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Ant Membracid Interaction and their Stoichiometric Relationship

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A B S T R A C T

Ant membracid interaction on three membracids, viz., *Leptocentrus taurus*, *Otinotus oneratus* and *Oxyrhachis taranda* of their respective host plants, viz., *Zizyphus jujuba*, *Tamarindus indica* and *Prosopis spicegera* were studied by field observations. The nymphs showed a strong myrmecophilous mutualism when they were regularly attended by the ants. A mean number of 78 *Leptocentrus taurus* nymphs were attended by the ant species *Formicaria brynnea* and its ant attendance was 92.8%. In *Otinotus oneratus*, a mean number of 84 nymphs were attended by *Componatus compressus* ants, with an ant attendance of was 87.5%. Whereas, *Oxyrhachis taranda*, 68 mean number of nymphs when attended by *Componatus compressus* ants, recorded ant attendance of 54.8%. The survival value of membracids nymphs was enhanced by the ant attendance. The results revealed that practically no nymphal mortality occurred in all the three membracids which had access to ants, and all the nymphs survived and became adults. The presence of ants, increased the survival rate of the membracid nymphs and decreased its mortality rate, and their survival rate by the presence and absence of ants was 67.14% and 38.88% for *Leptocentrus taurus*, 63.01% and 39.44% in *Otinotus oneratus*, and 76.78% and 35.48% in *Oxyrhachis taranda* respectively. The behaviour of the ants to the three membracid nymphs showed that the demand for the honey dew on the nymphs was not persistent but intermittent, and allowed sufficient interval for the fluid secretion. The ants actively moved back and forth among the nymphs, tickled the nymphs and made them eject the drop of anal fluid, pressed its mouth onto the drop, gripped it and moved away.

***Key words*:** *Leptocentrus taurus*, *Otinotus oneratus Oxyrhachis taranda*, *Formicaria brynnea*, *Componatus compressus*, Honeydew, Ant attendance, Nymphal survival rate

Though hemipterans are regarded as major pests to many plant species, ant-tended hemipterans may indirectly benefit their plant hosts through ant protection against external herbivores whose damage to the plant outweighs the cost of hemipteran infestation [1-4]. Many species of hemipteran insects are mutualistically associated with ant species, and. myrmecophily occurs within most families of the Sternorrhyncha and Auchenorrhyncha, including aphids, coccids and scales, and membracids [5-7]. A key component of the success of ant species in novel environments is the mutualistic interactions with homopterans in a consumer resource mutualism [8-10]. Moreover, ant membracid mutualism reduces predation and parasitism [2], [8], [11-18]. Membracids are phloem feeders, and produce an energy rich sugary excretion (a mixture of water, sugars, carbohydrates, proteins, and amino acids) called honeydew [2], [8]. Honeydew droplets that fall on the ground, and on the leaves beneath a group of treehoppers are used as cues by ants, which find the treehoppers and begin tending them [19], [21], as it represents their vital food resource [22-23]. Though the association of membracids with ants have been observed by several researchers, the complicated interaction involved in this relationship have been little understood. The present authors have reported a preliminary ant membracid interaction with reference to *Otinotus oneratus* and *Componatus compressus* [24]. The present research work reports on the ant membracid interaction between the membracid species, viz., *Leptocentrus taurus*, *Otinotus oneratus* and *Oxyrhachis taranda* and the ant species, viz., *Formicaria brynnea* and *Componatus compressus* with reference to ant attendance, membracid survival rate, honeydew, and factors influencing their relationship.

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MATERIALS AND METHODS

In order to study ant membracid interaction, three membracids (*Leptocentrus taurus*, *Otinotus oneratus* and *Oxyrhachis taranda*) on their respective host plants (*Zizyphus jujuba*, *Tamarindus indica* and *Prosopis spicegera*) were chosen. Five numbers of two year old respective host plants, spatially separated in an open field in Thiruvallur district of

Tamil Nadu, India were selected. Galleries of ant species, viz., *Formicaria brynnea* and *Componatus compressus* were established at the base of each host plant, when the density of membracid nymphs reached an optimum number. In each host plant, only the main stem was retained, while the side branches were cut off to facilitate in counting of ants, and the counted ants were removed simultaneously by making them come in contact with a stick to the stem of each plant. Then, the number of nymphs and adults of the membracids on the stem of the host plant was recorded. As long as the ant galleries or tunnels were not disturbed or blocked, the ants resumed their attendance on the membracids. Counts were also made on the five numbers of each host plant without ant attendance to determine the survival rate of nymphal membracids by dumping DDT powder (200g) at the base of stem of each host plant. Further, other factors involved in ant membracid interaction were also observed and recorded.

RESULTS AND DISCUSSION

The ant interaction with the membracids on its host plants varied. For *Leptocentrus taurus*, 46 number of branches belonging to 12 numbers of its host plant species, *Zizyphus jujuba* were examined, which had a mean number of 78 nymphs attended by the ant species *Formicaria brynnea* numbering 84, and its ant attendance was 92.8 percent. Whereas, in *Otinotus oneratus*, 28 number of branches belonging to 14 numbers of *Tamarindus indica*, when examined had a mean number of 84 nymphs attended by *Componatus compressus* ants numbering 96, with an ant attendance of 87.5 percent. In the case of *Oxyrhachis taranda*, 68 mean number of nymphs were attended by 124 *Componatus compressus* ants with an ant attendance of 54.8 percent when examined from 24 branches of 10 *Prosopis spicegera* plants (Table 1). The survival value of membracids nymphs was enhanced by the ant attendance. The results revealed that practically no nymphal mortality occurred in all the three membracids which had access to ants, and all the nymphs survived and became adults. The presence of ants, increased the survival rate of the membracid nymphs and decreased its mortality rate. On the other hand, it was vice-versa, when ants were absent. Amongst the three membracids studied, their survival rate by the presence and absence of ants was 67.14 percent and 38.88 percent for *Leptocentrus taurus*, 63.01 percent and 39.44% in *Otinotus oneratus*, and 76.78% and 35.48% in *Oxyrhachis taranda* respectively (Fig 1). Further, detailed observations on the behaviour of the ants to the membracid nymphs showed that the demand for the honey dew on the nymphs was not persistent but intermittent, and allowed sufficient interval for the fluid secretion. The ants actively moved back and forth among the nymphs, tickled the nymphs and made them eject the drop of anal fluid. When the liquid exuded, the ant pressed its mouth onto the drop, gripped it and moved away. At times, when the nymph failed to respond to the coaxing of the ant, the ants bit the sensory hairs of the anal tube, pushed its mouth into the anal tube and received the anal fluid.

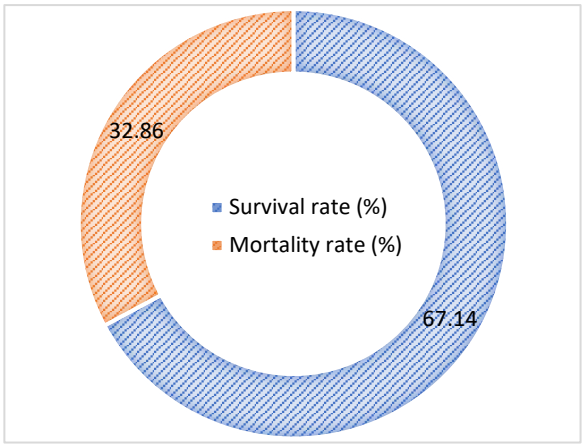
Table 1 Membracid nymphs attended by ants on their host plants

Membracid species	Host plant species	Ant species	No. of plants examined	No. of branches	Mean number of nymphs	Ant	
						Attended	Attendance (%)
Leptocentrus taurus	*Zizyphus jujuba*	*Myrmicaria brynnea*	12	46	78	84	92.8
Otinotus oneratus	*Tamarindus indica*	*Camponotus compressus*	14	28	84	96	87.5
Oxyrhachis taranda	*Prosopis spicegera*	*Camponotus compressus*	10	24	68	124	54.8

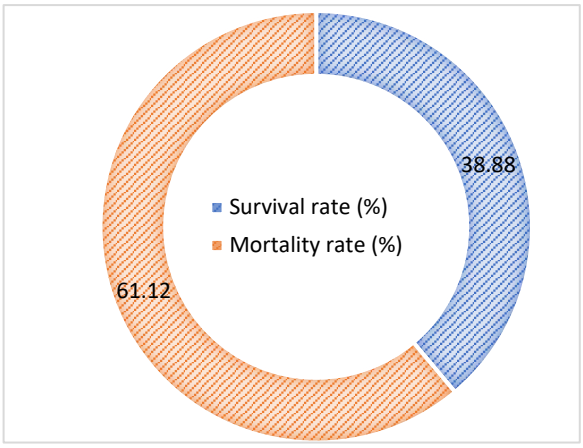
One of the fascinating phenomena with regard to the interspecific relationship of membracids is the myrmecophilous mutualism. Way [8] has reviewed the whole phenomenon of mutualism between ants and membracids. Hinton [25] and Wood [26] made excellent contributions supported by experimental data, with regard to the role of ants in the biological activities of the membracids. In general, the mutual relationship between the membracids and the ants seems to be much the same as that noticed between the aphids and the ants. The anal tubes of the membracid which is usually highly eversible and fringed with a circle of tactile sensilla and sensory setae near anal orifice, ejects out the honey dew in bubbles, when the ants tickle the sensory hairs of the anal orifice and eagerly consume them. For the continued mutualistic/symbiotic disposition of the ants and the nymphs of the membracids, an uninterrupted secretion of the anal fluid by the latter is a must, and this, in turn, is conditioned by the continuous sucking action of the plant sap by the nymph. According to Hood [27], the expulsion of the anal secretion through the caressing of ants enables the membracids to reduce the pressure with which the plant sap enters the gut. This theory has its own value considering the enormous quantity of the anal secretion expelled by many membracid nymphs and their constant association with ants. The interaction between ants and hemipterans has become a model system for studies of conditionality in mutualism, and variation in outcome is especially well documented for this system [28]. The benefits of mutualism are measured in terms of direct fitness such as the survival rate of nymphal population and the number of offsprings produced [14], [29], [30]. Many membracid species of the tropics have mutualistic relationships with honeydew harvesting ants [31], [32] and this relationship has significant consequences for membracids survival, since the ant species greatly reduce membracid mortality from predatory insects [33-34].

Ants of the genus *Camponotus* are described to be aggressive towards other arthropod groups, when they get close to the membracids, and tend to dominate and monopolize the food resource. They are also known to form ground nests beneath the host plant [35]. 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 [29], there is a high probability that the ant species that have ground nests are able to be involved in more mutualistic relationships with more membracid species, as observed in the present study. The attendance or non-attendance of ants may be quite accidental, and may depend on the chance proximity of ants. Chitra and Ananthasubramanian [36-37] reported a positive correlation between the number of membracids and the number of ants. The ant attended colonies of the membracids had the obvious benefit of protection from predators and a higher survival value for the nymphs has been substantiated in the present study, and the factor that accounted for ant attendance, as shown by the present study, was the optimum level of nymphal aggregations. Rajkumar *et al*. [24] reported *Otinotus oneratus* nymphs attended by *Componatus compressus*, and the ant attendance ranged from 56.5% to 92.9%. Similar observations were also made by Seni [38] on *Otinotus oneratus* and *Leptocentrus*

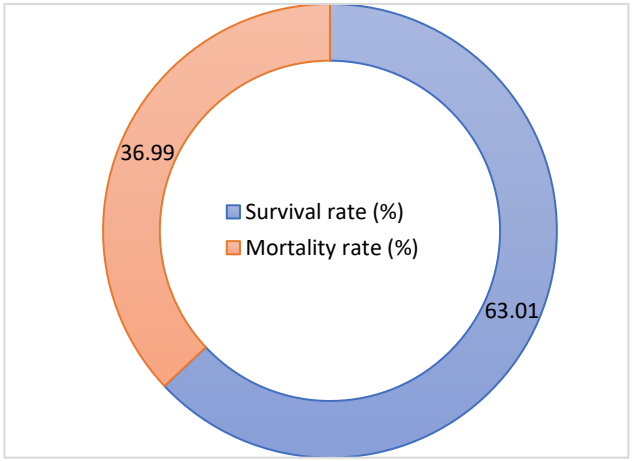
taurus, and by Sharma and Sundarraj [39] on *Leptocentrus longispinus*, *Otinotus oneratus* and *Oxyrhachis tarandus* which demonstrated the value of ant attendance in increasing the survival value of nymphs. The experimental results of Wood [26] also showed that larger groups of ant attended nymphs of *Enchenopa binotata* had a higher survival rate. The strength of associations between ant and honeydew producing insects, as well as the ability for ants to protect their symbionts from predators and parasites, vary greatly, even for the same pair of species among habitats [40]. Wood [26] noted membracids established mutualistic relationships with several ant species, not only provided protection to the nymphs by warding off the predators but also maintained the integrity of the nymphal aggregation when disrupted, by diminishing the alarm repose of nymphs, and reaggregation provided a means to retain effective alarm communication and facilitate ant attendance. On the other hand, Olmstead and Wood [41] observed a decline in the membracid population with decline in ant abundance owing to factors such as foraging patterns of the ants, distance of the tree or host plant from the ant colony, and the influence of nymphal group size on individual branches within a tree. Wood [26] reported that these factors influence how quickly the hatched nymphs are located by ants.



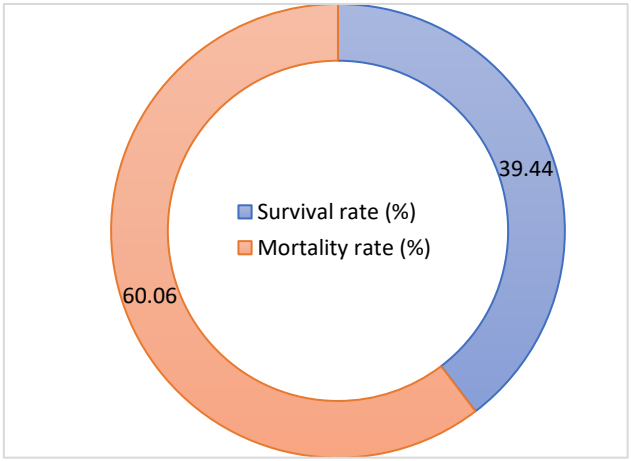
Leptocentrus taurus with *Myrmicaria brynnea*



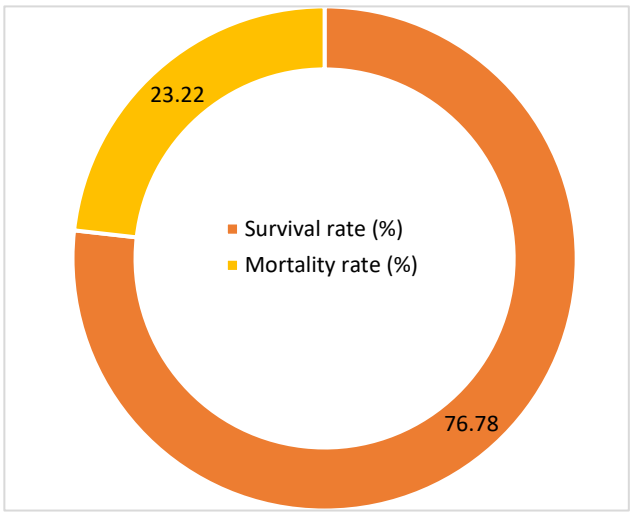
Leptocentrus taurus without *Myrmicaria brynnea*



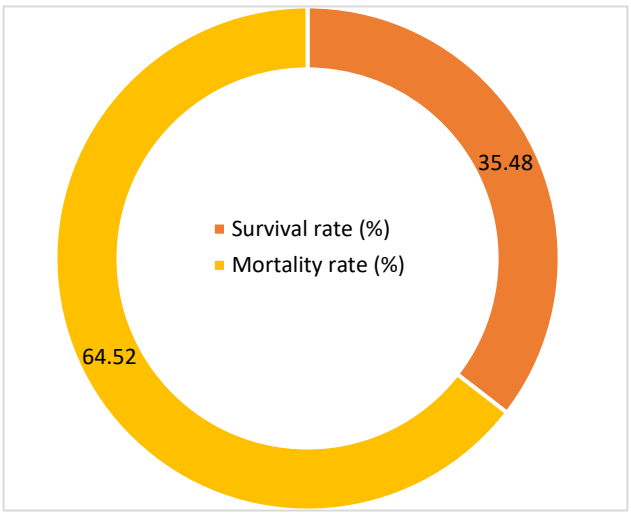
Otinotus oneratus with *Camponotus compressus*



Otinotus oneratus without *Camponotus compressus*



Oxyrhachis taranda with *Camponotus compressus*



Oxyrhachis taranda without *Camponotus compressus*

Fig 1 Effect of ant attendance on the survival rate of membracids

Factors influencing ant membracid relationship

Myrmecophilous interaction with ants are related to high degree of specificity, which often requires behavioural, chemical, and/or morphological adaptations of the participants to enable them to coexist with the ants. Ant hemipterans associations are generally regarded to be facultatively mutualistic [2-3], [28], since they have a density dependent effect [42], and ant membracid interactions have shown that the outcome of its association is contingent upon abiotic and biotic factors [43-44]. The mutualistic relationship between ants and treehoppers is conditional and can be affected by their physical and biological environment [12]. Studies have revealed that the outcome of ant membracid interactions can depend on factors such as temperature, membracid age [12], [45], identity and/or density of ants and membracids [12], [17], [42], host quality, the species of tending ants [11], [46], the aggregation size and the developmental stage of the honeydew producing membracids [12], [17], competition among honeydew producing insect aggregations for the services of ant mutualists [13], [45], [47], quantity and quality of honeydew [12], [29], [45], distance from servicing ant nests, nutritional status of ant colonies and the availability of alternative food resources of ants [45], the quantity of ants that are going to be attracted to interact in the mutualism [12], [29], [45], type, abundance of natural enemies [12-13], [16] and population of membracid enemies [48]. Moreover, mutualistic relationship tends to be more conditional when there is a third species involved in it [28].

Honeydew

The intensity of the mutualism between honeydew producing membracids and ants, depends, in part, on the relative attractiveness of honeydew to ants [11], [13], [45], [49]. Honeydew, a sugar rich liquid that contain a mixture of nutrients, is secreted by sap sucking hemipterans as a residue of partially digested plant sap, mixed products of the malpighian tubes [6], and further nutrients (specific amino acids and sugars), not found in the plant sap [19], [50]. Honeydew droplets contain a mixture of nutrients, *viz*., sugars, amino acids, amides, minerals, vitamins and proteins [19], [51]. Large membracid aggregations accumulate primarily on individual host plants that result in the production of large quantities of honeydew, which is the major component of many arboreal ant's diet and apparently is their main food source as well [6], [20], [35], [52-55]. Ants can detect qualitative and quantitative differences, as they preferentially tend those membracids on high quality hosts. Further, ants respond to changes in the composition and quantity of honeydew [56-58]. The quality and quantity of honeydew is variable, depending on different aspects like host plant, hemipteran age, and ant presence [20], [59]. Further, the host plant nutritional value and fitness can be a determinant of quality and quantity of honeydew too [59]. Ants, therefore, may respond more intensively to more profitable resources during honeydew collection activities [60-63]. Such differences in the reward for the foraging ant may be either larger volumes of honeydew [64], since quantity of honeydew is a critical factor in determining ant attendance [50], or higher quality honeydew that has preferred sugars or amino acids [13], [47], [50]. The quality of honeydew produced by membracids is another critical factor in determining the extent of ant attendance, because ants preferentially tend membracids that produce honeydew with a higher concentration of a particular trisaccharide called melezitose [50].

Trophobiosis

Trophobiosis (Trophikos: nourishment and biosis: life) is the by-product mutualistic relationship that exists between ants and herbivorous insects [6] [65-66]. This type of relationship occurs between some sap-sucking hemipterans, and arboreal ants [6], [54]. 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 [6]. The generalist or specialist ant membracid 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 [35], [59]. Further, ant assemblages can be affected by factors, like geographic location, season, and diurnal and nocturnal activity too [59].

Benefits for membracids

Benefits through mutualistic relationships with ants usually dependent upon variations in the environment [28], density of the interacting species, larger colony growth and size [67]. Factors such as the size and developmental stage of hemipteran aggregations, species and behaviour of ant partner, and predator abundance [12], [16], [42] also play a significant role while providing benefits to membracids. Ant attendance increases the feeding rate of membracids, its development, survival time of colonies [11], transportation of membracids to more favourable feeding sites of the plant with better quality sap supply, increased production of honeydew [8], provide some hygienic services, and improved sanitation in terms of honeydew removal [2], [8], thereby functioning as parental care takers, and thus increasing its reproduction rate [67-68].

Above all, ants providing 'unknowing protection' to the membracids by their mere presence, get themselves involved in the act of trophobiosis [69], by providing shelter and protection to the eggs, nymphs and adults, which leads to abundant decrease in their natural enemies. The mechanism of ant benefits to tended hemipterans often occurs via protection from natural enemies [8], [40], predators and parasitoids [2], [8], [11], [17-18], [54], [70], and parasitism [2]. Ants provide protection against frequent hemipteran predators, like ladybird beetle larvae and adults, syrphid fly larvae, lacewing larvae, parasitoid wasps, besides providing protection against general predators like spiders [12], [16].

Moreover, mechanistically, ants reduce fouling in membracids due to honeydew accumulation, by removal of their honeydew. In the absence of ants, the nymphs have to eliminate the honeydew by forcible extrusion, because uncollected honeydew may trap nymphs [71], and can result in the formation of sooty molds [72], block excretion, and increases its mortality risk caused by fungal attack [2-3], [73].

Benefits for ants

Studies have provided evidence that ants benefit from associations with hemipteran insects in terms of energy gain from the sugar rich food source produced by homopterans [8], [52], which is thought to result in higher colony growth rates [14].

Besides these, ant membracids interactions can also positively affect plant fitness, if the benefits of ant derived protection from herbivory outweigh the losses incurred by hemipteran feeding [52], [74]. Ant membracid mutualisms also involve a tritrophic system. Honeydew is consumed by ants either in direct association with the hemipterans (trophobiosis)

or indirectly when harvested from excretions accumulated on foliage and other plant surfaces [6], [8]. Ants protect membracids against predators, parasites and pathogens, and the associated plants against other herbivores, hence the tritrophic association can be often regarded as three-partner mutualism [2], [17], [45]. Given the importance of honeydew as a resource, it is expected and often observed that nutritious trophobioses are defended by ants against competitors and effectively monopolised [35], [75-78].

CONCLUSION

Ant membracid interaction has become a model system for studies of conditionality in mutualism. The benefits of mutualism are measured in terms of direct fitness such as the survival rate of nymphal population and the number of offsprings produced, and this relationship has significant consequences for membracids survival, since the ant species greatly reduce membracid mortality from predatory insects.

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