not to be close relatives, raising questions about whether kinship may play a role in the tolerance of other foundresses in the gall (Taylor & Miller 2014). However, work by Miller 1998a, which found that *T. coweni* foundresses were more likely to share galls on *A. patula* inflorescences when placed under conditions of high population density, regardless of relatedness, brings into question whether relatedness is a causal factor for gall sharing, or more of an incidental result of *Tamalia* ecology (for instance: winged morphs may deposit multiple (clonal) offspring at a single site, increasing the odds that foundresses in the same location would be clone-mates). The current study seeks to shed more light on how population density plays a role in determining gall-sharing rates, with particular attention to the role of spatial and temporal factors underlying gall distributions and resource availability.

Habitat Selection and the Plant Vigor Hypothesis

Many explanations have been proposed regarding why herbivorous insects choose some plants and plant organs over others. The Plant Stress Hypothesis, described by White in 1984, states that plants under stress (such as limited water) will be more susceptible to invasion because they tend to have higher concentrations of amino acids and other desirable nutrients for

herbivorous insects. In addition, it is thought that due to stress, the plants tend to delegate fewer resources to plant defenses (Rhoades 1979; White 1984; Williams & Cronin 2004). This explanation has generally been regarded as an incomplete way to describe insect distributions on plants, although it seems to have more predictive power in some settings than others (Price 1991; Cornelissen et al. 2008).

Another explanation—known as the plant vigor hypothesis (PVH), has commanded more attention in recent years. The PVH is described in detail in a 1991 paper by Peter Price, and states that insects will select more vigorous (larger, faster-growing) plants and plant modules. Additionally, in what is known as "preference-performance," the preference for these sites will be linked to higher fitness for the insects who colonize them (Craig et al. 1989; Price 1991).

Some of the most well-known work that supports the PVH is that of Thomas Whitham, who showed that for the galling aphid *Pemphigus betae*, the selection of larger leaves had clear and direct advantages for fitness (Whitham 1978). His work further suggested that sharing a leaf had measurable consequences, and that on shared leaves, galls in more distal positions produced, on average, fewer offspring than those in basal positions (Whitham 1980). One explanation for this came from the understanding that gall inducers can draw nutrients from surrounding plant areas. Larson and Whitham (1991) demonstrated that while all gall inducers on a leaf appeared able to draw in nutrients from the leaf they resided on, that only those at the base of the leaf reliably drew in nutrients from surrounding leaves as well. This finding highlights how galls may be affected by their specific location on the host plant, as well as by other nearby galls.

Many studies appear to align well with the PVH (Whitham 1978; Whitham 1980; Craig et al. 1986; Price & Clancy 1986; Caouette & Price 1989; Price 1989; Price 1991). A meta-analysis of related literature by Cornelissen et al. in 2008 suggested that, in general across

studies, insects do appear to show a preference for more vigorous plants and plant organs. However, it also showed that the degree to which vigorous plant parts were preferentially selected appeared to vary somewhat by insect feeding guild (such as chewers, sap suckers, stem-borers, leaf-rollers, and gall-formers).

Notably, Cornelissen et al. pointed out that there appears to be only mixed evidence of the preference-performance connection, and that while there are indications that many insects cluster around more vigorous plants and plant parts, only a few studies (such as Craig et al. 1989) seemed to verify a clear correlation between sites that were higher "preference," and higher fitness, and numerous studies showed weak (Fritz et al. 2000) or contradictory results (Santos et al. 2008).

One clear example of this inconsistency was a study of the galling aphid *Hormaphis hamameledis* (Rehill & Schultz 2001), which assessed the relationship between gall position and fitness in two consecutive years. The study showed that in both years, there was a strong preference for distal leaves along a shoot. However, leaf position was calculated to explain a significant amount of the variation in fitness in one year, but not the other—with galls on basal leaves having a higher fitness despite the apparent preference for more distal leaves. In addition, a fitness advantage was measured for galls on the distal half of the leaves themselves, but approximately three times as many galls were found in basal positions than in distal ones.

Despite general support for the PVH, many have also called the universality of its scope into question. Of the 71 studies that tested the PVH, only 17.8% tested both preference and performance, and of those, only half showed a fitness advantage associated with more vigorous plant modules (Cornellison et al. 2008). Some studies even showed directly contradictory results, and have measured *reduced* fitness on the most vigorous plant modules. One such study by

McKinnnon et al. in 1990 showed evidence for reduced fitness on the largest leaf shoots, and a U-shaped distribution pattern when examining gall fitness in relation to shoot size. The suggested explanation for this was that although larger shoots did provide a fitness advantage from a resource perspective, beyond a certain size the aphids were not able to effectively manipulate plant tissue, and the "gall-ability" (the responsiveness of the plant tissue to galling attempts) of these sites became reduced as a result.

From the literature as a whole, a general picture emerges: while the PVH is strong and has predictive power, it does not account for the entire story regarding how insects choose to distribute themselves on plants, and other variables besides plant vigor should be taken into active consideration. One such variable that arises repeatedly in many studies that appear to refute the PVH, is timing. Lorenz Rhomberg, in 1984, pointed out via his studies of a *Pemphigus* species closely related to that studied by Whitham, that its gall distributions could be explained simply by temporal factors alone. One of Rhomberg's chief criticisms of the PVH is that it broadly assumes aphids will *have* such abundant availability of resources that they'll be able to choose optimal sites. It is important to note that galling aphids are only able to induce galls on immature plant growth, and the maturation of plant tissue provides a limited window in which the aphids can induce their galls. The timing of bud burst may be somewhat variable across a region, as well as on a plant itself (Kummerow 1983), making the timing of the arrival of aphids and the availability of suitable plant tissue an intricate and consequential relationship (Yukawa 2000; Stone et al. 2002).

This variable pattern of available galling sites is visually evident on many *Arctostaphylos manzanita* (Ericaceae) shrubs, where leaf buds will emerge and mature at different times. In some cases—as may be influenced by one part of a plant falling consistently in the shade, and

another in the sun—these bud-burst time differences may be weeks apart. The new leaf bud will then open and elongate, and the leaves will mature starting at the base of the shoot, and ending with the youngest leaves at the tip. *Tamalia coweni*, which induces galls on immature *Arctostaphylos sp.* plant tissue—arriving very early at a bud that has yet to fully open may not have access to the inner leaves—which will ultimately become the most leaves closest to the tip of the shoot. In contrast, an aphid arriving late to a shoot may find the basal leaves no longer receptive to galling, and it will only have a choice of still immature leaves near the tip of the shoot—regardless of their quality or prior occupation. The aphids are obligate gall dwellers, and cannot survive for long periods outside of a gall. In addition, gall inducers are generally wingless, meaning they have limited mobility, and are unlikely to travel very large distances. Spatial and temporal constraints may therefore play a very strong role in the effective habitat choices that are available to an aphid at a given time.

While there may not be general consensus regarding the relationship between vigorous plant modules and fitness, one of the most consistent correlates of offspring count across aphid species is gall size. Many of the studies mentioned above show inconsistent or contradictory relationships between plant vigor measures and fitness, but most report consistent and significant positive relationships between gall size and the number of offspring a gall supports—a trend seen across the literature as a whole, both for galling aphids and other galling insects (Heard & Buchanan 1998; Rossi & Stiling 1998; McKinnon et al. 1999; Rehill & Schultz 2001). As such, assessing gall size is one of the more useful indicators of ultimate fitness for galling aphids, and is the main indicator of fitness used in the current study.

One of the main consistent themes that arises out of the relevant literature is the intricate coordination between the gall inducer and plant phenology, and the ultimate importance

of the effective gall-ability of sites over a consistent relationship with optimal plant resources. The current study aims to assess the aphid distributions and galling patterns within the context of *A. manzanita* host plant phenology, and to interpret the findings keeping in mind the specific constraints for this system. The existence of co-founding behavior among *Tamalia* adds an additional dimension to the assessment, and raises further questions regarding the costs and strategies surrounding habitat choice for galling aphids.

Major Objectives of the Study

The first aim of this study was to build upon the work done by Miller 1998, which found that the number of foundresses placed on a caged *A. patula* inflorescence was highly correlated with the incidence of cofounding, and that population density, rather than kinship, predicted gall sharing. One of the limitations to this study was that it assessed gall sharing in an artificial setting, where the free movement of foundresses was restricted—both spatially, as well as temporally, given all foundresses were placed at the same time. In addition, it looked at gall formation on inflorescences instead of leaves, where the galls are more commonly located. My study looked at leaf galls in their natural state, allowing for the free movement of foundresses when choosing galling sites.

The second aim of this study was to assess whether *T. coweni* population distributions align with the Plant Vigor Hypothesis. Due to limitations of the study, the focus was on the preference-performance aspect of the hypothesis, and assessed a) whether there were evident preferences in gall site location, b) whether these locations appeared to correlate with indicators of fitness, and c) whether site preference and performance appeared to be predictive of communal gall sharing.

CHAPTER II

MATERIALS AND METHODS

My study site was located at the Big Chico Creek Ecological Reserve (BCCER) in Butte County, California. The landscape in this area is a mixture of chaparral, oak woodland, and patches of grassland, and spans Big Chico Creek Canyon. To minimize the effects of slope, aspect, elevation, and surrounding vegetation, I collected all of my samples from a study plot spanning roughly 500m^2. This site is found on a gentle slope with a south-east aspect, about a third of a kilometer west of the Deer Creek Highway. The vegetation within the plot is a mixture of chaparral with scattered oaks woodland.

Two species of *Arctostaphylos* are found on this site: *A. manzanita* and *A. viscida.* To minimize the effect of host plant differences, I chose to sample only from *A. manzanita*. I standardized the selection of plants by eliminating those that were larger than three meters high by three meters wide, those without any galls, and plants that were senescent (as determined by being over fifty percent of the shrub dead).

Sampling began in late April 2015, and continued through mid-July of the same year. Galls first started appearing on plants at the study site in mid-March of 2015. In order to best capture final gall densities, sampling was delayed until a significant number of plants with active galls had a minimal number of immature leaves (less than 10% of shoots by estimation). As leaf development was not temporally uniform across plants at the site, this meant that not all shrubs were sampled at the same time. Individual shrubs were, however, sampled in their entirety on a single day. Because of this, seasonal developmental status of the plant was controlled for but external seasonal effects remained a variable that was noted but left for future examination. An attempt to minimize the effects of seasonal variance, both for the plants as well as for the aphids,

was made when dissecting galls; in the current study, only galls from a select window—roughly 2 weeks in late May to early June—were dissected and analyzed.

Galls were collected using a stratified random sampling method. A random number generator was used to determine a compass bearing, which was then used as the bearing for each transect. Transects were laid across a plant using string measuring tapes. A string was laid along the determined compass bearing for each meter of plant width, always at the center of each meter. For instance, a plant three meters wide would have three transects, one at half a meter, one at one and a half meters, and a third at two and a half meters. Each new plant shoot containing at least one gall and falling within ten centimeters of the transect in any direction was collected and promptly stored on ice. New shoots were defined as those originating from the current growing season, and were easily identified by the coloration of their stems and bract features at the base of the new growth.

Gall position and density was catalogued at the plant, shoot, and leaf scales. At the plant scale, this was noted by the location of the transect, and the number of galls per meter of transect. By shoot, leaves were assigned a catalogue number ascending from the base of the shoot to the tip. At the leaf scale, each leaf was visually divided into four quadrants, with the center point falling along the midrib halfway between the base and the tip of the leaf. Each gall was then assigned a quadrant number starting in the lower left quadrant moving clockwise. As such, the relative positions and densities of galls were determined at the leaf, growth, and plant scales.

Galls were transported from the field on ice to the lab, and immediately placed in a freezer, minimizing the chance aphids would leave their galls or move around. The time period of late May to early June was selected for detailed analysis, because this corresponds to the peak

season for *T. coweni* in the current region (see Discussion). Transects from this time period were chosen at random, and the galls from these were then analyzed in full. The gall age (early, active, or mature), its size (as estimated by an ellipsoid with length, height, and width measurements), number and age of foundresses (roughly estimated by "immature" = fewer than four molts and no offspring; "adult" = four molts and presence of at least one offspring; and "mature" = multiple offspring, and visible deflation in body size), offspring count, and arthropod associates in the gall were identified and catalogued. An estimation of the percent of leaf margin occupied was made for each leaf, with a clear grid overlay as an aid.

Final statistical analyses and data visualization were done using SPSS software. A binary logistic regression was used to determine whether an increase in population density correlated with the presence or absence of gall sharing on a leaf. A linear regression was then used to further determine if population density was predictive of the number of shared galls on a leaf. To determine differences such as gall size in different categories (such as gall per leaf densities), a combination of one-way ANOVA and Kruskal-Wallis tests were done. Most of the data had a positive skew, and thereby violated the assumption of normality required for the ANOVA tests. To remedy this, Log_{10} transformations were done so that the ANOVA and Tukey-HSD post hoc tests could be done. As an extra measure, the Kuskal-Wallis test (which does not have an assumption of normality) was used to verify the ANOVA results.

CHAPTER III

RESULTS

All galls were collected during the spring and summer of 2015. This summer was one in a succession of drought years for the area. While the effects of this were visible on water supplies and many other plants for the area, *A. manzanita*, a native California shrub and drought tolerant chaparral species, appeared to still be thriving. The first *Tamalia* galls of the season appeared alongside the budburst for the shrubs, which was well under way by early March. *Tamalia* appeared to thrive as well as its host plants despite the dry conditions, and ample populations were seen on a large number of shrubs across the study area (Miller, unpublished annual censuses of *Tamalia* galls at BCCER).

In total, 90 new seasonal shoots from 13 *A. manzanita* shrubs were examined in their entirety. These shoots contained 377 galled leaves, and 1,123 galls. Although galls were collected throughout the entirety of the season, these particular shrubs were chosen for examination because they were all sampled within a two-week span at the end of May and early June. This time period was chosen in hopes of examining galls within the peak of the *Tamalia* seasonal cycle. None of the examined galls contained discernable male or sexual female offspring. In the study area, sexual morphs are produced by third generation foundresses, and the presence of sexual morphs would suggest that the aphids were nearing the end of their seasonal cycle (Figure 1). It is likely that some portion of the younger foundresses from the sample, and those with very young offspring (which are difficult to distinguish as sexual morphs), belonged to this later generation. Overall, the examined galls were most likely a mixture of those made by original stem mothers and third generation foundresses, and were representative of the early peak season population for this area.

Nearly half of all galls (47.5%) occurred on leaves with only one or two galls, although leaves with three or more galls were strongly represented as well (Table 1). The number of foundresses on leaves ranged from zero to 25, with 11 leaves containing no foundresses (likely abandoned or preyed upon), and over half of leaves (53.3%) containing three or fewer (Table 2). Within galls, the majority (59.4%) were singly occupied (Table 3), and 32.3% of all galls were co-occupied, containing multiple foundresses. This percentage is well within the range of cofounding rates measured in other populations of *Tamalia* (Miller 1998). Eight point three percent of galls were empty (from the total sample, 2.9% of all leaves contained only empty galls, see Table 2). The reason they contained no aphids is unknown, although predation was not a clear cause, and abandonment was a possible alternative.

Table 1. Frequency Distribution:
Number of Galls on Leaves

Galls on Leaf	Frequency	Percent	Cumulative Percent
1	89	23.6	23.6
2	90	23.9	47.5
3	72	19.1	66.6
4	53	14.1	80.6
5	31	8.2	88.9
6	24	6.4	95.2
7	14	3.7	98.9
8	3	0.8	99.7
10	1	0.3	100.0
Total	377	100.0	

Of the co-occupied galls, nearly all contained two (67.9%) or three (23.8%) foundresses. Only around 8% contained four or more foundresses, and the few galls that contained 6 or more

Table 2. Frequency Distribution:
Number of Foundresses on Leaves

Foundresses on Leaf	Frequency	Percent	Cumulative Percent
0	11	2.9	2.9
1	84	22.3	25.2
2	59	15.6	40.8
3	47	12.5	53.3
4	42	11.1	64.5
5	32	8.5	72.9
6	25	6.6	79.6
7	15	4.0	83.6
8	13	3.4	87.0
9	22	5.8	92.8
10	9	2.4	95.2
11	9	2.4	97.6
12	3	0.8	98.4
13	1	0.3	98.7
14	2	0.5	99.2
17	2	0.5	99.7
25	1	0.3	100.0
Total	377	100.0	

collectively comprised less than 1% of all shared galls (Table 3). This distribution is well in line with the distributions of foundresses per gall collected by Miller from *Tamalia* galls on *A. patula and A. viscida* leaves and *A. patula* flower buds (Miller 1998b).

Table 3. Frequency Distribution: Number of Foundresses in Galls

Foundresses in Gall	Frequency	Percent	Cumulative Percent
0	93	8.3	8.3
1	669	59.4	67.9
2	245	21.8	89.7
3	86	7.6	97.3
4	22	2.0	99.3
5	5	0.4	99.7
6	1	0.1	99.8
8	1	0.1	99.9
9	1	0.1	100.0
Total	1123	99.7	

Aphid Density and Gall-Sharing Rates

The relationship between the number of foundresses on a leaf and the total number of galls (multiply or singly occupied) was best described by a power relationship (R^2= 0.743 p<<0.001) (Figure 2). In Figure 2, the dotted reference line is plotted along the path of y=x, in this case representing leaves where there is one foundress per each gall (n=669 galls). All points to the left of this line represent a leaf with at least one empty gall (out of 1,123 galls, 93 were empty), while points to its right represent leaves with at least one cofounded gall (n=361 galls). Notably, the instances of leaves without a cofounded gall diminished greatly for leaves with more than six galls, with at least one cofounded gall found on every leaf that had 7 or more galls (n=18 leaves).

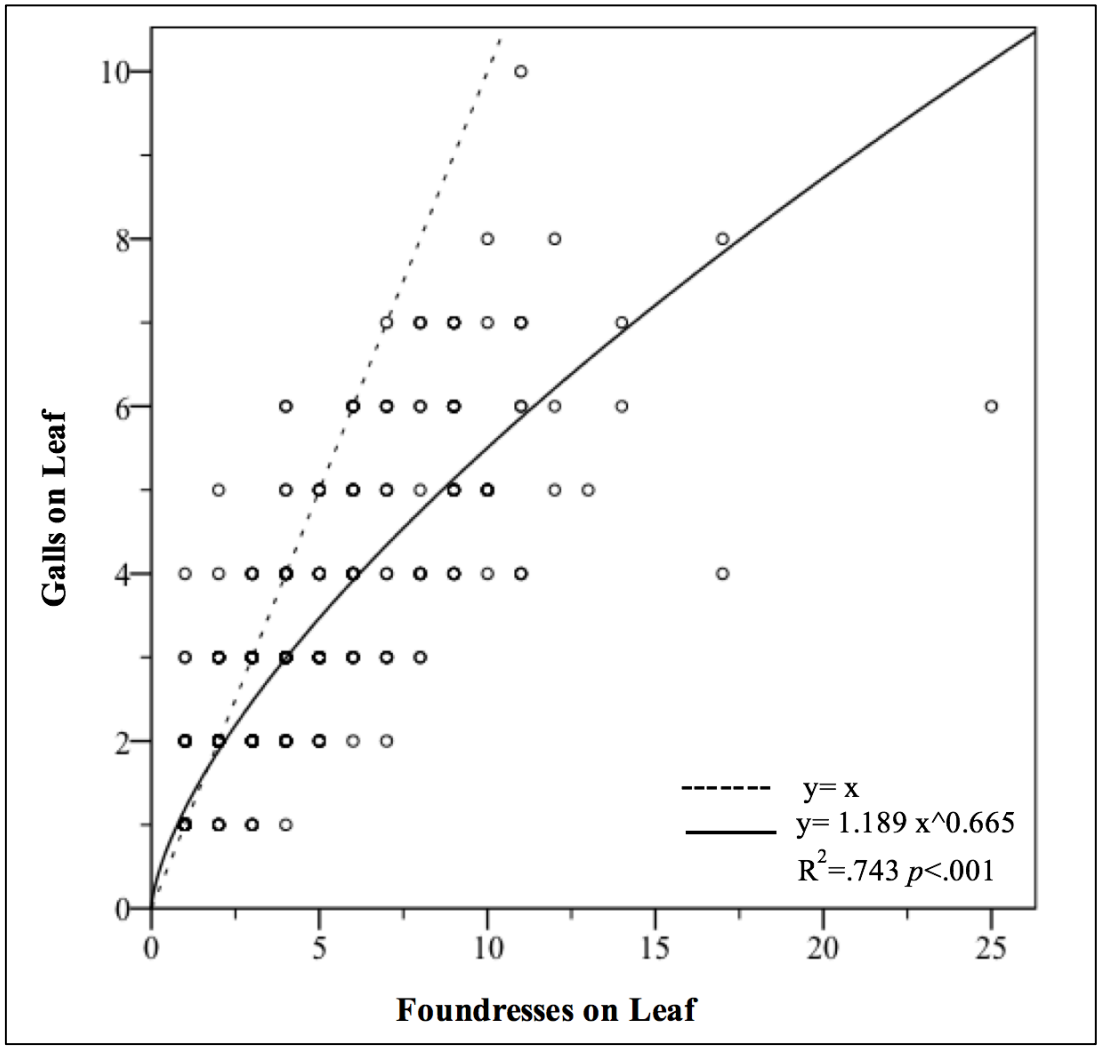

Figure 2. Foundresses on a Leaf vs. the Number of Galls on a Leaf
In total, 366 sample leaves with gall per leaf densities ranging from 1-10 galls/leaf were examined. The correlation between the total number of foundresses on a leaf and the number of galls on a leaf is shown above. The best fit to the data was a power curve, with the number of galls on a leaf increasing as the number of foundresses on a leaf became larger. For reference, a dotted line was plotted for y=x, which corresponds to leaves where there was one foundress per each gall on the leaf. Points to the left of this line represent leaves where all of which have at least one empty gall. Points to the right of y=x represent leaves where the number of foundresses is in excess of the number of galls, meaning that all leaves to the right of the dotted line have at least one shared gall.

Leaves with different numbers of foundresses and galls differed significantly in their rates of containing cofounded galls. Both measures of density (foundresses per leaf, and galls per leaf, respectively) were significant predictors of the presence or absence of cofounding on

leaves, but the headcount of foundresses on a leaf consistently proved to be the stronger of the two.

A binary logistic regression analysis was done to predict the presence or absence of cofounding on a leaf using the number of foundresses per leaf as a predictor. Given that 189 out of 366 sample leaves had at least one cofounded gall, the likelihood of correctly predicting the presence or absence of cofounding on a leaf was around 51% due to chance alone. The model chi squared value for the regression indicated that the foundress per leaf model offered a significant difference in predictive power from a constant only model ($\chi^2(1)= 298.285$, $p< 0.001$), and the Wald criterion indicated that foundresses per leaf was indeed a significant predictor variable ($p<0.001$).

Cox & Snell's $R^2= 0.557$, an approximate analog of the linear regression R^2, indicated that 55.7% of the variation in cofounding occurrence could be explained by the number of foundresses per leaf alone (the Nagelkerke R^2, a similar value although less of an analog to the common R^2, was 0.743). Prediction success overall was 86.1% (89.3% for absence of cofounding, 83.1% for presence thereof), a significant improvement from 51% due to chance alone. The Exp(B) value—the odds ratio—was 4.14, which indicated that the odds of a leaf containing a cofounded gall were 4.14 times greater with each additional increase of one foundress per leaf. For comparison, it is worth noting that in the current dataset, all leaves with 7 or more foundresses (77 leaves in total) contained at least one cofounded gall.

The same trend, although weaker, was seen when using the number of galls on a leaf as a predictor. The model chi squared evaluation showed that the galls per leaf model differed significantly from a constant-only model ($\chi^2(1)= 104.916$, $p<0.001$), and the Wald criterion indicated that galls per leaf was a significant predictor variable ($p< 0.001$). The Cox & Snell's

R^2= 0.249 (Nagelkerke R^2=0.332) indicated that 24.9% of the variation in cofounding occurrence could be explained by the number of galls on a leaf alone. Prediction success overall was 73.0% (69.5% for absence of cofounding, 76.2% for presence thereof), a significant improvement from 51% due to chance alone, although notably less accurate than the predictions using foundresses per leaf. The Exp(B) value was 2.153, which indicated that the odds of a leaf containing a cofounded gall were 2.153 times greater with each additional increase of one gall per leaf. For comparison, in the current dataset, all leaves with 7 or more galls (18 leaves in total) contained at least one cofounded gall.

The number of foundresses on a leaf was not only predictive of the occurrence of cofounding, but also of the number of cofounded galls on a leaf. A simple regression analysis showed a positive relationship between the number of foundresses on a leaf and the number of cofounded galls on a leaf, with a quadratic curve yielding a R^2 value of 0.800 (p<0.001) (Figure 3). A similar regression using galls per leaf as a predictor also yielded a positive, although weaker, relationship (R^2=0.377, p<0.001).

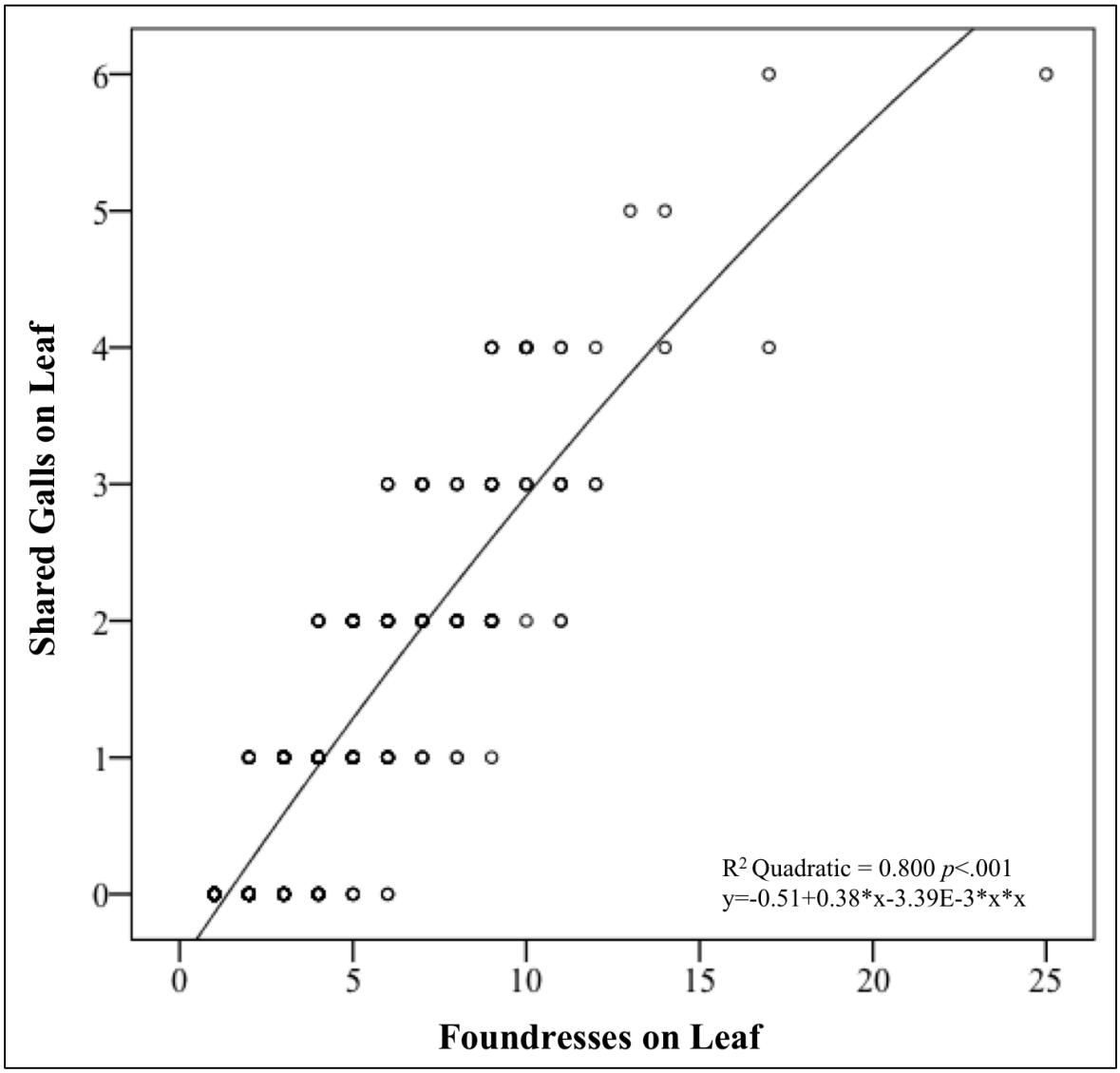

Figure 3. Foundress Density as a Predictor for the Number of Shared Galls on a Leaf
366 sample leaves were examined for cofounded galls. The total number of foundresses on a leaf was then used as a predictor for the number of cofounded galls on a leaf. The best fit to the data was a quadratic curve, with the number of shared galls on a leaf increasing as the number of foundresses on a leaf became larger.

Leaf Margin and Gall Sharing Rates

One limitation of using the number of galls and foundresses on a leaf as measures of density is they don't directly address the degree to which leaf resources are depleted. On *A. manzanita, T. coweni* induces its galls almost exclusively on the margin of newly forming leaves.

In the current dataset, out of 1,123 galls, only three were formed anywhere but the leaf margin (all three on the leaf midrib). As such, the percent of leaf margin occupied by galls was used as an additional measure of population density.

A binary logistic regression showed leaf margin to be a weak predictor of whether or not cofounding occurred on a leaf. A model chi squared test showed that the leaf margin model differed significantly from a constant-only model ($\chi^2(1)= 80.082$, $p<0.001$), and the Wald criterion indicated that leaf margin was a significant predictor variable ($p<0.001$). The Cox & Snell's $R^2= 0.226$ (Nagelkerke $R^2=0.301$) indicated that 22.6% of the variation in cofounding occurrence could be explained by the amount of leaf margin occupied alone. Prediction success overall was 71.9% (66.9% for absence of cofounding, 77.2% for presence thereof), a significant improvement from 51% due to chance alone, although notably less accurate than the predictions using foundresses per leaf, and roughly the same as the predictions using the number of galls per leaf. The Exp(B) value was 1.038, which indicated that the odds of a leaf containing a cofounded gall were 1.038 times greater with each additional increase of one percent margin occupied. For comparison, in the current dataset, 74 out 98 (75.5%) of leaves that had 100% of their margin occupied contained at least one cofounded gall.

Leaf margin was also a weak predictor of the number of cofounded galls on a leaf (Quadratic $R^2 =0.256$, $p<<0.001$) (Figure 4).

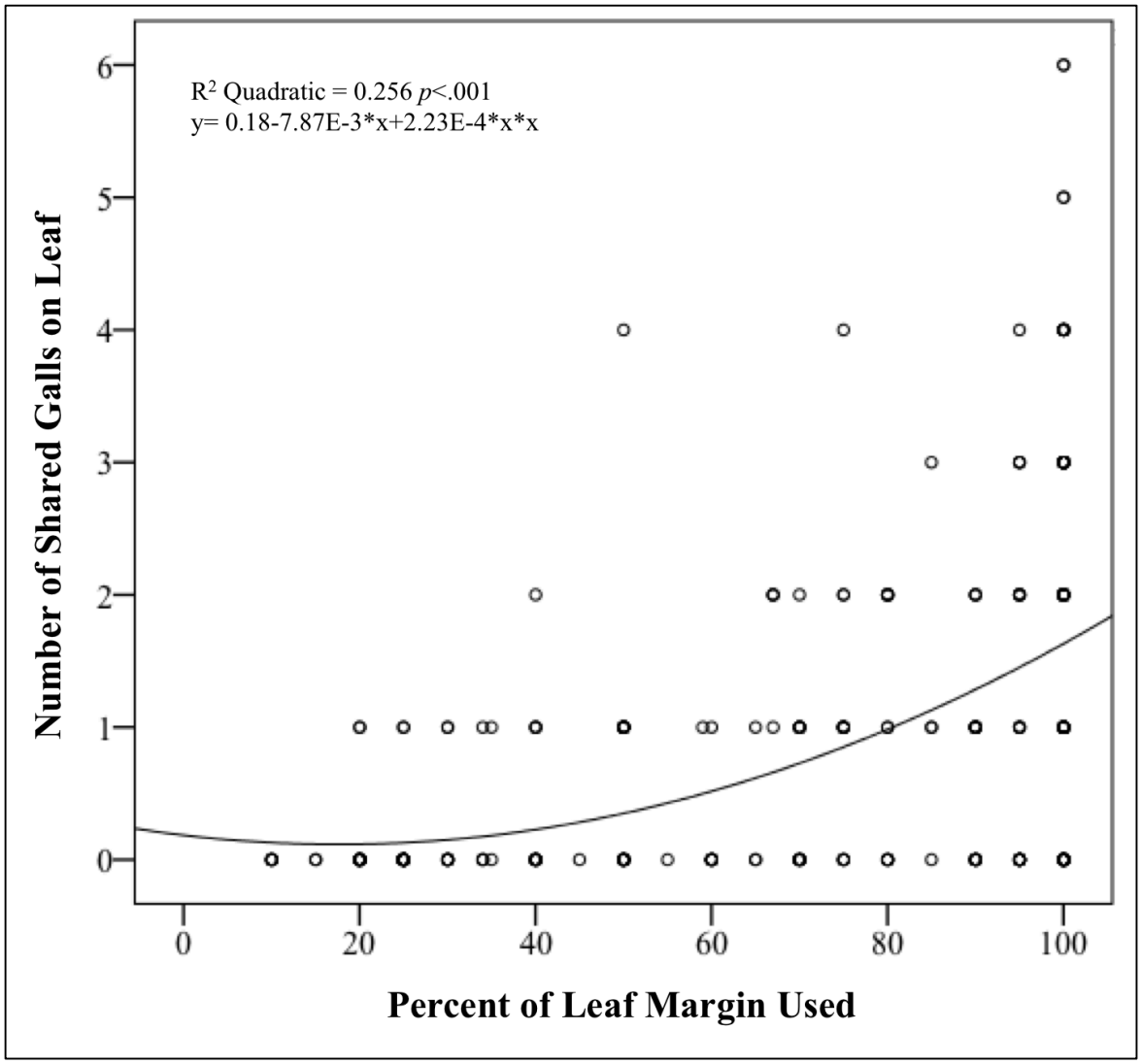

Figure 4. Percent of Leaf Margin Occupied vs. the Number of Shared Galls on a Leaf
312 sample leaves were examined for shared galls, and for each leaf, the amount of leaf margin that was occupied was estimated. The amount of occupied leaf margin was then used as a predictor for the number of shared galls on a leaf. The best fit to the data was a quadratic curve, with the number of shared galls on a leaf increasing as the number of foundresses on a leaf became larger.

While the number of foundresses per leaf and the number of shared galls per leaf had a positive correlation, the average number of foundresses in each shared gall remained comparatively stable across density categories. Out of 189 leaves with cofounded galls, the vast majority (91%) had an average number of foundresses per cofounded gall that ranged between 2 and 3 (Table 4). While this average did increase as foundress density increased, a simple linear

regression between the number of foundresses on a leaf, and the average number of foundresses per cofounded gall showed this to be a very weak positive correlation (R^2= 0.102, p<0.001). The same regression using the maximum number of foundresses in a cofounded gall on a leaf in place of the average did yield a much stronger, positive linear correlation, however (R^2=0.628, p<0.001). This suggests that while the upper limit of foundresses sharing a gall does increase as the number of foundresses on a leaf increases, that the vast majority of cofounded galls contain 2 or 3 foundresses across density categories.

Consequences of Gall and Leaf Sharing

Previous data suggests that gall size is a correlate of fitness and a predictor of the number of offspring a gall can support (Rehill & Schultz 2001; Heard & Buchanan 1998; McKinnon et al. 1999; Rossi & Stiling 1998). As such, gall size can be used as somewhat of a proxy for fitness, although the complexity of factors surrounding gall size should be noted. The current study did not examine the relationship between offspring count and gall size directly, but a cursory examination of galls with adult and mature foundresses (younger aphids, although their galls may have reached full size, won't have produced a full set of offspring yet) yielded a positive linear correlation between gall size and offspring count (n= 363, R^2=0.324, p<0.001) that aligns with similar data from other studies (Rehill & Schultz 2001, McKinnon et al. 1999). A more careful examination of this relationship, with control for the age of foundresses and other conditions would likely yield a more informative correlation. For the purposes of this study, the relationship between gall size and gall density was used as basis for an initial exploration of the consequences of gall and leaf sharing.

Effect of Gall Density on Gall Size

Gall size was examined across both gall per leaf and foundress per leaf densities. Although these two variables are related to one another, their relationship with gall size differs in a number of ways. The number of galls on leaf will be limited to a degree by the amount of physical space (specifically leaf margin) on a leaf, and beyond a certain point, adding subsequent galls would require diminishing gall size. The number of foundresses may increase far beyond the number of galls on a leaf, but adds further stresses to the leaf. Additional foundresses represent more aphids sapping resources from the leaf, although more foundresses also means, at least in theory, more pooled resources to induce the galls themselves.

As the leaf was the statistical unit, the average, minimum, and maximum gall sizes on each leaf were used as measures of gall size. Because sample sizes became very small at high densities, gall and foundress density categories were eliminated if they contained five or fewer data points. Volume measurements were not collected on the entire dataset (this began midway through when it became apparent this would be a valuable variable), so the samples involving volume comparisons are smaller than the total sample. The gall per leaf density categories for the following comparisons included: 1gall/leaf (n=49), 2 galls/leaf (n=66), 3 galls/leaf (n=48), 4 galls/leaf (n=32), 5 galls/leaf (n=16), and 6 galls/leaf (n=13).

Table 4. Frequency Distribution

Average Number of Foundresses in Shared Galls

Avg. Foundresses Per Shared Gall	Frequency	Percent	Cumulative Percent
2.00	100	52.9	52.9
2.25	6	3.2	56.1
2.33	9	4.8	60.8
2.50	13	6.9	67.7
2.60	2	1.1	68.8
2.67	6	3.2	72.0
2.75	2	1.1	73.0
3.00	34	18.0	91.0
3.33	2	1.1	92.1
3.50	6	3.2	95.2
4.00	6	3.2	98.4
4.17	1	0.5	98.9
4.25	1	0.5	99.5
4.50	1	0.5	100.0
Total	189	100.0	

The distributions for maximum, mean and minimum gall volume were positively skewed and violated the homogeneity of variance assumption for the ANOVA. Because of this, Kruskal-Wallis H tests were done instead, followed by a $\log_{10}$ transformation to achieve normality, and an ANOVA on the transformed data.

The $\log_{10}$ transformation failed to achieve normality for the maximum gall size distribution; however, Kruskal-Wallis ($\chi^2(5) = 5.089$, $p = 0.405$) and ANOVA $F(5, 218) = 1.241$, $p = 0.291$) tests agreed with one another, and were not significant.

A Kruskal-Wallis test showed that gall density did not have a significant effect on mean gall size, $\chi^2(5) = 6.080$, $p = 0.299$. An ANOVA on a $\log_{10}$ transformation of the data supported this result, and showed that the effect of gall/leaf density on average gall size was not significant, $F(5, 218) = 1.548$, $p = 0.176$.

In contrast to the maximum and mean gall sizes, there was a significant difference in minimum gall size across gall densities. The Kruskal-Wallis test showed a significant effect of gall density on minimum gall volume, $\chi^2(5) = 56.657$, $p < 0.001$, with a mean rank minimum volume score of 152 for 1 gall/leaf, 126.39 for 2 galls/leaf, 112.61 for 3 galls/leaf, 75.50 for 4 galls/leaf, 50.19 for 5 galls/leaf, and 56.31 for 6 galls/leaf. An ANOVA on $\log_{10}$ transformation of the data supported the Kruskal-Wallis H test, and showed that the effect of gall/leaf density on minimum gall size was significant, $F(5, 218) = 14.155$, $p < 0.001$. Post hoc comparisons using the Tukey HSD test indicated that the mean minimum volume for galls at 1 gall/leaf densities (M = 934.95, SE = 97.22) was significantly different than that for leaves containing 2 (M= 653.26, SE= 72. 15), 3 (M= 479.22, SE=50.57), 4 (M= 274.71, SE= 38.92), 5 (M= 177.13, SE= 31.22) and 6 (M= 187.11, SE=28.88) galls per leaf (all units are mm^3; see Figure 6).

In summary, gall density appeared to have little to no effect on the maximum size galls achieved, or on the average gall size on leaves. However, gall density did correspond with significant differences in the size of the smallest galls on leaves, with the smallest galls tending to occur on leaves with increasingly large numbers of galls (Figure 5, Figure 6).

Effect of Foundress Density on Gall Size

A similar trend for gall size was seen across foundress densities, as was seen across gall densities. The foundress densities per leaf included 1 (n= 48), 2 (n= 44), 3 (n= 32), 4 (n= 26), 5 (n= 22), 6 (n=12), 7 (n= 7), 8 (n= 8), and 9 (n=14) foundresses per leaf.

Maximum, mean and minimum gall volume distributions were all positively skewed, and all violated the homogeneity of variance assumption for ANOVA. Kruskal-Wallis tests showed the effect of foundress density on maximum ($\chi^2(8) = 8.725$, $p = 0.366$) and mean ($\chi^2(8) = 7.490$, $p = 0.485$) gall volumes was not significant. A subsequent ANOVA test on $\log_{10}$ transformation of the mean gall size data (which successfully achieved normality) corroborated this, and was not significant, $F(8,205)=0.666$, $p=0.721$. Although a $\log_{10}$ transformation did not achieve normality for the maximum gall size distribution, an ANOVA on the original data agreed with the Kruskal-Wallis test, and was not significant ($F(8, 205)=1.502$, $p=0.158$.

As was seen across gall densities, a Kruskal-Wallis test showed the effect of foundress density on minimum gall size to be significant ($\chi^2(8) = 39.334$, $p <0.001$), with a mean rank minimum volume score of 141.88 for leaves with 1 foundress, 110.31 for 2 foundresses/leaf, 120.23 for 3 foundresses/leaf, 106.85 for 4 foundresses/leaf, 87.64 for 5 foundresses/leaf, 79.33 for 6 foundresses/leaf, 83.31 for 7 foundresses/leaf, 45.69 for 8 foundresses/leaf, and 57.43 for 9 foundresses/leaf. A one way ANOVA on a $\log_{10}$ transformation of the data further supported this result, and showed the effect of foundress density on minimum gall size to be significant, $F(8, 205)=5.801$, $p <0.001$. Post hoc comparisons using the Tukey HSD test indicated that the mean minimum volume for galls at 1 foundress/leaf density (M= 954.91, SE= 101.40) differed significantly from the mean minimum volumes for leaves with 5 (M=365.58, SE= 50.49), 6 (M= 285.67, SE= 34.52), 8 (M=248.02, SE= 129.13), and 9 (M=212.60, SE= 31.76) foundresses per leaf. Minimum volumes on leaves with 2 foundresses (M= 558.53, SE= 70.20) differed significantly from leaves with 9 foundresses, and those on leaves with three foundresses (M= 695.59, SE= 116.10) differed significantly from leaves with both 8 or 9 foundresses (all units are Mm^3; see Figure 7 for corresponding pairwise confidence intervals).

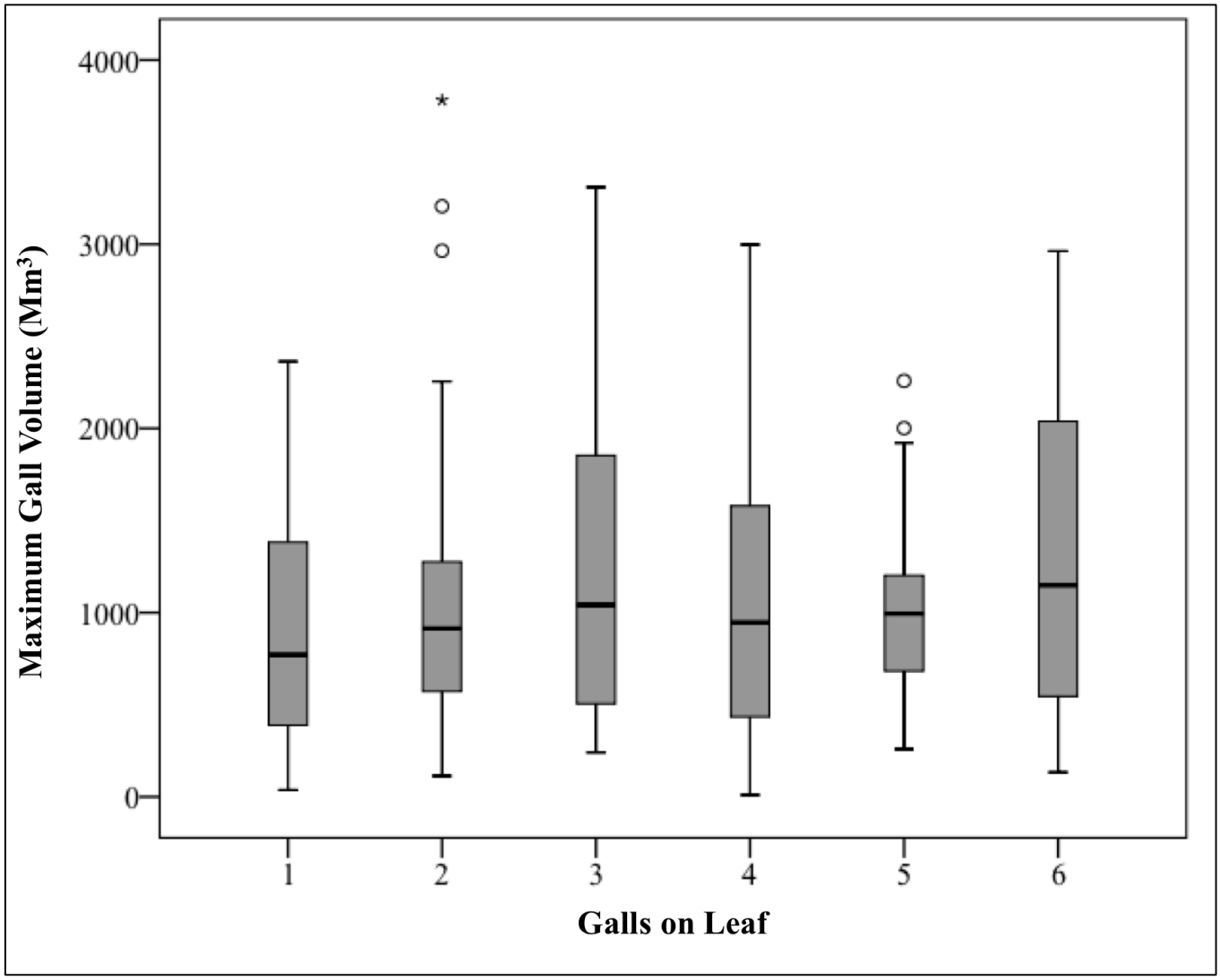

Figure 5. Gall Density as a Predictor for Maximum Gall Volume on a Leaf
The volumes of all galls were measured on 224 leaves with gall per leaf densities ranging from 1 to 6. No significant difference in the volume of the largest gall on each leaf was found across density categories.

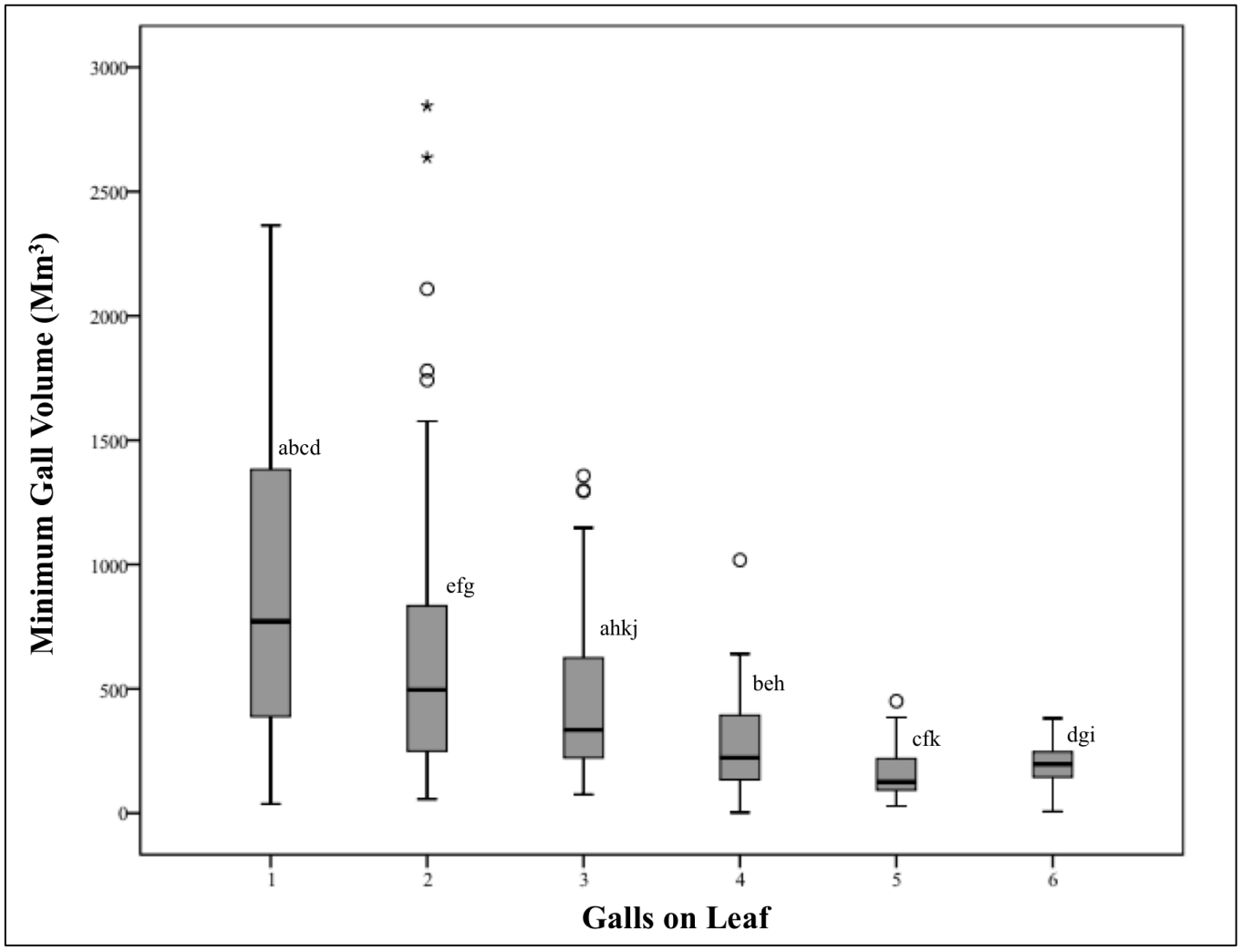

Figure 6. Gall Density as a Predictor for Minimum Gall Volume on a Leaf
The volumes of all galls were measured on 224 leaves with gall per leaf densities ranging from 1 to 6. The volume of the smallest gall on each leaf was then compared across gall density categories. Significant differences in minimum gall volume between pairs of density categories are indicated by letters.

Over all, foundress density, like gall density, appeared to have little to no effect on the maximum size galls achieved, or on the average gall size on leaves. However, foundress density did correspond with significant differences in the size of the smallest galls on leaves, with the smallest galls tending to occur on leaves with increasingly large numbers of foundresses (Figure 7, Figure 8).

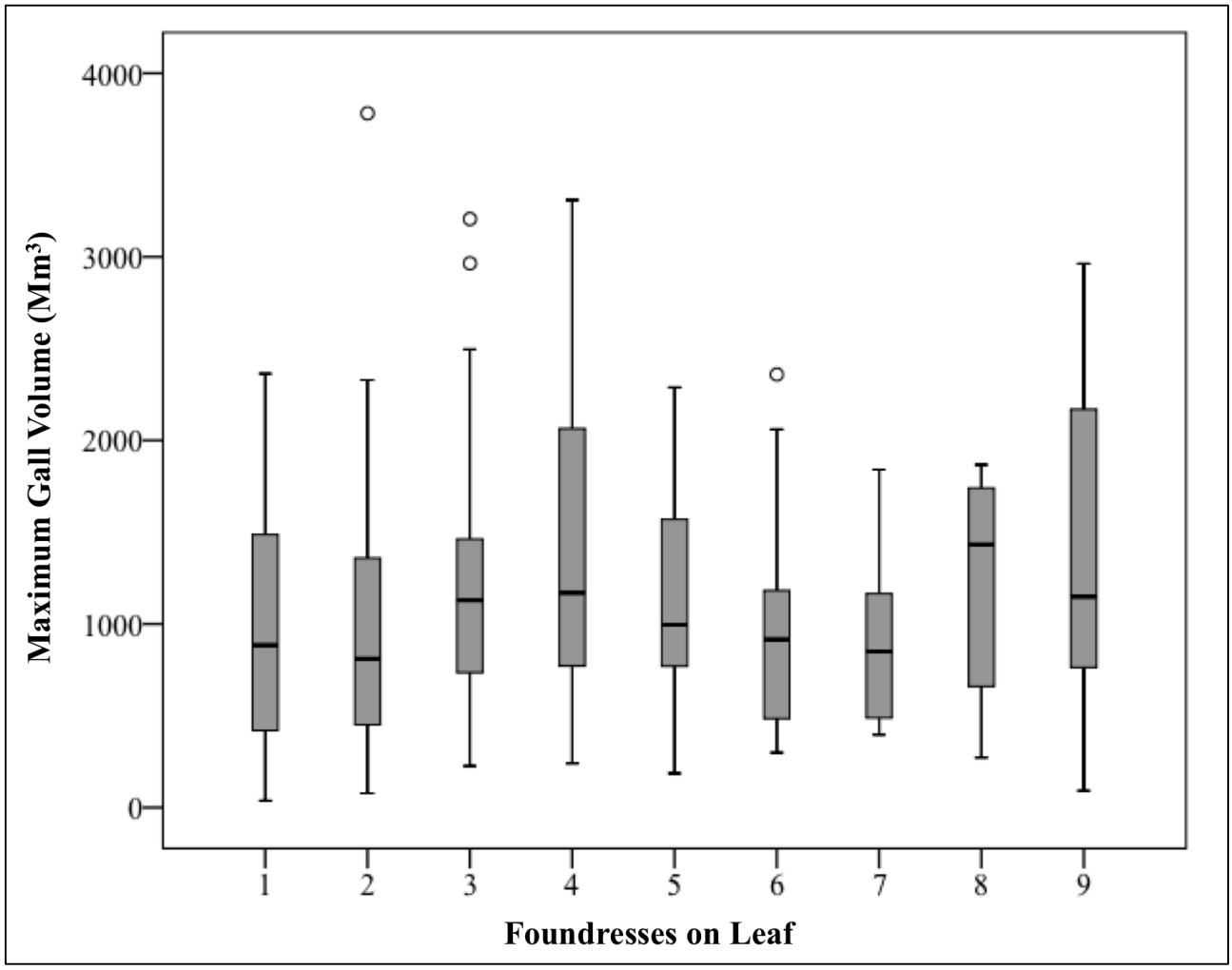

Figure 7. Foundress Density as a Predictor for Maximum Gall Volume on a Leaf
The volumes of all galls were measured on 213 leaves with foundress per leaf densities ranging from 1 to 9. No significant difference in the volume of the largest gall on each leaf was found across density categories.

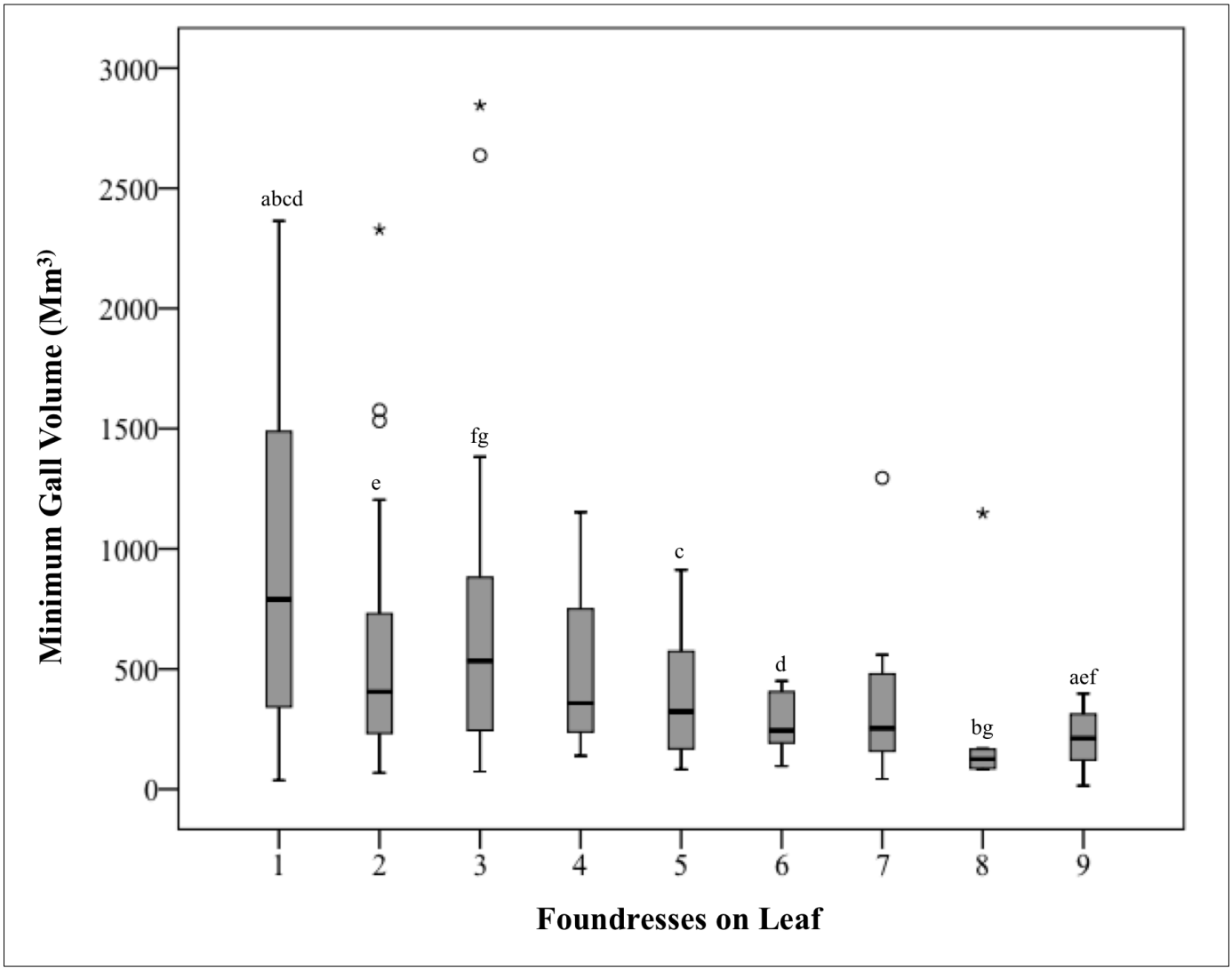

Figure 8. Foundress Density as a Predictor for Minimum Gall Volume on a Leaf
The volumes of all galls were measured on 213 leaves with foundress per leaf densities ranging from 1 to 9. The volume of the smallest gall on each leaf was then compared across gall density categories. Significant differences in minimum gall volume between pairs of density categories are indicated by letters.

Gall Sharing and Gall Size

Gall volumes with 1 (n= 289), 2 (n= 118), 3 (n=45), and 4 (n=11) foundresses were compared (sample sizes were too small to include for galls exceeding 4 foundresses). A check for normality showed the data was positively skewed, and failed the homogeneity of variance

assumption for an ANOVA. A subsequent Kruskal-Wallis test showed the effect of foundresses per gall on gall size to be significant ($\chi^2(3) = 23.978$, $p < 0.001$), with a mean rank of 219.84 for galls with 1 foundress, 224.28 for those with 2, 299.60 for those with 3, and 357.73 for those with 4. A $\log_{10}$ transformation of the data was then done to achieve normality, and an ANOVA then showed that the effect of the number of foundresses on gall volume was significant, $F(3, 475)=8.944$, $p < 0.001$. Post hoc comparisons using the Tukey HSD test indicated that the mean volume for galls with 1 (M = 815.09, SE = 33.45) and 2 (M=833.81, SE= 56.17) foundresses per gall were significantly different from the mean volumes of galls with 3 (M=1219.73, SE= 108.39) and 4 (M=1568.64, SE= 210.64) foundresses per gall (all units are Mm^3; see Figure 7 for corresponding pairwise confidence intervals). Over all, the number of foundresses in a gall appeared to have some effect on gall volume, with a higher number of foundresses per gall tending to correspond with larger galls (Figure 9).

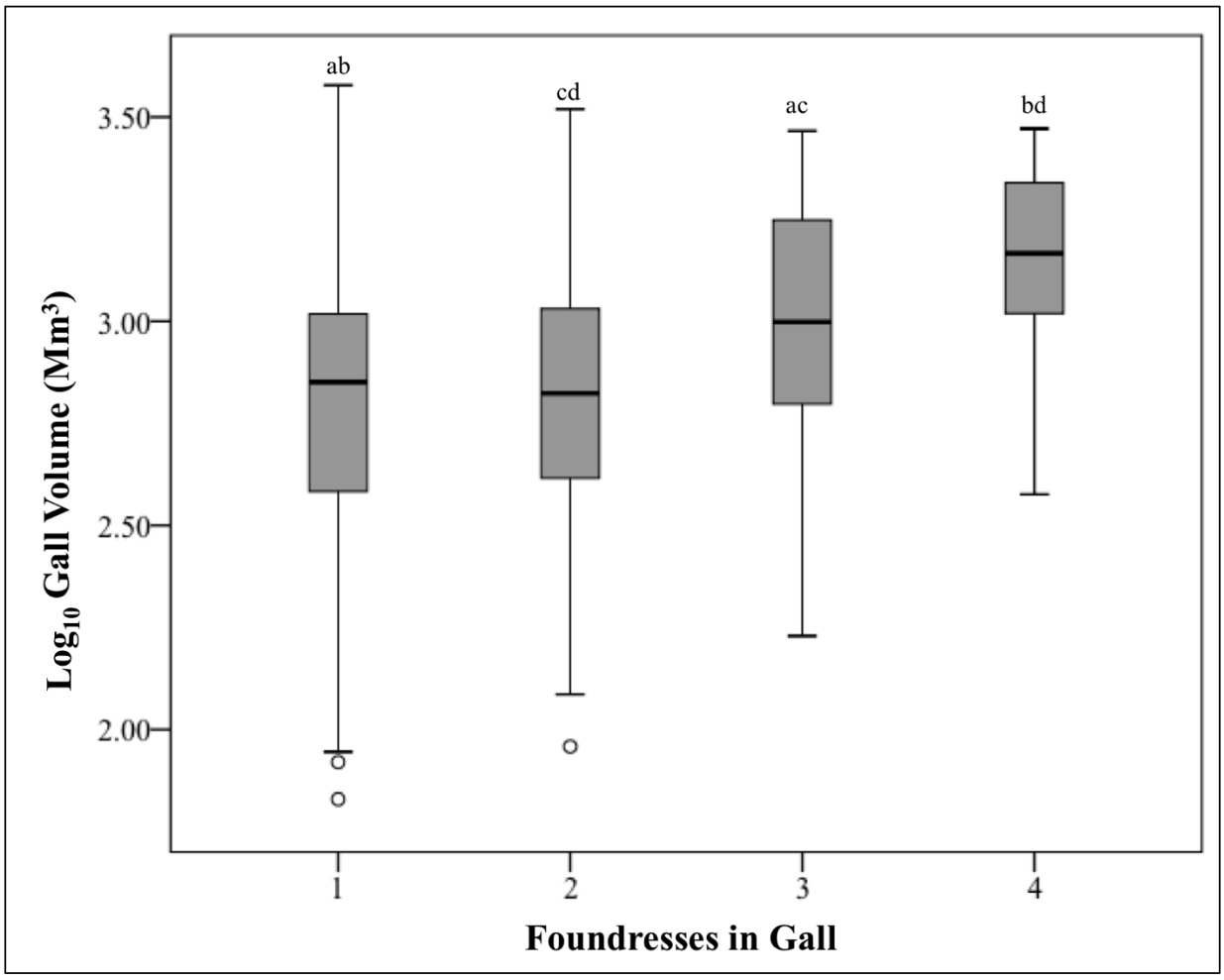

Figure 9. Foundress Count in Galls versus Gall Volume
The volume of 463 galls containing 1 to 4 foundresses was measured and compared between foundress/gall groups. Letters indicate significant differences between pairs of foundress/gall groups (p <.001 for all indicated significant differences).

Gall Position and Preferred Galling Sites

The importance of gall location on leaves and shoots is well documented, but to the knowledge of the author it has never been formally explored for *Tamalia* galls on these plant parts (Miller 1998a examined gall location on *A. patula* inflorescences). The position of a gall on a leaf may, among other things, alter its access to plant resources. For the current dataset, a simple assessment of galls in basal (lower half, closest to base of leaf and petiole) versus distal (upper half, closest to leaf tip) leaf positions was done. In a sample of 356 leaves comprising

1076 galls, 688 were found in basal positions, while 388 were in distal positions. If gall leaf position plays no role in the selection of gall sites, it would be expected that the numbers of basal and distal galls on the largely symmetrical, obovate *A manzanita* leaves would be roughly the same. A Chi^2 goodness of fit test to determine the likelihood that the observed galls came from a larger population with equal proportions of basal and distal galls was significant ($\chi^2(1) = 83.643$, $p < .001$), suggesting the observed deviation from an equal proportion is not random, and that leaf position does play a role. More galls were found in basal positions across all subsets of gall/leaf densities that were examined as well, with a Chi^2 goodness of fit test showing this difference to be significant for leaves with 1 ($\chi^2(1) = 44.507$, $p < 0.001$), 2 ($\chi^2(1) = 80.899$, $p < 0.001$), 3 ($\chi^2(1) = 13.5$, $p < 0.001$), and 5 ($\chi^2(1) = 7.026$, $p = 0.008$) galls (Table 5).

Table 5. Basal and Distal Gall Frequencies Across Gall Densities

Galls on Leaf	Basal Galls	Distal Galls	Leaves
1	65	8	73
2	149	29	89
3	135	81	72
4	118	94	53
5	94	61	31
6	73	71	24
7	54	44	14
Total	688	388	356

Gall Position and Gall Size

From a sample of 465 galls (empty galls and galls with immature foundresses were eliminated), volumes were compared between basal (N= 309) and distal (N=156) galls. An initial ANOVA violated the homogeneity of variance assumption, so an independent samples Mann-Whitney U test was done, which indicated that gall volume was greater for basal galls (*Mdn*= 826.551 Mm^3) than for distal galls (*Mdn*=614.907 Mm^3), *U*= 29912.000, $p<0.001$. The data was then transformed using a $\log_{10}$ transformation to achieve normality, and a subsequent ANOVA

verified that the effect of leaf position on gall volume was significant, $F(1, 463)=20.483$, $p<.001$ (Figure 10).

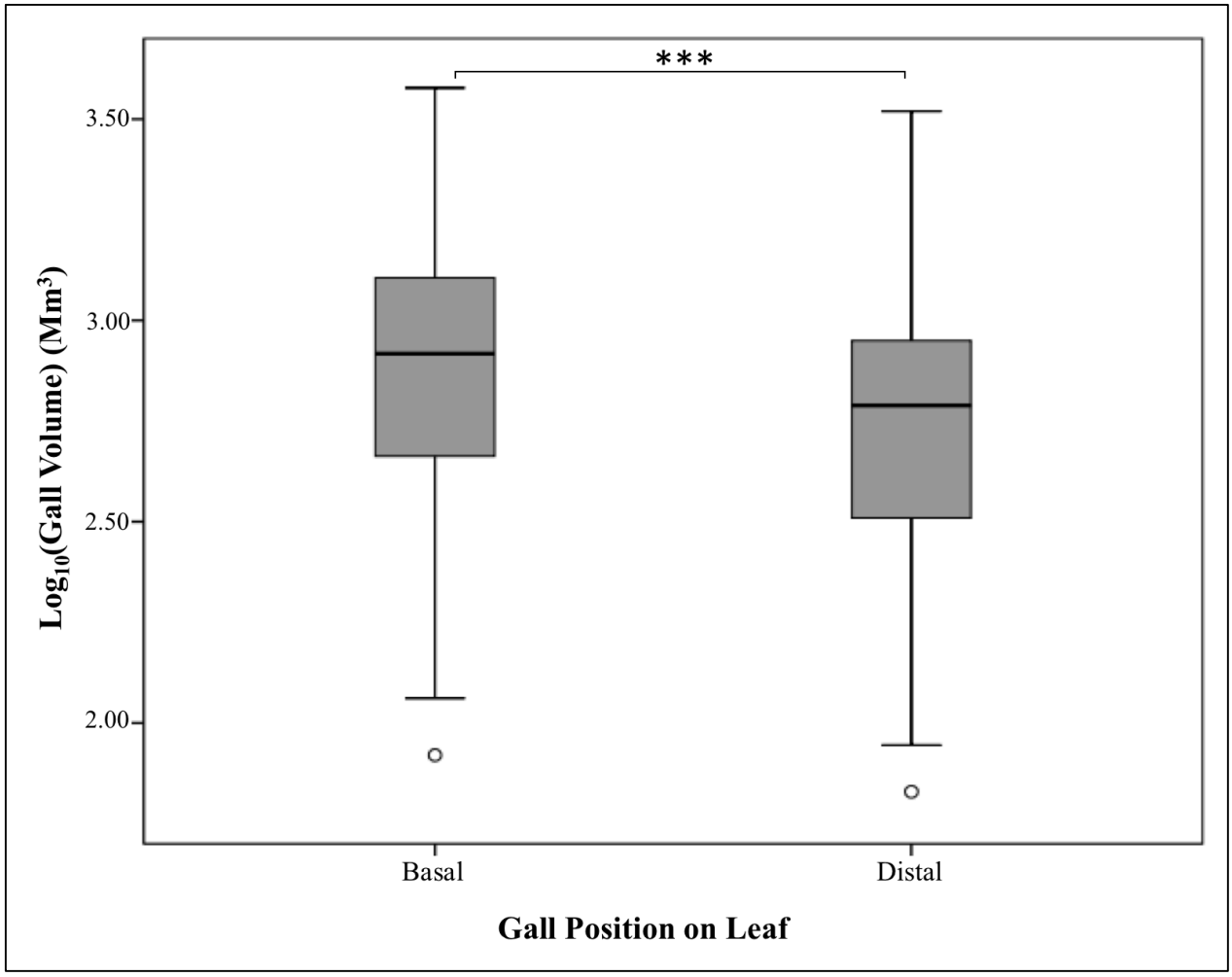

Figure 10. Gall Size in Basal and Distal Leaf Positions
The position of each gall on a leaf was analyzed; galls found on the bottom half of the leaf near the petiole were determined to be basal, and those on the top half of the leaf near the leaf tip were considered distal. The volume of basal (N= 309) and distal (N=156) galls were compared, showing the average volume of basal galls to be larger.

Gall Sharing in Basal and Distal Galls

Of 355 shared galls, 230 were in basal positions and 105 in distal positions. Although more basal galls were shared than distal ones, this proportion was highly reflective of the basal to distal proportion of the larger dataset. A Chi^2 goodness of fit test to see whether the proportion of

basal to distal cofounded galls differed from this proportion in larger gall dataset was not significant ($\chi^2(1) = 0.000$, $p = 0.991$). This suggests that shared galls are not more likely than singly occupied galls to be found in basal (or distal) positions, and provides no evidence for clustering of shared galls in one leaf position over the other.

CHAPTER IV

DISCUSSION

Gall-Sharing Rates and Population Density

The results of the current study showed a clear relationship between population density and gall sharing rates for *Tamalia coweni*. All three measures of density—foundresses and galls per leaf, as well as the amount of leaf margin occupied-- proved to be significant predictors of both cofounding on leaves, and the number of cofounded galls per leaf. The headcount of foundresses proved to be by far the strongest of the three, however. The reason for this, in part, can be explained by the fact that the number of galls on a leaf truncated off around 5 galls per leaf (88.9% of all leaves had five or fewer galls), but by comparison- the number of foundresses per leaf had a much larger spread—with roughly 87% of leaves having 9 or fewer foundresses. In addition to this, the number of foundresses per gall remained relatively even across densities, meaning that as the number of foundresses progressively exceeds the number of galls, the number of cofounded galls also tends to rise in a predictable fashion (as opposed to a more haphazard pattern of clustering huge numbers of foundresses in one gall on some leaves, and having a more even distribution on others). As *Tamalia* are the only aphids known to cofound their galls consistently, this pattern is notable in and of itself, although it stands alone without a greater context of aphids for comparison.

To a degree, the number of galls per leaf and the number of foundresses per leaf are closely related variables. Given the above assessment, it becomes somewhat clear why the number of galls per leaf is not as good a predictor of cofounding as the number of foundresses per leaf. Beyond a certain point, the number of galls that tend to be found on a leaf tapers off.

This is likely due to a space limitation. However, the number of foundresses per leaf has a much greater range than the number of galls per leaf, meaning that at high numbers of foundresses, the number of galls per leaf will be a poor predictor of additional cofounded galls. In addition, it is worth noting, that 25% of leaves had only a single foundress, meaning there *couldn't* be cofounding on that leaf, and that all of those data points will predict the absence of cofounding with perfect accuracy. In contrast, leaves with a single gall may or may not be cofounded- and there is no level at which there is certain accuracy for predicting cofounding when using galls as a measure.

If there is a strong relationship between cofounding rates and resource availability—that is, that foundresses on a leaf without enough space to create an additional gall would instead opt to share a gall—we would expect that the amount of available leaf margin would be a strong predictor of cofounding rates. The regression data suggests the amount of available margin is a significant predictor, although it is less accurate than both the head count of foundresses, and number of galls per leaf. There are a number of possible explanations for this. Leaf margin, like the number of galls per leaf, has no categories where there is assured accuracy, putting it at a disadvantage when compared with a head count of foundresses. One possible problem with leaf margin, is that unlike foundress and gall counts, it was estimated, and therefore likely less accurate. A number of things were done to mitigate this. When estimating, a clear overlay grid was used to help estimate difficult leaves. Still, however, some leaves had quite irregular gall orientations and were difficult to estimate, giving a certain margin of error. To account for this, the data analysis was done a number of ways-- using both raw, continuous data (0 to 100% of margin used), as well as groupings of data into categories (by 10%, 20% and 25% intervals). While estimation errors were likely, it is unlikely that estimations would incorrectly distinguish

between leaves with, for instance, 25% and 50% of leaf margin occupied. Doing the analyses with categories produced almost identical results, so the raw data was ultimately used.

Another possible explanation for why leaf margin is a relatively poor predictor of gall-sharing, is that available leaf space itself may not be a strong underlying factor driving cofounding. One possible explanation for this is if a significant amount of gall-sharing occurs due to late comers arriving at a leaf after it is close to maturity. In this scenario, an aphid might be unable to form a gall on a leaf, or the leaf tissue may no longer support the induction of quality galls. This study did not look at the relatedness of foundresses in galls and as such cannot determine whether or not foundresses sharing galls are clone mates deposited by the same mother at the same time; however, a casual assessment of foundress ages was done for each gall. If a gall was shared because of a late arrival, age difference between foundresses would be a telling marker of this. In the current data, out of 361 cofounded galls, 33 (9.1%) were marked as containing foundresses of visibly different instars (immature, adult, and mature, were the rough assessments used), a good proxy for age. While this is a small but notable proportion, it is almost certainly an underestimate. Foundresses go through four molts before reaching adult size—a process that can take a number of weeks. Over the course of this period, leaves mature, and an aphid arriving while an established foundress is still young, but after the optimal gall induction window for the leaf has passed, is very possible. In this scenario, visually noting age difference between aphids would be difficult, and certainly would not be picked up via the methods used in this study. Additionally, Taylor & Miller (2014) demonstrated that gall-mates are likely to be clone mates 50% of the time in doubly-occupied galls, which indicates a sizeable proportion of shared galls may have (non-clone mate) foundresses that likely arrived at different times.

The results of this study align very closely with those by Miller, in which manipulated population densities of *Tamalia* foundresses on caged *A. patula* inflorescences showed a strong correlation between the number of foundresses, and both the number of galls that were induced on each inflorescence and the number of those galls that were shared (Miller 1998a). The fact that the numbers from this study, where the aphids could move freely, align so closely with a similar study where the aphids were caged in place, reinforces the idea that the *effective* habitat selection—at least as far as foundress choice is concerned—may be relevant on a very local level.

Tamalia coweni and the Plant Vigor Hypothesis

The results of this study showed generally mixed support for the PVH; locations chosen more frequently showed some evidence of a fitness advantage, but overall, the importance of factors other than plant vigor—such as timing—appeared to offer important possible insight into the gall distributions that were observed.

Both foundress per leaf and gall per leaf densities were used to assess the effect population density had on gall size. Despite measuring somewhat differing consequences of density, in all cases these measures aligned with one another, so for simplicity they will be discussed together as simply population density. Density had no effect on the maximum gall size achieved on leaves, or on the mean volume of galls across density categories. This was a surprising finding. We might expect that as the number of galls per leaf increased, the strain on limited resources for the plant would increase, and fitness would decrease (unless, possibly, aphids were capable of controlling nutritional resources from the host plant). The current study did not assess offspring count in enough detail to verify that despite no gall size differences, there was also no difference in offspring count. However, given the strong amount of evidence

for gall size being a reliable correlate of offspring count, and the fact that in general, the current data aligns with this correlation as a whole—there is no strong indication there would be a difference.

However, in a notable deviation from the max and mean gall size, the volume of the smallest galls on a leaf differed significantly across density categories, with smaller galls generally being found on leaves with increasingly high densities. While numerous studies have looked at similar measures regarding the relationship between gall density and volume, the picture that emerges from these studies is complicated, with higher densities being linked to both smaller and larger gall sizes (and resulting increased fitness), as well as some showing no strong correlation (Rehill & Schultz 2001; Stiling & Moon 2005; Santos 2011).

The current study suggests that one possible explanation for these conflicting results may be that in some cases the answer may be a bit more complicated. If the maximum and mean gall sizes do not appear to be affected by population density, limitations of plant resources alone may not play a predominant role in gall size achievement. One way to square this with the trend seen for the minimum gall sizes in the current study, is that, beyond the limitations of nutrition from the host plant, timing may play a key role in determining gall size. If the largest galls are the first ones to be formed on a leaf, they would effectively have a head start from a resources perspective. In addition, galls initiated later would not only face potential crowding-itself limiting gall size as late-comers must utilize whatever limited and irregular gall spaces are still available, but in addition, late comers would likely initiate their galls as the window of gall-ability for the leaf was closing. The leaf tissue itself may no longer be as optimal for gall induction, which may result in sub-optimal galls.

Galls in the basal half of leaves were significantly larger on average than those in distal positions. In addition, a notable majority of galls were located in basal positions. While the size difference between basal and distal galls may make sense from a plant resources may be plausible—especially in light of evidence that basal galls may be able to deploy a broader range of resources than distal galls (Whitham 1978), it is worth noting that another plausible explanation for the size difference between basal and distal galls is timing. The predominance of basal galls is most pronounced in leaves that have only one or two galls, suggesting that more often than not, these are the first locations chosen on a leaf when all sites are open. If basal galls tend to be the first galls initiated, they not only would have had a potential advantage by an initial period of low competition for plant resources, but they also likely had the longest period of gall induction that spanned the period of optimal receptivity to galling in the leaf tissue. These may be contributing factors to why basal galls tend to be larger than distal ones.

This explanation would not necessarily answer the question of *why* basal sites are chosen more frequently than distal ones, however. One possible explanation for this preference, is that basal sites may provide limited protection from predators and the elements before galls can enclose them (Rehill & Schultz 2001). While leaves on *A. manzanita* eventually are exposed in a growth with alternating leaves, they begin in an enclosed leaf bud, which opens before elongating in maturity. Very young aphids might find protection from the hot sun, as well as some predators, by remaining immersed in the early leaf bud, and initiating galls near the base of the leaves. Once their galls are established, they would then be protected by their own enclosures. Aphids arriving later would find limited basal positions available, and would not have the protection of the early leaf bud—making later galls potentially riskier to initiate.

There was no evidence whatsoever that basal galls were more or less likely to be cofounded than distal galls. In fact, the proportion of basal to distal cofounded galls was almost identical to the proportion of basal to distal galls over all. If gall sharing were an attempt to cluster around optimal galling sites, we might expect to see more cofounded galls in some parts of the leaf than others. At least on a basal to distal measure—despite a strong majority of galls being found in distal sites, there is no evidence that cofounding itself occurs more in basal positions. If cofounding tended to occur when multiple foundresses arrived late to a leaf, and chose to share the limited space left to them, we might expect slightly more cofounding to occur in distal positions, which may tend to be founded later. While these scenarios can't entirely be ruled out, the current data does not provide any indication that they are at play. Instead, as the number of foundresses on a leaf rises, so does the number of cofounded galls.

Galls with three and four foundresses tended to have, on average, larger volumes than galls with only one or two foundresses. Within the current study, it is difficult to assess what is cause and what is effect in this scenario, but a number of explanations may be plausible. If additional foundresses were present during the gall initiation process, the pooled resources for manipulating the plant tissue would be greater, and could in theory result in a larger gall. If the foundresses showed up after the initial growth phase, they may have chosen larger galls over smaller ones, due to a greater amount of space being desirable. While this explanation seems logical, there are a few reasons it may be less plausible. For one, it assumes the foundresses would be actively measuring gall size. In addition, it assumes that aphids arriving late to a leaf would have equal access to all the galls on that leaf in the first place. As galls mature, the outer walls become tough and the opening effectively closes, making it difficult or potentially

impossible for aphids to enter. It is possible that larger galls take longer to grow and to reach this kind of maturity, and as such have a longer window during which they could be invaded.

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