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THE ROLE OF ANTS IN MEMBRACIDAE PARENTAL CARE

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I really want to thank my Dad, my guardian angel, for fighting until the end, just for us. You will always be in my mind and my heart, thank you for rearing me the way you did, for teaching me as many good things as you could, and for showing me that nothing can stop you from fighting for what you want, not even illness. I promise you that this is the first step to accomplish all the dreams that we had together, hope you can see me wherever you are, and hope you are proud of every single step I take from now on. I will always love you. To my mom for being always there when I needed her and when I needed the right words to keep on going. To all of my family for always being there and believing in me. Juan Felipe for being my friend, my companion, for helping me to develop the ideas to write this paper, for being there in the best and worst years of my life, for always knowing what to say when i didn't understand why life works this way. To my friends, for being such great partners in this crazy journey, you made everything easier and happier. To Andre for being such a great teacher, for helping me out and letting me work with you. To Dimitri for introducing me to the insect world. To la Pontificia Universidad Javeriana for these great years of learning, and finally I want to thank every single person that supported me this last year, it hasn't been easy to move on, but thank to you all for the heartfelt words.

CONTENT

1. ABSTRACT

The mutualistic relationship between ants and treehoppers is known for the benefits that ants provide in exchange for food, including protection against natural enemies and increase in female fecundity. The aim of this review is to integrate the information that exists about parental care in Membracidae when associated to ants. This study was evaluated by conducting a review on 39 published studies. Results showed that the mutualistic relationships between species can be generalists or specialists, in term of the quantity of ant species that interact with a single membracid species and vice versa. Ants take care of membracids in any of their juvenile life stages (eggs, nymphs), being more common the interaction with nymphs. The reduction in nymph predation rates is a result of ant-guarding, and not parental care. The reproductive bout in females is strictly linked to ant-guarding and brood parasitism. This study confirmed that treehoppers transfer parental care behavior to ants and the main purpose for parental care is to attract ants.

2. PROBLEM STATEMENT

Treehoppers (Hemiptera: Membracidae) are a group of phytophagous sap sucking hemipterans, with a piercing and sucking stylet that helps them feed from woody and herbaceous plant phloem (Lin, 2006). Membracids can exhibit three ways of social interaction, either a solitary mode of life, a nymphal or adult aggregation and an all life stages sub social behavior with various degrees of maternal care (Tallamy & Wood 1986; Lin 2006; Torrico-Bazoberry et al. 2014). Some lineages of membracids that live in aggregations and have some level of parental care are known to have a mutualistic relationship with arboreal ants. Membracid females are able to transfer parental care behavior towards eggs and nymphs to ants, as a new benefit of mutualism (Bristow 1982).

The interaction between these groups is a facultative by-product mutualistic relationship in which hemipterans give honeydew, as a reward to ants, in exchange for different benefits (Morales et al 2008). Benefits include removing excess honeydew that can lead to mold infestation, protecting from weather, increasing fecundity and growth rate and decreasing development time. Protection against natural predators and parasitoids is generally accepted as the most important benefit (Bristow, 1984; Moreira & Del-Claro 2005; Morales et al. 2008; Fagundes et al 2012; Fagundes et al. 2013). Since this relationship is not obligated and that females incur in energy costs due to parental reproductive bout and self-protection, the main purpose for parental care might only be to attract ants (Billick et al. 2001; Zink 2003a). Although there are some membracid species that exhibit parental care and do not interact with ants.

The ant-membracid mutualism has attracted interest since the last years of the past century due to the fact that it comprises many benefits to both of the groups involved, as well as coevolutionary adaptations to fulfill these benefits (Delabie 2001). Moreover it has gain ecological importance, as it is seen as a key example of symbiotic relationships that needs to be deeply investigated because of the multiple factors that affect the mutualism, but also for the effect that this mutualism has over the surrounding arthropod community and the host plants (Delabie 2001; Morales et al. 2008; Freitas & Rossi 2015). Due to the fact that the mutualism can have an impact on the structure and stability of the surrounding arthropod community, that can lead to a decrease in the herbivory rate of other groups, different than the hemipterans, the positive and negative effects that this mutualism has over the host plant fitness, imply that this ant-membracid interaction can be used as a case of biological control (Eubanks & Styrsky 2006; Zhang et al. 2012; Freitas & Rossi 2015).

Due to the relevance and importance of this mutualism it is necessary to understand the role of ants towards the membracid aggregations, specially the juvenile stages, and how this leads to certain behaviors and adaptations by the membracid, specially the adult females. The aim of this review is to integrate the information that exists about parental care in Membracidae when associated to ants, and analyze the adaptations that are linked to the behaviors that lead to this mutualistic association.

3. THEORETICAL FRAMEWORK

Trophobiosis

Trophobiosis is the by-product mutualistic relationship that exists between ants and herbivorous insects (Delabie 2001; Fagundes et al. 2012; Fagundes et al. 2013). This type of relationship occurs between some lineages of sap-sucking hemipterans, some families of lepidopterans and arboreal ants (Fritz 1983; Delabie 2001; Perotto et al. 2002). Trophobiotic relationships probably evolved from a predator-prey interaction that changed when ants started to be attracted to honeydew, because this was a more stable and continuous source of nutrients than extra-floral nectaries (Delabie 2001).

The mutualistic relationship between ants and treehoppers is conditional and can be affected by their physical and biological environment (Cushman & Whitham 1989). Factors such as season in which the mutualism takes place, membracid age (Cushman & Whitham 1989, 1991), aggregation density, quantity and quality of honeydew (Cushman & Whitham 1989, 1991; Morales 2002), distance from servicing ant nests, nutritional status of ant colonies and the availability of alternative food resources of ants (Cushman & Whitham 1991) can influence the time that it would take for the mutualism to take place and the quantity of ants that are going to be attracted to interact in the mutualism (Cushman & Whitham 1989,1991; Morales 2002). Moreover, mutualistic relationship tends to be more conditional when there is a third species involved in it (Bronstein, 1994). The host plant nutritional value and fitness can be a determinant of quality and quantity of honeydew (Fotso et al. 2015).

Honeydew is a sugar-rich liquid that contain a mixture of nutrients, and is secreted by sap-sucking hemipterans as a residue of partially digested plant sap (Delabie 2001; Perotto et al. 2002) and mixt products of the malpighian tubes (Delabie 2001). Honeydew is the major component of many arboreal ant's diet and apparently is their main food source as well (Fritz 1983; Del-Claro & Oliveira 1999; Blüthgen et al. 2000; Delabie 2001; Zhang et al. 2012). Honeydew droplets contain a mixture of nutrients, such as sugars, amino acids, amides, minerals, vitamins and proteins (Del-Claro & Oliveira 1996; Moreira & Del-Claro 2005). The quality and quantity of honeydew is variable, depending on different aspects, such as host plant, hemipteran age, ant presence (Del-Claro & Oliveira 1999; Lundgren 2009; Fotso et al. 2015). Although honeydew is the product supporting the mutualistic relationship, it is also a way for the membracids to alert ants of their presence by flicking it away from the plant (Del-Claro & Oliveira 1996; Moreira & Del-Claro 2005).

Parental care

Parental care is seen as an altruistic trait in which the offspring receive benefits at the expense of parent fitness (Wong 2013). In insects, parental care after egg hatching appeared independently in ten different orders (Mas & Kölliker 2008). In hemipterans, parental care has several origins and has evolved several times, most of the times as a extensive protection care of eggs and nymphs against predators and parasitoids (Zink 2003b; Lin et al. 2004).

Parental care main purpose in membracids is to protect egg masses, maintain nymphal aggregation and deter predators and parasitoids. Egg-guarding by adults acts to increase the hatching success of eggs (Bristoe 1982; Zink 2002). Female parental care in some groups of Membracidae can involve facilitated feeding for nymphs, this behavior can be led by juveniles that influence the relationship to make it last, but this also implies an energetic cost for the adult (Mas & Kölliker 2008; Torrico-Bazoberry et al. 2014).

Parental care behavior in treehoppers can be modified by the presence of ants. Females may abandon their eggs and nymphs before or after the time they usually do in absence of ants (Bristow 1982). Females stay with their brood during their first nymphal stages, or until they get to an adult stage to establish the presence of ants (Bristow 1982; Wong 2013). The necessity of females to establish ant presence in an early life stage, is because these can increase the survivorship of nymphs (Del-Claro & Oliveira 1996).

Protection against natural enemies

The ant-membracid mutualism has several benefits for treehoppers, but protection against natural predators and parasitoids is generally accepted as the most important (Del-Claro & Oliveira 1999; Fagundes et al. 2013; Ants that are engaged in mutualistic relationships with trophobionts defend them from natural enemies (Freitas & Rossi 2015). Ant species that attend trophobionts are territorial, can feed on different sources of sugar and are opportunistic, predator or scavenger (Delabie 2001). Arboreal ants are attracted to food rewards found as extrafloral nectaries or hemipteran honeydew (Delabie 2001; Campos & Camacho 2014). Mutualistic ants tend to monopolize their food source by building nests around or over the membracid aggregation, and exhibiting aggressive behaviors towards other arthropod groups (Blüthgen et al. 2000; Fotso et al. 2015)

Ants association with membracids involves a high level of ecological, morphological and behavioral variation within both groups, which in many cases provides mutual benefit, including an increase in both groups population number (Blüthgen et al. 2000; Fotso et al. 2015). Due to aggressive behavior towards other arthropod groups in order to protect membracid, the adjacent arthropod community can substantially reduce its abundance and richness. The reduction of other herbivores can result in plant fitness, when the losses incurred by hemipteran feeding are outweighed (Moreira & Del-Claro 2005; Zhang et al. 2012; Freitas & Rossi 2015).

Female fecundity

Female fecundity can be measured in terms of reproductive bout. Semelparous females only have one reproductive bout and tend to take care of their offspring during all stages of development, to ensure that a high percentage of their offspring get to an adult stage (Trumbo 2013; Wong 2013). Iteroparous females are capable of having multiple reproductive bouts and tend to abandon their young to lay a second clutch of eggs thus increasing their offspring and ensuring that at least one is reaching adulthood (Zink 2003a; Trumbo 2013; Wong 2013). In membracids some species are Iteroparous, yet are involved in parental care, this type of behavior leads to adaptations that can help in performing both, such as cooperative care or brood parasitism and ant-guarding(Trumbo 2013).

Cooperative care or brood parasitism is the case in which one female takes care of more than one egg clutch or many females oviposit in the same egg clutch and just one of them takes care of them all (Zink 2005; Trumbo 2013). This is a female tactic in response to kinship and ecological constraints, which might involve the low capacity of females to provide adequate maternal care or to increase the fecundity of iteroparous females (Zink 2003b; Trumbo 2013). This tactic might be seen as a response to increase the fitness of the offspring. Laying eggs in an already established egg clutch, could mean a safer place, compared to a new clutch if it has closer proximity to natural refuges or ant guards, or just because the later oviposited eggs are placed in the middle of the egg mass, which means being more protected from predation due to positional effects (Zink 2003).

4. OBJECTIVES

1. General objective

To recognize the main features of the ant-Membracidae symbiotic relationship

2. Specific objectives

1. Provide a comprehensive summary of ant Membracidae-offspring interaction
2. Review the evidence that treehoppers transfer parental care behavior to ants
3. Discuss the proposition that the main purpose for parental care is to attract ants

5. METHODOLOGY

Literature search

The literature search was done using the university data bases as well as google scholar, using "Ant-Membracidae mutualism", "Ant-Membracidae Parental care", "Parental care associated to Ants", "Trophobiosis Parental care", "Parental care Membracidae" as keywords, in both sources and in the citations used in reviews of related topics (Way 1963, Tallamy & Wood 1986, Buckley 1987, Delabie 2001, Lin 2006, Zhang 2012, Trumbo 2013, Wong 2013). I only considered studies including ant-membracidae mutualism, studies including trophobiosis with only other non-hemipteran groups were excluded for the data analysis, as well as studies that did not had either parental care, membracid life history or mutualism as its main topic.

Literature and data selection

The studies selected to be included in the analysis were those that portrait membracid-ant relationships, in which membracid and ant species names were mentioned, as well as membracid life history, and that mentioned in some way an interaction of ants with membracid immature life stages. Studies about the life history of species that were known to have ant mutualism, were taken into account to complete the information needed for the meta-analysis, although sometimes this did not focus on the relationship with ants.

Data analysis

The information was gathered in charts that relate which species of Membracidae interact with which species of ants, during which stages of development ants were present and had a role of protection, the interaction behaviors within and between the species, that range from the capacity of Membracidae females to exhibit more than one reproductive event, cooperative care or brood parasitism within Membracidae females and ants aggressive behavior towards the associated arthropod community. An analysis was conducted on each of the variables mentioned above independently.

6. RESULTS

Thirty-nine publications met the criteria stated for the meta-analysis (Table 1). These studies included analyses of 28 species of membracid, belonging to 16 genus. *Enchenopa* was the genus with more species reported to have ant mutualism (4) followed by *Campylenchia* (3), *Enchophyllum* (3), *Publilia* (3), *Aconophora* (2), *Membracis* (2), *Vanduzea* (2), *Bilimeki* (1), *Bolbonata* (1), *Calloconophora* (1), *Entylia* (1), *Erechtia* (1), *Eunusa* (1), *Guayaquila* (1), *Notocera* (1), and *Tragopa* (1).

In those studies, 54 species of ants were discussed to have ant-membracid mutualism, belonging to 4 subfamilies: Formicinae (55,55%), Myrmicinae (25,92%), Dolichoderinae (11,11%) and Ectatomminae (7,40%). *Camponotus* was the most common genus in these studies, with 16 species (30,18%), followed by *Formica*, with 11 species (20,75%). *Camponotus rufipes* was the ant species that interacted with most membracid species (4), being the most generalist, and more than 10 species of ants have mutualism with just one species of membracidae. At the same time only 3 species of Membracidae interact with only one species of ants, *Azteca* sp. is found in this type of associations with *Eunusa concolor* and *Vanduzea* sp being these species the most specialist.

Table 1. Membracidae-Ant interaction and life history characteristics

Genus	Species	Mutualistic Ant species	Reproductive strategy	Brood Parasitism	Abandonment after egg hatching when ants take care	Life stage Ant-tend	Reference
Aconophora	*A. ferruginea*	*Camponotus abdominalis, C. novogranadensis, C. sexguttatus, C. simillimus, Zacryptocerus porrasi*	?	?	No	?	Lin 2010; Letourneau & Choe 1987
	A. teligera	Camponotus aff. blandus, C. abdominalis, C. renggerri, C. rufipes, Ectatomma tuberculatum	?	?	?	?	Dansa et al. 1992
Bolbonata	B. sp.	*Dolichoderus quadridenticulatus*	?	?	?	Nymphs, Adults	Blüthgen et al. 2000
Calloconophora	*C. pugionata*	*Camponotus crassus, C. fastigatus, C. novogranadensis, C. rufipes, C. senex, Cephalotes pusillus, Crematogaster sp., Pheidole sp., Pseudomyrmex gracilis*	?	?	Yes	Eggs, Nymphs	Fagundes et al 2011; Fagundes et al 2013
Campylenchia	*C. latipes*	?	?	?	?	Nymphs	Lin 2010
	C. hastata	?	?	?	?	Nymphs, Adults	Lin 2010
	C. sp	*Camponotus atriceps, C. linnaei, C. planatus, Dolichoderus lutosus, Dorymyrmex sp., Forelius pruinosus, Monomorium cyaneum, Paratechina longicornis, Pseudomyrmex simplex*	?	?	?	?	Gove & Rico-Gray 2006
Enchenopa	*E. binotata*	?	Semelparous	Yes	Yes	Nymphs	Matausch 1912; Wood 1982, 1983
	E. brasiliensis	*Camponotus aff. blandus, C. crassus, C. ruffipes, Crematogaster sp., Ectatomma quadridens, Pheidole sp., Pseudomyrmex aff. gracillis, P. aff. palidus.*	Iteroparous	Yes	Yes	Eggs,Nymphs, Adults	Moreira & Del-Claro 2005
	E. gladius	?	Iteroparous	Yes	?	Nymphs, Adults	Lin 2010
	E. ignidorsum	?	Iteroparous	Yes	?	Nymphs, Adults	Lin 2010
	E. sericea	*Camponotus rufipes, Ectatomma tuberculatum*	Iteroparous	Yes	Yes	Nymphs, Adults	Hinton 1977; Perotto 2002
Enchophyllum	*E. dubium*	?	?	?	?	Nymphs, Adults	Lin 2010
	E. melameucum	?	?	?	?	Nymphs, Adults	Lin 2010
Entylia	*E. bactriana*	*Camponotus ferrugineus, Formica sp, Prenolepsis imparis, Tapinoma sessile*	Iteroparous	Yes	Yes	Nymphs	Olmstead & Wood 1990

Table 1. Continued

Genus	Species	Mutualistic Ant species	Reproductive strategy	Brood Parasitism	Abandonment after egg hatching when ants take care	Life stage Ant-tend	Reference
Erechtia	*E. sp.*	*Cephalotes atratus*	?	?	?	?	Blüthgen et al. 2000
Eunusa	*E. concolor*	*Azteca sp.*	?	?	No	Nymphs, Adults	Mckamey 1992
Guayaquilla	*G. xiphias*	*Brachymyrmex sp., Camponotus abdominalis, C. crassus, C. lespesi, C. pallescens, C. renggeri, C. rufipes, C. Sericeiventris, C. aff. blandus, Cephalotes atratus, Crematogaster sp., Ectatomma edentatum, Ectatomma planiden, Pheidole sp., Zacryptocerus clypeatus, Z. Pusillus.*	Iteroparous	?	Yes	Eggs, Nymphs	Del-Claro & Oliveira 1996, 1999, 2000; Quental et al. 2005; Freitas & Rossi 2015
Membracis	*M. fuscata*	?	?	?	?	Nymphs, Adults	Lin 2010
	M. mexicana	?	?	?	Yes	Nymphs, Adults	Lin 2010; Hinton 1977
Notocera	*N. sp.*	?	?	?	Yes	Nymphs	Lin 2010
Publilia	*P. concava*	*Formica exsectoides, F. fusca, F. integra, F. pergandei F. rubicunda, F. subsericea*	Iteroparous	Yes	Yes	Nymphs, Adults	Messina 1981; Morales 2000, 2002; Zink 2003a, 2003b, 2005; Morales et al 2008
	P. modesta	*Crematogaster sp., Formica altipetens, F. obscuripes, F. occulta, F. oreas*	Semelparous	No	No	Nymphs, Adults	Cushman & Whitham 1989, 1991; Billick 2001; Reithel & Billick 2006; Reithel & Campbell 2008
	P. reticulata	*Myrmica americana, M. lobicornis fracticornis, Tapinoma sessile,*	Iteroparous	?	Yes	Nymphs, Adults	Bristow 1982, 1984
Tragopa	*T. sp.*	*Cephalotes atratus, Dolichoderus quadridenticulatus*	?	?	?	?	Blüthgen et al. 2000
Tropidaspis	*T. sp.*	*Dolichoderus quadridenticulatus*	?	?	?	?	Blüthgen et al. 2000
Vanduzea	*V. arquata*	*Crematogaster sp., Formica sp, F. subsericea*	?	?		Nymphs	Fritz 1983; Cocroft 2003
	V. Sp	Azteca sp.	?	?	?	?	Blüthgen et al. 2000

?: Unknown or undocumented information.

Parental care

The membracid species that interact with ants in a mutualistic relationship, exhibit maternal care. The studied species could be classified in 2 major types of parental care. In the 1st type, females remain on eggs until hatch, and actively maintain aggregated nymphs until its last instar and defend them from potential predators, this type can be called complete parental care. The 2nd type, females remain on eggs until hatch and the 1st two nymphal instars and after that they abandoned their broods to ant care, this type can be called incomplete parental care. The complete parental care was only reported to occur in 3 species (11,11%), the incomplete parental care was reported to occur in 10 species (37,03%). Ants can establish a relationship with membracids in any moment of their life cycle, being eggs, nymphs or adults. In the first two life stages parental care by ants can take place. Ants only take care of eggs in the mutualism established with 3 species of membracid, while they take care of nymphs in all the species that were included in the study, the mutualism with adults is seen to happen in 14 species (Fig 1).

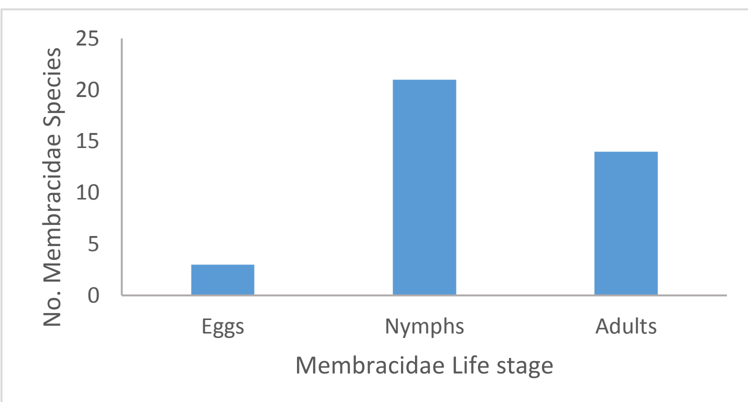

Fig 1. Life stage in which Ant-Membracidae mutualism occur.

Protection against natural enemies

The ant-membracid mutualism significantly decreased immature predation, this lead to an increase in the survivorship of the same group, while at the same time lead to an increase in the total number of new adults (Wood 1982; Bristow 1984; Cushman & Whitham 1989; Olmstead & Wood 1990, 1991; Del-Claro & Oliveira 2000; Morales 2002; Billick et al. 2001; Perotto et al. 2002; Cocroft 2003; Moreira & Del-Claro 2005; Fagundes et al. 2013). Out of the thirty-eight publications used for the analysis, thirteen focused on the effect that had ant-membracid mutualism on the immatures survivorship due to a decrease in predation (Table 2). There is a consensus in the studies that there is an increase in the number of total membracids aggregated in the presence of ants as a consequence of an increase in the survivorship specially of nymphs.

The presence of adult females in the egg and nymphs aggregation has been seen as a way of attracting ants, more than to actually protect immatures from predators. There is a consensus in the information establishing that adult females don't play a significant role in the increase of immature survivorship as a consequence of predator's decrease (Table 2). In presence of ants the total abundance of predators seen around membracids aggregations are diminished, the presence of adult females is generally not seen as a factor that influenced this abundance, with or without ant presence. Only one study stated that adult females had an influence in nymph survivorship, but only when ants were not present (Del-Claro & Oliveira 2000).

Table 2. Effect of ant and adult membracidae presence over immature protection against natural enemies

Reference	Species	Life stages	Host plant	Effect of ant presence over immature membracid predation	Effect of adult membracids presence over immature predation
Wood 1982	*Enchenopa binotata Complex*	Eggs and nymphs	*Robinia pseudoacacia*	Decrease predation	No effect
Bristow 1984	*Publilia reticulata*	Nymphs	*Vermonia noveboracensis*	Decrease predation	No effect
Cushman & Whitham 1989	*Publilia modesta*	Nymphs	*Helenium hoopesii*	Decrease predation	No effect
Olmstead & Wood 1990	*Entylia bactriana*	Eggs and nymphs	*Ambrosia artemisiifolia, Cirsium arvense, Cirsium vulgare*	Decrease predation	No effect
Cushman & Whitham 1991	*Publilia modesta*	Nymphs	*Helenium hoopesii*	Decrease predation	No effect
Del-Claro & Oliveira 2000	*Guayaquila xiphias*	Eggs and nymphs	*Didymopanax vinosum*	Decrease predation	Decrease predation only in absence of ants
Morales 2000	*Publilia concava*	Nymphs	*Solidago altissima*	Decrease predation	No effect
Billick et al. 2001	*Publilia modesta*	Nymphs	*Chrysothamnus viscidiflorus*	Decrease predation	No effect
Morales 2002	*Publilia concava*	Nymphs	*Solidago altissima*	Decrease predation	No effect
Perotto et al. 2002	*Enchenopa sericea*	Nymphs	*Caesalpinia gilliesii*	Decrease predation	No effect
Cocroft 2003	*Vanduzea arquata*	Nymphs	*Robinia pseudoacacia*	Decrease predation	No effect
Moreira & Del Claro 2005	*Enchenopa brasiliensis*	Nymphs	*Solanum lycocarpum*	Decrease predation	No effect
Fagundes 2013	*Calloconophora pugionata*	Eggs and nymphs	*Myrcia obovata*	Decrease predation	No effect

Female fecundity

Female fecundity can be measured by the amount of times a female is able to oviposit or to have multiple reproductive events. In treehoppers, reproductive bouts seems to be related to strategies that allow them to keep their offspring cared, even if is not by them. Out of the 27 species of Membracidae included in the study, only the reproductive bout behavior of ten has been documented, eight are iteroparous and two are semelparous.

Female fecundity can be increased by strategies as ant-guarding and brood parasitism. The relationship between Reproductive bout and ant-guarding as well as brood parasitism is direct. Out of the 8 species that are iteroparous, 6 have egg-dumping and brood parasitism behavior, 2 are unknown or have not been documented. Out of the 2 species that semelparous, 1 exhibit these behaviors while the other doesn't (Fig 2).

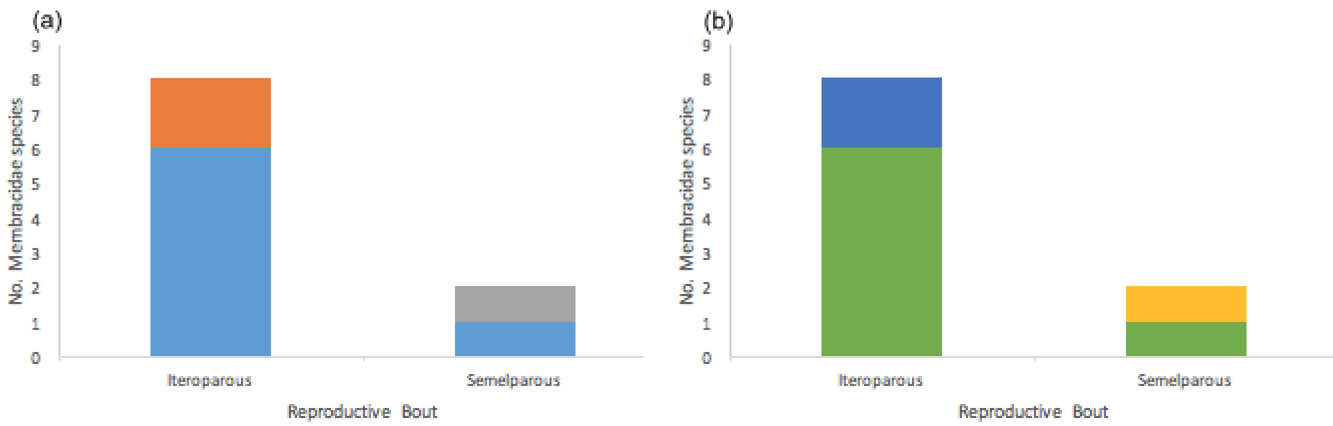

Fig 2. The relationship between the fecundity, in terms of reproductive bout, and the social behavior adaptations. (a). Relationship between reproductive bout and young abandonment, Green: There is young abandonment, Blue: There is no information, Yellow: There is no abandonment. (b). Relationship between reproductive bout and brood parasitism, Blue: There is brood parasitism, Orange: There is no information, Gray: There is no brood parasitism.

7. DISCUSSION

The generalist or specialist ant-membracidae relationship is a consequence of various factors that affect the ant assemblage. Ants might choose their trophobiotic partner according to their behavioral patterns, including territoriality over the food resource, dietary requirements, amount and type of sugars and carbohydrates they need, characteristics of the host tree that can influence the honeydew quality and quantity (Blüthgen et al. 2000; Fotso et al. 2015). Ant assemblages can be affected by factors such as geographic location, season, and day and night activity (Fotso et al. 2015).

The territoriality over the food source can be seen in different ant species that present different adaptations to maintain this behavioral pattern. There are ants as *Camponotus rufipes* and *Ectatomma* spp. that are described to be aggressive toward other arthropod groups, including in some cases even other ants species, when they get close to the membracids and tend to dominate and monopolize the food resource. These species are also known to form ground nests beneath the host plant (Blüthgen et al. 2000). Taking into account that one of the factors that affect the mutualism between ants and membracids is the distance between the nests and the host plant (Morales 2002), there is a high probability that the ant species that have ground nests are abler to be involved in more mutualistic relationships with more membracid species, as it happens with *Camponotus rufipes.*

Azteca sp. is an ant species that also has a territorial behavior over the food source, although it is shown in a different way. This species as well as *Dolichoderus bidens, D. quadridenticulatus* and *Crematogaster* sp. are able to build arboreal nests around or next to the membracid aggregation that they are tending. *Azteca* sp. is known to build its nest around the membracid aggregation giving shelter to the later and keeping it isolated from interacting with other ant species or arthropod groups in general. This behavior might explain why *Eunusa concolor* and *Vanduzea* sp. are only known to interact with *Azteca* sp (Blüthgen et al. 2000; Delabie 2001).

Ant-membracid mutualism can be seen as a way to avoid going through parental care, and evade the costs that come with it. The main cost that parents have to undergo when expressing parental care is to invest energy to protect the offspring and spending time in taking care of an amount of offspring to make sure it gets to an adult stage. These behaviors diminish the possibility of protecting itself and having another reproductive event and increase the probability of having more offspring. For a parent to stay and take care of their offspring, and for parental care to maintain and evolve, the benefits must outweigh the costs (Wood 1978; Mas & Kölliker 2008). Then the reasons to stay would be that the oviposition site is good in terms of food quality, is a refuge from predators or has a high ant presence (Zink 2003a).

In membracid species that exhibit parental care and do not have a mutualistic relationship with ants, it can be seen that some species can have, as part of their social behavior, egg dumping as a way to increase their offspring, but although this can happen females always tend to express a complete parental care of at least one of their broods (Torrico-Bazoberry et al 2014). Some of these species, such as *Umbonia crassicornis* have developed defensive adaptations towards predators as a cryptic coloration and hardness of the pronotum (Wood 1978). Membracid species that interact in a mutualistic relationship do not have this type of adaptations to protect themselves from predators, other than, transferring the parental care to ants. Females will stay with their broods until hatching to state the presence of ants, and assure this relationship with the nymphs will keep on going.

In order to provide parental care as protection from natural enemies, the parents must have less probabilities to be attacked (Wong 2013). The species that do not interact in mutualism with ants have adaptations in order to protect their broods, as is the case of *Umbonia crassicornis* which has vibrational communication between nymphs and adults in order to alert adult females of the presence of predators. Females in order to protect their brood have defensive behavior that includes wing fanning and kicking hind legs (Cocroft 2001, 2002; Ramaswamy & Cocroft 2009).

Within the species that interact in mutualism with ants only *Guayaquila xiphias* exhibits some kind of defensive behavior as the one just mentioned and in the absence of ants (Del-Claro & Oliveira 2000). *Publilia concava* has vibrational communication with ants to alert them of the presence of predators. Ants are shown to increase their aggressive behavior, and to reduce their attack time in response to the signal (Morales et al. 2008). Although this social behavior adaptation leads to the protection of immatures from natural enemies, adults are not taking care of their broods to protect them. Adult Females in many cases will only stay by their brood to receive the benefits of the mutualism with ants, although there is no parental care that really benefits their offspring in terms of protection. This might support the proposition that the main purpose of parental care is to attract ants.

The semelparity hypothesis states that semelparous species exhibit parental care while iteroparous won't. Nevertheless there could be opportunistic iteroparous organisms that can have parental care and multiple reproductive events at the same time, but only if there were to have resources to do it (Tallamy & Brown 1999). In membracids that interact with ants although the reproductive bout of all is not known or documented, there seems to be a tendency in which females are iteroparous and exhibit some degree of parental care, at least to attract ants and establish the mutualism. Taking into account the semelparity hypothesis those species that are reported to be iteroparous are just opportunistically iteroparous thank to ant-guarding and brood parasitism, that are strategies to keep doing parental care while females have multiple reproductive events (Tallamy & Brown 1999). Another possibility is that the semelparity hypothesis is incorrect and an alternative point of view is that this species are really iteroparous and this trait appeared when the cost of maternal care was reduced by offloading care to other individuals, as it happens in brood parasitism and ant-guarding (Trumbo 2013).

8. CONCLUSIONS

Parental care behavior can be transfer to ants, as it can be seen that adult females, that interact in mutualism with ants, tend to abandon their broods when ants are present.

Parental care is used by treehoppers to attract ants and obtain the benefits of mutualism, adult females don't have any impact over juvenile's protection.

Iteroparity is a trait that is spread through the species that interact with ants in mutualism, and is related to either having mutualism with ants, have brood parasitism or both.

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