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**Differential Maternal Defense Behavior in Three Species of Treehoppers
(Hemiptera: Membracidae)**

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ABSTRACT

Maternal care in the animal kingdom can vary immensely from species to species, but the reason for its ubiquity underlies an evolutionary impulse to pass on favorable genes to the next generation. In treehoppers, maternal care increases the rate of offspring survival through species-specific levels of protection from both predation and parasitism. To investigate the factors that influence maternal care, I introduced a variety of animate and inanimate stimuli to both brooding and non-brooding treehoppers in three species: *Antianthe expansa*, *Alchisme grossa*, and *Umbonia crassicornis*. By quantifying their responses as proxies for energy output, I concluded that maternal defense is a species-specific phenomenon that is distinct from personal defense, relies primarily on kinesthetics rather than visual input, and is stimulus-dependent. This type of species-specificity is likely governed by different types of environmental pressures that necessitate the evolution of direct defense behaviors or inter-species mutualisms.

Cuido Maternal en Tres Especies de membrácidos (Hemiptera: Membracidae)

RESUMEN

El cuidado maternal en el reino animal puede variar enormemente de una especie a otra, pero la razón de su ubicuidad subyace a un factor evolutivo de transmitir genes favorables a la siguiente generación. En membrácidos (Membracidae), el cuidado maternal aumenta la tasa de supervivencia de las crías a través de niveles específicos de protección contra la depredación y el parasitismo. Para investigar los factores que influyen en el cuidado maternal, introduje directamente una variedad de estímulos animados e inanimados a las hembras con y sin huevos o ninfas de tres especies: *Antianthe expansa*, *Alchisme grossa* y *Umbonia crassicornis*. Al cuantificar sus respuestas como aproximaciones de consumo de energía, concluí que la defensa maternal es un fenómeno específico de la especie que es distinto de la defensa personal. Además, se basa principalmente en la cinestética en lugar de la entrada visual, y es dependiente del estímulo. La especificidad de cuidado maternal según la especie probablemente se rige por diferentes tipos de presiones ambientales que requieren la evolución de comportamientos de defensa directa o mutualismos con otras especies.

The biological foundation underlying both parasitoid-host and predator-prey relationships stems from an innate struggle for survival characterized by adaptive evolution, natural selection, and specialization over time. Treehoppers (Membracidae), in particular, experience parasitism of their eggs from many species of wasps; some of which can be as small or even smaller than the eggs themselves (Godoy et al. 2006). Predation by comparably large invertebrates such as spiders, flies, beetles, and mantids is also common for many treehoppers despite their hard exterior, cryptic coloration, and ant mutualists (Godoy et al. 2006).

As a result, some species of treehoppers have evolved varying levels of subsocial maternal behavior in an effort to protect their brood from both parasites and predators (Godoy et al. 2006). This type of behavior, in contrast to its solitary and gregarious counterparts, distinguishes itself by having the mother facilitate the survival, growth, and development of her offspring (Eickwort 1981). For some species, maternal care may be limited to the passive use of their bodies as shields for their eggs until they hatch, although abandonment prior to hatching may still occur (Haviland 1925). For others, maternal care may extend beyond passive protection through kicking, shaking, and wing vibrations, in response to potential threats (Godoy et al. 2006). In either case, the survival of the offspring often times hinges on the presence of the mother (Cocroft 2002).

However, subsocial behavior of hemipterans also increases the risk of predation and decreases fecundity of egg-guarding mothers (Tallamy and Schaefer 1997). Some researchers suggest that the advent of ant mutualisms and adult aggregations were responses to the heightened risks associated with subsocial behaviors (Gadelha et al. 2016). In exchange for honeydew produced by nymphal or adult excretion, the ants provide protection against potential predators (Gadelha 2016). This mutualism with ants and their propensity to aggregate en masse suggests that there is some visual, kinesthetic, chemosensory or acoustic component relevant to the distinction of friend or enemy. For many treehoppers, the presence or absence of these ants may dictate the nature and extent of their maternal defense.

In my study, I addressed the following questions: (1) does defense behavior of brooding treehoppers depend on the type of stimulus and (2) how does this defense behavior differ among treehopper species. I used *Alchisme grossa*, *Antianthe expansa*, and *Umbonia crassicornis* to study the differential maternal defense behaviors across this diverse family of insects.

METHODS

Subject Selection

All experimental subjects for this study were found in the Monteverde area between 13 November and 25 November. Four brooding mothers with egg masses and one non-brooding mother of *Alchisme grossa* were extracted from the leaves of *Acnistus arborescens* (Guitite trees). No two subjects were ever found occupying the same branch. Each branch containing *A. grossa* was then cut, transplanted into a jar containing water, sealed with parafilm, and placed in a large glass housing for the remainder of the experiments. The same procedure was carried out for two *Antianthe expansa* with egg masses and three *A. expansa* with nymphs. In all cases, adult *A. expansa* were observed to be in groups of three or more with ants and nymphs always close by. One *Umbonia crassicornis* with nymphs was found on an unknown Fabaceae tree and experiments were done on site for this species. Three types of stimuli were used for this study: a stink bug, caterpillar, and a Guitite leaf.

Threat Introduction

Animate “predators” (stink bug or caterpillar) were introduced to brooding mothers using a leaf vector. The leaf was used to mimic a quasi-natural setting to prevent the stinkbug or caterpillar from being prematurely startled prior to each trial. In order to ensure that the predator would make contact with the mother, vinegar was applied with a pincel along the edges and underside of the leaf to deter the predator from moving elsewhere. Physical contact between the predator and the mother or her egg sac and thirty seconds thereafter constituted one trial. At least two minutes were allotted before the initiation of the next trial. For trials in which a treehopper was not on an egg mass, I waited until the subject was stationary to introduce the stimulus.

Fresh Guitite leaves were used as inanimate stimuli for *A. grossa* and *A. expansa* while leaves from the associated Fabaceae plant were used for *U. crassicornis*. One leaf was held to the pronotum of each treehopper for either 5 seconds or 10 seconds. The response during the application of the stimulus and 30 seconds thereafter constituted one trial.

Response Scoring Determination

In order to provide a quantitative measure for the various defensive responses of the treehoppers, I assigned scores to each type of response. Each score was determined based on response frequencies during preliminary observations and relative projected energy outputs. For each trial, the responses were recorded, quantified, and summed as follows: 0: stationary passive defense, 1: movement away from the egg mass, 2: lateral shaking, 3: kicking, 4: wing vibrations, and 5: flying away (Table 1). Statistical analyses of differential maternal defense for the various stimuli were performed using two-sample, two-tailed t tests of the mean and standard deviation values.

Table 1. Response Score Quantification

Score	Name	Behavior in response to stimulus
0	Stay	Remaining stationary; passive defense
1	Movement away	Walking away
2	Shake	Shaking of the body laterally
3	Kick	Kicking of the stimulus using its hindlegs
4	Wing vibration	Flapping its wings for intimidation
5	Fliy	Flying away

RESULTS

Maternal defense response is species-specific

To understand the species-level variability of maternal defense behavior, I assessed the differential response frequencies of *A. expansa*, *U. crassicornis*, and *A. grossa*. Because I was only interested in the types of defenses present in each species, I disregarded the nature of the stimulus for simplification. For *A. expansa*, only three types of responses were observed: passive defense, shaking, and walking away; for *U. crassicornis*, all except flying away was observed; for *A. grossa*, all responses were observed (Figure 1).

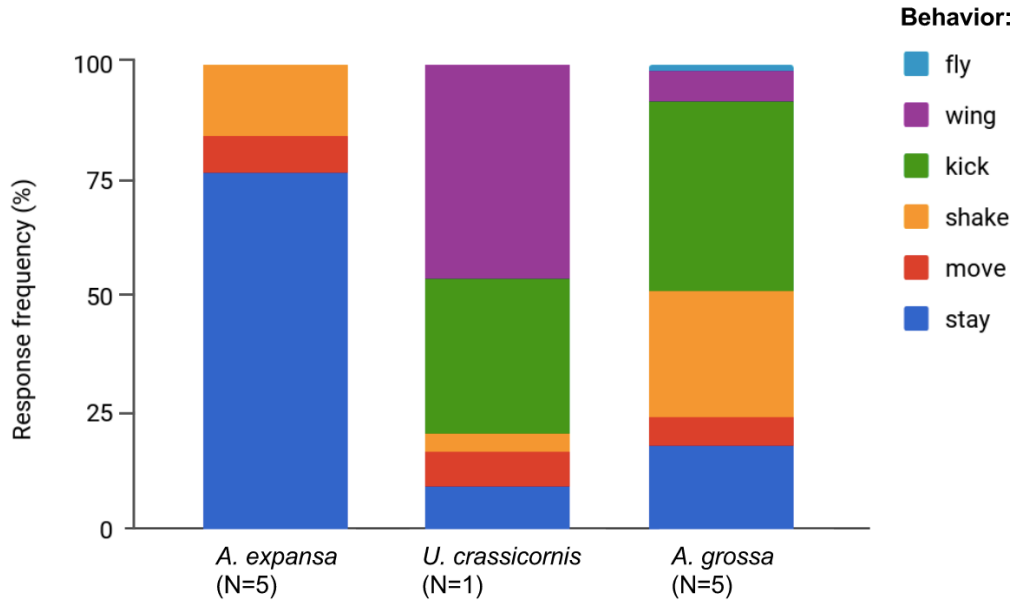


Figure 1. The range of maternal defense responses to any type of threat is species-specific.

Passive maternal defense throughout brooding is variable and species-specific

To further understand the extent of passive maternal care, I recorded the percentage of mothers who were present on an egg sac every morning for 14 days. *U. crassicornis* remained with her nymphs every day of the study while *A. grossa* and *A. expansa* both showed varying levels of passive maternal care (Figure 2). However, because experiments for *U. crassicornis* were done on site as compared to the other two species in the lab, I cannot omit the possibility that this type of behavior was environmentally-dependent.

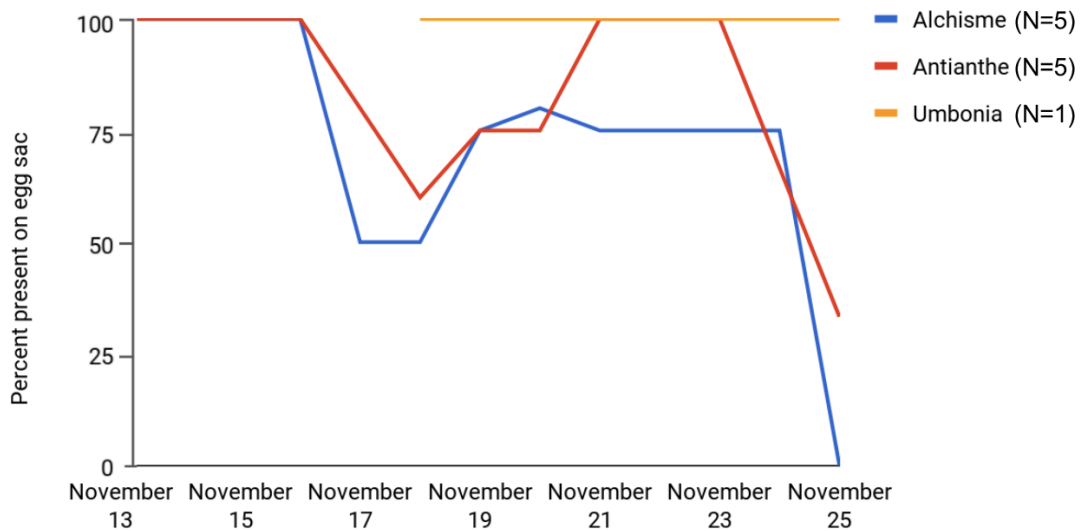


Figure 2. Maternal presence of *U. crassicornis* is persistent while *A. grossa* and *A. expansa* demonstrate inconsistency of presence throughout the brooding process.

The extent of maternal care is stimulus-dependent

Maternal defense behavior is kinesthetic, not visual

To isolate a possible visual component to maternal defense, I compared the responses of one mother to leaves held in front of her and leaves that made physical contact with her pronotum. I then repeated these experiments in the dark and observed their responses using red light. Because I only wanted to isolate the possibility of visual detection of potential threats, I limited my trials to one individual. Regardless of the presence of light, physical contact was necessary for the elicitation of a defensive response (Figure 3).

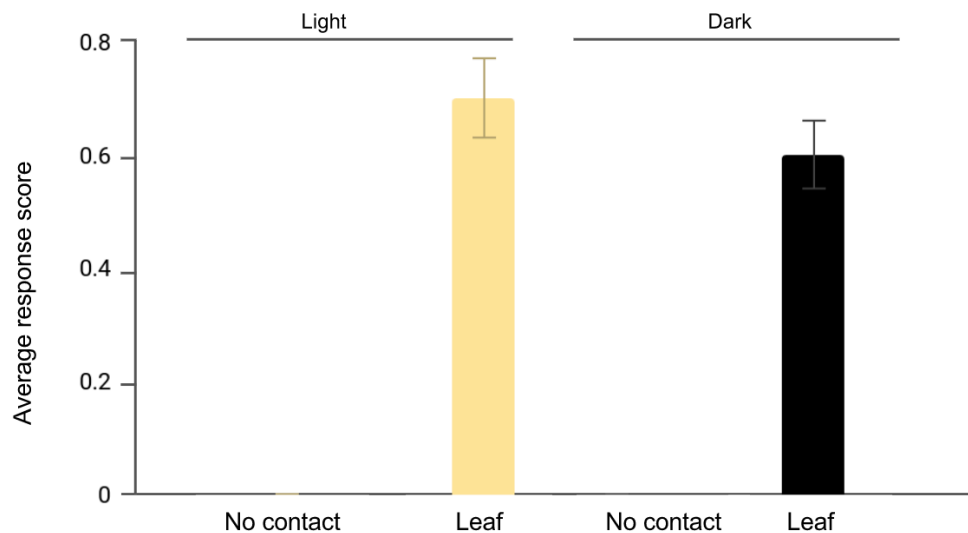


Figure 3. Physical contact with the mother is necessary to elicit a defensive response. (N=1)

Maternal defense behavior could be temporally-dependent

In order to assess whether the duration of a stimulus is important in maternal defense, I subjected each treehopper to leaf stimulation for five or ten seconds. For all three species, the average response score was higher when the stimulus was prolonged (Figure 4). However, only *U. crassicornis* showed a statistically significant difference in average response scores with regard to the duration of the stimulus. This result is reported with the caveat that I only observed the behavior of one individual of *U. crassicornis*.

Treehopper mothers display a heightened defensive response for animate stimuli

In order to determine whether treehopper mothers can distinguish between animate and inanimate stimuli, I provoked a defensive response through the introduction of either an insect or a leaf. For all three species, the average response score was greater for animate stimuli, but only *A. grossa* and *U. crassicornis* displayed statistical differences between the stimuli (Figure 4).

Next, because treehoppers must grapple with both predation from larger invertebrates and parasitism of their eggs from smaller wasps, I investigated how the size of animate threats affects maternal defense response. Thus, I used stink bugs of comparable size to the treehopper and first instar caterpillars as my predation and parasitoid size surrogates, respectively. For all three

species, the treehopper mothers do not significantly alter their behavior in response to size. However, because caterpillars and stink bugs are different in more ways than just size, this conjecture may be unfounded.

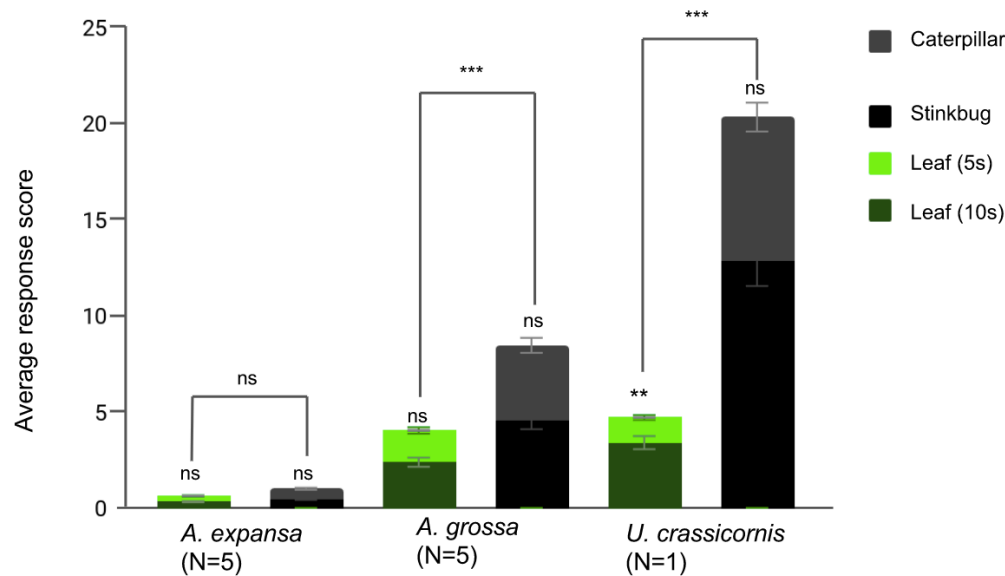


Figure 4. Average response score of maternal defense is higher for larger, animate stimuli and for prolonged inanimate stimuli as compared to their associated counterparts. ** $p < 0.01$, *** $p < 0.001$; ns, not significant.

A. grossa can recognize individuals of its own species

Because adult *A. grossa* have been observed to aggregate in nature, I sought to understand their behavior when faced with a “familiar” stimulus. On eight separate, unabated occasions, I observed more than one *A. grossa* mother on the same leaf under laboratory settings. These aggregations normally involved more than one female within five centimeters of each other and with at least one female occupying the space atop an egg mass. The particular individual atop an egg mass varied by occasion. During physical interactions among individuals in these situations, I frequently noted only passive defensive behaviors, such as remaining stationary or walking away. Typical responses to animate stimuli such as kicking or wing vibrations were rarely observed.

Personal defense is distinct from maternal defense in A. grossa

To distinguish between maternal defense and personal defense, I conducted threat-mimicry experiments on *A. grossa* who were not guarding an egg sac. Regardless of the threat type (animate or inanimate), treehopper mothers who were actively guarding an egg sac displayed a heightened response score as compared to astray individuals. This experiment was limited to *A. grossa* because they showed the greatest variability in response types and the highest frequency of egg mass abandonment.

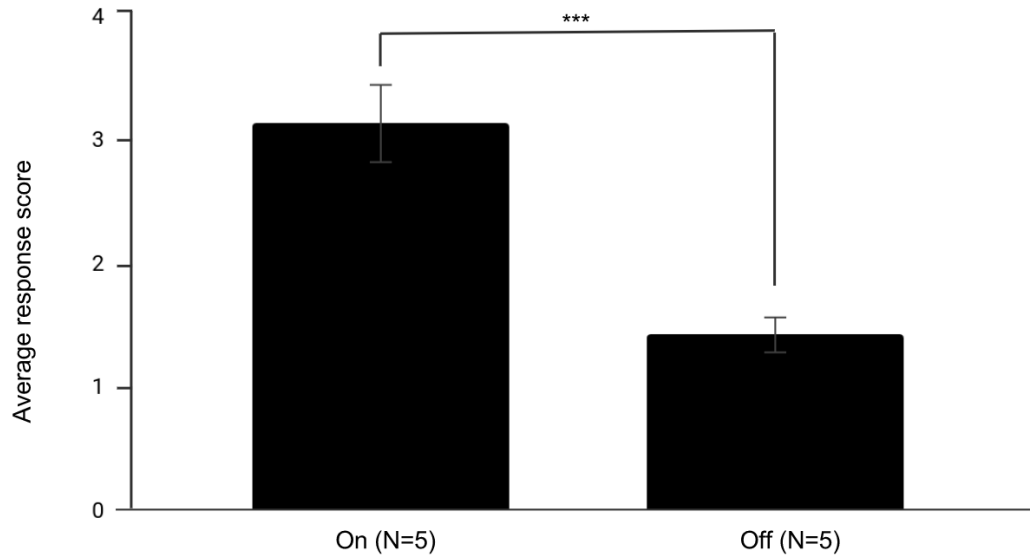


Figure 5. Average response score of maternal defense in *A. grossa* is higher when the mother is guarding her egg sac than when she is not. *** $p < 0.001$

DISCUSSION

Variation in defensive responses with regard to the type of stimulus revealed an acute ability to kinesthetically, not visually distinguish between different types of threats (Figure 3). Anatomically, this provides some evidence to previous notions that the pronotum has a sensory function (Wood 1984). This decreased reliance on vision likely stems from the evolutionary adaptation for substrate-borne acoustic communication as the primary form of threat detection (Cocroft 1999). The elevated average response score displayed across all three species for animate stimuli may be (1) because of an innate energy allocation mechanism that responds to more genuine threats or (2) because the leaf stimulus, unlike the caterpillar and stinkbug, did not induce substrate-borne vibrations before making to physical contact; thus, the difference in response scores may also rely on the mother's ability to detect the threat prior to its arrival. Although there was no difference in the response scores with regard to the type of animate stimulus (caterpillar or stink bug), the treehopper mothers demonstrated the ability to distinguish between conspecifics and hetero-conspecifics. This ability likely stems from the integration of substrate vibrations and pheromone communication in maternal defense (Cocroft 1999). Furthermore, the duration of a stimulus seemed to play a significant role in the level of responses of the treehoppers. This determination may also be the result of yet another energy allocation mechanism that prevents the waste of unnecessary energy on ephemeral stimuli. Additionally, there were always undefined refractory periods between successive kicks, further suggesting that the duration of the stimulus may play a role in the determination of a defense response. Taken together, I propose that the stimulus-dependent response scores stems from a kinesthetically-dependent reaction optimized to energy conservation.

Phylogenetic patterns of trait divergence among Membracidae tribes reveal a potential tradeoff between ant mutualisms and extended maternal care (Olmstead and Wood 1990b) (Figure S1). With regard to the species in my study, *A. grossa* and *U. crassicornis* occupy the Hoplophorionini tribe while *A. expansa* occupies the Smiliini tribe. Moreover, neither *U. crassicornis* nor *A. grossa* were ever found in the presence of ant mutualists; while *A. expansa*

was always found in the presence of ant mutualists. The extended range of behaviors and increased average response scores among *U. crassicornis* and *A. grossa*, as compared *A. expansa*, may suggest that the advent of ant mutualisms contributed to this evolutionary divergence (Figure 1 and 4). It thus stands to reason that individuals like *A. expansa* who benefit from the protection of mutualists would not require the energetically-costly adaptations designed for the personal or maternal defense as seen in *A. grossa* and *U. crassicornis* (Figure 1). However, this then begs the question: why don't *A. grossa* and *U. crassicornis* have ant mutualists?

One hypothesis for the evolution of this proposed tradeoff between ant mutualisms and extended maternal care involves elevational gradients (Wood 1984). Because higher altitudes preclude the development of robust ant populations, treehoppers who occupy such areas likely evolved advanced degrees of personal and maternal defense, like *A. grossa* and *U. crassicornis* (Wood 1984, Janzen et al. 1976). This finding thus gave rise to the notion that treehoppers with ant mutualists are ancestral to those without and that hoplophorioninines like *A. grossa* and *U. crassicornis* secondarily lost their association with ant mutualists (Costa 2006). However, because *A. expansa*, its ant mutualists and *A. grossa* are all often found occupying *Acnistus arborescens* trees, *A. grossa* likely began its evolutionary history occupying higher elevation trees, but through time, returned to occupy those in lower elevations. Thus, the absence of ant mutualisms for *A. grossa* is not limited by ant abundance; but perhaps (1) because ants can distinguish between different sources of honeydew. Like most Membracids, *A. grossa* excretes honeydew as part of their plant sap diet. Therefore, there may be some difference in honeydew composition that dissuades ants from approaching *A. grossa*. Or (2) because ants have learned over time that interactions with non-mutualists may result in bodily harm. Correspondingly, the evolution of ant mutualisms likely precludes the development of kicking behavior to prevent the inadvertent kicking of mutualist ants. However, further research into the precise sensory and genetic variables of ant mutualisms is required to completely understand this ant-treehopper relationship.

The large bodies and sharp lateral pronotal horns of *U. crassicornis* and *A. grossa*, also suggests a deviation from a reliance on hymenopteran mutualists. For *U. crassicornis*, these pronotal adaptations are essential to their defense against anuran predation (Wood 1977). In fact, removal of their sclerotized pronotum greatly increases their rate of predation (Wood 1993). These tribal distinctions in protective behavior and physical anatomy thus give credence to the proposed phylogenetic relationship that *U. crassicornis* and *A. grossa* are more closely related to each other than they are to *A. expansa* (Dietrich 2001).

Additionally, extended maternal behavior has been closely linked to semelparous individuals who are limited to only one brood throughout its lifetime (Wood 1984). Evolutionarily speaking, abandonment of egg masses is likely to be low and maternal defense energy output is likely to be high in semelparous individuals as compared to their iteroparous counterparts (individuals who can lay eggs more than once in their lifetime). Empirical ovipositional data suggests that *U. crassicornis* is obligatorily semelparous (Wood and Dowell 1984). Despite my low sample size for this species, its persistent presence with the nymphs throughout my study and its consistently high energy output further highlights this suggestion (Figure 2 & Figure 4). This type of parental behavior is in contrast to those of *A. grossa* and *A. expansa* who demonstrated a strong propensity for egg-mass-abandonment and lower levels of average response scores for any given stimulus (Figure 2). Although members of the Hoplophorionini tribe were originally believed to be exclusively semelparous, one research

group observed two individuals of *A. grossa* tending to two distinct egg masses during different periods of the year (Torrico-Bazoberry et al. 1984). *A. grossa*, thus may be either facultatively or moderately iteroparous. And despite the lack of evidence regarding ovipositional behavior in *A. expansa*, their observed rate of abandonment may also suggest either facultative or moderate iteroparity. There are also hypotheses that suggest that brooding iteroparous individuals have a tendency to aggregate in an effort to increase the probability that ants will tend to them (Torrico-Bazoberry et al. 1984). During my initial subject collection, adult individuals of *A. expansa* were always found aggregated in groups of three or more with ants and nymphs present, thus further strengthening the case for iteroparity in *A. expansa*.

The observed frequency of brooding aggregations of *A. grossa* suggests a more complex type of extended maternal care than originally proposed (Wood 1993). However, this type of behavior is not limited to *A. grossa*, as fellow membracids *Publilia concava* and *Polyglypta dispar* have also demonstrated similar “egg-swapping” behavior (Zink 2003a and Eberhard 1986). Here, I propose two hypotheses for this unusually high incidence of brooding aggregations. My first hypothesis considers the possibility of brood parasitism in which one female deposits eggs into the existing clutch of a conspecific (Zink 2003a). This type of behavior has been observed in *A. grossa* but the benefits for both the parasite and recipient are not fully understood (Torrico-Bazoberry et al. 1984). In the case of *Publilia concava*, brood parasitism does not reduce the hatching success of host eggs, increases the lifetime fecundity of the parasitic mother, and increases lifetime clutch count (Zink 2003a). However, unlike what I observed in *A. grossa*, parasitism by *Publilia concava* does not involve any type of maternal egg guarding post-oviposition. For example, in most of my observed cases, a mother who had “adopted” a new egg mass displayed typical maternal defense behavior as if it were her own. This distinction between *A. grossa* and *P. concava* in post-parasitism defense behavior may stem from regional and temporal differences of brooding that for *P. concava*, results in maternal death prior to egg hatching (Wood 1993). My second hypothesis for the high incidence of brooding aggregations that I observed in *A. grossa* considers the possibility of cooperative care. Although largely undocumented in treehoppers, individuals that engage in cooperative care have been shown to benefit from aggregations through the creation of a nutrient sink in the host plant that provides food for both the adults and the nymphs (Lin 2006). To exclude the possibility that they were sharing leaves due to some nutritional deficiency, I introduced a fresh leaf after the initial aggregation (19 November). Throughout the remainder of the study, I never observed any treehoppers occupying this alternate food source. Interestingly, for the last three days of my study, one *A. expansa* individual was consistently found atop an abandoned *A. grossa* egg mass. Although these events were only observed under laboratory settings, they may suggest that either the egg mass itself or the modifications made by the original mother provides some sort of additional nutrient source that fresh leaves cannot supply. Female adult aggregations of *A. grossa* have also been observed to decrease the rate of parasitism of eggs through a potential cooperation among egg-guarding mothers (Camacho et al. 2014). Although in my study, a maximum of three *A. grossa* mothers aggregated at one time, these hypotheses may provide a viable explanation for the high incidence of maternal aggregations.

In sum, by quantifying their responses as a proxies for energy output, I concluded that maternal defense is a species-specific phenomenon that is distinct from personal defense, relies primarily on kinesthetics rather than visual input, and is stimulus-dependent. This type of species-specificity is likely governed by different types of environmental pressures that necessitate the evolution of direct defense behavior or inter-species mutualisms. However, these

results and hypotheses are reported with the caveat that the various animate stimuli (caterpillars and stink bugs) used in this study are not known predators of these treehoppers. Further research involving their natural predators may provide a more robust depiction of the various factors involved in maternal defense recognition and behavior.

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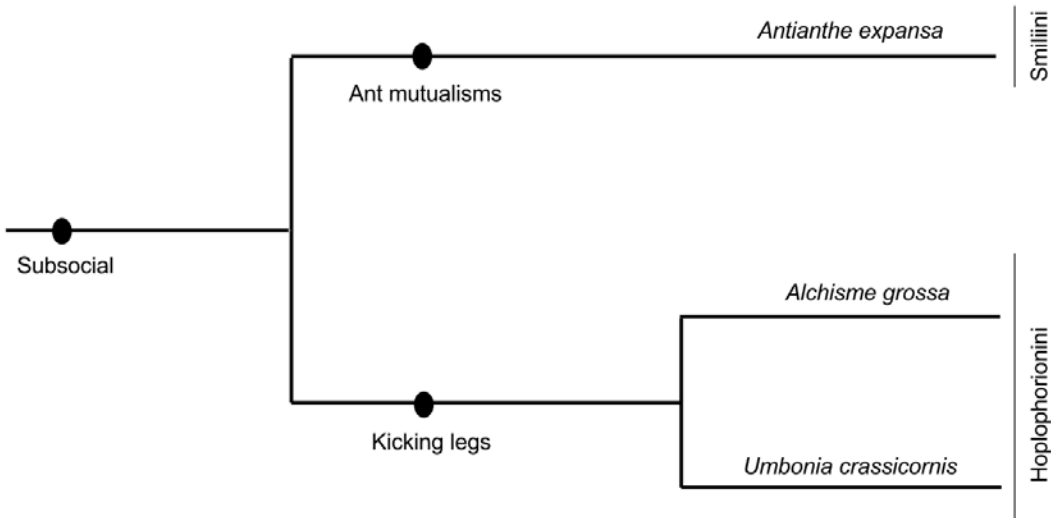
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Supplemental Information



S1. Abbreviated phylogenetic relationship among *A. expansa*, *A. grossa*, and *U. crassicornis*. Tribal affiliations are listed to the right. Adapted from Dietrich et al. 2006.