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ETHOLOGY OF SOME MEMBRACIDS ON ITS HOST PLANTS

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AUTHORS' CONTRIBUTIONS

This work was carried out in collaboration among all authors. Author KR managed the analyses of the study. Authors KR, ST, SA and MV managed the literature searches. Authors KR and ST wrote the first draft of the manuscript, performed the statistical analysis, and edited the final draft of the manuscript. All authors read and approved the final manuscript.

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ABSTRACT

Membracids have received adequate attention for its taxonomic, habitual, behavioural and bioecological studies. In the present study, the behavioural aspects (feeding, communal life, resting, mimicry and colouration, oviposition, incubation, ecdysis, and parental care) of three membracids, *viz*., *Leptocentrus taurus*, *Otinotus oneratus* and *Oxyrachis taranda* on its host plants were studied by regular field observations at frequent intervals. The present study brought to light more salient behavioural features of membracids on its respective host plants. Hence, studies on other species of membracids exposed to different host plants may bring out additional behavioural aspects.

Keywords: Membracid; *Leptocentrus taurus*; *Otinotus oneratus*; *Oxyrachis taranda*; behaviour.

1. INTRODUCTION

The family Membracidae, tropicopolitan in distribution, includes 2500 species, and comprises small to medium sized phytophagous insects belonging to the Auchenorrhynchous Homoptera. These insects are popularly known as 'cow bugs', 'horn bugs' and 'tree hoppers' for their tree jumping/hopping arboreal habits. Membracids have received adequate attention for its taxonomic work [1,2], ecological facets [3-6], habitual aspects [7], behavioural and bioecological studies [8-17]. Ananthasubramanian and Ananthakrishnan [9] and Devarajan [17] made preliminary studies on the

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population dynamics and fluctuations of the common membracid species, *Otinotus oneratus* and *Oxyrachis rufescens* respectively. Later, Rajkumar et al. [18-21] reported on the population dynamics of three membracids, *viz*., *Leptocentrus taurus*, *Otinotus oneratus* and *Oxyrachis taranda* in relation to the environmental parameters on its host plants. Thereafter, a lacunae on studies related to membracids occurred for a decade. Therefore, in the present study the behavioural aspects of three membracids on its host plants has been investigated.

2. MATERIALS AND METHODS

The present study was carried in Thiruvallur district of Tamil Nadu, India, from March 2007 to February 2009. The membracids species and their host plants chosen for the study are presented in Table 1. Nylon nets with medium sized meshes were tied on to host plants to enclose the eggs, nymphs and adults of membracids for close observation of its behavioural aspects, *viz*., feeding, communal life, resting, mimicry and colouration, oviposition, incubation, ecdysis and parental care by regular field observations at frequent intervals. A total of five observations were recorded/observed for each behavioural study.

3. RESULTS

3.1 Feeding

The rostrum of nymphs and adults was seen thrust into the host plant tissues. The first, second and third instars was found feeding on the tender twigs especially on the fleshy succulent parts of the host plant. The adults and later instars were found feeding together on the leaf axils and internodal regions of the stem. Adults of *Leptocentrus taurus* and *Otinotus oneratus* preferred the hard woody tissues, whereas, *Oxyrachis taranda* favoured the inflorescence axis of their host plant. *Leptocentrus taurus* invariably occupied the tender tips of the free hanging prop root of *Ficus benghalensis*, whereas, in the other two host plants, the terminal tender shoots were occupied more for feeding. The feeding sites of *Otinotus oneratus* adults and nymphs preferred the twigs/branches of its host plants which were one or two years old. *Oxyrachis taranda* remained in the midrib near the base of the lamina and favoured the lower leaf surface of their host plants.

3.2 Communal Life

Leptocentrus taurus nymphs and adults were entire solitary, whereas, in *Otinotus oneratus*, the nymphs were gregarious and the adults were solitary, and in *Oxyrachis taranda*, both the nymphs and adults were gregarious.

3.3 Resting Posture

Majority of the three membracid species rested with its head directed downwards. In *Leptocentrus taurus*, the percentage of heads directed downwards in adults and nymphs ranged from 85-93% and 82-95%, and for *Otinotus oneratus* it was 80-100% and 70-90%; and in the case of *Oxyrachis taranda* it was 80-100 % and 65-100% respectively (Fig. 1).

3.4 Mimicry and Colouration

The adults of *Leptocentrus taurus* and *Oxyrachis taranda* while at rest on the leaf axils with their horns outside the axils, appeared as an inanimate object, as its horns mimicked a stipular spine. The nymphs of *Otinotus oneratus* were dark brown in colour, and mimicked the thorns of the host plant.

3.5 Mating

Mating occurred three to six days after adult emergence. Observations on the duration of pre copulating period in *Leptocentrus taurus*, *Otinotus oneratus* and *Oxyrachis taranda* lasted for 15-45, 25-60, and 20-40 minutes respectively. During the establishment of sexual contact, the abdomen of the male was bent, its elytra raised, and body vibrated rapidly on closer observation. The male moved towards the female, turned around and effected sexual contact. The abdomens of both male and female were raised, and the male clasped the female, and the copulating pair remained with their abdomens raised to give the figure of inverted 'V'.

3.6 Oviposition

The arrangement of eggs differed in the three membracid species. In *Leptocentrus taurus*, the eggs were completely hidden from view as it was laid on the free hanging slender prop roots of its host plant. *Otinotus oneratus* lodged a row of eggs below the bark of its host plant. The eggs of *Oxyrachis taranda* were arranged in two rows in an alternating fashion. The two rows of eggs diverged at one end and converged at the opposite end.

In all the three membracid species examined, the eggs were elongate, oval in shape, shining white in colour with a smooth operculum and chorion. In *Leptocentrus taurus*, the eggs ranged from 220-290 arranged in egg slits on it host plant *Ziziphus jujuba*. The eggs were 0.7-0.17mm in diameter and 0.75-1.75

mm long. Just before hatching, the eggs were found to swell, and recorded an increase of 1.5 times their original size, and the colour changed to dull white. In *Otinotus oneratus*, the eggs were arranged in slits, and ranged from 160-220 on its host plant *Tamarindus indica*. The eggs were 0.22-0.25mm in diameter and 0.70-0.95mm long. The eggs were elongate with one end smooth and broadly rounded, which was embedded in the plant tissue during oviposition. The opposite end was slightly narrower and had the operculum. In *Oxyrachis taranda*, the number of eggs ranged from 340-420 on its host plant *Prosopis spicigera*. The eggs were 0.27-0.36mm long and 0.9-1.1mm wide, elongate with a yellowish white chorion which was smooth and vitreous.

The mortality rate of the eggs laid by the membracid species on its host plants differed based on years and seasonal periods. For *Leptocentrus taurus*, on *Acalypha wilkesiana*, it ranged from 50.0-78.0% in 2007-2008, and 40.4-72.7% in 2008-2009, and its seasonal average during premonsoon, southwest, northeast and winter was 63.5, 59.0, 58.0 and 57.0% respectively. In *Ficus benghalensis*, it was 42.8-80.9% in 2007-2008, and 33.3-78.2% in 2008-2009, and its respective seasonal average values were 62.0, 55.0, 57.0 and 55.0%. While for, *Ziziphus jujuba* the respective values were 50.0-79.1% in 2007-2008, and 25.0-79.1% in 2008-2009, and its respective seasonal average value was 58.5, 58, 56 and 56.5%. In *Otinotus oneratus*, the mortality rate of eggs ranged from 40.0-76.4% in 2007-2008, and 41.0-75.0% in 2008-2009, with a seasonal average of 65, 59, 52 and 55% respectively in *Pithecellobium dulce*. For *Tamarindus indica* it ranged from 38.9-72.2% in 2007-2008, and 41.3-70.4% in 2008-2009, with the seasonal average of 58.0, 53.0, 45.0 and 49.0% respectively. For *Terminalia catappa*, the respective values ranged from 43.7-68.5% in 2007-2008, and 33.3-88.8% in 2008-2009, and the seasonal average values were 56, 59, 48 and 59% respectively. In the case of *Oxyrachis taranda*, on *Acacia arabica*, the egg mortality rates varied from 30.7-59.5% in 2007-2008, and 33.3-71.8% in 2008-2009, and the seasonal average was 52, 52, 42 and 45% respectively. For *Crotalaria juncea*, the respective value ranged from 35.8-74.1% in 2007-2008, and 28.5-67.7% in 2008-2009, with a seasonal average of 54, 49, 45 and 48% respectively. While on *Prosopis spicigera*, it had a mortality rate of 28.9-84.5% during 2007-2008, and during 2008-2009, it was 23.7-77.5%, with respective seasonal average values of 55, 39, 35 and 45% (Fig. 2).

Table 1. Membracid species and their host plants selected for the present study

Membracid species	Host plant species	Family	Nature
Leptocentrus taurus Fabricius	*Acalypha wilkesiana* Müll.Arg.	Euphorbiaceae	Herb
	Ficus benghalensis L.	Moraceae	Tree
	Ziziphus jujuba Mill.	Rhamnaceae	Tree
Otinotus oneratus Walker	*Pithecellobium dulce* (Roxb.) Benth.	Fabaceae	Tree
	Tamarindus indica L.	Fabaceae	Tree
	Terminalia catappa L.	Combretaceae	Tree
Oxyrachis taranda Fabricius	*Acacia arabica* (L.) P.J.H. Hurter & Mabb.	Fabaceae	Tree
	Crotalaria juncea L.	Fabaceae	Herb
	Prosopis spicigera L.	Fabaceae	Tree

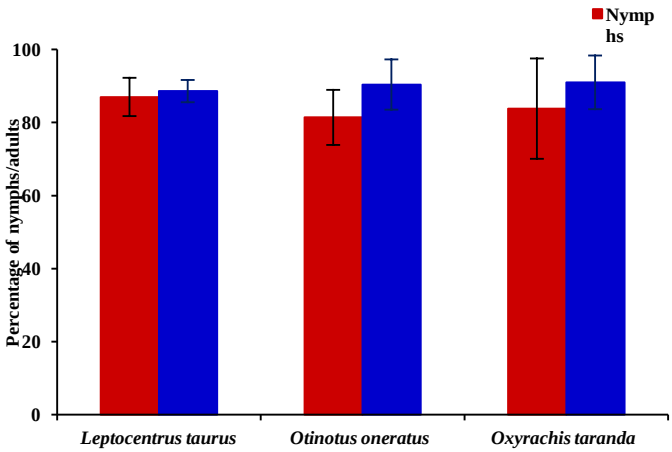

Fig. 1. Resting posture of membracids

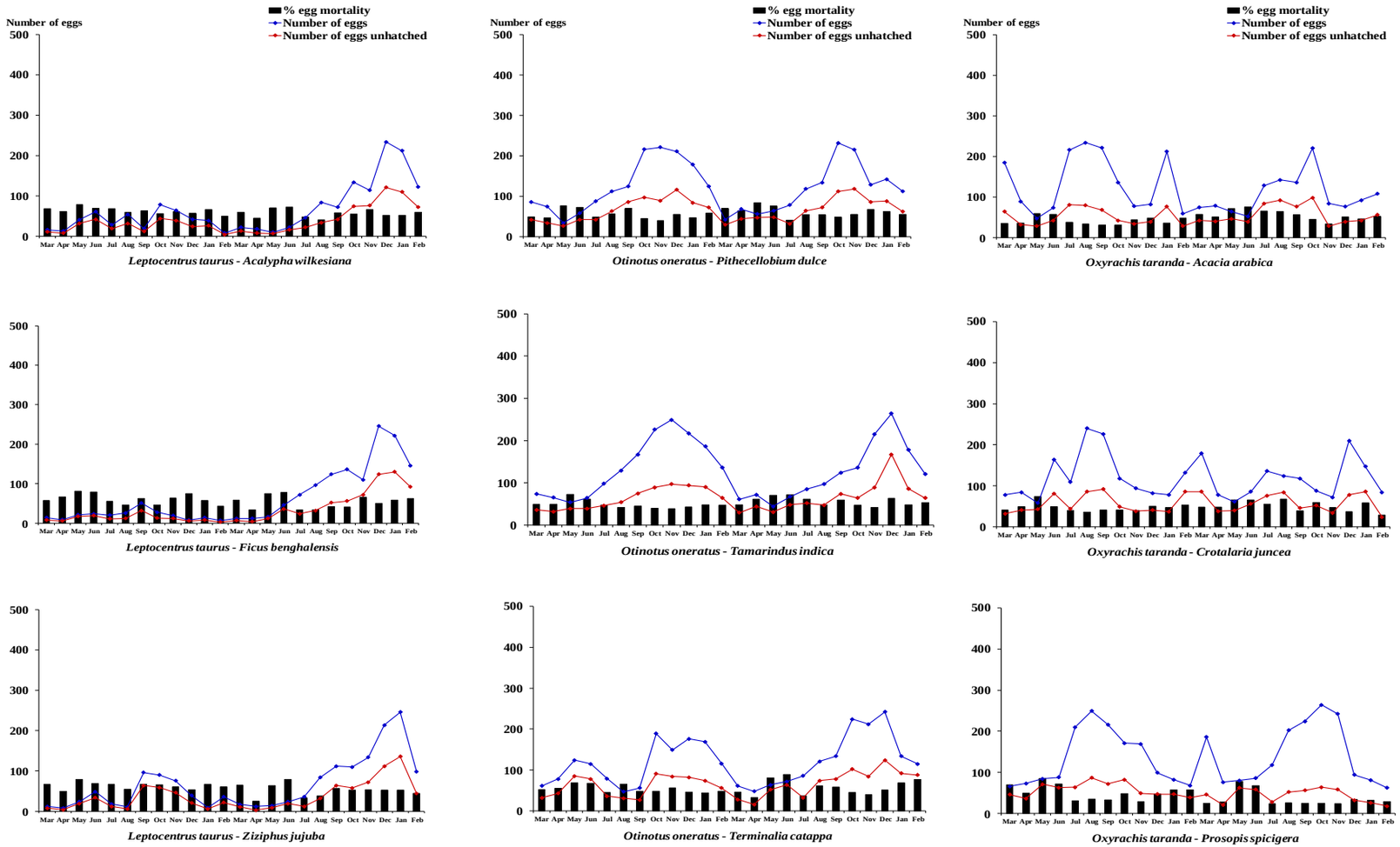

Fig. 2. Egg mortality rate of membracids on its host plants

3.7 Incubation

The incubation period of *Leptocentrus taurus* on *Acalypha wilkesiana*, *Ficus benghalensis* and *Ziziphus jujuba*; *Otinotus oneratus* on *Pithecellobium dulce*, *Tamarindus indica* and *Terminalia catappa*; and *Oxyrachis taranda* on *Acacia arabica*, *Crotalaria juncea* and *Prosopis spicigera* throughout the study period revealed a temperature that ranged from 29.3-33.7°C. The minimum incubation period was observed during December 2007, January 2008, November 2008 and December 2008 under conditions of high relative humidity, low temperature and excess moisture.

Hatching occurred with a minimum of seven days and a maximum of 11 days. The respective time for the entire process of eclosion in *Leptocentrus taurus*, *Otinotus oneratus* and *Oxyrachis taranda* was 35-55, 10-30 and 30-35 minutes respectively. Hatching occurred during the early hours of the day when the ambient temperature was low, and before hatching, a slight enlargement of the egg was observed. The process of eclosion was similar in all three membracid species in the present study except for the time required for the completion of the process. The hatching membrane covering the embryo ruptured and the egg cap was pushed upward by the first instar. The head projected out, and the body of the nymph exhibited rhythmic back and forth movements in its attempt to squeeze out, and finally the nymphs slowly moved apart and rested for some time.

3.8 Ecdysis

All three membracids underwent five moults. The earlier instar took less time than the later ones. The first instar of all membracid species completed ecdysis in about 30 minutes, and the mean time taken for moulting by the fifth instar of *Leptocentrus taurus*, *Otinotus oneratus* and *Oxyrachis taranda* was 35, 34 and 42 minutes respectively. The duration (in days) of egg stage for *Leptocentrus taurus* on *Acalypha wilkesiana*, *Ficus benghalensis* and *Ziziphus jujuba* was 9, 8 and 11 respectively. For *Otinotus oneratus*, on *Pithecellobium dulce*, *Tamarindus indica* and *Terminalia catappa*, the respective values were 9, 10 and 7. In the case of *Oxyrachis taranda*, on *Acacia Arabica*, *Crotalaria juncea* and *Prosopis spicigera*, it was 9, 9 and 11 respectively. The fifth nymphal stage exhibited the longest duration, and the mean time taken for moulting by the fifth nymphal stage in *Leptocentrus taurus*, *Otinotus oneratus* and *Oxyrachis taranda* was 35, 34 and 42 minutes respectively. The duration of each nymphal (I, II, III, IV and V) stages (in days) varied in three membracid species and even in the same species on its host plants. For *Leptocentrus taurus*, it was 6, 5, 5, 5 and 8 in *Acalypha wilkesiana*; 7, 6, 7, 6 and 9 in *Ficus benghalensis*; and 7, 4, 3, 5 and 9 in *Ziziphus jujuba* respectively. In *Otinotus oneratus*, it was 8, 4, 5, 6 and 8 in *Pithecellobium dulce*; 8, 5, 5, 4 and 9 in *Tamarindus indica*; and 6, 4, 4, 5 and 8 in *Terminalia catappa* respectively. While for *Oxyrachis taranda*, it was 8, 5, 5, 4 and 8 in *Acacia arabica*; 8, 5, 5, 4 and 9 in *Crotalaria juncea*; and 9, 5, 6, 4 and 10 in *Prosopis spicigera* respectively (Fig. 3).

3.9 Parental Care

The brooding females of membracids exhibited great tenacity for the protection of her eggs. The females of *Leptocentrus taurus*, *Otinotus oneratus* and *Oxyrachis taranda* remained in the egg slits and exhibited parental care for a period ranging from 5-8, 7-14, and 6-12 hours respectively. Further, it was observed that in all membracids, when probed with a needle, it resulted in more tenacious grip of egg masses, and when continuously disturbed, the brooding female moved away from the branch and then resumed 35, 30 and 27 minutes respectively. The female kicked at the needle with her hind legs, and opened and closed her elytra. When the stimulus was sustained on, the female slowly moved away to the other side of the twig, only to return to her egg mass in a short time.

4. DISCUSSION

4.1 Feeding

Membracids are continuous feeders and feed at almost any hour of the day, but their active feeding time appears to be during the mid-afternoon. The feeding behaviour of membracids is similar to that of other homopteran bugs. The strong and stout rostrum or beak is very well adapted for piercing the tissues of the host plants. Funkhouser [4] stated that very little energy was spent during feeding, and the insect remained in one spot for a long time. The feeding sites of the membracid nymphs and adults on their host plants are often specific. As a rule, nymphs, especially in their early stages, prefer tender and succulent parts of twigs, petioles, peduncles or pedicels. Ananthasubramanian and Ananthakrishnan [8,9] reported that the nymphs of *Eucoccosterphus tuberculatus* occurred gregariously either near the terminal parts of the peduncles or on the young aggregated fruits of their host plant *Morinda tinctoria*. Nixon and Thompson [11] reported that *Micrutalis calva* nymphs feed on flower stalks and leaflets between the veins, whereas adults feed on the floral parts and leaf rachis. Geetha [22] also reported that the first to fourth nymphal stages of *Tricentrus pilosus* chose the young, slender free hanging prop

roots while the later nymphs and adults moved upward to the relatively woody basal part of the prop roots. In the present study, the effect of feeding on host plants by the membracids was not deleterious, particularly when the host plant had woody tissues. However, the two gregarious membracids, *Leptocentrus taurus* and *Otinotus oneratus* brought significant damage to *Tamarindus indica* and *Ziziphus jujuba*. The feeding sites, *viz.*, tender stem or inflorescence axis or young pods, dried and fell down due to the sucking action caused by these two membracids.

4.2 Communal Life

Most membracid species exhibit gregariousness, living in group in a sub social manner [8,9]. In some species, the adults also remain gregarious, but in many instances, they become solitary. In the present study it was observed that the membracids exhibited both solitary and gregarious behaviour. Further, an interesting aspect in the membracid was that, when disturbed, they hop out or fly away, but after a while returned to the same twig and remained together marking a sub gregarious behaviour.

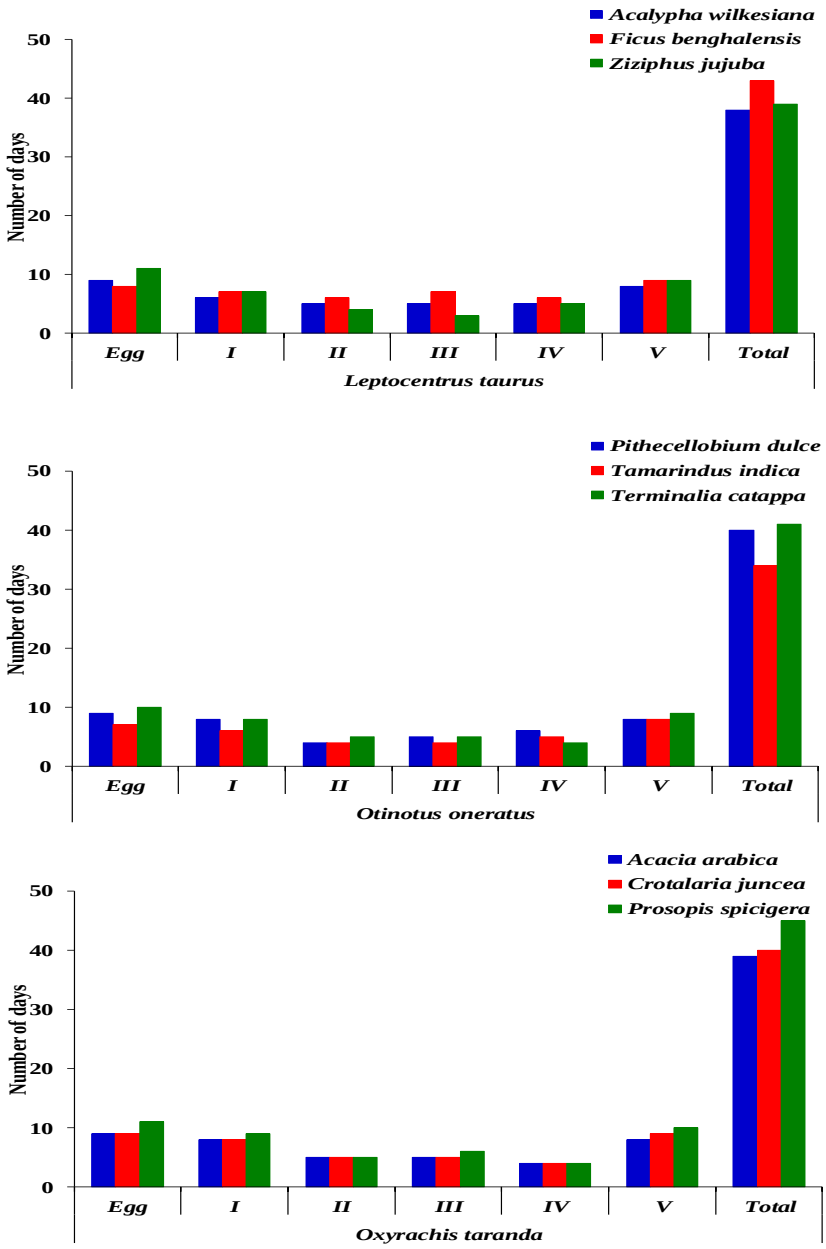

Fig. 3. Incubation period and post embryonic development of membracids on its host plants

4.3 Resting Posture

A peculiar behaviour of membracids in general is their resting posture. Funkhouser [4] stated that majority of adults rests with its head pointing towards the branch, or pointing downwards if it is in the trunk, and whether this characteristic attitude is assumed in order to increase their resemblance to the thorns, twigs or irregularities of growth of their host wound be a matter of conjecture. In the present observations also, it was found that the three species of membracids rested with a posture of their head ends directed downward. In the opinion of the present investigation, this characteristic may be advantageous for the insect to jump down to the substratum or ground at the slightest indication of danger; and when the insect usually hops to an adjacent branch or falls to the ground, it is out of sight to the predator. In general, nymphs when disturbed adhered more tenaciously to the twigs, and the same was observed in the nymphal stages of the three membracids studied.

4.4 Mimicry and Colouration

The grotesque pronotal development of membracids and their colour pattern are interesting phenomena in the context of mimicry and colouration [23]. The membracid body shape and colour blends so perfectly with the bark, leaves, flowers, buds, stipules, spines or seeds of their respective host plants, that they remain quite inconspicuous and derive protection from predators enhancing their survival value significantly. The same was observed in the present study too where the three membracids mimicked a stipular spine and thorns of their host plants, and blended with their background with respect to colouration. Ananthasubramanian and Ananthakrishnan [8,9] proved the value of cryptic colouration and mimetic behaviour in the survival rate of membracids. In general, the nymphs are leafy green, particularly on their dorsal aspect, and thus they blend with their background, and with the colour of their host plants. Nymphs which occupy the leaf axils of their host plants mimic the auxiallry buds making them inconspicuous for a casual observer and to their natural enemies too. Ananthasubramanian and Ananthakrishnan [9] pointed out the superficial resemblance of membracids to the parts of their host plants, wherein, the pronotal anterior process of the last nymphal instar of *Leptocentrus varicornis* mimicked the stipular spine of *Ziziphus jujuba*, and the suprahumeral horns of *Leptocentrus taurus* resembled the stipular spines of *Capparis sepiaria*. The colouration and the body contour of *Eucoccosterphus tuberculatus* resembled to a great extent the immature dried fruits of its host plant *Morinda tinctoria*.

4.5 Mating

Mating behaviour of all three membracids in this study did not vary and appeared to confirm to a general plan. Mating ritual contains four components as observed in *Platycotis vittata* by Wood et al. [24], which involved, (i) male attraction to female, (ii) selection of male by female, (iii) pre copulation, and (iv) establishment of sexual contact. In the first stage, two or more males are attracted to a female. The males walk up and down the host plant, and the female walks slowly around the twig and remains motionless for a while. The males then move and positions themselves by the side of the female, and the female kicks off the males by her legs and moves away in a spiral manner around the twig. This behaviour is repeated until a single male is allowed to remain by her side which marks the end of the second stage of mating. In the pre copulatory period, one female and a single male alone are involved, and this period lasts from a few minutes to several hours followed by sexual contact. All these components were observed in the three membracids studied.

4.6 Oviposition

During oviposition, the female protrudes her ovipositor holding it nearly at right angles to the body and thrusts it into the plant tissues. It was found that the ovipositing sites of membracids were determined by the distance of the oviposition site from the base of the twig, and the age of the stem. As a rule, they prefer branches which are one or two years old for oviposition. The arrangement of eggs in the egg slits also differed in the three species of membracids studied. Further, the initiation and the termination of oviposition phases differed in terms of time. The number of eggs in each egg mass of the different species of membracids varied as the present observation revealed. The difference in the incubation period appear to be spectacular during various seasons of the year due to the effects of temperature, moisture, and humidity as extreme temperature and low humidity retard embryonic development [25]. The same factors influenced the findings of the present study too. The nymphs become slow in its movement, eventually stop feeding and undergoes moulting. Moulting invariably occurs when the ambient temperature is low (during the early hours of the morning and late in the evening). The first region to show the ecdysial pit was epicranial structure. The split extended forward and backward on the head capsule, then along the entire length of the trophi and subsequently extended backward through the cervical sclerites on the thorax. Chitra [25] stated that as the soft parts of the insect gradually freed from the old exoskeleton, the latter became more or less crumbled only to be consumed by the insect.

4.7 Incubation

The duration of egg stages differed in the three membracid species. The incubation period was found to be significant during different seasons of the year due to the influence of temperature, relative humidity and rainfall [8,9]. In the present study too, temperature accelerated the embryonic development, and hatching occurred in less than seven days, irrespective of relative humidity, and the incubation period prolonged to 11 days.

4.8 Ecdysis

Moulting time differs with regard to nymphal stages as well as with the ambient physical factor, as moulting normally occurs in the morning when the temperature is low [8,9]. The duration of each nymphal period was dependent upon abiotic factors (temperature, relative humidity and rainfall), and on its host plant too, as a relatively high temperature was found to accelerate the nymphal development which was observed in the present study too. The discarded exoskeleton which often remains attached to the twig for several days revealed the chaetotaxy of the nymph.

4.9 Parental Care

One of the interesting social interactions exhibited by the membracids in the context of their ethology is the various degrees of parental solicitude [26]. The evolution of parental care represents an extraordinary breakthrough in the adaptations of organism to their environment. Insect parental adaptations comprise a continuum of care ranging from passive egg guarding to an array of complex grooming, feeding and protective behaviours. The parental care can be categorized into three primary behaviours: (a) those that physically protect the young from danger, (b) those that provide resources vital to the offspring, and (c) those that facilitate offspring feeding. Wilson [27] reported maternal care in membracids in the context of survival of eggs and nymphs. Observations on the brooding membracid females in the present study clearly indicated that the peculiar orientation of its resting posture enabled the female to cover almost the entire egg mass.

5. CONCLUSION

The present study brought to light more salient features of membracids behaviour on its respective host plants. Hence, studies on other species of membracids exposed to different host plants may bring out additional behavioural aspects.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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