



Communal Gall Sharing Enables Interspecific Brood Parasitism in *Tamalia* Gall Aphids

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ABSTRACT

I sought to evaluate the hypothesis that primitive social behavior, in the form of aphids sharing gall space, facilitates the evolution of specialized inquilines exploiting this behavior. Because gall-inducing *Tamalia* aphids reproduce parthenogenetically, gall-mates are, potentially, clonally related, theoretically reducing conflict within the gall. Consequently, mean levels of relatedness were estimated for foundresses sharing galls. Phylogenies of gall-inducing *Tamalia* aphids and their inquilines were generated to pinpoint the origins of the inquiline clade. Further, I evaluated the hypothesis that maintenance of inquiline populations is a function of density dependence in the host aphid species. Field trials were carried out to compare modes of dispersal of gall-inducers and inquilines within and between host plants. The abundance and density of both gall-inducers and inquilines were monitored on populations of host plants. The presence of inquilines appears to depend on the abundance of the host aphid. The high tolerance of gall-inducing females for others in the gall appears to enable its exploitation not only by additional gall-inducers but also by *Tamalia* inquilines, close relatives acting as obligate social parasites of gall-inducers. The origin and maintenance of *Tamalia* inquilines may be consistent with a pattern of density dependence, but the ecological factors associated with this remain unclear.

Key words: gall, aphid, inquiline, *Tamalia*

Introduction

Unlike the majority of gall-inducing insects, the aphids (Hemiptera) and thrips (Thysanoptera) are distinctive in that they occupy hollow, rather than solid galls on their host plants. Thus these insects undergo development and reproduction within an arena in the confines of the gall, potentially setting the stage for social behavior as well as its

exploitation by social parasites. Because all aphids reproduce through parthenogenesis for at least a portion of their life histories, aphid reproduction may occur clonally as well as sexually. Thus selection acts upon the entire aphid clone (Janzen 1977), which comprises a set of distinctive *morphs*, each specialized for some aspect of the species life history (Dixon, 1998, Abbot, 2011).

The life history of a typical species of gall

aphid involves a sessile, gall-inducing generation alternating with alate (winged) morphs adapted for dispersal from the gall. The gall-inducing progenitor of the clone, or stem mother, is apterous (wingless), with greatly reduced legs and sensory organs; she is highly fecund as well. (In this paper, I refer to all apterous gall-inducing morphs as *foundresses*.) By contrast, the dispersive, asexual morph is winged, with relatively well-developed legs, eyes, and antennae; she is proportionately less fecund, owing to the physiological constraints of investment into wing musculature and associated locomotory apparatus (Dixon and Kindlmann, 1999). A series of parthenogenetic generations culminates in an annual sexual generation yielding novel genotypes (Wool, 2004, Simon et al., 2002).

Tamalia aphids and their host plants, woody shrubs in the Ericaceae, are restricted to North America, with centers of biological diversity in California and Mexico. Upwards of six gall-inducing species of *Tamalia* have been described, including at least one inquiline species (*Tamalia inquilinus*); additional species of inducers and inquilines await description (Miller et al., 2015). *Tamalia* aphids constitute a distinct taxon, only distantly related to other gall-inducing Aphidoidea; hence, they represent an independent origin of gall induction (Remaudière and Stroyan, 1984). The evidence strongly suggests that inquilines and gall-inducers are sister taxa, inquilines having originated from a common gall-inducing ancestor, perhaps in conjunction with a host-plant shift (Miller and Crespi, 2003).

Here I argue that the permeability of the *Tamalia* aphid gall, together with the high level of tolerance among foundresses for sharing gall space, facilitates or *enables* its exploitation by conspecific gall-inducers and, by extension, congeneric inquilines. This remarkable circumstance arises as a consequence of the variably clonal structure of aphid populations, as well as the tolerance for intruders by foundresses. First-instar *Tamalia* foundresses have three options for gaining access to critical gall space for development and reproduction: they may locate a suitable site for gall induction on the host plant, join another foundress in

establishing a gall, or (especially if they are late-comers) invade a gall and share it. Co-occupation of galls is frequent and widespread in *Tamalia* aphids: of 143 populations surveyed between 1993~2017, inspection of 13,700 galls indicates at least 74 of these populations show some level of gall co-occupation (unpublished results). This striking form of elementary sociality is distinctive of *Tamalia* aphids (Miller, 1998a). By contrast, numerous examples exist of agonistic behavior in other gall aphids, ranging up to gall usurpation or even lethal combat (Whitham, 1979, Inbar, 1998, Footitt and Maw, 2018).

When foundresses share gall space, they do so at a significant cost *per capita*: survival rates are highest for foundresses occupying galls singly, declining with increasing numbers of foundresses sharing galls. Similarly, *per capita* rates of reproduction vary inversely with the number of foundresses per gall, although this is not necessarily true for *total* numbers of foundresses and offspring produced in jointly-occupied galls (Miller, 1998b). Mutual tolerance among co-foundresses occurs in many social insect systems, such as ants (Heinze et al., 2017) and wasps (Hunt and Toth, 2017), and may be regarded as a critical enabling mechanism for the origins of sociality in animal groups (Krafft et al., 1994, Prokopy and Roitberg, 2001), but it seems puzzling in the case of *Tamalia* aphids, given its negative fitness consequences. This apparent paradox may find a resolution within the context of group kinship considerations. Because *Tamalia* and other aphids reproduce clonally for at least a portion of their life cycle, the possibility is raised that clonal groups of foundresses may share gall space, reducing to zero any theoretical conflict among them. Hence natural selection acts on the entire genotype, which comprises multiple animals in the case of clonal societies (Janzen, 1977, Stern and Foster, 1996). There is no evidence for kin discrimination between *Tamalia* foundresses, as is true of other taxa investigated for this behavior (Aoki et al., 1991, Miller, 1998b).

As with gall-inducers, *Tamalia* inquilines must occupy galls to complete development and reproduction. Unlike their host aphids, inquilines are unable to initiate galls, acting as obligate parasites. The early stages of gall

induction offer the best opportunities for access by intruders. Inquilines may, alternatively, enter mature, desiccated galls that have opened and released their occupants (the winged, dispersing generations of the host aphids) (Miller, 2004). Typically, inquilines are borne by winged morphs, either hatching from eggs or produced live; but inquilines differ from their gall-inducing hosts by possessing additional flexibility in their life history. Rather than undergoing a strict sequence of sessile gall occupation alternating with a winged, dispersing generation, adult inquilines may produce additional apterae either remaining within their natal gall, or dispersing on foot seeking additional galls to invade.

Genetic evidence from mitochondrial, nuclear, and endosymbiont DNA markers reveals differential rates of evolution in *Tamalia* gall-inducers and their inquilines. Three lines of data support this assertion: 1) the rates of base-pair substitution in mtDNA are 2.5-3 times faster in the genomes of inquilines than that of gall-inducers, 2) haplotype network analysis of populations suggests greater structure in those of inquilines, and 3) host-associated differentiation (HAD) is stronger in inquilines than in gall-inducers (Miller and Crespi, 2003, Miller et al., 2015). The causes of accelerated evolution and HAD in inquilines are not clear, but are likely ecological in nature (Turcotte et al., 2011). These may include greater population viscosity and structure arising from important life history differences, including distinct modes of dispersal. Reduced population sizes of inquilines, relative to those of their host aphids, may cause genetic bottlenecks resulting from greater dynamics of inquiline populations across years. These, in turn, can yield increased population structure and accentuate genetic drift, potentially causing substantial evolutionary change in populations (Wright, 1931, Akimoto, 1988, Funk et al., 2001). Greater population densities of gall-inducers and host plants may engender the origin and maintenance of inquilines, as a consequence of density-dependent processes (Brown and Brown, 1986, Savolainen and Vepsäläinen, 2003). In this paper I explore some ecological and life-history aspects of *Tamalia* aphids potentially sufficient

to promote rapid evolution in inquilines. Specifically, I evaluate the hypothesis that gall-inducers and inquilines employ contrasting strategies of dispersal, reflecting their differing life history patterns.

Materials and Methods

Overview

My research program has combined investigative methods in the laboratory, including standard molecular genetics applications, with original observations and experimental trials in wild populations of aphids and their host plants. Because the biology of *Tamalia* aphids remains, to a considerable degree, imperfectly understood, I have undertaken detailed studies of the natural history and ecology of aphid populations on three principal species of host plant, *Arctostaphylos patula*, *Arctostaphylos viscida*, and *Arctostaphylos manzanita* (Ericaceae), in the Sierra Nevada and Cascade mountain ranges of California, USA, beginning in 1993 and continuing to the present. One of my primary goals was documenting the occurrence and frequency of communal gall occupation in *Tamalia coweni*, and this I accomplished by sampling galls randomly along transects of the host plants, then dissecting and examining the gall contents under a stereoscopic microscope (Miller, 1998a). In a second, experimental field study, I investigated the consequences of communal gall occupation, as well as the potential for kin discrimination among gall foundresses (Miller, 1998b). To reveal kin structure of communal foundresses, galls were sampled and aphids genotyped using amplified fragment length polymorphism (AFLP) protocols (Taylor and Miller, 2014).

Tamalia inquilinus was previously unrecognized, suggesting it existed as a cryptic species (Hebert et al., 2004) until its formal description by Miller and Sharkey (2000). In a prior field-based investigation of inquiline ecology, I estimated survival and reproduction rates by gall-inducers sharing galls with inquilines, comparing those against galls containing gall-inducers only (Miller, 2004).

Construction of *Tamalia* phylogenies has

been carried out using a variety of molecular markers, including aphid mtDNA, nDNA, and DNA of the aphid endosymbiont *Buchnera* (Miller and Crespi, 2003, Miller et al., 2015). This work was performed to 1) establish that the inquiline clade composed a monophyletic group; 2) situate inquiline *Tamalia* within the context of the entire genus, to pinpoint their origins; 3) elucidate patterns of diversification and host-race formation between *Tamalia* aphids and their host plants.

Ecological study of *Tamalia* populations

In this long-term project with my colleague, Colleen Hatfield, we have investigated *Tamalia* aphid populations and their host plants at the Big Chico Creek Ecological Reserve, at California State University, Chico. Specifically, our study populations comprise a 1-hectare mosaic of scrub and oak-pine forest at 550 meters elevation in the Cascade-Sierra foothills. A significant element of this community are the approximately 600 *Arctostaphylos* shrubs, including 400 individuals of *A. manzanita* and 200 of *A. viscida*. Like many fire-adapted plants, *Arctostaphylos* spp. require fire for sexual reproduction (Anacker et al., 2011).

Wildfires in 1999 yielded a highly patchy distribution of surviving trees and shrubs: this irregular pattern of burning opened bare ground in which new *Arctostaphylos* could be established during the following growing season (the year 2000). I estimate that 152 of the total 155 shrubs classified as “juveniles” germinated in 2000, implying that the surviving juvenile plants comprise a single cohort precisely 16 years old (as of 2016). The approximately 350 remaining plants in the study are classified as “mature” individuals, their origins dating back to earlier episodes of fire. Beginning in 2008, all juvenile plants were assigned unique three-digit identities; a randomly drawn subset of mature plants (25 of each species) was similarly coded. The lack of galls on juvenile *Arctostaphylos* shrubs prior to 2008 provided a natural experiment in which arrival rates of gall-inducers and inquilines putatively originating from galls on nearby mature shrubs could be compared, to estimate their relative rates of dispersal and colonization.

Monitoring study plants

Starting in 2008, I inspected all juvenile plants during each growing season, for the presence of any *Tamalia* galls. Up to two galls were collected annually from each plant, representative of different portions of the shrub. I stored sample galls at 4°C until dissection under the microscope. Inspection of fresh galls permitted detection of active gall-inducers as well as any inquilines present. In addition to sampling galls during the growing season, all remaining galls were counted at the conclusion of the growing season in an annual *gall census*. Care was taken to count only those galls produced in a given year: this was verified by including galls only on new branch growth. In addition to counting all new galls on study plants, estimates were made of maximum dimensions of height and breadth, to the nearest cm. These metrics were then used to estimate shrub volume, approximating the surface area of a cone. Gall density was estimated as the mean number of galls/m² of shrub surface area. The annual gall census and shrub measurements were performed as a class activity involving undergraduate students in my general ecology course at California State University, Chico.

Dispersal trials

In this experiment, I tested the hypothesis that inquilines exit their natal galls to seek additional galls in which to develop and reproduce (*gall-exit trials*). Hence I predicted first-instar inquilines would be captured leaving galls disproportionately more often than gall-inducers. In May-Jun 2003, Jun 2006, and Jun 2008, a total of 83 galls (designated “source galls”) on *A. viscida* approaching maturity were selected systematically and marked with flagging. The adhesive material Tanglefoot (Scotts Miracle-Gro, Marysville, Ohio, USA) was then applied to the entire petiole supporting the leaf, potentially trapping any insects exiting the gall on foot. Galls were monitored every three days until aphids were thus trapped on petioles, or for a maximum of 2 weeks. I then collected all trial galls, and, under a stereoscopic microscope, recorded the identity and number of all trapped insects, before dissecting the presumed source galls to record their contents. First-instar gall-

inducers and inquilines are readily distinguished by the presence of capitate setae on the gall-inducers only; setae on inquilines are tapered (Miller and Sharkey, 2000).

In a second experiment, I quantified differences in dispersal rates between gall-inducers and inquilines (*inter-gall dispersal trials*). Specifically, I predicted that inquilines were the more likely to exit galls on foot and appear in neighboring galls. Clusters of newly-mature *A. viscida* galls (from which developing alates had dispersed) were selected haphazardly. With a laboratory pipettor (Eppendorf, Hamburg, Germany) about 100 μ l of fluorescent insect tracking powder (Exosect Ltd, Winchester, UK) were injected into a gall, designated the "donor gall." After monitoring for 1-2 weeks, the donor gall and all neighboring mature galls on the same branch tip ("potential recipient galls") within 0.5 m walking distance were collected and their contents examined under an ultraviolet lamp. Minimum walking distance was estimated (to the nearest 1 cm) between donor galls and all potential recipient galls, which were then collected and their contents examined for evidence of aphid movement between galls.

Results

For the purposes of this study, I established as useful plants only those juveniles surviving long enough to have produced galls, or which were still alive as of 2016 (i.e., had not yet been colonized): this totaled 127 plants (Figure 1). Of these, 96 juvenile plants had been colonized at least once by 2016; 31 plants had never had galls within the time frame of this study. The estimated mean lag between first appearance of galls on juvenile host plants and first detection of inquilines was 2.56 years (SEM 0.3 years, $n = 59$). This is likely an overestimate of the true value, as plants were sampled only during the growing season, and generally once per year. In 18 of 59 cases, gall-inducers and inquilines first appeared in sample galls on identical dates, indicating a high efficiency rate of inquilines locating host aphid galls. Once plants had been colonized by gall-inducers and inquilines, the frequency of inquilines in galls stabilized at ~10%. Based on data for the 2016 season, a

preliminary linear regression analysis showed no significant association between inquiline abundance and gall density ($F = 0.135$, $n = 66$, $p = 0.716$).

I completed a total of 83 gall-exit trials. As expected, all aphids trapped were first-instar larvae. The number of trials with inquilines trapped was 19; by contrast, only 3 trials captured gall-inducers, in spite of the greater abundance of gall-inducers in *Tamalia* populations generally. The total number of inquilines trapped (82) likewise exceeded that of gall-inducers (5), reflecting greater activity of inquilines presumably seeking galls to enter. A test of independence indicated the appearance of inquilines in Tanglefoot traps was highly dependent on the presence of adult inquilines within donor galls, under the assumption that first-instar aphids arose from adults present within adjacent galls ($X^2 = 60.52$, with Yates's correction for continuity ($n = 107$, $P < 0.001$)). Corroborating this was the observation that in 5 of 6 instances of the inquilines trapped by Tanglefoot, the donor gall was found to contain adult inquilines.

I completed 70 inter-gall dispersal trials, inspecting a total of 313 potential recipient galls. Ten galls showed evidence of inter-gall dispersal, in the form of either marked larvae or their exuvia. In nine of these, first-instar inquilines were detected; in one instance, a first-instar gall-inducer was identified, suggesting that marked aphids appearing in potential recipient galls are more likely to be inquilines than gall-inducers. In nine of ten cases, I found marked animals in the nearest neighbor gall. Mean distance of dispersal was 3.3 cm (± 2.8 cm SD).

Discussion

Tamalia gall-inducers and inquilines show striking differences in dispersal patterns within host plants and gall occupation rates, apparently reflecting their distinct life history strategies. These may be considered at two spatial scales: a coarse-grained scale (movement in meters or tens of meters) for colonization of new plants, by alate adults; and a fine-grained scale (movement in cm) for dispersal between galls on the same host plant, by ambulatory first-instars.

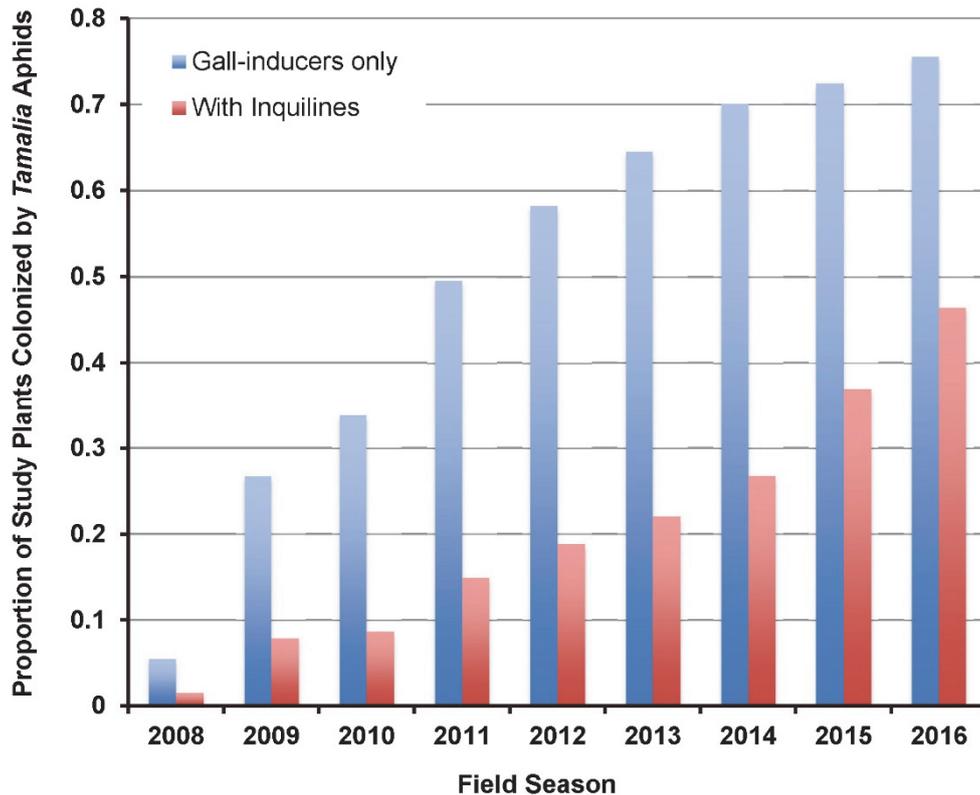


Fig. 1. Cumulative colonization by *Tamalia* aphid gall-inducers and inquilines, as a proportion of the total set of juvenile *Arctostaphylos viscida* and *Arctostaphylos manzanita* plants in the study population at the Big Chico Creek Ecological Reserve, 2008-2016.

The juvenile plants in my study population were first colonized in 2008, nine years following the 1999 wildfire. Figure 1 demonstrates an increasing rate of colonization of plants, which begins to attenuate in 2012 until 2016, the most recent year for which data are available. By contrast, the frequency of inquilines in galls increases only gradually at first, then accelerates in 2014~2016, suggesting inquiline colonization of plants proceeds according to properties spatially different from those of the gall-inducers. These trends indicate that, at some point, inquiline colonization rates will reach an asymptote approaching that of the proportion of plants colonized by gall-inducers. Because the detection probabilities (Mackenzie et al., 2006) of inquilines are lower than that of gall-inducers, colonization rates by inquilines are likely underestimates. A minimum dispersal-distance hypothesis, as has been proposed for benthic marine propagules, may best explain aerial patterns of dispersal in

relatively weak fliers such as aphids (Dixon, 1998, Shanks et al., 2003).

According to my experimental evidence, first-instar *Tamalia* inquilines were significantly more likely to appear in Tanglefoot traps than were gall-inducers, and more likely to move between galls. This pattern of activity is consistent with the hypothesis that inquilines readily seek and occupy gall space (Miller, 2004). A minority of first-instar gall-inducers may also act as opportunists by invading established galls (unpublished data). Alternatively, first-instar inquilines may develop inside their natal gall rather than exiting. Both patterns of behavior may be a function of density dependence, such that crowding within a gall promotes inter-gall dispersal. Another important biological aspect of *Tamalia* inquilines is the reproductive flexibility of adult apterae within the gall: these females may invest differentially in apterous or alate (pre-winged) offspring, perhaps owing again to conditions of density (Gilbert, 1980, May et al.,

1981) but this hypothesis remains to be documented in detail. Such a pattern would be consistent with the general flexibility of aphid clones making investment decisions in offspring as a function of crowding (Dixon and Kindlmann, 1999, Shibao et al. 2010), as well as the hypothesis that the interspecific inquiline strategy originated from an intraspecific, opportunistic one.

In a broader, ecological context, *Tamalia* gall-inducing aphids and their inquilines are characteristic of xeric plant communities in North America, where periodic fire plays a critical role in maintaining host plant populations of these specialist insects. The spatial and temporal aspects of ecological succession following wildfire have evidently provided an evolutionary backdrop in which gall induction by *Tamalia* aphids has originated; opportunistic strategies employed by *Tamalia* inquilines may well be derived from similar intraspecific behaviors in *Tamalia* gall-inducers. The precise roles of density dependence on colonization rates, reproductive investment decisions, and dispersal both within and between galls remain to be elucidated, but hold promise for future investigations. For example, high-precision global positioning system technology (Trimble Inc., Sunnyvale, California, USA) may be applied to develop detailed maps revealing the patterns of colonization and dispersal by both *Tamalia* gall-inducers and inquilines. These, in turn, can facilitate evaluating whether inquiline populations are indeed highly structured and more subject to genetic bottlenecks than those of the gall-inducers. Such data may additionally test the hypothesis that alate *Tamalia* aphids act as “aerial plankton” by moving randomly among host plants according to a minimum-dispersal model (Shanks et al., 2003, Williams et al., 2005).

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Tamalia 屬造瘿蚜蟲的蟲瘿空間共享習性致使種間的巢寄生行為

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摘 要

本研究藉由蚜蟲可共享蟲瘿空間的習性進而促使客居者特化出利用蟲瘿之行為，檢測原始的社會昆蟲行為假說，因造瘿蚜蟲 *Tamalia* 屬行孤雌生殖，瘿室內成員應皆為同胞近親，理論上可減少瘿內的衝突，故可藉由分析共存於蟲瘿內的各幹母的親緣關係，建構 *Tamalia* 屬瘿蚜及其客居者的系統發生來瞭解客居者的起源。本研究也進一步探討客居者維持族群與寄主蚜蟲之間有無符合密度應變假說，比較野外造瘿者及客居者於寄主植物的種內及種間散佈模式，並監測造瘿者及客居者在寄主植物上的豐度及密度，結果顯示客居者存在與否取決於蚜蟲寄主的豐度。造瘿蚜蟲對於其他物種可並存於瘿內的高度容忍性，促使其他造瘿者及 *Tamalia* 客居者利用此一習性，這些與造瘿者近緣的客居者也演化為專一性的群居寄生者。*Tamalia* 客居者的演化起源及族群維持可能與寄主的族群密度關聯，但相關的生態因素則仍有待發掘。

關鍵詞：蟲瘿、蚜蟲、客居者、*Tamalia*