

The Ecology of Inquilinism in Communally Parasitic *Tamalia* Aphids (Hemiptera: Aphididae)

DONALD G. MILLER III¹

Department of Biological Sciences, California State University, Chico, CA 95929-0515

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ABSTRACT I report the first example of communal parasitism in galling aphids and quantify the effects of gall invasion by the inquiline aphid *Tamalia inquilina* Miller on its host, *Tamalia coweni* (Cockerell). On populations of the host plants *Arctostaphylos* spp., both *T. coweni* and *T. inquilina* exhibited facultatively communal behavior and co-occupied galls with no apparent agonistic interactions. Although total reproductive output of adult offspring was similar between galls containing *T. coweni* alone and galls with both species, the allocation of brood was skewed toward that of the inquiline; hence, *T. inquilina* is a parasite of *T. coweni*. The presence of *T. inquilina* had no significant effect on survivorship of *T. coweni* in mixed-species galls. *T. inquilina* successfully reproduced in open galls abandoned by *T. coweni*, and under these circumstances was best characterized as commensal rather than parasitic. My data indicated *T. inquilina* was significantly more likely to move between galls, supporting the hypothesis that the inquiline actively seeks galls to invade. As frequent occupants of unsealed galls, *T. inquilina* may incur higher risks of predation and desiccation than *T. coweni*; experimental evidence showed that at least one specialist predator preferred *T. coweni* to *T. inquilina* and that *T. inquilina* withstood experimental desiccation for significantly longer periods than did *T. coweni*. I suggest the distinctive morphology of *T. inquilina* is a correlate of the ecology of its parasitic life history on *T. coweni*.

KEY WORDS *Tamalia*, communal, inquiline, aphid, parasite

THE ECOLOGY OF EXPLOITATION is a diverse and important theme in the evolution of animal behavior. Among the forms of exploitation are brood parasitism, in which conspecifics or heterospecifics reduce their parental investment by depositing young or eggs into nests of other individuals (Friedmann 1928, Yom-tov 1980, Tallamy 1985, Rothstein 1990). A variation on the theme of brood parasitism is social parasitism, which in a broad sense, involves the exploitation of social behavior through appropriation of brood care or useful nesting space by often closely related species (Schmid-Hempel 1998, Savolainen and Vepsäläinen 2003). The success of both brood and social parasitism is likely to be dependent on their frequency relative to the exploited individuals or species (Barnard and Sibly 1981, May and Robinson 1985). However, social parasitism is more intrusive in that it may involve the continued presence not only of juvenile stages but adults of the parasitic species (Wilson 1971, Buschinger 1986).

Social parasitism is known from a variety of taxa, especially the termites, ants, social bees, and wasps (Wheeler 1919, Michener 1974, Field 1992), although it has been reported in groups as diverse as mammals and myxobacteria (Jones 1997, Fiegna and Velicer

2003). Among the more specialized of insect social parasites are inquilines, which obligately invade nests of their hosts because they are unable to establish their own. The social Hymenoptera and staphylinid beetles provide numerous examples of inquiline species, all of which are highly specialized and often overlooked because of their cryptic habits and frequent close resemblance to their host species (Fisher 1983, Reed and Akre 1983, Kistner 2004). As a historically understudied group comprising multiple, independent origins of social behavior, sociality and its exploitation in aphids have only recently received much attention from behavioral ecologists (Ozaki 1995, Abbot et al. 2001, Foster 2002). Although there is a growing literature on the ecology and evolution of aphid sociality, few if any published examples of interspecific social parasitism exist for this group.

Sociality in aphids is typically associated with galls, adventitious growths of plant tissue induced by the specific feeding activities of these sap-sucking insects. As nutritious, protective domiciles, aphid galls constitute an essential resource typically occupied and defended by solitary females (foundresses) against intrusion by competitors (Price et al. 1987, Wool and Burstein 1991, Moran 1993). Like thrips galls, but unlike dipteran and hymenopteran galls, aphid galls are typically hollow: the resultant gall space constitutes an

¹ Corresponding author, e-mail dgmiller@csuchico.edu.



Fig. 1. Inquiline aphid, *T. inquilina* (top), co-occupying a gall on *A. viscida* with its host, *T. coweni* (bottom). *T. inquilina* is markedly more pubescent and sclerotized than *T. coweni*. Both specimens ≈ 1 mm in length.

arena in which behavioral interactions among gall inhabitants can occur relatively freely; furthermore, these galls may house numerous individuals representing overlapping generations (Rohfritsch and Shorthouse 1982, Forrest 1987, Crespi and Worobey 1998). In some aphid species, females invade galls intra- or interspecifically, expelling or even killing the occupant in the process (Aoki and Makino 1982, Akimoto 1989, Akimoto and Yamaguchi 1997, Inbar 1998). In contrast, foundresses of the manzanita leaf-gall aphid, *Tamalia coweni* (Cockerell), can establish galls solitarily or with other females. Thus, *T. coweni* behaves as a facultatively communal species (Miller 1998a). A recently described species, *Tamalia inquilina* Miller, specializes in entering occupied or abandoned galls of *T. coweni* (Miller and Sharkey 2000) (Fig. 1).

The life cycles of *T. coweni* and *T. inquilina* are closely coordinated where they co-occur in western North America. Newly emerged foundresses of *T. coweni* induce galls singly or in groups by repeated probing with their mouthparts along the edges of leaves or on incipient flower buds on the host plant, *Arctostaphylos* spp. (Ericaceae), during spring and summer. The *early phase* of gall induction (Mani 1964) provides a period of at most a few days for possible intrusion by predators or by other *Tamalia* aphids into

the still-open gall. During the *trophic phase* of development, the gall is sealed and foundresses complete their growth and reproduction. After about 4 wk, the gall dries and splits open, releasing adults with wings, marking the *mature phase* (Mani 1964) of gall development. Offspring are either winged asexual females, which disperse and deposit a second generation of foundresses on the host plant, or winged, sexual females and males, which disperse, mate, and produce the overwintering eggs, thus completing the life cycle (Miller 1998a). Mature-phase galls are again vulnerable to intrusion not only by predators of *T. coweni* but potentially by inquiline *Tamalia* aphids. Both inquilines and foundresses require at least temporary residence within galls for their survival, as do all known *Tamalia* (Remaudière and Stroyan 1984). Like *T. coweni*, the first generation of *T. inquilina* is wingless and emerges from overwintering eggs: these wingless females enter galls as first instars during the early phase of induction and begin reproducing alongside *T. coweni* after reaching adulthood. At least some of their offspring develop wings, which emerge from mature-phase galls before dispersing to larviposit another generation of wingless females that will in turn enter still-available galls of *T. coweni*. An unknown fraction of *T. inquilina* offspring apparently remains wingless throughout development and may disperse from their natal galls as first instars, possibly invading other early- or mature-phase galls of *T. coweni* and maturing and reproducing therein. Like *T. coweni*, *T. inquilina* completes its life cycle with the production of winged males and winged sexual females, the latter of which mate and oviposit after dispersing from their natal galls.

In this study, I characterize and quantify communally parasitic behavior by *T. inquilina* on *T. coweni*. I show that the inquiline significantly reduces production of host offspring but has only a negligible effect on host survivorship. I show that inquilines occupy and reproduce within abandoned galls, with no direct impact on the host species. Strong circumstantial evidence has implicated *T. inquilina* as an obligate associate of *T. coweni* (Miller and Sharkey 2000); here, I provide experimental evidence directly confirming this. As obligate invaders of galls, *Tamalia* inquilines are more likely to move between galls under experimental and natural conditions, hence they may incur additional risks of exposure to predation and desiccation outside the gall. I show experimentally that inquilines are less attractive to at least one important predatory species and withstand desiccation significantly longer than do foundresses. These behavioral and morphological attributes appear as part of an adaptive syndrome in this novel form of social parasitism.

Materials and Methods

Study Populations. Foundresses (*T. coweni*), inquilines (*T. inquilina*), and associated predators were studied on populations of the host plants *Arctostaphylos manzanita* C. Parry and *Arctostaphylos viscida* C.

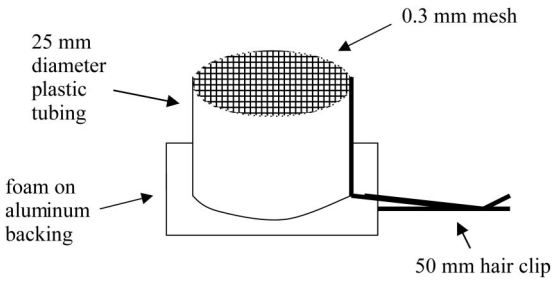


Fig. 2. Clip cage design used for experimental manipulation and collection of *Tamalia* aphids emerging from galls. Cage fits over gall and contains aphids without injuring host plant.

Parry at the California State University Big Chico Creek Ecological Reserve (BCCER), Butte County, CA; *A. viscida* and *Arctostaphylos patula* E. Greene at the University of California Blodgett Forest Research Station, El Dorado County, CA; and *Arctostaphylos glauca* Lindley at the University of California Deep Canyon Research Station, Riverside County, CA during April–August 1995–2003. As is typical of most species of *Arctostaphylos*, these populations are subject to a pronounced seasonal drought, presenting physiological challenges both to the host plant and to plant-feeding insects (Price et al. 1987, Hileman et al. 2001). Although their life histories and ecology are clearly distinct and here treated as such, both *T. coweni* and *T. inquilina* may represent species complexes (Miller and Crespi 2003).

Impact of Inquilines on Host Fecundity and Fitness. Samples of galls were taken over the entire growing season from host plants, and gall contents were examined by means of a stereoscopic dissecting microscope. Particular attention was paid to the timing of both gall establishment by *T. coweni* and the appearance of inquilines in galls; as far as possible, I classified all aphids by developmental stage (instar). As used here, “foundress” refers to either the first or second galling generation of *T. coweni*, and “inquiline” to any wingless individual of *T. inquilina*. Maximum length and width of galls were measured to the nearest 0.1 mm using a reticle mounted on a stereoscopic dissecting microscope: gall volume was estimated assuming galls approximated an ellipsoid with volume $4/3\pi R_1 R_2^2$, where R_1 is one-half the long axis of the gall and R_2 is one-half the transverse axis of the gall. In a general predator survey, the frequency and identity of any predators were noted: particular attention was paid to the timing of the appearance of predators relative to development of the gall.

Production of offspring by foundresses both in the presence and absence of inquilines was compared using spring-clip cages placed over 44 trophic-phase galls in the field and monitored weekly. Cages were constructed of sections of 25-mm-diameter plastic tubing, covered on one end with fine netting (0.3 mm mesh) and attached to spring-loaded hair pins that were glued to a 30-mm square piece of foam on aluminum backing (Fig. 2); these were modifications of

the cage design in MacGillivray and Anderson (1957). I collected and identified all adult offspring emerging from galls, following the key provided in Miller and Sharkey (2000). Using adult offspring as estimates of reproductive success afforded not only greater accuracy in their identification but helped control for juvenile mortality within the gall, which increases to significant levels, especially late in the growing season. Once galls had matured and dried, I dissected them and identified all occupants, dead and alive. Separation of foundresses from inquilines can be done readily even in a desiccated state, because inquilines bear the recognizable features of greater sclerotization (the degree of rigidity of the cuticle; Chapman 1982), greater pubescence, and longer antennal length than do foundresses (Miller and Sharkey 2000). To monitor productivity of late-season galls, I caged a separate sample of 20 mature-phase galls and collected and identified all emergent aphids over a 4-wk period. At the end of the growing season, I collected these galls and recorded their contents.

Life History and Behavioral Syndromes of the Inquiline. To test whether inquilines can induce galls under experimental conditions, I marked 13 treatment groups, each comprising three first-instar inquilines (aphids generally <1 wk old), and 11 control groups of three first-instar foundresses with fluorescent animal tracking powder, and caged them over developing inflorescences of *A. patula*. In the laboratory, aphids were dissected from galls and transferred with a fine artist’s brush to cages consisting of 20-mm-long sections of clear plastic drinking straws (5 mm in diameter) that were stoppered with cotton wool at both ends and that fit snugly over the lowermost secondary stalk of each experimental inflorescence; trials were transported to the field on ice. After transfer to inflorescences, I placed spring-clip cages over each trial: these protected them and helped maintain position of the cotton wool as the inflorescences expanded. I assigned trials randomly to test plants, except that in no case were experimental aphids placed on the same individual plants from which they were collected. The cages were collected after 4 wk, and aphid survival and gall establishment rate were recorded. Because any survivors had molted and were thus no longer identifiable by fluorescent powder, the presence of marked exuvia (shed exoskeletons remaining from the first molt) was used to identify aphids and their most recent location before molting.

To monitor dispersal of any aphids from, and potentially between, galls, I placed 250 cages over trophic-phase galls in the field and inspected them every 2–3 d for 4 wk: all aphids emerging were collected and identified to species and instar. To determine whether inquilines, foundresses, or both enter galls under experimental conditions, I collected aphids from galls and marked them with fluorescent animal-tracking powder, using a fine artist’s brush. I caged 22 groups of three first-instar inquilines and six groups of three first-instar foundresses over mature galls. Gall and cage contents were collected after 1 wk, and the location of any marked individuals was recorded.

Table 1. Effect of the presence of inquilines on productivity of *Tamalia* galls

Gall occupants	Gall phase	<i>n</i>	Adult foundress offspring produced	Adult inquiline offspring produced
Foundresses only	Trophic	24	8.9 ^a (3.0)	—
Foundresses with inquilines	Trophic	20	1.2 ^b (0.7)	7.8 (2.9)
Inquilines only	Mature	10	—	2.7 (1.4)

^a and ^b significantly different (Mann-Whitney test, $P < 0.05$; two-tailed).

The potential adaptive value of the morphology of inquilines relative to foundresses was explored through manipulations of exposure to predators and experimental dessication. *Leucopis* sp. larvae (Diptera: Chamaemyiidae), which are common natural predators of *T. coweni* (Miller 1998a), inquilines, and foundresses were collected from mature galls. In each of 10 trials prepared, five adult inquilines and five adult foundresses were transferred with a fine brush to an opened (and emptied) gall in a 100 by 15-mm petri dish. Five *Leucopis* larvae, ranging anywhere from the second to the fifth instar, were introduced to the gall, and each trial was observed continuously for up to 120 min under a dissecting microscope. Once positioned, each experimental animal was free to move out of the gall. I recorded all direct contacts with the mouthparts by *Leucopis* larvae on the aphids and scored the rate of successful attachment and penetration of the cuticle (once firmly attached, the larva feeds by ingesting body fluids of the aphid, resulting in a noticeable decrease in the size of the aphid). No animal was used in more than one trial; successive attacks by the same predator on the same aphid were not recorded.

To compare the ability of inquilines and foundresses to withstand dessication, therefore simulating evaporative demand outside the gall, 21 adult foundresses and 26 adult inquilines were obtained from trophic-phase galls and transferred to a petri dish, which was placed in a convection (drying) oven at 40°C. The aphids were monitored every 5 min, and their survival rates were recorded: an aphid was scored as still alive if its legs or antennae showed movement.

Statistical Analysis. Statistical procedures were performed with SYSTAT (Wilkinson 1989) and Biostat Basics (Gould and Gould 2002). Nonparametric statistical methods were applied in the analysis of results when data were non-normally distributed (Kolmogorov-Smirnov goodness-of-fit tests on original or transformed data, Lilliefors $P < 0.01$).

Results

Impact of Inquilines on Host Fecundity and Fitness.

The contents of 200 galls on *A. viscida* at BCCER were sampled. Of these, 178 contained at least one foundress or inquiline; predation or abandonment may account for the remaining 22 empty galls. One hundred sixty-one galls contained at least one foundress, and the mean foundresses per occupied gall was 1.10 ± 0.03 (SE; range, 1–5); 58 galls contained at least one inquiline, and mean inquilines per occupied gall was 2.09 ± 0.23 (range, 1–9). Production of adult offspring by foundresses was significantly higher in the absence

of inquilines than when inquilines co-occupied galls (Mann-Whitney test: $U_{20, 24} = 344$; two-tailed $P < 0.05$), although the number of offspring reared to adulthood for foundresses and inquilines combined was about the same for parasitized and unparasitized galls (Mann-Whitney test, not significant; Table 1). Inquiline production of adults exceeded that of foundresses in parasitized galls, but not significantly so (Mann-Whitney test: $U_{20, 20} = 268.5$; two-tailed $P = 0.07$; Table 1). Of 20 mature-phase galls monitored, 10 contained at least one foundress or inquiline and 7 contained at least one living inquiline; none contained living foundresses. Inquiline production of adult offspring continued 2 wk after the last foundress offspring were recorded and ranged from 1 to 12 per gall (Table 1).

Although the presence of inquilines was associated with a decrease in the reproduction of foundresses, inquilines had no measurable effect on foundress mortality rates. In samples of 149 galls containing solitary foundresses and 36 galls with a single foundress and one or more inquilines, 21.1% of foundresses failed to reach adulthood in the absence of inquilines; 20.0% died prematurely when at least one inquiline was present in the gall (χ^2 test for independence; $\chi^2 = 0.01$, $n = 185$, $df = 2$; not significant). Similarly, the presence of multiple inquilines in galls had no significant effect on inquiline mortality rates: in 42 galls sampled containing at least one inquiline, there was no observed mortality before adulthood in any inquilines collected, although as many as nine co-occupied a single gall.

The presence of inquilines had no significant effect on gall size (volume) in early- and trophic-phase galls (early-phase galls containing solitary foundresses only; $79.5 \pm 17.1 \text{ mm}^3$, $n = 11$; galls with one or more inquilines present in addition to solitary foundresses, $112.7 \pm 46.9 \text{ mm}^3$, $n = 32$; for trophic-phase galls, $984.2 \pm 106.6 \text{ mm}^3$, $n = 62$ and $1,003.9 \pm 182.7 \text{ mm}^3$, $n = 27$, respectively; t -tests, $P > 0.5$). Mature-phase galls, by definition, no longer respond with further growth to feeding by galling aphids. When present, additional foundresses do not significantly increase gall size beyond that achieved by solitary foundresses (unpublished data).

The gall-induction experiments provided no evidence that inquilines can induce galls in the absence of foundresses. Twenty of 39 inquilines were recovered 1 wk after trials were set up: all died before establishing galls. In contrast, 21 of 33 foundresses survived long enough to establish 18 galls (test of proportions; $Z = 5.53$, $P < 0.0001$); taken together,

these experimental data confirm that *T. inquilina* is obligately associated with *T. coweni*.

Life History and Behavioral Syndromes of the Inquiline. Although both inquilines and foundresses dispersed from galls and were trapped in cages, inquilines were significantly more likely to do so: 15/42 (36%) of all inquilines collected in cages or caged galls were outside galls; 16/160 (10%) of all foundresses collected were outside galls (test of proportions; $Z = 4.11$, $P < 0.0001$). Of 15 marked inquilines recovered from the gall invasion experiment, 6 had entered galls; of three marked foundresses recovered, none had entered galls. These data are consistent with the hypothesis that inquiline dispersal rates between galls exceed those of foundresses. In field-collected samples of 100 early-phase, 270 trophic-phase, and 430 mature-phase galls, first-instar inquilines were the sole occupants of four mature-phase galls and never occupied early- or trophic-phase galls in the absence of foundresses. First-instar inquilines occurred alongside foundresses in 7 early- and 10 mature-phase galls, but in only 1 trophic-phase gall. These data support the possibility that the trophic-phase gall, being relatively well sealed, is the stage of gall development during which invasion by inquilines is least likely.

In samples of 83 early-phase, 31 trophic-phase, and 63 mature-phase galls inspected for predators of *Tamalia*, *Anthocoris whitei* Reuter (Heteroptera: Anthocoridae), a common predator at all stages of its development, and *Leucopis* sp., a common predator during its juvenile stages, were observed exclusively in mature-phase galls (one or more *A. whitei* in 16/63 and *Leucopis* in 7/63 galls). This suggests that aphids in mature galls are not only vulnerable to invasions by inquilines but also to predation. The single sampling date of galls representing all phases of development from the same population of the host plant controlled for effects of seasonality in the appearance of predators.

In the predator choice experiments using *Leucopis* larvae on adult foundresses and inquilines, successful *Leucopis* attacks resulted in continuous feeding for at least 1 min to a maximum of >120 min before observations ended (one larva was still feeding on a *Tamalia* aphid after >232 min of discontinuous observation). Although larvae were equally likely to encounter and contact foundresses and inquilines (29 contacts with foundresses versus 26 with inquilines, $\chi^2 = 0.16$, $df = 1$, not significant), larvae preferentially attacked and consumed foundresses over inquilines (11/29 observed contacts between *Leucopis* and foundresses led to successful attacks versus 0/26 for inquilines; G -test for goodness-of-fit, $G = 16.55$, $P < 0.001$). When *Leucopis* larvae contacted *T. inquilina*, they seemed to reject them quickly, unlike most contacts with *T. coweni*. In the desiccation trials, inquilines survived outside galls at 40°C significantly longer than did foundresses (200 ± 71 versus 130 ± 46 min); Wilcoxon signed-ranks test, $Z = 3.42$, one-sided $P < 0.001$).

Discussion

Most published examples of social parasitism involve the exploitation of the eusocial (highly social) taxa (Michener 1974, Hölldobler and Wilson 1990). For example, inquiline ants exploit the elaborate reproductive division of labor in ant societies, often with the result that offspring of the inquilines are reared by their adoptive colony (Aron et al. 1999). Although *Tamalia* societies are relatively simple and exhibit no apparent specialized behaviors or morphologies distinctive of eusocial systems, *T. inquilina* obligately invades galls and reduces fitness of its facultatively communal host *T. coweni*. In this inclusive sense, *T. inquilina* acts as a social parasite (Wilson 1971, Buschinger 1986, Bourke and Franks 1995, Schmid-Hempel 1998). Like its host, the inquiline facultatively occupies galls communally: multiple females share galls and breed together, but apparently not through active cooperation. Although inquilines may compete directly with foundresses for host plant resources by feeding and reproducing within the gall, no overt agonistic behavior occurs. This is the first report of communal parasitism in social aphids in the framework of a quantified cost and benefit analysis of the overall effects of parasitism on fitness.

At least six of the seven known species of *Tamalia* exhibit facultative communal behavior in which females co-occupy galls and breed jointly within the gall space (unpublished data). Recent molecular evidence indicates the inquiline clade branched off after the galling life history evolved in ancestral *Tamalia*, possibly in association with a shift in host plant species (Miller and Crespi 2003). Gall invasion involving closely related species is seen also in the facultative inquiline aphid *Eriosoma yangi* Takahashi, which similarly may have evolved inquiline behavior in conjunction with a host plant shift (Akimoto 1988). The close phylogenetic affiliation of *Tamalia* inquilines and foundresses parallels the hypothesized origins of numerous socially parasitic species from ancestral clades of the host species: such labels as agastoparasitism or adelphoparasitism have been applied in these cases (Ronquist 1994, Hunter and Woolley 2001, Foitzik et al. 2003). In *Tamalia*, communal behavior may be considered an ancestral state with mutual tolerance of group members an important first step in the evolution of social behavior (Krafft et al. 1994). Such intraspecific communal behavior, with its attendant risks of intraspecific brood parasitism, may have facilitated invasion and exploitation by incipient inquilines at the origins of interspecific parasitism (Brockman 1993, Zink 2000, Neumann and Moritz 2002).

A parallel is found in the socially parasitic ants, where polygyny (meaning multiple reproductive females in a single colony: common in ants, Buschinger 1986; but rare in galling aphids, Miller 1998a) in the host is a likely precondition for the evolution of inquilinism (Bourke and Franks 1991). Like *Tamalia* inquilines, inquiline ant species tend to occupy polygynous colonies and are themselves polygynous

(Buschinger 1986). Unlike many or most species of ants, and apparently all described species of galling aphid, *Tamalia* societies exhibit no overt agonistic behavior. In the case of intraspecific communal galling, this can be understood readily as additional foundresses impose only a minor demonstrable cost in fitness to their adopters, and indeed may be acting mutualistically under the possibility they constitute clonal groups (Miller 1998b). However, the inquiline competes effectively with its host, implying that selection should favor territorial behavior in *Tamalia* foundresses. The lack of territoriality in *Tamalia* foundresses is striking and parallels the evolutionary puzzle of how various brood and social parasites in a number of taxa, including birds (Yom-tov 1980), fish (Sato 1986), mammals (Jones 1997), wasps and bees (Field 1992), ants (Buschinger 1986), and lace bugs (Tallamy and Horton 1990) succeed in deceiving and exploiting their hosts (Wilson 1971, Johnsgard 1997). There are at least three possible reasons why such territorial behavior has not evolved. First, no evidence of discrimination by *Tamalia* aphids has yet been shown, and these and other aphids may simply lack the necessary neurological and genetically mediated mechanisms needed for precise discrimination of kin (Aoki et al. 1991, Stern and Foster 1996, Miller 1998b, Abbot et al. 2001). In a co-evolutionary arms race between parasite and host species (Dawkins and Krebs 1979), any ability evolving in the host species to recognize parasites comes at a potential cost of discrimination against the host itself (Johnsgard 1997, Lotem and Nakamura 1998). Hence foundresses attempting to eject inquilines from their gall risk ejecting other foundresses as well, some of which may be clone-mates (Miller 1998b). Second, by invading galls early and remaining within them, inquilines may be masked as aliens by adsorbing any chemical signature of the gall or its colony on their cuticle, as occurs in socially parasitic butterflies and wasps (Akino et al. 1999, Sledge et al. 2001). Third, although establishing a gall represents a significant investment in time and energy, the risks of fighting may discourage territorial behavior by foundresses against conspecifics or inquilines (Price et al. 1987, Zahavi and Zahavi 1997, but see Whitham 1979).

When inquilines invaded galls occupied by foundresses, they reduced host reproductive success but had only a negligible effect on host survival rates. Although the proportion of host offspring raised to adulthood was significantly lower in parasitized versus unparasitized galls, total offspring output was about the same for both outcomes. This situation is similar to that of intraspecific brood parasitism in the burying beetle *Necrophorus vespilloides* Hbst., in which females rear the same number of offspring irrespective of whether they are parasitized, even though parasitized females raise significantly fewer of their own offspring (Müller et al. 1990). Like the ecology of inquilinism in *Tamalia* galls, the few previously published studies quantifying the impacts of inquilinism in other plant-feeding hemipterans, cynipid wasps and cecidomyiid flies have reported reduced rates of host

survival, reproduction, or both (Roskam 1992, Ronquist 1994, Heard and Buchanan 1998, Sanver and Hawkins 2000, Yang et al. 2001). However, *Tamalia* inquilines not only invade occupied galls but regularly enter mature, abandoned galls and survive long enough to reproduce, with no direct effect on the host aphid species. Thus this interspecific interaction does not constitute parasitism but may instead be characterized as commensalism, in which one species benefits while the other is unaffected (Begon et al. 1990); Wilson (2000) further refines commensalism involving nests as nest commensalism. The commensal guild of arthropods occupying galls abandoned by the gall-inducers has been described as "successori" by Mani (1964), many of which enter galls seeking shelter, food or both. A multitude of animal species, including not only insects but other arthropods, reptiles, amphibians, birds, and mammals will take advantage of abandoned nests, burrows, and other protective domiciles, but typically few such successori are specialists in exploiting domiciles created by close phylogenetic relatives (Friedmann 1928, Mani 1964, Trenham 2001, Averill-Murray et al. 2002, Mendonça and Romanowski 2002). Apparently, *Tamalia* inquilines are capable of using resources in mature galls abandoned by foundresses possibly for reasons of predation, reduced nutrient quality, or increased evaporative demand. These late-season, senescent galls are unlikely to be highly productive, as shown by the low number of offspring produced by inquilines in mature galls, but this opportunistic life history strategy is consistent with the ability of inquilines to compete successfully in galls still occupied by foundresses.

It is important to note the nonmanipulative nature of this portion of the study. By caging and monitoring naturally occurring galls rather than attempting controlled releases of inquilines into existing galls, it was assumed that inquilines entered galls based primarily on their availability and not based on any preference for poorly defended galls harboring decrepit foundresses. That any evidence for agonistic interactions between foundresses and inquilines has yet to be found, in examinations of thousands of galls (unpublished data), is support for this assumption. However, experimental releases of inquilines into caged galls would permit controlled tests of the alternative hypothesis that *T. inquilina* invades galls in a discriminatory fashion, based on an assessment of the likelihood of successful reproduction therein.

Tamalia inquilines show a significantly greater degree of mobility than foundresses, as evidenced by their exit rates and the capacity to enter galls. Although foundresses likely disperse between galls as well, the distinctly greater rates of mobility in inquilines reflect substantial differences in their respective life-history strategies. Selection of aphid clones comprising single genotypes may favor risk-reducing strategies such as dispersal and developmental plasticity, both of which occur in *Tamalia* and in other parthenogens (Hamilton and May 1977, Janzen 1977, Miller 1998a, Poulin 2003). Inter-gall dispersal has been well documented in an array of galling aphids with such

techniques as sticky traps and molecular markers (Setzer 1980, Aoki 1982, Akimoto 1989, Ozaki 1995). The lack of evidence for discrimination by gall occupants against such interlopers is thought to facilitate this mode of exploitation (Abbot et al. 2001).

My data suggest inquilines incur a relatively high risk of exposure to predators and to desiccation, the latter of which is a constant threat to gall-dwelling insects experiencing arid conditions during the growing season (Price et al. 1987, Morris et al. 1999). The same temporal "window of opportunity" for invasion and exploitation of established galls imposes an increased likelihood of encountering natural enemies (Stone and Schönrogge 2003). However, under experimental conditions, inquilines experienced a significantly reduced rate of attack by a specialist predator and survived desiccation significantly longer than did foundresses. It is not yet clear what factors lend inquilines greater immunity to predators and to evaporative demand, but their distinctive morphology may be important in this regard (Fig. 1): compared with foundresses, adult inquilines are densely pubescent and exhibit significant sclerotization.

The distinct morphogenetic patterns of inquilines may provide further clues about their ecological role with foundresses. In aphid species in which usurpation or defense of galls occurs, specialized morphology for combat is most pronounced in the first instar (Aoki 1977, Aoki and Makino 1982). Greater sclerotization would likewise be expected in first-instar inquilines if it were to facilitate usurpation of galls occupied by *T. coweni*. But exactly the reverse pattern occurs: first-instar inquilines appear unsclerotized, whereas the adult appears by far the most heavily sclerotized stage. This developmental pattern further suggests that the adult morphology of inquilines is more an adaptation to desiccation and predation (both risks of which are more likely in mature galls) rather than a correlate of fighting ability against other gall aphids. The precise degree of differences in sclerotization between inquilines and foundresses remains to be quantified.

Neither the details of the mechanism by which *T. coweni* induces galls nor the events by which the ability to induce galls was lost in the ancestral *T. inquilina* are known. As obligate invaders of galls, inquilines may lack the appropriate probing behaviors or chemical or genetically mediated factors necessary to stimulate a gall. A better understanding of the etiology of gall induction may provide clues about the origins and loss of the galling habit in *Tamalia* as well as in other galling arthropods (Stone and Schönrogge 2003). That *Tamalia* inquilines are effective competitors with foundresses and can successfully reproduce in abandoned and possibly low-quality galls suggests a trade-off occurred between maintaining the ability to initiate galls and the efficiency in extracting nutrients from established galls during selection for the inquiline life history in *Tamalia*. One approach toward quantifying any competition for nutrients between inquilines and foundresses might involve comparing their developmental rates by weighing them over time: this could be carried out with galls containing

foundresses only and with mixed-species galls. Finally, similar examples of inquiline parasitism probably exist in other communal galling societies, e.g., galling thrips (Morris et al. 1999), but perhaps have been overlooked because of close biological similarities between host and parasite: discovering further such examples will require careful taxonomic and ecological investigation.

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