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Biology, feeding and oviposition preference of *Helopeltis theivora*, with notes on the differential distribution of species of the tea mosquito bug species complex across elevations

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Abstract

Cocoa (*Theobroma cacao* L.) is an important beverage crop and commercially grown as a plantation crop. With the changing climate, the tea mosquito bug species complex, viz., *Helopeltis theivora*, *H. bradyi* and *H. antonii*, is emerging as a major threat to cocoa cultivation in India. Among the species of this complex *H. theivora* is responsible for causing considerable damage. The present investigations were carried out to find a weak link in the life cycle of *H. theivora* so it can be managed effectively. Specimens of the tea mosquito bug were found to first appear during the first week of September in South India. *Helopeltis theivora* requires on average 29.28 days to complete its life cycle on cocoa. The highest level of natural mortality was recorded in the first-instar nymph. The total developmental period of the fifth-instar nymph was significantly longer than that for the other nymphal instars. The sex ratio reflects that the population is highly female-biased, which may contribute to the dominant nature of this species in the cocoa ecosystem. Observation of the feeding and oviposition behavior of *H. theivora* revealed that the insect prefers to feed and oviposit on developing pods rather than on leaves and shoots. Analysis of the species distribution of tea mosquito bug at different elevations revealed that cocoa gardens situated less than 300 meter above mean sea level are dominated by *H. theivora*, whereas gardens situated more than 300 meter above mean sea level are dominated by *H. bradyi*. This separation of species across elevation may be driven either by abiotic or biotic factors.

Keywords

behavior; biology; cocoa; *Helopeltis* species; species distribution; tea mosquito bug

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Introduction

Cocoa is one of the world's important cash crops and commercially grown as a plantation crop in India. It is native to the Amazon region of South America and was originally consumed as a bitter energy drink, 'xocoatl', by Mayans and Aztecs; later, with the addition of milk and sugar, chocolate was made of it. In India it was introduced in the Western Ghats and plains, and from 1970 onwards became an integral part of palm-based cropping systems. It now covers an area of 82 940 hectares in India, covering the states of Kerala, Karnataka, Tamil Nadu and Andhra Pradesh, with a production of 18 920 tonnes annually. The Indian chocolate industry and confectionaries are predicted to require 60 000 tonnes of dry beans for the year 2025, while current production requires 45 000 tonnes (DCCD, 2014). In recent years cocoa cultivation has been facing threats due to several factors, viz., pests and diseases, inadequate irrigation, climate change, lack of quality planting material, and improper management.

Among these threats, the occurrence of insect pests and diseases is one of the key factors causing low production and reducing productivity of cocoa. More than fifty pest species have been documented from perennial stands of cocoa in different cropping systems throughout the world (Entwistle, 1972). Among these pests, the tea mosquito bug (TMB), *Helopeltis* spp. (a species complex; Heteroptera: Miridae), has emerged as a major pest of cocoa in South India. Being a polyphagous pest, TMB is able to do damage in cocoa gardens adjoining cashew plantations irrespective of the season (Devasahayam, 1985). TMB is recognized as 'capsids' in many African countries and considered as one of the most important insects affecting cocoa cultivation across the globe (Mariau, 1999).

In India, this species complex is one of the most serious sucking insect pests of cocoa, being responsible for causing up to 40% yield loss (CPCRI, 1993; Padi, 1997). Nymphs and adults of this mirid suck the cell sap from leaves, young shoots, peduncles, and pods. The injury made by the suctorial mouth parts of the insect cause exudation of a resinous gummy substance from the feeding punctures (Thube et al., 2016). The tissues around the point where the stylet enters become necrotized due to infection with secondary plant pathogens. These feeding lesions turn pinkish brown after 24 hours and become black within 2-3 days. Affected shoots show long black lesions and may cause die-back in severe cases. TMB infests the economically important part of cocoa tree, i.e., the pod, and even small amounts of damage caused by the insect pest may lead to heavy quantitative loss directly as well as qualitative loss indirectly (Muhamad & Way, 1995).

Because *Helopeltis* is a pest species affecting introduced crops, studying its biology and behavior is very important for finding weak links in the life cycle of this bug in order to formulate effective management strategies against this pest. The entire *Helopeltis* species complex, comprising *Helopeltis theivora* Waterhouse, 1886, *H. bradyi* Waterhouse, 1886 and *H. antonii V.* Signoret, 1858, is reported from cocoa ecosystems, but reports on its species distribution across elevation gradients are scarce. The objectives of this work were to study the biology and behavior (of the focal species *H. theivora*), and to characterize the distribution patterns of the *Helopeltis* species complex associated with cocoa at different elevations in the southern part of India. The results are expected to provide ecological knowledge that is useful for implementing integrated pest management strategies of this pest in cocoa gardens. The present investigation also confirms the existence of a species replacement strategy in TMB *Helopeltis* spp. at different elevation levels.

Material and methods

Biology

All research regarding the biology and behavior of *H. theivora* was carried out at the experimental farm of the Central Plantation Crops Research Institute, Regional Station, Vittal, Karnataka, India (12°45′N, 75°4′E; 90 m above mean sea level [ASL]) during 2017 and 2018.

Aluminum rearing cages developed by Sundararaju & John (1992) were fabricated with slight modifications for studying the biology and behavior under laboratory conditions. Gravid females of TMB were collected from the experimental farm and species-level identity was confirmed using the keys in Stonedahl (1991). Gravid females were allowed to lay their eggs on fresh cocoa pods kept in the rearing cages. The respiratory processes of eggs projecting from the surface of the pods were indicative of the presence of eggs. The eggs laid on the pods were maintained in the laboratory and observations on fecundity, incubation period and egg hatchability were recorded. The hatchability was calculated by dividing the total number of nymphs that emerged by the total number of eggs that were laid and then multiplied by 100 to express it as a percentage.

Thirty newly hatched nymphs of *H. theivora* were transferred individually into nymphal rearing cages containing fresh pods. The nymphs were observed daily in order to record the molting period of each instar. The molted skin was removed soon after each molt to avoid mixing up the casted skins of different instars. The duration of all nymphal instars, of both males and females, was recorded throughout the experiment.

The survival rate of *H. theivora* was calculated by recording the death of individuals from all instars and of adults during the developmental time. The mating behavior of newly emerged males and females was studied in laboratory conditions. Mating patterns with respect to preferable time for successful mating of males and females were studied. The sex ratio was calculated using the number of males and females that emerged from four replicates (each replicate included fifteen nymphs).

Feeding and oviposition preference

Choice test. In a choice test the feeding and oviposition preference of TMB on cocoa shoots and pods was studied. Freshly emerged adults of TMB were released into aluminum cages containing a uniform number of cocoa shoots and pods. One pair

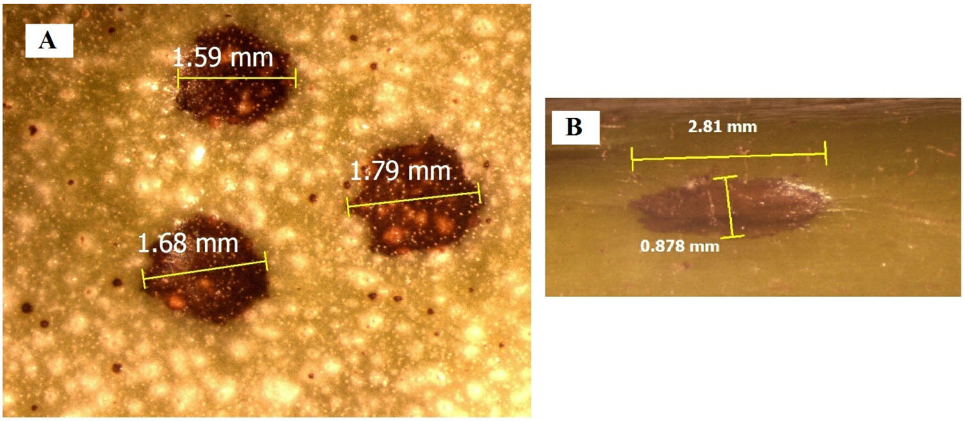

Figure 1. Shape of feeding lesions produced by *Helopeltis theivora* on pods (A) and shoots (B).

of adults per cage was considered as a replication. Fifteen such replications were maintained in this experiment. The number of feeding lesions produced on pods and shoots by each pair of adults was recorded 24 h after their introduction. Fifteen of these feeding lesions were randomly selected and the diameters of these lesions were measured under a stereomicroscope (Leica M10, equipped with an EC4 Digital camera). To study the oviposition preference, one pair of females was released into an aluminum rearing cage containing both cocoa pods and shoots. One pair of females per cage was considered as one replication and 15 such replications were maintained. The number of eggs laid on pods and shoots was recorded separately.

No choice test. One pair of adults was released per cage containing either cocoa pods or shoots. Each pair was considered as a replication and 30 such pairs were allowed to feed separately on either cocoa pods or shoots. The number and size of feeding lesions produced, and number of eggs lain on pods and shoots were recorded separately. The data thus obtained were also quantified further in terms of number of lesions produced/pair/day on pods and shoots, respectively.

Data on the number and diameter of feeding lesions recorded in the choice and no-choice tests were further used to calculate the actual area of pods and shoots damaged by a pair of adults. The shape of feeding lesions produced on pods was circular (fig. 1A) whereas on shoots the shape of lesions was ellipsoid (fig. 1B). The area of the circular lesions was calculated using the formula $A = \pi r^2$, where A is the area and r is the radius of the feeding lesion. The area of ellipsoidal lesions was calculated using the formula $A = \pi ab$, where A is the area of the ellipsoid feeding lesion produced on shoots, a is the length of the maximal axis ‘a’ and b is the length of minimal axis ‘b’.

For the *in-vivo* study, a field survey was conducted in 10 different TMB-infested cocoa gardens located in the Dakshin Kannada district of Karnataka. Ten randomly sampled plants per garden were observed and the number and diameter of feeding lesions per five shoots and pods were recorded. The mean number of lesions, diameter of feeding lesions and number of eggs laid on pods and shoots were recorded separately and subjected to analysis for understanding the feeding and oviposition preference in real field conditions.

Species distribution across the elevation gradient

Survey and sample collection. A survey was conducted at different elevation levels in the major cocoa-growing areas of Karnataka (Bantwal, Puttur, Mangalore, Sullia, Balehonnur and Shivamogga), Kerala (Idukki) and Tamil Nadu (Kodaikanal and Kumbarayoor) states of India. Ten TMB-infested cocoa gardens were selected from each location. Randomly, fifty cocoa trees were surveyed and adults were collected from each garden.

Species identification. The taxonomic identities of all the collected specimens were confirmed using morphological characteristics. Taxonomic characters such as pronotal coloration, color pattern on hind leg, structure of lobal sclerite, female genital chamber and parameres were observed and the identity of specimens was confirmed using the keys in Stonedahl (1991).

Further, species identity was confirmed through molecular characterization. DNA was extracted from legs and antennae of the adult individuals using the Qiagen DNeasy Blood and Tissue Kit® (QIAGEN Strasse 1, Hilden, Germany), following the manufacturer's protocols. The remainder of the body of the respective individuals is kept as voucher specimens at ICAR-CPCRI-RS, Vittal, Karnataka. PCR reactions were performed to amplify the partial mitochondrial cytochrome oxidase (*MT-COI*) gene using a 50 μl reaction volume containing 25.0 μl GoTaq® Green Master Mix (Promega Corporation, Madison, WI, USA), 2.0 μl each of the forward (LCO1490 5′-GGTCAACAAATCATAAAGATATTGG-3′) and reverse (HCO2198 5′-TAAACTTCAGGGTGACCAAAAAATCA-3′) primers (Folmer et al., 1994) (10 pmol/μl), 2.0 μl DNA and 19.0 μl sterile water. Thermocycling (Bio-Rad T100, Hercules, CA, USA) consisted of an initial denaturation at 94°C for 3 min, followed by 30 cycles of denaturation at 94°C for 20 s, annealing at 50°C for 30 s, extension at 72°C for 30 s, and a final extension at 72°C for 5 min. The amplified product was evaluated by electrophoresis on a 1.0% agarose gel (Sambrook, 2001). PCR purification (Bioline Meridian Bioscience, Bioline GmbH, Luckenwalde, Germany) was done and purified products were sent for Sanger sequencing (Agrigenome Pvt. Ltd., "SmartCity Kochi", Infopark Road, Kakkanad, Kerala, India). Obtained sequences were aligned using BioEdit (Biological sequence alignment editor – Tom Hall, http://www.mbio.ncsu.edu/BioEdit/bioedit.html) and blasted in the NCBI (http://www.ncbi.nlm.nih.gov/) as well as the BOLD database (http://www.boldsystems.org/). Sequence similarity was analyzed with the available sequences and sequences were deposited in NCBI.

Species distribution. After exact identification of the species, the fraction of the population occupied by each species at a particular elevation level was worked out. Surveyed areas were grouped into different elevational ranges, i.e., 0-300, 301-600,

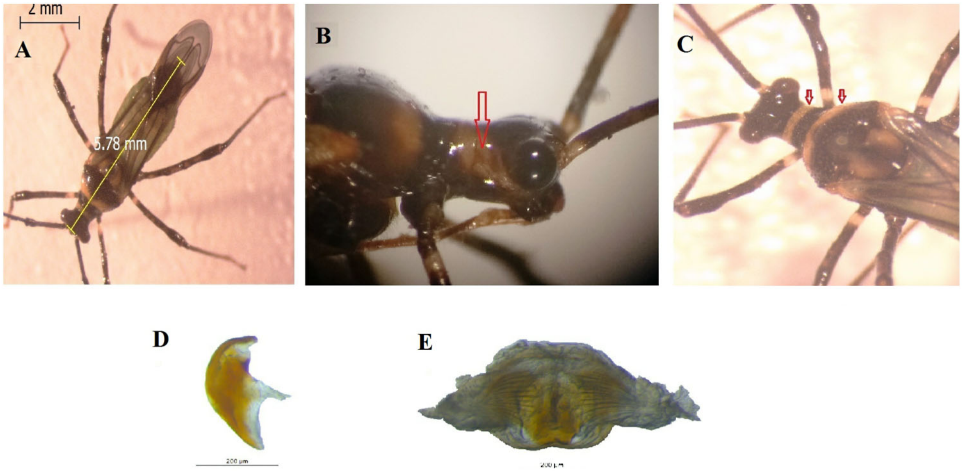

Figure 2. *Helopeltis theivora*. (A) Adult; (B) head with lateral pale stripe; (C) bi-colored pronotum; (D) lobal sclerite; and (E) female genital chamber.

601-900, 900-1200 and >1200 m and the dominant species in each group was identified.

Statistical analysis

Data collected in the biology and behavioral studies were expressed as mean ± SE. Difference between developmental period of nymphal instars was examined via one-way ANOVA and means were separated by Duncan's Multiple Range Test. Statistically significant differences between number of feeding lesions on pods and shoots as well as actual area of feeding were analyzed by independent samples t-test at 0.01% level of significance using SPSS software (v. 15.0 – IBM, Armonk, NY, USA).

Results

In the field, the presence of TMB was first noted during the first week of September. *Helopeltis theivora* was recorded as the dominant species at the research farm of ICAR-CPCRI, Regional Station, Vittal, Karnataka, during this study. The species' identity was confirmed by observing taxonomic characters such as elongate, dark brownish to greenish bugs (fig. 2A); head with pale stripe laterally (fig. 2B); antennae with first segment pale; pronotal collar bicolored (fig. 2C); lobal sclerite of male genitalia quite large with a relatively small base, bluntly pointed at apex (fig. 2D); right paramere reduced and pointed at apex; left paramere longer, with curved apex; and female genital chamber with numerous well-developed rings distally and separate throughout (fig. 2E).

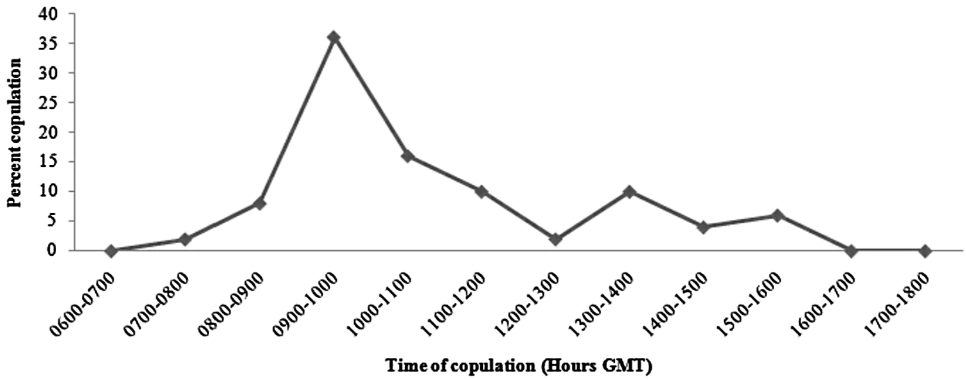

Figure 3. Mating pattern of *Helopeltis theivora* during photophase.

Biology

After molting of the fifth-instar nymph, adults take 9.4 ± 0.51 days till first mating, i.e., the pre-mating period. The average mating period per pair recorded is 1.24 h. The mating pattern of adult males and females is depicted in fig. 3. Most adult mating pairs were observed during the morning, 9-11 AM. After every successful mating the adult female takes 3.8 ± 0.2 days for oviposition, i.e., the pre-oviposition period. The mean incubation period of eggs is 8.1 ± 0.39 days. An average number of 9.0 ± 0.32 eggs per female was recorded during the first day of oviposition. The mean fecundity was quite high, with 78.63 ± 1.69 eggs/female. The mean percentage of egg hatchability was 79.74%. Among all nymphal instars, the developmental time of the fifth-instar nymph was significantly longer (ANOVA: $F_{4,70} = 170.66$, $P < 0.01$) than that of the other stages with 72.01 h. The mean developmental period of all the nymphal stages is depicted in table 1. Adult females and males lived for 20.87 ± 0.72 and 15.67 ± 0.68 days, respectively. The total developmental period for *H. theivora* was 29.28 days (table 1). Finally, among all nymphal instars 65.32% reached the adult stage. The highest natural mortality was recorded in first-instar nymphs followed by second instars with 80.17 and 93.46% survival, respectively. The survival frequency of all nymphal and adult stages is depicted in table 2. The male to female sex ratio was 1:1.65; this indicates that the population of *H. theivora* is female-biased.

Feeding and oviposition preference

The mean number of feeding lesions and the actually damaged area on pods and shoots caused by *H. theivora* in choice and no-choice tests by a pair of adults after 24 h of rearing are shown in table 3. The mean number of feeding lesions and the actual area of feeding were observed to be significantly higher on pods than on shoots in both choice and no-choice tests (independent samples t-test for choice test; $t_{28} = 17.73$, $P < 0.01$ and $t_{28} = 16.52$, $P < 0.01$; for no-choice test; $t_{28} = 16.33$, $P < 0.01$ and $t_{28} = 15.97$, $P < 0.01$).

Table 1.
Mean developmental period of different stages of *Helopeltis theivora*.

Instar/stage/sex	Mean developmental period (hours) ± SEM
1st instar	$38.32^{d} \pm 1.06$
2nd instar	$47.24^{c} \pm 0.85$
3rd instar	$48.32^{c} \pm 0.88$
4th instar	$58.37^{b} \pm 1.12$
5th instar	$72.01^{a} \pm 0.99$
Total nymphal period (days)	11.01
Male	15.67* ± 0.68
Female	20.87* ± 0.72
Mean adult duration	18.27
Total life cycle (days)	29.28

*Duration in days.
Means in columns followed by different small letters are significantly different according to Duncan's multiple range test ($P < 0.05$).

The data generated from the field survey (fig. 4) support our laboratory study and prove that *H. theivora* prefers pods for feeding as well as oviposition.

Species distribution across the elevation gradient

Samples collected during the survey were subjected to morphological characterization, which confirmed that only two species of TMB, viz., *H. theivora* and *H. bradyi*, are damaging cocoa at different elevations. Sequencing of the mitochondrial cytochrome oxidase gene yielded 679 and 595 bp fragments for *H. theivora* and *H. bradyi*, respectively. A BLAST search for the sequences obtained for *H. theivora* and *H. bradyi* showed the highest hits for the respective species. The *COI* gene sequences of *H. theivora* and *H. bradyi* have been submitted to GenBank under accession numbers MH628465 and MH628466. The dominance and distribution of TMB species at different elevations is depicted in fig. 5. At low elevation, i.e. <300 meter ASL, *H. theivora* was predominant whereas in cocoa gardens situated at >300 meter ASL, *H. bradyi* was the dominant TMB species.

Table 2.
Mean percentage survival of different stages of *Helopeltis theivora*.

	Mean percentage survival (%)						
Instars/stages	Egg	1st	2nd	3rd	4th	5th	Adult
% Survival	79.74	80.17	93.46	95.37	97.19	99.06	99.89
SEM (±)	1.56	2.07	0.91	0.83	0.89	0.84	0.11

Table 3.
Mean number of lesions with actual area of feeding per pair of adult per day.

Test	Plant parts	Number of feeding lesions/pair ± SEM	Actual area of feeding/pair/day ± SEM (mm)	Number of eggs laid on first day of oviposition/female ± SEM
No choice	Pods	184.8 ± 10.07	472.14 ± 27.32	10.2 ± 0.32
	Shoots	19.4 ± 1.05	35.26 ± 2.36	2.2 ± 0.42
Choice	Pods	179.06 ± 9.94	457.49 ± 27.59	9 ± 0.32
	Shoots	2.33 ± 0.6	3.30 ± 0.15	0.33 ± 0.24

$n = 15$ replications.

Discussion

Tea mosquito bugs, among which *H. theivora*, have recently emerged as a major insect pest of cocoa. Nevertheless, very few reports are available on their biology, behavior, seasonal incidence, and distribution in cocoa ecosystems, while the study of the seasonal incidence is much required for the appropriately timed application of management strategies. Throughout the period of study, no incidence of *H. theivora* was seen during the southwest monsoon (June-September). This may be attributed to the non-availability of the preferred host stage or the unfavorable climatic condition during this period. The occurrence of TMB in the field was first noted during the first week of September.

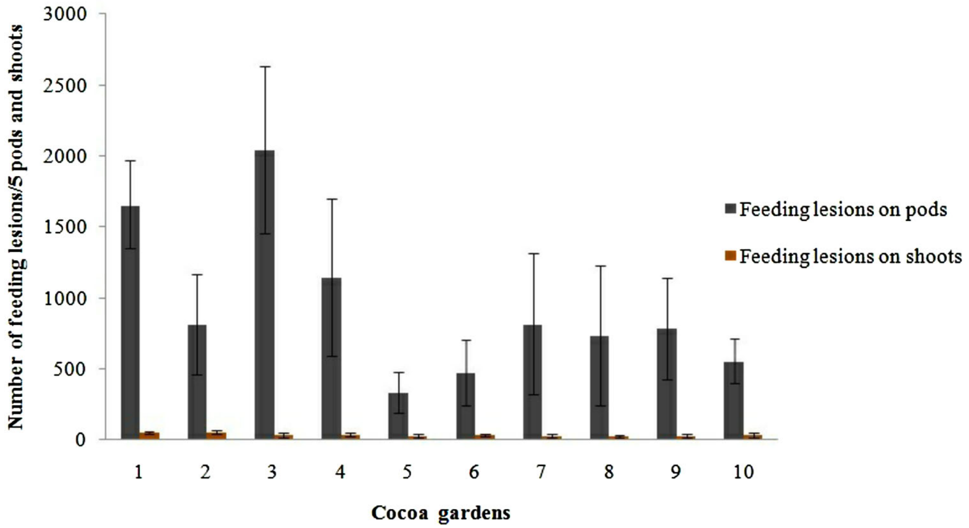

Figure 4. Number of feeding lesions on samples collected from field during survey (error bars reflect SEM of feeding lesions on 5 pods/shoots).

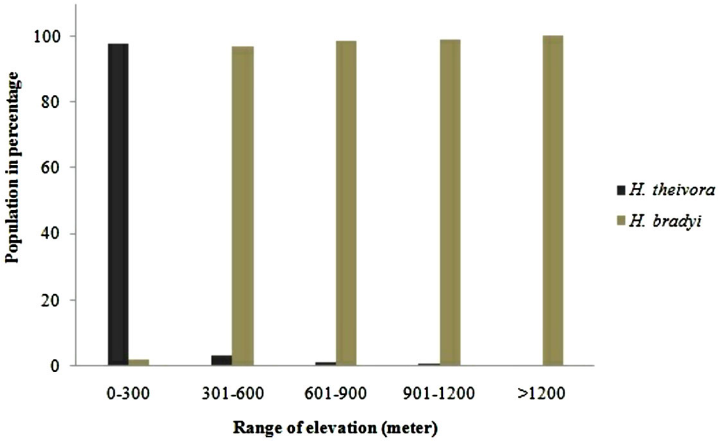

Figure 5. Distribution and dominance of *Helopeltis* spp. across the elevation (based on sampling of 10 gardens/range of elevation).

After completion of their nymphal instar stages and pre-mating period, courtship predominantly occurs in the morning hours. This preference for the morning hours for mating may be due to the courtship pheromone activity of virgin females being at a maximum or to the availability of favorable climatic conditions during that time period. Our results for the pre-oviposition period (3.8 ± 0.2 days) and mean fecundity (78.63 ± 1.69) are in agreement with the report of Roy et al. (2009) on tea. Srikumar & Bhat (2012) reported substantially lower mean egg hatchability in cashew (66%); whereas, our study recorded 79.74% egg hatchability in cocoa. This variation may be due to a difference in nutritional composition and variation in the turgor pressure at the oviposition site. The longer duration for the fifth-instar nymph (72.01 h) may be required for its preparation to undergo the precious molt. Higher numbers of feeding lesions with more diameter produced by fifth instar nymph may be attributed to the intake of more food to create enough tension on the cuticle for molting into the adult stage. The mean developmental periods of all the nymphal instars concur with those in the report of Srikumar & Bhat (2012).

Srikumar & Bhat (2012) reported the longevity of *H. theivora* males and females to be 23.17 and 24.67 days, respectively. However, in the present study, reduced longevity of adult males and females may be attributed to variations in the host plant and rearing material. Survival rate of nymphal instars is moderate (65.32%) and in agreement with the report of Roy et al. (2009). The maximum natural mortality in first-instar nymphs, may be due to the presence of a very delicate proboscis and the absence of optimal feeding sites to suck the cell sap. Female-biased sex ratio reported in this study may be one of the reasons that *H. theivora* has become a dominant species of the TMB in cocoa ecosystems situated at lower elevations.

Preference of cocoa pods for feeding and oviposition may be due to the various reasons viz. higher turgor pressure in pods, which is required for the easy sucking of cell sap and oviposition, the availability of strong feeding/oviposition stimulants that initiate and maintain continuous feeding/ovipostion on pods and the high nutritional qualities of pods as compared to other parts.

During field surveys we observed that the occurrence of the pest increases with the availability of developing pods. A very contrasting result was observed by Pillai et al. (1984), who noted that the commencement of population development of TMB (*H. antonii*) was synchronous with the emergence of new flushes in cashew plantations. A relation between feeding habits and oviposition preferences are observed in the present investigation and we noted that oviposition occurred within or very close to the feeding lesions, as reported by Muhamad & Way (1995). Thus, *H. theivora* prefers to feed and oviposit on tender shoots/flushes in cashew and on pods in cocoa, which reflects differential feeding and oviposition behavior. However, in the present investigation all egg-laying was found to be done on small immature and developing pods rather than on shoots and mature pods, probably to make it easy for the newly hatched nymphs to start feeding immediately to meet their nutritional requirements. Wheeler (2001) mentioned that the feeding and oviposition habits of Miridae are not easily characterized and additional information will definitely improve our knowledge of their peculiar feeding and oviposition behavior.

Understanding the pattern of species distribution and community structure and their underlying drivers along environmental gradients remains a key challenge in insect ecology. Many insect species are widely distributed along elevation gradients, such that populations living at the upper and lower altitudinal extremes experience different environmental conditions, especially with respect to the local/micro climate. This has clear implications for our general understanding of the biology and distributions of such species. The study of species' ecology along altitudinal gradients may provide clues to the likely response of both species and communities to climate change over time (Hodkinson, 2005). Altitude affects not only the species richness but also the species composition of insect communities (Whittaker, 1952). In the present investigation, a first attempt to assess the TMB species distribution across the elevation gradient was made by conducting a survey in cocoa fields situated from 0 to 2134 meter ASL. Two species of TMB (*H. bradyi* and *H. theivora*) were separately infesting cocoa at different elevation. This species variation across the elevation gradient may be due to the presence of the ecological strategy called 'species replacement' or 'species shipment' along altitudinal gradients; this strategy is found among diverse groups such as grassland bugs (Auchenorrhyncha) and dung-feeding flies (Sepsidae) in northern England (Randall et al., 1981), horseflies and grasshoppers in the French mountains (Claridge & Singrao, 1978) and satyrid butterflies in Venezuela (Adams & Bernard, 1981). The reasons behind the separation of these two *Helopeltis* spp. at different elevations may be to avoid interspecific competition, variation in micro-climatic conditions or variation in biotic and abiotic factors at the different elevation levels. Thus, the population density pattern of a particular insect species reflects changes in the host-plant's phenology, quality, and density and variation in the populations of specific parasitoids and predators.

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Author contributions

Conceived and designed the experiments: SHT, GKM and CM. Performed the experiments: SHT and TPPR. Contributed materials/analysis tools: EA and JCT. Wrote the paper: SHT, GKM and TPPR. All authors analyzed the results and approved the final version of the manuscript. SHT carried out the research work carried out at ICAR-Central Plantation Crops Research Institute, Regional Station, Vittal, Karnataka, India

Conflict of interest and disclosure

The authors declare that they have no conflict of interest. The authors confirm that there are no financial disclosures for this study.

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