BIOLOGY AND HOST PLANTS SELECTION OF THE DARKLING BEETLE *MESOMORPHUS VILLIGER* BLANCHARD (COLEOPTERA: TENEBRIONIDAE)

Thesis submitted to the UNIVERSITY OF CALICUT

in partial fulfillment of the requirements for the degree of **DOCTOR OF PHILOSOPHY IN ZOOLOGY**

By SEENA C. M.

Under the Guidance of **Dr. SABU K. THOMAS**



P. G. & RESEARCH DEPARTMENT OF ZOOLOGY ST. JOSEPH'S COLLEGE DEVAGIRI, (AUTONOMOUS) CALICUT - 673 008, KERALA.

FEBRUARY 2018



P.G. & RESEARCH DEPARTMENT OF ZOOLOGY ST. JOSEPH'S COLLEGE DEVAGIRI (AUTONOMOUS) CALICUT - 673 008, KERALA www.devagiricollege.org email: sabukthomas@gmail.com

Dr. Sabu K. Thomas Associate Professor

Certificate

Certified that the thesis entitled "BIOLOGY AND HOST PLANTS SELECTION OF THE DARKLING BEETLE MESOMORPHUS VILLIGER BLANCHARD (COLEOPTERA: TENEBRIONIDAE)" submitted by Mrs. Seena C.M. to the University of Calicut for the award of degree of Doctor of Philosophy in Zoology, is a bonafide record of research work done by her in this department. This work has not been previously formed the basis for any award of degree or diploma.

Mrs. Seena C.M. has successfully completed the preliminary qualifying examination prescribed by the University of Calicut.

Place: Devagiri Date: **Dr. Sabu K. Thomas** Supervisor & Guide



P.G. & RESEARCH DEPARTMENT OF ZOOLOGY ST. JOSEPH'S COLLEGE DEVAGIRI (AUTONOMOUS) CALICUT - 673 008, KERALA www.devagiricollege.org email: sabukthomas@gmail.com

Dr. Sabu K. Thomas Associate Professor

Certificate

Certified that the publication, "Seena C.M. and Sabu K.T. 2013. Defensive Glands of the Darkling Beetle Mesomorphus villiger Blanchard (Coleoptera: Tenebrionidae) Psyche, pp 3." is published in a peer reviewed journal.

Place: Devagiri

Dr. Sabu K. Thomas Supervisor & Guide

Date:

Declaration

I do hereby declare that the thesis entitled "Biology and host plants selection of the Darkling beetle Mesomorphus villiger Blanchard (Coleoptera: Tenebrionidae)" submitted to the University of Calicut for the award of degree of Doctor of Philosophy in Zoology has not been formed the basis for the award of any other Degree, Diploma, Associateship, Fellowship and represents the original work done by me.

Place: Devagiri Date:

Seena C. M.

Acknowledgements

I express my profound sense of gratitude to my Guide and Supervisor Dr. Sabu K. Thomas, Associate Professor, Post Graduate and Research Department of Zoology, St. Joseph's College Devagiri (Autonomous), Calicut. I am extremely thankful for his valuable guidance, strong emotional support and constant encouragement throughout the course of this study which helped me to complete it successfully.

I express my sincere thanks to Dr. Sibichen M. Thomas, Principal, St. Joseph's College Devagiri (Autonomous), Calicut and Rev. Fr. Dr. Benny Sebastian, former Principal, for providing institutional facilities during the course of my research work.

I express my sincere thanks to Dr.George Mathew, Head, Post Graduate and Research Department of Zoology, St. Joseph's College Devagiri (Autonomous), Calicut, Dr. A. T. Thomas, former Head, for providing me the required facilities throughout my research work and for their support and encouragement. I wish to express my sincere thanks to all the staff members of the department for all the help rendered during the course of my research.

I am extremely thankful to Mr. K. T. Thomachan, associate Professor, Department of Economics, St. Joseph's college, Devagiri, for expertise regarding software based statistical analysis.

I thank the University Grants Commission, for providing financial support in the form of UGC-JRF fellowship.

I am extremely thankful to my friends, Dr. Nithya Sathiandran, Dr. Arunraj C., Dr. Nirdev P. M., Dr. Shiju T. Raj, Dr. Simi Venugopal, Dr. Sobhana K.A., Dr. Aswathi P, Mrs. Subha Babu, Mrs. Prameela, Mrs. Binsha P., Mr. Akhil S.V., Mr. Jithmon V.A., Mrs. Sruthi M.C, Ms. Divya M, Ms. Ashly Kurian and all other research scholars in the Entomology Research Lab, St.Joseph's College Devagiri (Autonomous), Calicut, for their help throughout my research work. I wish to express my thanks to lab assistants in the Post Graduate and Research Department of Zoology, St. Joseph's College Devagiri (Autonomous), Calicut, for their valuable co-operation and help.

I am deeply indebted to my family for their wholehearted support, inspiration and co-operation which formed the basis of my research. work.

Above all I thank Almighty for providing me the health, patience and strength to complete the study.

Seena C.M.

Dedicated to my family and teachers...



CONTENTS

	Page No.
Chapter 1: INTRODUCTION	1
1.1. Biology and habits	
1.2. Host plants and host plant preferences	
1.3. Reproductive performance on preferred host plants	
Chapter 2: REVIEW OF LITERATURE	9
2.1. Distribution and Biology of Mesomorphus villiger	
2.2. Host plants and host plant preferences	
2.3. Reproductive performance on preferred host plants	
Chapter 3: MATERIALS AND METHODS	13
3.1. Biology and habits	
3.2. Host plants and host plant preferences	
3.3. Reproductive performance on preferred host plants	
Chapter 4: RESULTS	25
4.1. Biology and habits	
4.2. Host plants and host plant preferences	
4.3. Reproductive performance on preferred host plants	
Chapter 5: DISCUSSION	42
5.1. Biology and habits	
5.2. Host plants and host plant preferences	
5.3. Reproductive performance on preferred host plants	
Chapter 6: CONCLUSIONS	57
Chapter 7: REFERENCES	60

LIST OF TABLES

- Table 1Duration (in days) of egg, larval, pupal and adult stages of
Mesomorphus villiger fed with Rubber leaves.
- Table 2Fecundity, egg hatchability, larval survivability and pupal
survivability of Mesomorphus villiger.
- Quantity (mm^2) of leaves consumed (mean \pm SD) by Table 3 *Mesomorphus villiger* in no-choice and multiple choice experiment tests.

Two-way ANOVA for feeding preference of MesomorphusTable 4villiger with respect to the leaf type and leaf age in no-choiceand multiple choice experiment tests.

- Table 5 One-way ANOVA for the quantity of tender and senescent leaves consumed by *Mesomorphus villiger* in no-choice and multiple choice experiments.
- Table 6Tukey multiple comparisons (t- test) of the variation in the
feeding preference of *Mesomorphus villiger* towards tender and
senescent leaves of Jackfruit and Rubber with all other leaf
types in no-choice and multiple choice experiment tests.

Tukey multiple comparisons (t- test) of the variation in the
feeding preference of *Mesomorphus villiger* towards tender and
senescent leaves of Cocoa, Flowering murdah and Raintree
with all other leaf types in no choice and multiple choice
experiment tests.

Tukey multiple comparisons (t- test) of the variation in the
feeding preference of *Mesomorphus villiger* towards tender and
senescent leaves of Tamarind, Mango, Wild jack and Cassia
with all other leaf types in no choice and multiple choice
experiment tests.

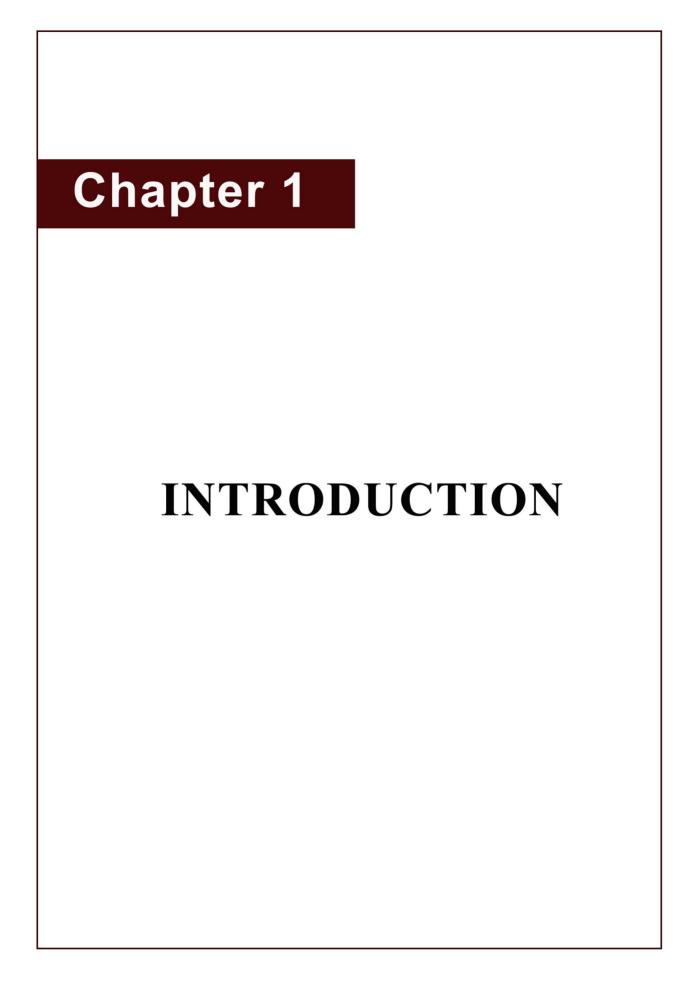
Tukey multiple comparisons (t- test) of the variation in the feeding preference of *M. villiger* towards tender and senescentTable 9 leaves of Mexican lilac, Cashew, Macaranga and Indian kino with all other leaf types in no choice and multiple choice experiment tests.

Comparison of the fitness and performance of various life cycle Table 10 stages of *Mesomorphus villiger* with Rubber and Jackfruit as host plants.

LIST OF PLATES

Plate 1	(A) Mesomorphus villiger aggregation on bark of a tree, (B) on
	drainage pipes, (C) on sunshade of a building, (D) multilayered
	aggregation and (E) on detached wall paint.

- Plate 2 Experimental set up for (A) No-choice and (B) Multiple choice leaf disc tests.
- Plate 3 Life cycle of *Mesomorphus villager:* (A&B) Eggs, (C&D) Larvae, (E&F) Pupae, (G) *Mesomorphus villiger* Adult.
- Plate 4 Larval instars of *Mesomorphus villiger*: (A) First, (B) Second, (C) Third, (D) Fourth, (E) Fifth, (F) Sixth, (G) Seventh, (H) Eighth, and (I) Ninth instars.



INTRODUCTION

1.1. Biology and habits

Mesomorphus villiger Blanchard 1853, (Coleoptera: Tenebrionidae) is a darkling beetle belonging to the tribe Opatrini. Members of the genus *Mesomorphus* Seidlitz 1893, are distributed in Palearctic (Iran, Afghanistan, Pakistan, China and Nepal), Oriental (India, Sri Lanka, Thailand, Andaman Islands, Burma, Laos, Java, Bali, Sumatra, Borneo, Malaysia, Vietnam and Philippines), Australian (Queensland, Papua New Guinea and New South Wales), Afro tropical (South Africa, Tanzania, Ivory Coast, Ethiopia, Namibia, Madagascar, Cameroon and Kenya), Neotropical (Brazil, Colombia, Ecuador and Peru) and Nearctic regions (Alaska) (Kaszab 1963; Schawaller 2000; Ferrer 2000, 2002a, 2002b, 2008; Lobl and Smetana 2008).

There are a total of 86 species reported from this genus globally (Kaszab 1963; Ferrer 2000, 2002), 27 from Asia (Ferrer 2002), 16 from India and nine species from South India. The Indian species include *M. indicus*, *M. curtus*, *M. gridellii*, *M. crassiusculus*, *M. villiger*, *M. striolatus*, *M. kulzeri*, *M. latisculus*, *M. foveolatus*, *M. punctatithorax*, *M. birmanicus*, *M. meridionalis*, *M. brevis*, *M. feai* and *M. rugulosus* and the species reported from south India include *M. indicus*, *M. gridellii*, *M. villiger*, *M. striolatus*, *M. kulzeri*, *M. punctatithorax*, *M. meridionalis*, *M. punctatithorax*, *M. striolatus*, *M. kulzeri*, *M. punctatithorax*, *M. meridionalis*, *M. punctatithorax*, *M. striolatus*, *M. kulzeri*, *M. punctatithorax*, *M. feai* and *M. rugulosus* and the species reported from south India include *M. indicus*, *M. gridellii*, *M. villiger*, *M. striolatus*, *M. kulzeri*, *M. punctatithorax*, *M. meridionalis*, *M. brevis* and *M. rugulosus* (Arunraj 2013). Members of the genus *Mesomorphus* are gregarious, and their species aggregate in large numbers in favourable places to preserve moisture during the dry season, where they remain inactive for long periods, waiting for the favourable conditions for reproduction

(Ferrer 2002a). They fly and are attracted to lights (Ferrer 2002b) and are seen under stones or under the barks and in the holes or cracks of the trees. Some members of the genus *Mesomorphus* show, aggregation on tall trees like Red lauan tree (*Shorea siamensis*) in Thailand, where the trunk was covered up by swarms of *Mesomorphus* (Jolivet 1998).

Mesomorphus villiger has been reported as a nuisance pest from India (Sitaramaiah *et al.*, 1999), Nepal, Afghanistan, Siberia, Australia, Africa (Madagascar) (Schawaller 2000) and Sri Lanka (Kaszab 1979). *M. villiger* reported as a nuisance pest in the Rubber plantation belts of Vietnam (Viet Nam Net 2013). They are reported from Palearctic region (Japan, Nepal, South Korea, Afghanistan, China, Taiwan, Russia and Australia) by Lobl and Smetana (2008).

Mesomorphus villiger is a small litter dwelling nocturnally active beetle belongs to the detritivorous guild (Arunraj 2013) and these beetles occur under rocks and in leaf litter with the larvae living in the soil or scavenging on the ground at night (personal observations). These beetles commonly present in the leaf litter of many trees especially in the Rubber plantations in South India (Arunraj and Sabu 2012). It is reported as an egg predator of orthopterans in Iranian rice fields and grass lands (Ghahari *et al.*, 2009) and as a stored grain pest in China (Yan *et al.*, 2010). They showed aggregation on Sal tree (*Shorea robusta*) in Uttar pradesh, India (Hegde *et al.*, 2013). *M. villiger* has been reported as a pest in Tobacco growing belts of Andhra pradesh, and is known as tobacco ground beetle. Here, only the larvae are known to cause injury (Sitaramaiah *et al.*, 1999), which nibble and gnaw at the base of newly transplanted tobacco seedlings, resulting in death and thereby creating gaps in the field, sometimes to an extent of 50–60% of the area.

It is observed from the coastal areas of Kozhikode, Malappuram and Trissur Districts in Kerala. Invasion of huge population of these beetles in to residential buildings and their persistent stay during monsoon season create nuisance to the locals. Their nocturnal movements and release of an irritating, odoriferous quinonic secretion that causes mild skin burns (Seena and Sabu 2013), makes it a nuisance pest in many regions of the South Western Ghats. In the residential area of South Western Ghats it is commonly called as 'erumamootta'.

Mesomorphus villiger often misidentified as *Luprops tristis* Fabricius 1801, the Rubber litter beetle, due to its similarities in morphology and the aggregation pattern. Unlike *Luprops, M. villiger* occurs in non-Rubber belts also. *M. villiger* were collected from the litter of Mango (*Mangifera indica* Linnaeus 1753), Cashew (*Anacardium occidentale* Linnaeus 1753), Rain tree (*Albizia saman* (Jacq) Merr 1891) and Rubber (*Hevea brasiliensis* (Willd. ex Adr. De Jus) M⁻ull. Arg. 1865) (Seena and Sabu 2013). The high abundance of these beetles in the residential buildings and the frustrating nocturnal movements make them a serious nuisance pest in both Rubber plantation and non-Rubber belts and also in many urban localities. They do not sting or bite, but when disturbed, they release an irritating odoriferous quinonic secretion that causes skin burns and eye irritations (Seena and Sabu 2013). Aggregation of these beetles seen in dark, undisturbed areas where they remain dormant for a period of about six months during the wet monsoon season. *M. villiger* aggregates on tile roofed buildings, on bricks, under bark of tree like *Albizia saman*, hollow wooden blocks, coconut fronds and husks, crevices below boulders in the premises of the buildings (Plate 1).

Except for short notes on developmental stages by (Joshi 1962) on tobacco leaves from Northern region (Andhra pradesh) no details about its biology, behaviour and host plants are known.

1.2. Host plants and host plant preferences

Presence of *M. villiger* in various plant litter types including Rubber, Mango, Cashew and Rain tree along the coastal belts of Kerala (Seena and Sabu 2013) indicates that the *M. villiger* is sustaining on the leaves of these trees. Other litter shedding plants seen near their aggregation sites include Cassia (*Cassia fistula* Linn. 1753), Cocoa (*Theobroma cacao* Linn. 1753), Flowering murdah (*Terminalia paniculata* Roth. 1821), Indian beech (*Pongamia pinnata* (L.) Pierre 1899), Indian kino (*Pterocarpus marsupium* Roxb. 1795), Jackfruit (*Artocarpus heterophyllus* Lam. 1789), Macaranga (*Macaranga peltata* Müll. Arg. 1866), Mango, Mexican lilac (*Gliricidia sepium* (Jacq.) Kunth 1842), Rain tree, Rubber, Tamarind (*Tamarindus indica* L. 1753) and Wild jack (*Artocarpus hirsutus* Lam. 1789).

Litter stands of these plants might be serving as the breeding and feeding habits for the beetles. Hence, it is essential to determine the feeding preference of *M. villiger* towards the leaf litter of the various litter contributing trees from where its presence have been noticed and the trees present around their aggregation sites whose litter must be contributing to the population build-up of the

beetle in region where its higher incidence is observed. Data on the feeding preference towards leaf litter of various potential plants and identification of the most preferred host plants will enable control of the beetle by removing the leaf litter of the host plants from the agri-belts where it is present as a nuisance beetle.

Studies on Rubber litter beetle *L. tristis* present in the same geographical belts by (Sabu *et al.*, 2012) reported that *L. tristis* feed up on many other plants in addition to Rubber litter present in the area. Feeding preference of *L. tristis* towards tender leaves of most plants and the preference of herbivorous beetles towards nutrient rich tender leaves have been recorded. However based on the presence of *M. villiger* in various regions including Rubber plantations and non-plantation belts, it is hypothesised that *M. villiger* is not a specialist feeder and feed on the leaf litter of most plants and its abundance is arising from the availability of leaf litter of number of host plants and it may not be having feeding preference towards tender leaves which are not always available.

Lack of data on the feeding preferences of *M. villiger* towards various host plants necessitate its study on host plant selection and feeding preferences. Data generated would be helpful in understanding host plant related variations in life cycle and reproductive potential and in identifying the potential of the major host plants and breeding habitats and also is expected to contribute towards development of control strategies to prevent the population build-up of *M. villiger* and its possible spread to new regions.

5

1.3. Reproductive Performance on preferred host plants

Insect reproductive strategies and performance of offsprings are greatly influenced by host plant quality and for a poor quality host, females may decrease the number and /or quality of eggs (Leather and Burnand 1987). Host quality is a complex concept which includes various factors like levels of nitrogen, carbon, trace elements, defensive compounds that positively or negatively affect the performance of plant feeding insects (Awmack and Leather 2002). Parameters of insect performance that influenced by host nutritional quality includes developmental time, body mass of pre-adult stages (Alonso et al., 2001), fecundity and longevity (Wu and Li 1992). When host plant shift exists, nutritional quality of host becomes the key factor which determines the phenotype of herbivorous insects and lead to phenotypic plasticity where, same genotype produce different phenotypes on different hosts (Via et al., 1995) by adaptation to their local hosts (Mopper 1996). Inferior host quality results in prolonged pre-imaginal stage and indirectly affect fitness by increased vulnerability to weather and natural enemies (Campos et al., 2003).

No data is available on the reproductive performance of *M*. *villiger* except for studies by Joshi (1962) on the larval development of *M*. *villiger* using media such as dried cow dung, farmyard manure, soil, mixture of farmyard manure and soil, and soil collected from the pit where tobacco leaves were dumped. Hence it is necessary to analyse the reproductive performance of *M*. *villiger* involving the mating, oviposition, fecundity and mortality on the most preferred host plants which can be done only after identification of their preferred hostplants.

Objectives

- 1. Biology and habits.
- 2. Identification of major host plants and host plant preferences.
- 3. Reproductive performance on the preferred host plants.

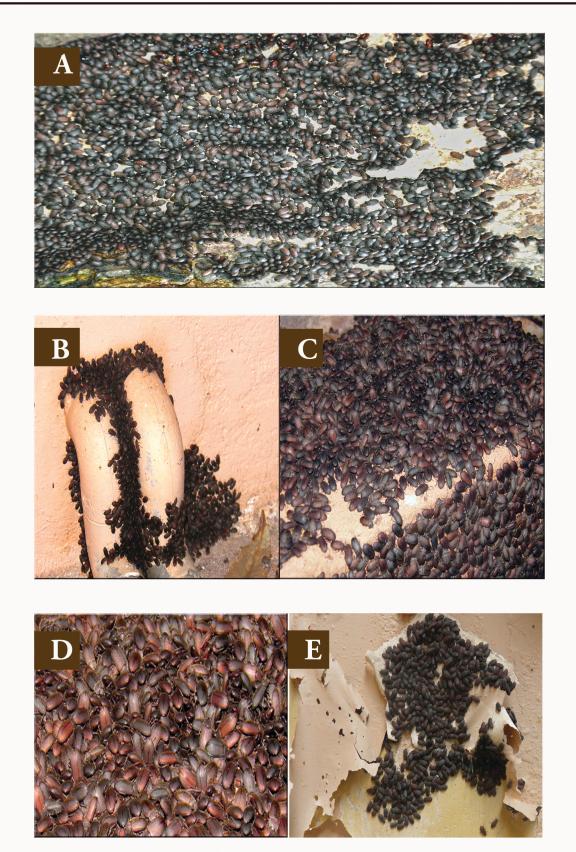


Plate 1. (A) *Mesomorphus villiger* aggregation on bark of a tree,(B) on drainage pipes, (C) on sunshade of a building, (D) multilayered aggregation and (E) on detached wall paint.



REVIEW OF LITERATURE

REVIEW OF LITERATURE

2.1. Distribution and Biology of Mesomorphus villiger

The first taxonomic studies on the genus *Mesomorphus* was done by Kaszab (1963) who worked on Palaearctic and Oriental species of *Mesomorphus*. MichitakaChoj (1978) reported *M. villiger* from Nansie Islands, Japan. Ferrer (2002) worked on the genus *Mesomorphus* and described two new species from India (*M. lilligi* and *M. schawallari*). Arunraj (2013) discussed about the presence of *M. villiger* in South India.

Jacobson (1975) reported that root, leaf and seed extracts in alcohol of *Pongamia glabra* were found to show insecticidal activity against *M. villager*. Sitaramaiah *et al.*, (1999) reported *M. villiger* as a pest of tobacco in Andra pradesh, India. It is also reported as a stored grain pest in China (Yan *et al.*, 2010). Stockholm Convention on Persistent Organic Pollutants (2011) tested the efficiency of Monocrotophos, Chlorpyrifos, fenvalerate and Carbaryal over endodulfan on *M. villiger*. It is reported as an egg predator of orthopterans in Iranian rice fields and surrounding grass lands (Ghahari *et al.*, 2009). Arunraj and Sabu (2012) worked on a methodology on the sex determination of *M. villiger* based on the presence or absence of a notch in the 8th abdominal sternite. Seena and Sabu (2013) reported it as a home invading nuisance pest in South India. Aggregation behaviour of *M. villiger* was reported by Hegde *et al.*, (2013) on Sal tree (*Shorea robusta*) in Uttar pradhesh, India.

Joshi (1962) studied the biology of *M. villiger*, and provided a short description on its life cycle stages. Joshi and Pavate (1963) studied on its

biology by periodic regression analysis. Seena and Sabu (2013) worked on the defensive gland of *M. villiger* and provided details of the morphology of the gland and mode of release of the defensive secretion.

2.2. Host plants and host plant preferences

No record of work on host plants of *M. villiger* reported yet. Seena and Sabu (2013) reported the presence of *M. villiger* under the litter of various host plants including Rubber, Jack fruit, Cashew, Mango and Rain tree.

Analysis of the feeding preference in *L. tristis* (Sabu and Vinod 2009) showed that all developmental stages of these beetles have strong preference towards fallen tender leaves and lowest preference towards senescent leaves indicating that leaf age is a major attribute determining food selection and food preference of L. tristis. Equal preference towards tender and mature Cocoa leaves, presence of patches of Cocoa plantations and the scarce distribution of other host plants in Rubber plantation belts leads to the proposal that in the absence of tender and mature Rubber leaves, Cocoa becomes the major host plant of L. tristis (Sabu et al., 2012; Aswathi 2013). Feeding preference in flea beetles, Phyllotreta cruciferae Goeze 1777 and P. Striolata Fabricius 1803 for nine cruciferous plants and field peas by choice and no-choice tests using seedlings at the cotyledon and first-true-leaf stages found that both species show host preferences among species in the family Cruciferae (= Brassicaceae) and that these preferences changed with host age and leaf type (Palaniswamy and Lamb 1992). Multiple-choice feeding preference assays on larvae and adults of the chrysomelid beetle, Microtheca punctigera Achard 1917, on various host plants indicated higher preference of larvae for mustard and Chinese cabbage and adults (both females and males) for mustard (Menezes *et al.*, 2005).

Larval survival and development of *Epilachna vigintioctopunctata* on solanaceous, cucurbitaceous and leguminous plants were examined for seven local populations from Japan, Thailand, Malaysia and Indonesia revealed that solanaceous plants are the major host plants of E. Vigintioctopunctata in Southeast Asia and this species is unable to complete its life cycle solely on cucurbitaceous plants (Yoichi and Haruo 1999). Analysis of feeding preference of Heliconius eratophyllis 1775 Fabricius (Lepidoptera: Nymphalidae) larva with choice tests using leaf discs of on young and older leaves of Passiflora suberosa Linnaeus 1753 revealed greater preference and growth rate of the insect on younger leaves (Rodrigues and Moriera 1999). Leaf preferences of the serpentine leaf miner, *Liriomyza trifolii* Burgess 1880 (Diptera: Agromyzidae) on differently aged leaves of potato plant in choice and no-choice experiments showed that they exhibited a preference for the larger, older, lower leaves, although the middle leaves were superior for the growth and development of the young stages which may be due to factors other than resource quality for larvae (Fracknath 2005).

Study on the effect for four host plants namely Tobacco, Cowpea, Sweet potato and Chinese cabbage on the biology and food utilisation of cut worm *Spodoptera litura* Fabricius 1775 (Lepidoptera: Noctuidae) revealed that all biological parameters of the larvae and adult were affected by the host plants (Xue *et al.*, 2010). Influence and mechanism of different host plants namely, Cabbage (*Brassica oleracea var. capitata*), Soybean (*Glycine max*), Cowpea (*Vigna*)

11

unguiculata), Sweet potato (*Ipomoea batatas*), Cotton (*Gossypium* spp.), alligator weed (*Alternanthera philoxeroides*), on the growth, development and fecundity of the common cutworm *Spodoptera litura* to understand host suitability of plant infesting insect species revealed that Cabbage, Cotton and Sweet potato were more preferred food for *S. Litura* (Shahout *et al.*, 2011).

2.3. Reproductive performance on preferred host plants

No record of work on Reproductive performance of *M. villiger* reported yet. Host plant quality induces changes in larval and adult performance of Willow Leaf Beetle *Plagiodera versicolora* Laicharting 1781, (Ishihara and Ougushi 2006). Fecundity of the herbivorous insects is determined by the quality of host plants (Awmack and Leather 2002). Reproductive performance of *L. tristis* in relation to leaf age of Rubber tree revealed that availability of tender leaves with high nitrogen and moisture content during the post-dormancy phase of *L. tristis* is a critical factor that determines the survival of *L. tristis* adults and the subsequent generation (Sabu *et al.*, 2014). Influence of the larval host plant on reproductive strategies of cerambycid beetles was studied by Hanks (1999).



MATERIALS AND METHODS

MATERIALS AND METHODS

3.1. Biology and habits

Mesomorphus villiger for this study were collected from a residential building at Thrissur, Kerala $(10^0 \ 10' \ and \ 10^0 \ 46' \ N$ and $75^0 \ 57'$ and $76^0 \ 54' \ E)$ (Natural resources data bank Thrissur 2014) by last week of October 2012. Collected beetles were maintained in large circular clay vessels (13 x 35cm) with coconut husks to provide a hiding place to aggregate, capped with nylon mesh net and placed in an environmental chamber (YORCO, India) at relative humidity 51% and temperature 26°C (representing the average temperature and humidity in the aggregation site) till the beetles arouse from dormancy by last week of November.

Study was conducted from 2012 December to 2014 November in St. Joseph's College, Devagiri, Calicut $(11^015N, 75^050E)$. Pre-dormant beetles maintained in the laboratory were used for biology studies. Sexing was done initially with the sternal notch methodology (Vinod *et al.*, 2008; Arunraj and Sabu 2012) which involved forceful extrusion of genitalia of adult and was later done based on pupal sexual dimorphic feature. Sex ratio was noticed and paired male and female kept together in separate plastic containers (Tarson19 x 10 cm) to observe mating behaviour and were fed with wilted tender leaves of Rubber, major host plant seen in their aggregation sites. 25 such plastic containers were kept in a plastic tray. Unfed leaves were removed daily along with the faecal pellets to avoid fungal contamination. Water soaked cotton ball was placed in the containers, and

was moistened at regular intervals. Moisture level in the plastic containers was also maintained by spraying water in the morning and evening hours.

Adults were removed after oviposition. Number of eggs hatched and duration of egg development were recorded. Emergence of newly hatched larvae noticed. The first instar larvae were transferred into separate containers with fresh leaves. To make it possible to follow the development of successive larval instars, two larvae per container were used. This avoided the inhibitory effect of crowding on larval development in tenebrionids (Tschinkel and Wilson 1971). Larvae were monitored every 12 hour interval with the development time of instars determined from the exuviae left behind.

The pre-moulting larval behavioural pattern noticed and the duration for each moulting period was recorded. The time of oviposition and adult emergence were recorded for calculating the total period. Pupated larvae were collected and kept in separate containers till the emergence of adults. Newly hatched adults, both males and females were maintained in separate plastic containers and the sex ratio and longevity were recorded.

Behaviour of the newly emerged adults, larvae, pupae, preaggregation and post-aggregation phases observed both in the field and lab set-ups. Efforts were taken to understand the behaviour during the pre-aggregation phase, home invasion and post aggregation return to the field.

3.2. Host plants and host plant preferences

Test insects: Study was carried out during February-March 2015 at Department of Zoology, St. Joseph's College, Devagiri, Calicut. Beetles used

14

for the study were collected from the Rain tree litter in the Devagiri College campus, located 6 km east from the Malabar Coast at Calicut (11°15 N, 75°50 E). Collected beetles were maintained in clay vessels (13 x 35 cm) placed in an environmental chamber (YORCO, India) at relative humidity 69% and temperature 34°C and were fed with both tender and senescent leaves of all the 14 leaf types commonly seen in the region. The beetles were deprived of food for 24 hrs before starting the feeding experiments.

Host plants: Details of the 14 potential host plants used for analysis are placed below:

- i. *Albizia saman* (Fabaceae, Fabales; Common and local name: Raintree): is a large evergreen tree native to tropical America now widespread throughout the humid and sub-humid tropics. Naturally occurs on savannahs (grasslands) and in deciduous forests and riparian corridors. Grows best in the lowlands from sea level to 300m (1000 ft) with rainfall 600–3000mm (24–120 in). It is noted as a promising agro forestry species with most important use as a shade tree in parks, pastures, and roadsides since this species leaflets fold together at night and in wet weather, allowing the rain to fall through and the grass can grow right up to the trunk. The tree produces copious pods with a sweet pulp suitable as a dry season feed supplement. Their long black pods and the leaves are rich in tannins and they are used to feed livestock (National tropical botanical garden 2013; Duke 1983).
- ii. Anacardium occidentale (Anacardiaceae, Sapindales; Common and local name: Cashew): was originally spread from Brazil by the Portuguese and is

15

widely grown for Cashew kernels popularly known as "Cashew nuts" (Nadgauda *et al.*, 2005; Rao *et al.*, 1998). Although it is an evergreen tree, during pre-summer period prior to flowering large quantities of old leaves of Cashew are shed (Sabu *et al.*, 2012).

- iii. Artocarpus heterophyllus (Moraceae, Rosales; Common and local name: Jackfruit): is a tall evergreen tree with spreading canopy. Although an evergreen tree, large quantities of old leaves are shed during summer vegetative flush. It is a common tree in the Rubber belts as farmers use its fruits and seeds as a food item, leaves for fodder and stem for timber (Elevitch and Manner 2010).
- iv. Artocarpus hirsutus (Moraceae, Rosales; Common name: Wild jack; Local name: Aini, Anjili): is a tall evergreen tree species that is endemic to the Western Ghats (Ramesh *et al.*, 1997). Large quantities of old leaves are shed during summer vegetative flush. It is a common tree in the Rubber belts as planters allow a few trees to grow in the midst of Rubber plantations due to the high commercial value of its wood and its taller canopy which do not interfere with growth of Rubber plants (Sabu *et al.*, 2012).
- v. *Cassia fistula* (Fabaceae, Fabales; Common name: Cassia; Local name: Kanikonna): is a deciduous tree of deciduous forests ranging from tropical thorn to moist through subtropical thorn to moist forest zones and is a native of India. It produces yellow flowers in drooping racemes, making it an extremely showy tree in bloom with only flowers and no leaves (Orwa *et al.*, 2009a). It is a common ornamental tree in the surroundings of residential

buildings as its flowers are considered as an auspicious first sight at the crack of dawn on the day of Vishu, a new year festival celebrated in the region (Database on State of Environment 2010). Leaf shedding occurs during December–February period and flowering during March–April period.

- vi. Gliricidia sepium (Jacq.) Kunth 1842. (Fabaceae, Fabales; Common name: Mexican lilac; Local name: Sheemakonna): is a medium-sized leguminous tree which occurs in abundance throughout its native range in Pacific coast of Central America and has also been used extensively outside its native range in the Caribbean, the Philippines, India, Sri Lanka and West Africa. It is used for plantation shade, green manure, living fence posts, firewood and livestock fodder, and also as an ornamental tree and forage crop in cut-and-carry systems (Rico-Gray et al., 1991). Leaves are rich in protein, highly digestible and low in fibre and tannin. It makes a good hedge but needs frequent pruning and is used as a shade tree for Coffee and Cocoa. Though it is one among the most widely cultivated multipurpose tree, its use in commercial livestock production systems is limited due to palatability constraint. Its ability to fix atmospheric nitrogen and recycling of soil nutrients as it produces much litter has lead to its wide spread use as a green manure (Elevitch and Francis 2006). They shed their leaves from January to May (Simons and Stewart 1994; Orwa et al., 2009b).
- vii. *Hevea brasiliensis* (Euphorbiaceae, Malpighiales; Common and local name: Rubber): is a deciduous tree with a major annual leaf shedding during December, leaf flush in January, and flowering in February. Rubber

17

plantations of about half a million hectares are present along the western slopes of the Western Ghats in the South Indian state of Kerala (Sabu and Vinod 2009).

- viii. Macaranga peltata Müll.Arg. 1866 (Euphorbiaceae, Malpighiales; Common name: Macaranga; Local name: Vatta): is a deciduous tree native to Sri Lanka and India. It is a resinous tree, up to 10m tall, with velvety hairy young parts. The tree is common throughout the Western Ghats. Its bark is used for making pulp and match sticks. Leaves are good green manure with high nitrogen and potash content. Trees are also grow as a shade tree for Coffee and as a tree for aforestation programmes due to its ability to grow fast (Saminathan and Vetrichelvan 2012; Nair and Nair 1999).
 - ix. *Mangifera indica* (Anacardiaceae, Sapindales; Common and local name: Mango): is an evergreen tree, indigenous to the Indian subcontinent. Although an evergreen tree, large quantities of old leaves are shed during summer vegetative flush. The leaf-flushing period can have one to five flushing events with the whole canopy flushing in synchrony or in patches (Bally 2010). The most common native variety, *Nattumavu*, in the Rubber belts was selected for the study.
 - x. *Pongamia pinnata* (L.) Pierre 1899 (*Fabaceae*, Fabales; Common name: Indian beech; Local name: Pongam): is native to Southern and Eastern Asia and Australia (Groom 2012). Historically, this plant has been used in India and neighbouring regions as a source of traditional medicines, animal fodder, green manure, timber, fish poison and fuel. The tree has been identified as a

resource for agro-forestry, urban landscaping and the bioameloriation of degraded lands (Scott *et al.*, 2008). *P. pinnata* is a preferred species for controlling soil erosion and binding sand dunes because of its dense network of lateral roots (Sangwan *et al.*, 2010) and is being used as a medicinal plant in India. The leaves are known to have antiseptic properties and the press cake leftover from oil extraction is used as a liniment. It is also an important source of firewood in arid areas (Orwa *et al.*, 2009c).

- xi. Pterocarpus marsupium Roxb. 1795 (Fabaceae, Fabales; Common name: Indian Kino Tree/ Malabar Kino Tree; Local name: Venga): is a large deciduous tree native to Sri Lanka with a restricted distribution to southern part of India. The tree distributed in deciduous forest throughout the India (Varghese 1996) and is commonly found in the Western Ghats. It is a deciduous tree undergoing rapid synchronous leaf fall during the pre-summer period (Mishra *et al.*, 2006). It is a biannual plant with two flowering seasons per year. It is exploited for its medicinal bark and latex and also for its timber. The count of this tree species is declining in the wild and therefore it has been placed in the vulnerable list of red data book (World Conservation Monitoring Centre 1998).
- xii. *Tamarindus indica* L. 1753 (*Fabaceae*, Fabales; Common and local name: Tamarind): is a slow-growing, long-lived massive tree with high resistance to wind. Normally their leaves are evergreen but may shed briefly in very dry areas during the hot season. Tamarind is native to Tropical Africa and has been introduced into India long ago and often been reported as indigenous

also in India. The wood is valued for fuel, for it gives off an intense heat. The galls on the young branches are used in tanning. The leaves are eaten by cattle and goats, and furnish fodder for silkworms in India and West Africa (National tropical botanical garden 2013; Morton 1987).

- xiii. *Terminalia paniculata* Roth. 1821 (Combretaceae, Myrtales; Common name: Flowering murdah; Local name: Maruthu): is a tropical deciduous tree with a broad natural distribution in the Western Ghats, India and is endemic to Peninsular India. It is the most dominant tree in the moist deciduous forests of Western Ghats. The leaf fall in the tree occurs in the November–December period and leaf flush during January-February period. Bark is used in ayurvedic medicine and tannin obtained from the bark is a substitute for wattle tannin (Pillai and Chandrashekara 2011). The tree is planted in home gardens and agricultural landscapes as a multipurpose tree for providing support to pepper and potential sources of green manure (Sanker and Chandrshekara 2002).
- xiv. Theobroma cacao Linnaeus 1753 (Malvaceae, Malvales; Common and local name: Cocoa): is an evergreen tree native to Central America and South America. It was introduced as a crop plant into many Tropical African and Asian countries for Cocoa seeds which are used to make Cocoa powder and chocolate (Frankis and Schulz 2010). As it grows well in the under storey of Rubber, it is a common tree in the Rubber plantation belts in the region.

Experimental analysis: Tender and senescent leaves of the proposed host plants were collected from a non-Rubber agriculture landscape at Chelavoor close to

Calicut. Freshly sprouted leaves of five to ten days of age (identifiable by smaller size, smooth texture, and bright green or brown colour) were categorised as tender leaves and were collected from the tree branches of same height. Senescent leaves that are yellowish brown in colour were removed by a gentle flicking of the leaf from the trees. Collected leaves were brought to the laboratory and leaf discs (400 mm²) of each leaf type were prepared, except tamarind where compound leaves with small leaf lets are present, two small leaf discs (50mm²) were used instead of a single leaf disc. Prepared leaf discs were kept under ambient conditions for 24 hrs.

Multiple choice and two choice leaf disc tests were performed in the second week of February 2013 on successive days. For all the 14 host plants, feeding preference towards tender and senescent leaves (two-choice leaf disc tests: hereafter referred as no-choice tests as it involves a single host plant) were carried out. Multiple choice leaf disc tests with tender and senescent leaf age classes were conducted for all the 14 host plants. For no-choice tests, one tender and one senescent leaf disc of each host plant was placed in a plastic containers (Tarson-19 x 10cm). For multiple choice tests, leaf discs (400mm²) of each leaf type were cut and were individually marked with odourless marker pen that enabled their identification (Plate 2). In no-choice experiments, two teneral beetles and in multiple choice experiment four teneral beetles were introduced into the centre of the vessel and allowed to feed for 24 hrs (8 am to 8 am). Fifteen replicates were maintained for each host plant in no-choice experiments and for each leaf age class in multiple choice experiment. Leaf area consumed was estimated using a one mm^2 mesh size-reticulated paper glued on a glass slide. Amount of leaf disc consumed during the tests was estimated by subtracting the unconsumed area from the initial area of 400 mm² (Sabu *et al.*, 2012).

Data Analysis:

Based on the quantum of leaves consumed in multiple-choice experiments, tender leaves of host plants with leaf consumption of >100 mm were broadly classified as most preferred; 10 to 100 mm as moderately preferred and 1 to 10 mm as low preferred. In senescent leaves of host plants with leaf consumption of >10 mm were broadly classified as most preferred; 1 to 10 mm as moderately preferred and <1 mm as low preferred host plant categories. Feeding recorded in no-choice experiment was used to analyse the preference towards tender and senescent leaf age classes for each host plant and to measure the extent to which the beetle will feed on each host plant leaf when other leaf resources were not available as in monoculture plantations.

All analyses were done following square root transformation of the data (Weiss 2007). Significance levels of the variation in the quantity of leaf consumed among the leaf types and leaf ages were assessed with two-way ANOVA and pair wise differences among leaf types with Tukey-Kramer post hoc tests (*t*-tests). Significance level of the variation in the quantity of leaf consumed between the tender and senescent leaves of each leaf type was assessed with oneway ANOVA. Significance was determined at P < 0.05. All statistical analyses were performed by using Minitab 16 Academic Software for windows (Minitab 2010).

22

3.3. Reproductive performance on preferred host plants

Beetles were collected from their aggregation sites used for this study. Study was conducted from November 2015 to June 2017 in the Department of Zoology, St. Joseph's College, Devagiri, Calicut, Kerala. Collected beetles were reared and maintained in separate clay vessels (13 x 35cm) capped with nylon mesh net and placed in an environmental chamber (YORCO, India) on tender leaves of Rubber and jackfruit. For the experiments Rubber leaves were collected from branches of the same height of a randomly selected tree in the middle of an 18 year old Rubber plantation, RRII 105 clone (Wild. Ex ADR. De Jus), to avoid possible inter plant variation in leaf quality. Following Sabu and Vinod (2009), freshly sprouted leaves of five days of age were categorised as tender and used to rear adult and larvae.

For Jackfruit, old leaves are regularly shed and new ones are produced, during summer vegetative flush large quantities of old leaves are replaced with new ones. Tender leaves of seven days of age were used for the experiments because of slow leaf expansion rate than Rubber, which were collected from a healthy tree with 20 years of approximate age. Collected leaves were kept frozen at 0°C in plastic containers.

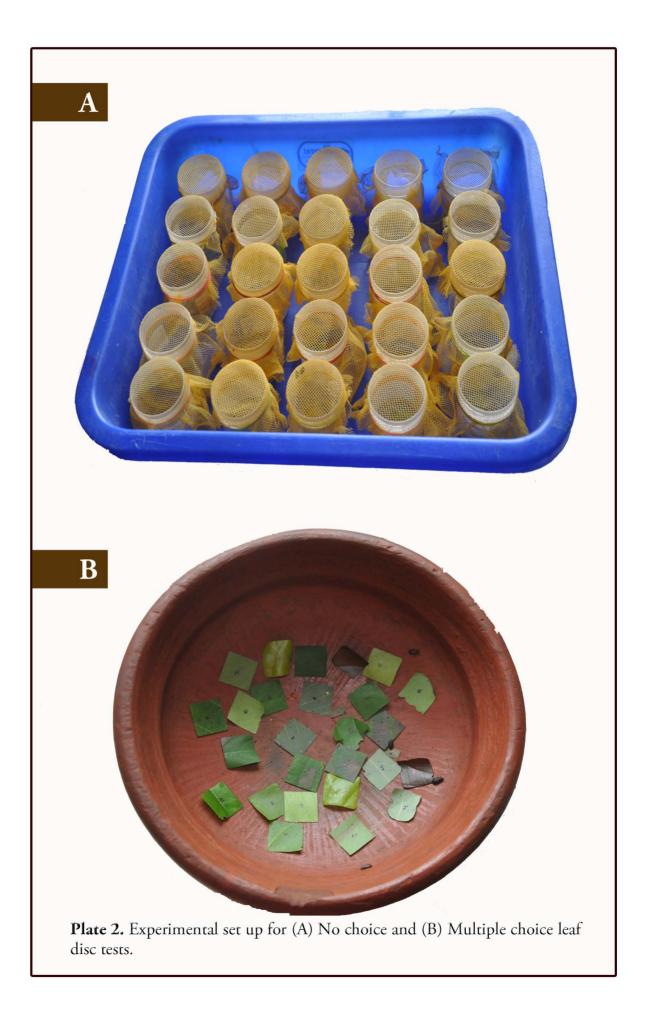
Ten replicates for each leaf type were maintained. Thus, a total of 20 beetle pairs were analyzed. A parallel stock of 10 pairs was maintained on each leaf type to replace individuals lost by mortality during the intermediate stages of the experiment. Each replicate comprised one male-female pair in a small clay vessel (8 x 5 cm) covered with nylon mesh and kept in the environmental chamber.

A small, moist piece of cotton placed on the net served as a source of water, and the excreta were removed on a daily basis. The eggs produced were counted and transferred into sterile plastic vials ($5.5 \times 4.5 \text{ cm}$) using a moist fine hair brush. For each pair, pre-oviposition period and the fecundity were recorded.

Fifty eggs laid during the first 24 hours of oviposition were transferred to Petri dishes (9 x 1.5 cm) in the environmental chamber and monitored at six hour intervals. The number of eggs hatched and the duration of egg development were recorded. Neonate larvae that hatched within a six hour period were transferred to labelled plastic vials (5.5 x 4.5 cm) with a moist, fine hair brush. Larval instars and adults were fed sliced tender leaves of respective plants. The durations of the larval and pupal stages were recorded.

Data Analysis:

Variations in reproductive performance on the two selected leaf types were analysed by one way ANOVA.





RESULTS

RESULTS

4.1. Biology and habits

Life biology of *M. villiger* involved four stages namely egg, larva, pupa and adult (Plate 3). It has univoltine life cycle with a single brood/generation per year.

Oviposition and egg: Pairing season of the adult *M. villiger* was noticed towards the end of January and mating pair formation started by first week of February in both laboratory and field conditions. Paired beetles were kept in separate vials laid eggs by last week of February, with a pre-oviposition period of 16 ± 1.41 days (Table 1). Oviposition was a nocturnal event (91.3%) except for a few incidences during day time (6.7%). Eggs were laid singly and measuring 0.70 ± 0.01 mm in length and 0.49 ± 0.01 mm in diameter, white and oval, sticky and delicate. In laboratory, eggs were found attached to the leaves or on the sides and bottom of the clay pot (Plate 3). In the field beetles were noticed in the middle layer of litter and also under small pebbles. Eggs were found attached to the leaf litter singly and having the covering of soil and faecal matter. Fecundity was 64.5 ± 20.96 (Table 2). Oviposition period was from last week of February to last week of March, lasting 25.6 \pm 3.81 days (Table 1). Eggs were laid daily and at intervals of 3–4 days. Average egg hatchability was 40.6 ± 12.19 (63.26 %). Egg incubation period was 5.27 ± 0.46 days. Towards the end of egg phase, eggs turned from white to yellowish in colour.

Larva: The number of instars varied from seven to nine (Plate 4). Most of the larvae (80%) pupated during seventh instar and 10% during 8th and 9th instars.

They were fast moving, elongate, cylindrical, with abdominal tip tapering posteriorly, three pairs of legs, and superficially resemble small wireworms (typical false wire worm type) (Plate 3 and 4). Body was convex dorsally and slightly flattened ventrally. Each segment bears two lateral pairs of fine whitish setae. The last abdominal segment carried a pair of brown appendages. Newly hatched larvae were white and transparent. A shade of brown is observed after moulting into the third instar to give a yellowish-brown appearance. The pale colour tinge returns to that of the first/ second instar larva when preparing to moult, however, it darkens again on the same day. The larvae gradually grow in size with every moult. Larvae preferred to feed on fresh tender leaves, when both tender and senescent Rubber leaves were provided. It was observed to bore in the top loose soil provided in the culture vessels. They were present in the loose soil in field conditions. They are active during night and remained idle under leaf litter during day time, and showed movement when disturbed.

Larval instar duration for 1st instar was 3.13 ± 0.35 days; 2nd instar was 3.27 ± 0.59 days, 3rd instar was 3.73 ± 1.28 days, 4th instar was 4 ± 0.65 days, 5th instar was 5 ± 0.76 days, 6th instar was 5.47 ± 0.52 days, 7th instar was 8.33 ± 2.5 days, 8th instar was 8.89 ± 2.13 days and 9th instar was 9.47 ± 1.26 days. Larval duration ranges from 32 to 51 days. Total larval duration for the beetle with one to seven instars was 32.93 ± 0.95 days; one to eight instar was 41.8 ± 1.09 days and one to nine instars was 51.2 ± 1.10 days. The first instar larvae measured 3 mm in length. 2nd instar 3.8 mm, 3rd instar 5 mm, 4th instar 6.2 mm, 5th instar 7.4 mm, 6th instar 9 mm, 7th instar 10.6 mm, 8th instar 11.1 mm and 9th instar 12 mm. There was no

variation in morphological features except size between the instars. First three instars showed 63%, second three instar showed 53% and last three instars showed 49% mortality. For four to five hours prior to each moulting the larva became sluggish and skin splits dorsally over the head and thorax and the next instar emerges. After a short duration of inactivity (2–10 minutes) the moulted larvae started feeding. Overall larval mortality rate was 55 % (55 \pm 7.21).

Pupa: Yellowish in colour and measured 6.2 ± 0.63 mm in length and 3.9 ± 0.32 mm breadth. Pupae were naked and with the occasional exception of a slight abdominal movement, they were inactive. Pupae were whitish yellow on emergence but turn yellowish with age, being brown at the time of emergence. The pupal duration was 5.6 ± 1.06 days and survivability was 85.90% (Table 2). Differentiation between the two sexes was possible at the pupal stage with the terminal end of female having a pair of small appendages which were very much reduced in male. The pupae were seen in soil below leaf litter in the field and in the clay pot under leaf litter in the laboratory. Pupae were found singly both in lab and in field.

Adult: Pupae moulted into teneral adult stage by second week of May. Teneral adults were light brown in colour with soft chitinous exoskeleton. The exoskeleton became hard within two to three days and beetles got the typical reddish brown or black colour. Adult stage of *M. villiger* involved three phases namely predormancy, dormancy and post-dormancy. Adult longevity was 398.8 ± 19.92 days (Table 1). Sex ratio of *M. villiger* estimated was 60% female and 40% males, both

in field and laboratory conditions. Same ratio was observed among the dead beetles also.

Pre-dormancy phase: This phase lasted for of 30.8 ± 2.09 days. Teneral adults started feeding after two to three days and active for 30.8 ± 2.09 days. During this stage, all were litter dwelling and nocturnally active. Beetles were seen under the litter of major litter shedding trees like, Rubber, Mango, Cashew and Raintree in the field. Adults in the laboratory set up were fed on tender Rubber leaves. Mortality rate during this phase was 3%.

Dormancy phase: Dormancy phase of *M. villiger* lasted for six months from June to November. Mesomorphus villiger enterd in to dormancy in reponse to simulated wet conditions in laboratory. In the field they entered in to nearby buildings in large population (Plate 1) and settled on the wall, ceilings of the building and crevices with the onset of monsoon rain during June. Aggregated beetles were surface active during night for a week and entered in to a prolonged period of dormancy for six months from June to November. They aggregated in single layered to multi layered (5-6 layers of beetles) cluster. No feeding, no mating pair formation and egg production were noticed during the dormancy period. Dormancy observed in M. villiger was diapause, while in Luprops it was oligopause (Sabu et al., 2008), which is intermediate between quiescence and diapause (Mansingh 1971; Dank 1987; Leather et al., 1995). Mortality rate during dormancy was 39.6%. High degree of mortality was noticed in the field also, as dead beetles were found in dormancy sites, towards the end of dormancy period during the last week of October. Dead beetles with equal proportion of male and

female were observed in the laboratory setup and also in field conditions. The dormancy period lasted for 184.5 ± 5.06 days in laboratory conditions and the beetles came out from dormancy during last week of November to first week of December in the laboratory and in the field.

Post-dormancy phase: post-dormancy phase of *M. villiger* lasted for 193.7 ± 12.32 days from first week of December to second week of February. Beetles in experimental set up became active by December–January and started feeding on the leaves and took shelter in the litter. By first week of December, the aggregated beetles in the buildings moved out towards the litter in the field. By third week of December no beetles were observed in the building.

Following 60–70 days of feeding, mating pairs appeared in the laboratory set up during first and second week of February. They completed egg laying by last week of February, the pre-dormant beetles again entered in to dormancy stage after the monsoon rain and were dead during May to June period. Parent generation (post-dormant beetles) entered into dormancy along with new generation (pre-dormant) beetles but could not complete another phase of dormancy in the second year as all were dead during the first two months of dormancy period. Mortality was in the range of 20% during first week of May, 30% by second week of May and 50% by second week of June. 100% mortality was recorded by last week of June indicating that no post-dormant beetles survived beyond June.

In the field, various life cycle stages of *M. villiger* was observed during different periods. Eggs were observed during first week of February to second week of March indicating the presence of mating pairs in field; larvae of various stages were recorded from last week of February to first week of May and pupae and teneral adults from first week of May to second week of May. Adults were observed from second week of December till last week of May through January, February, March and April months. No adults, larvae and pupae were recorded in the field during June to November period.

4.1. Host plants and host plant preferences

Variation in the quantity of leaves consumed by *M. villiger* among the fourteen leaf types and between the leaf ages, in both no-choice and multiple choice experiments was recorded (Table 3).

Tender–Senescent leaf preference: Analysis of the feeding preference towards tender and senescent leaves of various host plants revealed that tender leaves were preferred over senescent leaves for 13 out of 14 host plants and equal preference towards both tender and senescent leaves of one host plant in no-choice test (Table 3 and 5). The tender leaf preferred host plants were Indian kino $(5.9 \pm 4.15, 1 \pm 0.95)$, Tamarind $(32 \pm 12.90, 1.15 \pm 1.22)$, Indian beech $(3.8 \pm 2.42, 0.65 \pm 0.78)$, Rubber (261.8 ± 35.79, 1.85 ± 1.44), Jackfruit (167.2 ± 27.64, 0), Cashew (11.25 ± 6.34, 0.35 ± 0.52), Mango (25.85 ± 17.83, 0), Wild jack (24.55 ± 16.93, 1.8 ± 2.11), Macaranga (9.09 ± 6.77, 2.65 ± 2.11), Rain tree (26.1 ± 11.92, 2.75 ± 3.43), Flowering murdah (61.8 ± 23.33, 3.4 ± 1.59), Cocoa (84.4 ± 22.77, 2.45 ± 2.98) and Cassia (21.45 ± 14.14, 1 ± 0.61). Equal preference for both tender and senescent leaves Mexican lilac (15.6 ± 6.97, 18.7 ± 11.33) was recorded (Table 3).

Comparison of tender leaf consumption in no-choice tests showed that Rubber and Jackfruit were the most preferred host plants; Cocoa, Flowering murdah, Mexican lilac, Cashew, Cassia, Wild jack, Rain tree, Tamarind and Mango were the moderately preferred host plants. Indian-beech, Indian kino and Macaranga were the low preferred groups (Table 3).

No- Choice Experiments

Tender Leaves: All the 14 leaf types were consumed by *M. villiger* at varying quantities (Table. 3). Rubber and Jackfruit leaves were the most preferred leaves and the consumption was 3–4 times higher than the quanity of moderately preferred leaves such as Mango, Cashew, Cassia, Wild jack, Rain tree, Tamarind, Mexican lilac, Cocoa and Flowering murdah. Rubber was preferred over all other 13 leaf types and Jackfruit over 12 leaf types. *M. villiger* showed no variation in the quantity of Cocoa and Flowering murdah leaves consumed, and Cocoa and Flowering murdah leaves consumed, and Cocoa and Flowering murdah leaves consumed, and Cocoa and Flowering murdah leaves were preferred over 10 leaf types (Mango, Cashew, Cassia, Wild jack, Rain tree, Tamarind, Mexican lilac, Indian beech, Indian kino and Macaranga). Rubber and Jackfruit were most preferred; Cocoa, Flowering murdah, Mango, Cashew, Cassia, Wild jack, Rain tree, Tamarind and Mexican lilac were the moderately preferred leaf types. Indian beech, Macaranga and Indian kino were the low preferred leaves.

Senescent Leaves: Consumption of senescent Mexican lilac leaves was very high compared to all other leaves (Tables 3, 4 and 5), and it is the most preferred senescent leaf type. Flowering murdah, Rain tree, Cassia, Wild jack, Indian kino,

31

Cocoa, Tamarind, Rubber and Macaranga were the moderately preferred leaf types. Jackfruit, Mango, Cashew and Indian beech were the low preferred types.

Multiple-Choice Experiments

Tender leaves: *M. villiger* consumed all the 14 leaf types at varying quantities. Jackfruit (234 ± 24.78) and Rubber (159.9 ± 22.38) leaves were the most preferred host plants as these two leaves were consumed at exceptionally high quantities (>100 mm). Cashew (34.7 ± 23.29), Mango (24.43 ± 11.21), Flowering murdah (54.35 ± 36.88), Wild jack (34.85 ± 23.42), Rain tree (27.2 ± 18.56), Mexican lilac (59.58 ± 28.65), Cocoa (28.3 ± 14.42) were the moderately preferred leaf types (between 10 mm and 100 mm) (Tables 3, 4 and 5) and Tamarind (8.08 ± 6.62), Indian beech (3.56 ± 2.69), Macaranga (5.75 ± 3.37), Indian kino (1.8 ± 1.78) and Cassia (9.13 ± 6.86) were the low preferred leaf types (<10 mm).

Senescent leaves: Leaves of Mexican lilac (58.5 \pm 33.39) and Flowering murdah (22.73 \pm 31.04) were the most preferred leaf types in senescent leaf category (mean value >10mm) (Tables 3, 4 and 5). Cassia (1.8 \pm 4.46), Rain tree (7.05 \pm 8.95), Indian kino (1.85 \pm 1.70) and Macaranga (1.38 \pm 1.64), were the moderately preferred leaf types (mean value between 1mm and 10 mm). Jackfruit (0.25 \pm 0.43), Mango (0.05 \pm 0.1), Indian beech (0.35 \pm 0.62), Cocoa (0.23 \pm 0.52), Tamarind (0), Rubber (0.18 \pm 0.16), Wild jack (0.05 \pm 0.1) and Cashew (0.03 \pm 0.08) were the low preferred leaf types (mean value

Comparison of the consumption of Tender and Senescent Leaves

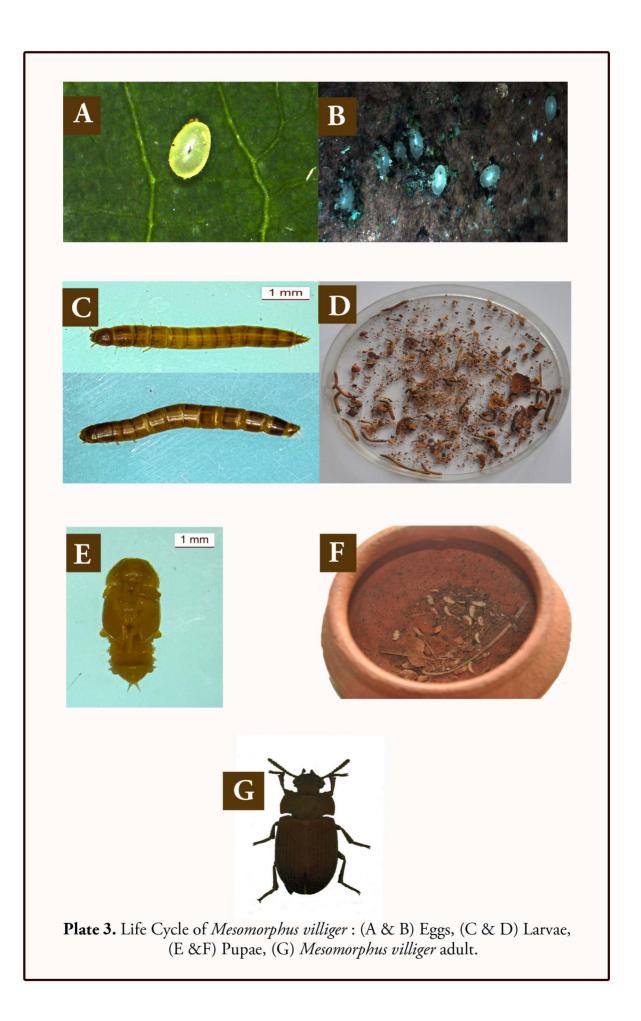
Comparison of the consumption of tender and senescent leaves of 14 host plants in no-choice experiments revealed that *M. villiger* preferred tender leaves of 13 host plants except Mexican lilac. Both tender and senescent leaves of Mexican lilac were equally preferred (Tables 3, 5–9). Comparison of the tender and senescent leaves consumed in multiple choice experiments revealed that *M. villiger* preferred tender leaves of most of the host plants except Mexican lilac and Indian kino (Table 3, 5–9). *M. villiger* showed equal preference towards both tender and senescent leaves of Mexican lilac and Indian kino.

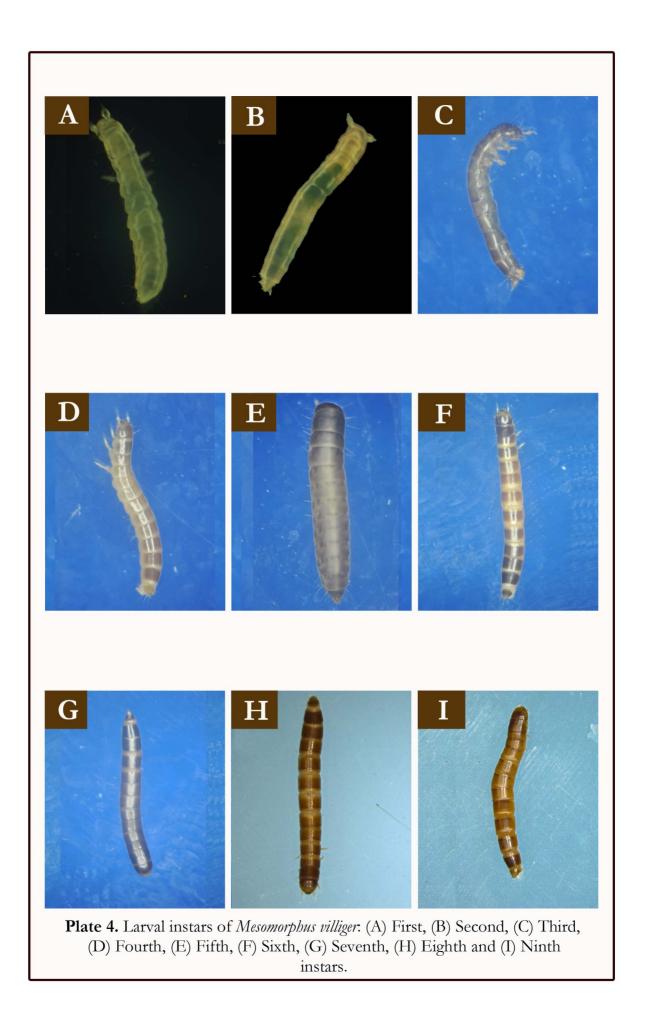
4.2. Reproductive performance on preferred host plants.

Mesomorphus villiger completed various stages of their life cycle on both Rubber and Jackfruit (Table 10). Variation of fitness and reproductive performance in terms of pre-oviposition period, fecundity, egg incubation period, egg hatchability, larval duration, pupal duration, larval survivability, pupal survivability and longevity on Rubber and Jackfruit indicate the existence of influence of host plants.

Pre-oviposition period showed significant difference between Rubber and Jackfruit. Pre-ovipositon period was prolonged when Jackfruit used as host plant. Beetles took more days for egg laying when Jackfruit used as host plant (19.7 \pm 2.26 days) than on Rubber (16 \pm 1.41 days). Fecundity, the reproductive parameter with utmost importance in determining the influence of host plant for phytophagous insects was 46.1 \pm 14.28 eggs for Jackfruit and 64.5 \pm 20.98 eggs for Rubber. Egg incubation periods for Jackfruit was 5.6 \pm 0.69 days and for Rubber was 5.2 \pm 0.52 days with p value > 0.05.

Hatchability of eggs, larval survivability and pupal survivability did not show any difference between Rubber and Jackfruit. Longer duration for larva was recorded with Jackfruit 54.5 \pm 2.76 days and for Rubber was 50.8 \pm 2.20 days, with p<0.05. Adult longevity of beetles varied greatly among Rubber and Jackfruit. Adult longevity recorded for those feeding on Rubber was 398.8 \pm 19.92 days and for Jackfruit was 374.1 \pm 22.82 days.





Sl. No	Stage	Mean ± SD
1	Egg	5.27 ± 0.46
2	1 st instar larva	3.13 ± 0.35
3	2 nd instar larva	3.27 ± 0.59
4	3 rd instar larva	3.73 ± 1.28
5	4 th instar larva	4.00 ± 0.65
6	5 th instar larva	5.00 ± 0.76
7	6 th instar larva	5.47 ± 0.52
8	7 th instar larva	8.33 ± 2.5
9	8 th instar larva	8.89 ± 2.13
10	9 th instar larva	9.47 ± 1.26
11	Larval duration from 1 st to 7 th instars	32.93 ± 0.95
12	Larval duration from 1 st to 8 th instars	41.8 ± 1.09
13	Larval duration from 1 st to 9 th instars	51.2 ± 1.10
14	Рира	5.6 ± 1.06
15	Adult longevity	398.8 ± 19.92
16	Pre-dormancy period	30.8 ± 2.09
17	Dormancy period	184.5 ± 5.06
18	Post-dormancy period	193.7 ± 12.32
19	Pre-oviposition period	16 ± 1.41
20	Oviposition period	25.6 ± 3.81

Table 1. Duration (in days) of egg, larval, pupal and adult stages of *Mesomorphusvilliger* fed with Rubber leaves.

Table 2 . Fecundity, egg hatchability, larval survivability and pupal survivability of
Mesomorphus villiger.

Sl. No.	Parameter	Mean ± SD
1	Fecundity (no. of eggs per female)	64.5 ± 20.98
	Parameter	%
2	Larval survivability	45.10%
3	Pupal survivability	85.90%
4	Egg hatchability	63.26%

Table 3. Quantity (mm^2) of leaves consumed (mean \pm SD) by *Mesomorphus villiger* in no-choice and multiple choice experiment tests.

	Tende	r leaves	Senescent leaves		
Host plants	No choice	- · · · · · · · · · · · · · · · · · · ·		Multiple choice	
Wild jack	24.55 ± 16.93	34.85 ± 23.42	1.8 ± 2.11	0.05 ± 0.1	
Cashew	11.25 ± 6.34	34.7 ± 23.29	0.35 ± 0.52	0.03 ± 0.08	
Cassia	21.45 ± 14.14	9.13 ± 6.86	1 ± 0.61	1.8 ± 4.46	
Cocoa	84.4 ± 22.77	28.3 ± 14.42	2.45 ± 2.98	0.225 ± 0.52	
Jackfruit	167.2 ± 27.64	234 ± 24.78	0	0.25 ± 0.43	
Mango	25.85 ± 17.83	24.43 ± 11.21	0	0.05 ± 0.1	
Flowering murdah	61.8 ± 23.33	54.35 ± 36.88	3.4 ± 1.59	22.73 ± 31.04	
Indian beech	3.8 ± 2.42	3.58 ± 2.69	0.65 ± 0.78	0.35 ± 0.62	
Rain tree	26.1 ± 11.92	27.2 ± 18.56	2.75 ± 3.43	7.05 ± 8.95	
Rubber	261.8 ± 35.79	159.9 ± 22.38	1.85 ± 1.44	0.18 ± 0.16	
Mexican lilac	15.6 ± 6.97	59.58 ± 28.65	18.7 ± 11.33	58.5 ± 33.39	
Tamarind	32 ± 12.90	8.08 ± 6.62	1.15 ± 1.22	0	
Macaranga	9.09 ± 6.77	5.75 ± 3.37	2.65 ± 2.11	1.38 ± 1.64	
Indian kino	5.9 ± 4.15	1.8 ± 1.78	1 ± 0.95	1.85 ± 1.70	

No-choice						
Source	SS	df	MS	F	p value	
Leaf type	562.01	13	43.23	36.80	<.05	
Leaf age	831.71	1	831.71	707.98	<.05	
Leaf type \times Leaf age	622.72	13	47.90	40.78	<.05	
	Multiple	e- Choice	<u>!</u>			
Source	SS	df	MS	F	p value	
Leaf type	1,456.275	13	112.02	55.24	<.05	
Leaf age	1,320.413	1	1,320.41	651.13	<.05	
Leaf type × Leaf age	1,233.231	13	94.86	46.78	<.05	

Table 4. Two-way ANOVA for feeding preference of *Mesomorphus villiger* with respect to the leaf type and leaf age in no-choice and multiple choice experiment tests.

Table 5. One- way ANOVA for the quantity of tender and senescent leaves consumed by *Mesomorphus villiger* in no-choice and multiple choice experiments.

	No-choice test		Multiple-	choice test
Leaf types	F	p value	F	p value
Wild jack	17.33	0	69.67	0
Cashew	29.22	0	80.65	0
Cassia	16.10	0	17.19	0
Cocoa	114.98	0	86.47	0
Jackfruit	712.06	0	2775.62	0
Mango	31.55	0	109.63	0
Flowering murdah	66.70	0	5.94	0.03
Indian beech	11.48	0.01	12.96	0
Rain tree	22.13	0	10.82	0
Rubber	674.53	0	1734.03	0
Mexican lilac	0.13	0.73	0.03	0.87
Tamarind	45.19	0	29.23	0
Macaranga	4.58	0.04	10.76	0
Indian Kino	8.23	0.02	0.01	0.91

Table 6. Tukey multiple comparisons (t-test) of the variation in the feeding preference of *Mesomorphus villiger* towards tender and senescent leaves of Jackfruit and Rubber with all other leaf types in no-choice and multiple choice experiment tests.

	Tende	r leaves	Senescent leaves		
Host plants	No choice	Multiple choice	No choice	Multiple choice	
Jackfruit/ Indian beech	0	0	0.17	0.97	
Jackfruit/Indian kino	0	0	0.08	0.14	
Jackfruit/ Macaranga	0	0	0.00	0.30	
Jackfruit/ Cashew	0	0	0.47	0.61	
Jackfruit/ Mexican lilac	0	0	0	0	
Jackfruit/ Cassia	0	0	0.05	0.52	
Jackfruit/ Wild jack	0	0	0.04	0.68	
Jackfruit/ Mango	0	0	1	0.68	
Jackfruit/ Rain tree	0	0	0.01	0.00	
Jackfruit/ Tamarind	0	0	0.10	0.55	
Jackfruit/ Flowering murdah	0	0	0.00	0	
Jackfruit/ Cocoa	0	0	0.01	0.91	
Jackfruit/ Rubber	0	0	0.01	0.10	
Rubber/ Indian beech	0	0	0.22	0.97	
Rubber/Indian kino	0	0	0.41	0.14	
Rubber/ Macaranga	0	0	0.50	0.30	
Rubber/ Cashew	0	0	0.06	0.62	
Rubber / Mexican lilac	0	0	0	0	
Rubber/ Cassia	0	0	0.53	0.52	
Rubber/ Wild jack	0	0	0.60	0.68	
Rubber/ Mango	0	0	0.01	0.68	
Rubber/ Rain tree	0	0	0.79	0.00	
Rubber/ Tamarind	0	0	0.36	0.55	
Rubber/ Flowering murdah	0	0	0.27	0	
Rubber/ Cocoa	0	0	0.98	0.91	

Table 7. Tukey multiple comparisons (t-test) of the variation in the feeding preference of *Mesomorphus villiger* towards tender and senescent leaves of Cocoa, Flowering murdah and Rain tree with all other leaf types in no-choice and multiple choice experiment tests.

	Tende	r leaves	Senescent leaves	
Host plants	No	Multiple	No	Multiple
	choice	choice	choice	choice
Cocoa/ Indian beech	0	0	0.24	0.94
Cocoa/ Indian kino	0	0	0.42	0.18
Cocoa/ Macaranga	0	0	0.48	0.36
Caocoa/ Cashew	0	0.51	0.07	0.54
Cocoa/ Mexican lilac	0	0	0	0
Cocoa/ Cassia	0	0	0.55	0.59
Cocoa/ Wild jack	0	0.53	0.62	0.60
Cocoa/ Mango	0	0.63	0.01	0.60
Cocoa/ Rain tree	0	0.71	0.76	0.00
Cocoa/ Tamarind	0	0	0.38	0.48
Cocoa/ Flowering murdah	0.11	0.01	0.26	0
Flowering murdah/ Indian beech	0	0	0.02	0
Flowering murdah/ Indian kino	0	0	0.06	0
Flowering murdah /Macaranga	0	0	0.67	0
Flowering murdah/ Cashew	0	0.07	0	0
Flowering murdah/ Mexican lilac	0	0.47	0	0
Flowering murdah/ Cassia	0	0	0.09	0
Flowering murdah/ Wild jack	0	0.06	0.11	0
Flowering murdah/ Mango	0	0	0	0
Flowering murdah/ Rain tree	0	0	0.41	0
Flowering murdah/ Tamarind	0.01	0	0.05	0
Rain tree/ Indian beech	0	0	0.14	0
Rain tree/ Indian kino	0	0	0.27	0.12
Rain tree/ Macaranga	0.02	0.00	0.69	0.50
Rain tree/ Cashew	0.04	0.30	0.04	0.00
Rain tree/ Mexican lilac	0.19	0	0	0
Rain tree/ Cassia	0.45	0	0.37	0.02
Rain tree/ Wild jack	0.77	0.32	0.43	0.00
Rain tree/ Mango	0.84	0.91	0.01	0.00

Table 8. Tukey multiple comparisons (t-test) of the variation in the feeding preference of *Mesomorphus villiger* towards tender and senescent leaves of Tamarind, Mango, Wild jack and Cassis with all other leaf types in no-choice and multiple choice experiment tests.

	Tende	r leaves	Senesce	nt leaves
Host plants	No	Multiple	No	Multiple
	choice	choice	choice	choice
Tamarind/ Indian beech	0	0.24	0.76	0.53
Tamarind/ Indian kino	0	0.05	0.93	0.04
Tamarind/ Macaranga	0	0.70	0.12	0.11
Tamarind/ Cashew	0.01	0	0.34	0.93
Tamarind/ Mexican lilac	0.05	0	0	0
Tamarind/ Cassia	0.16	0.77	0.77	0.22
Tamarind/ Wild jack	0.34	0.00	0.70	0.85
Tamarind/ Mango	0.39	0.00	0.10	0.85
Tamarind/ Rain tree	0.51	0.00	0.24	0.00
Mango/ Indian beech	0.00	0.00	0.17	0.66
Mango/ Indian kino	0.00	0.00	0.08	0.06
Mango/ Macaranga	0.03	0.00	0.00	0.15
Mango/ Cashew	0.07	0.25	0.47	0.93
Mango/ Mexican lilac	0.26	0.00	0	0
Mango/ Cassia	0.58	0.00	0.05	0.29
Mango/ Wild jack	0.92	0.27	0.04	1
Wild jack/ Indian beech	0.00	0	0.45	0.66
Wild jack/ Indian kino	0.01	0	0.76	0.06
Wild jack/ Macaranga	0.03	0	0.23	0.15
Wild jack/ Cashew	0.08	0.97	0.18	0.93
Wild jack/ Mexican lilac	0.31	0.01	0	0
Wild jack/ Cassia	0.65	0.00	0.92	0.29
Cassia/ Indian beech	0.01	0.14	0.55	0.54
Cassia/ Indian kino	0.02	0.03	0.84	0.41
Cassia/ Macaranga	0.09	0.50	0.20	0.70
Cassia/ Cashew	0.19	0.00	0.22	0.25
Cassia/ Mexican lilac	0.56	0	0	0

Table 9. Tukey multiple comparisons (t- test) of the variation in the feeding preference of *Mesomorphus villiger* towards tender and senescent leaves of Mexican lilac, Cashew, Macaranga and Indian kino with all other leaf types in no-choice and multiple choice experiment tests.

	Tende	r leaves	Senescent leaves	
Host plants	No choice	Multiple choice	No choice	Multiple choice
Mexican lilac/ Indian beech	0.02	0	0	0
Mexican lilac/ Indian kino	0.07	0	0	0
Mexican lilac/ Macaranga	0.26	0	0	0
Mexican lilac/ Cashew	0.46	0.01	0	0
Cashew/ Indian beech	0.12	0	0.52	0.59
Cashew/ Indian kino	0.27	0	0.30	0.05
Cashew/ Macaranga	0.68	0	0.01	0.13
Macaranga/ Indian beech	0.24	0.42	0.06	0.32
Macaranga/ Indian kino	0.48	0.12	0.14	0.67
Indian kino/ Indian beech	0.63	0.44	0.70	0.15

Table 10. Comparison of the fitness and performance of various life cycle stages of *Mesomorphus villiger* with Rubber and Jackfruit as host plants.

Sl. No	Parameter	Rubber	Jackfruit	p value
1	Larval duration	50.8 ± 2.20	54.5 ± 2.76	< 0.05
2	Larval survivability	0.45 ± 0.05	0.44 ± 0.05	> 0.05
3	Pre oviposition period	16±1.41	19.7 ± 2.26	< 0.05
4	Egg incubation period	5.2 ± 0.52	5.6 ± 0.69	> 0.05
5	Pupal survivability	0.86 ± 0.07	0.80 ± 0.85	> 0.05
6	Egg hatchability	0.65 ± 0.09	0.64 ± 0.09	> 0.05
7	Adult longevity	398.8 ± 19.92	374.1 ± 22.82	< 0.05
8	Pupal duration	5.4 ± 0.97	5.7 ± 1.09	> 0.05
9	Fecundity	64.5 ± 20.98	46.1 ± 14.28	< 0.05



DISCUSSION

DISCUSSION

5.1. Biology and habits

Life cycle of *Mesomorphus villiger* was univoltine and it involves egg, larval, pupal and adult stages. Seasonality in life cycle was distinct as it could breed only once during the summer season (February, March and April) in the region. As monsoon rains starts in the region before the beetles could enter into reproductive phase, the new generation adults started home invasion and dormancy by the month of June. Thus during the monsoon season adults were forced to remain in dormancy, that lasted for six months from June to November. The name 'Tobacco ground beetle' given to *M. villiger* due to the damage it caused to tobacco seedlings (Sitaramaiaah *et al.*, 1999) is misleading as *M. villiger* feeds and grows on many non-tobacco plants and is present in non-tobacco regions.

During the present study the number of larval instars in *M. villiger*, was found to range between seven and nine. Joshi (1962) reported that there was no fixed number of larval instars in *M. villiger*, with the number ranging from five to fourteen. Allsopp and Adams (1979) reported that soil-dwelling tenebrionid larvae characteristically have numerous stadia but with considerable variation between individuals. This phenomenon was showed by many tenebrionids including, *Tenebrio molitor* Linnaeus 1758, with 12–24 instars (Ludwig 1956; Ludwig and Fiore 1960; Urs and Hopkins 1973), *Gonocephalum simplex* Fabricius 1801, with 11–13 instars (Breniere 1960) and *Zophobas atratus* Fabricius 1775, with 12–13 instars (Quennedey *et al.*, 1995), *Lagria hirta* Linnaeus 1758, with seven to eight instars (Zhou and Topp 2000).

42

Although instar number was frequently considered to be invariable within species, intra specific variability in the number of instars, referred as developmental polymorphism (Schmidt and Lauer 1977) was not an exceptional phenomenon. Moreover, within species, instar number is perhaps usually considered to be constant in most insects. Still, there are a considerable number of species in which instar number varies intraspecifically (partially reviewed by Calvert 1929; Uvarov 1966; for Orthoptera, Wigglesworth 1972; Corbet 1999 for Odonata). The causes of the variation in number of instars include genetic variation (Zhou and Topp 2000), diapause (Yin and Chippendale 1974), compensatory growth on poor quality substrates, sexual dimorphism, temperature, growth rates or even larval gregariousness (reviewed by Wigglesworth 1972). Hence further empirical analysis are required to understand the exact factors behind the intra specific variability in the number of instars of *M. villiger*.

Larval period of *Mesomorphus villiger* ranged from 33 to 51 days. In most insects, the developmental period from egg to adult varied considerably according to the prevailing environmental conditions. Instar number tends to increase under adverse rather than favourable conditions (Esperk *et al.*, 2007). Among the environmental factors, temperature (Ballmer and Pratt 1989; Adachi 1994; Shintani and Ishikawa 1997), photoperiod (Goettel and Philogene 1978), food quality and quantity (Nijhout 1975; Jones *et al.*, 1980), rearing density (Leonard 1968, Adachi 1981, Morita and Tojo 1985), and humidity (Collins *et al.*, 1989; Beckett and Evans 1994) were the most common ones affecting the instar number in various insects. Low humidity, presence of injuries and low food quality (mature leaves, diet lacking some important component) and quantity (transient starvation), increase the instar number in many insect species (Esperk *et al.*, 2007). Hence, the variation in larval development duration of *M. villiger* is attributed to the following factors viz., temperature, photoperiod, food quality and quantity and rearing density based on the earlier studies and further empirical analysis are required to pinpoint the exact reasons for *M. villiger*.

Sexual dimorphic morphological differences, in the form of a pair of papillae on ventral region of eighth abdominal sternite of the female pupae and no such structures on the male pupae, have practical significance. These features can be used as the simplest and least destructive method for sex differentiation of *M. villiger* instead of the sternal notch methodology which leads to death of the adults (Sabu *et al.*, 2008). However, univoltinism and the seasonality of pupal stage, species with its occurrence confined to the pre-summer periods, makes sexing based on pupal morphology impossible during other seasons as pupae are not available and only adults specimens becomes available. Hence sexing of adults based on sternal notch methodology (Sabu *et al.*, 2008) is the only option during other periods.

Dormancy: The adult stage duration estimated was 398.8 ± 19.92 days and the adult stage involved three distinct phases:- pre dormancy (30.8 ± 2.1), dormancy (184.5 ± 5.06) and post dormancy (193.7 ± 12.32). Pre dormancy is the period of maturation and accumulation of food reserves to tide over the expected dormancy period. As in *L. tristis* (Sabu *et al.*, 2008), if it does not rain during the period, teneral adult beetles use this period for feeding and storing up reserve food

material to sustain during the dormancy. If early rains occur, teneral adults also will be forced to enter into dormancy making the beetles less prepared for the prolonged dormancy. If pre dormancy is prolonged due to late onset of monsoon rainfall, it will enable maturation of all the teneral adults and stocking up of reserve food materials which makes the adult beetles better prepared to tide over the dormancy period.

Mortality: Mortality of *M. villiger* was high in dormancy condition both in lab studies and natural conditions. As the beetles depend upon reserve food materials to sustain during the dormancy period, it could be the low accumulation of the reserve food materials by the adult beetles due to prolonged larval period and shorter time period available for feeding during the pre-dormancy period that lead to higher mortality during dormancy. The lesser mortality of *L. tristis* on rubber leaves with longer pre dormancy period and shorter larval duration and instars substantiates the above observations.

High mortality was observed in all stages of *M. villiger* compared with another litter dwelling tenebrionid beetle *L. tristis* in the region with similar habitat requirements. Egg mortality was 36.74% compared to 6% in *L. tristis*; larval mortality was 55% with 4% in *L. Tristis* and pupal mortality was 14.10% with 1% in *L. tristis*. High egg mortality and larval mortality could be the major reasons for the lesser population build up of *M. villiger* in the region unlike the *L. tristis* which has a much lower egg mortality and larval mortality (Sabu *et al.*, 2008). Low pupal mortality compared to the egg and larval phases indicates that the egg and larval stages are the vulnerable phases in the life cycle of the *M*. *villiger*. Another factor to be considered is the higher number of larval instars (7–9) and prolonged larval phase in *M. villiger* compared to the fixed number of larval instars (5) in *L. tristis* which lead to the proposal that lesser larval instars enables attaining early maturity and reaching the adult stage early by *L. tristis*. Similarly, pre dormancy mortality of adult was 3% compared to 1% in *L. tristis* and mortality during dormancy was 39.6% compared to 21.2% in *L. tristis*. Along with high egg and larval mortalities, higher mortality of adults during dormancy is also noted as the reason for their lower abundance and population build up of *M. villiger* compared to *Luprops* in rubber plantation belts in the region.

Aggregation: Aggregation during diapauses is common among insects as an energy and water conserving mechanism (Wolda and Denlinger 1984; Denlinger 1986; Danks 1987). Aggregation observed during the dormancy and the shift in position during the dormancy are thermoregulatory mechanisms of *M. villiger* to get protection from adverse habitat conditions as reported in *L. tristis* from the region (Sabu *et al.*, 2008). Moisture, photoperiod, temperature, food availability, and food quality are the recognized dormancy induction cues (Mansingh 1971; Tauber and Tauber 1976; Masaki 1980; Danks 2003; Sato 2003; Wang *et al.*, 2006; Vinod and sabu 2010). Mass entry of *M. villiger* in to shelters in response to the onset of monsoon rains together with general affinity of tenebrionids towards dry conditions (Watt 1992; Endrody- Younga and Tschinkel 1993) and the same behaviour pattern analysed in *L. tristis* with similar habitat affinities (Vinod and Sabu 2010) indicate that wetness of the habitat conditions induced migration of *M. villiger* towards shelters and into dormancy in the region.

Sex ratio: Present study provides the data that female biased sex ratio exists in *M. villiger* and its implications need further extensive studies. According to the sex allocation theory (Trivers and Willard 1973), female should adjust her progeny's sex when the fitness returns from one sex are higher than those from the other. Females control sex ratio through resource allocation to male and female progeny when the fitness benefits of producing sons or daughters differ (Godfray and Werren 1996). Various factors such as local mate competition (LMC) (Hamilton 1967), resource competition (Clark 1978), maternal quality (Trivers and Willard 1973), mate attractiveness (Burley1981) and variable environment (Charnov *et al.*, 1981) affect how a mother adjusts her progeny's sex ratios to maximise the fitness returns.

It becomes clear from the biology studies and from the presence of prolonged dormancy in *M.villiger*, among the various factors cited above, variable environment proposed by Charnov *et al.*, (1981) controls the sex ratio of *M. villiger* in the study region. Review revealed that there is very limited studies on the effect of climate and environmental factors in determining sex ratio and it was recently shown (Bonal *et. al.*, 2015) that temperature and rainfall timing can bias insect ratio. Hence the female biased sex ratio in *M. villiger*, might be related to the unpredictability of environmental conditions (duration of rainy season that will lead to longer dormancy phase or limitations on food availability after dormancy) which controls the life histories of *M. villiger*.

If the rain fall is delayed that will lead to prolonged dormancy and lack of dry litter habitat conditions and delayed availability of tender leaves during the post dormancy phase and reduction in the effective foraging time for pre dormancy beetles which is detrimental for the future generation as it affects their ability to tide over the dormancy period with accumulated reserve food and it leads to all sorts of unpredictability for the future generation. Hence the recorded female biased sex ratio will lead to higher number of eggs, larvae and adults and female biased sex ratio might be compensating the high mortality rates recorded in the egg and larval stages and also it might be a strategy of the *M. villiger* to handle the above unpredictabilities. However we lack data to know whether a male can mate with many females (polyandry) and polyandry will ensure maintenance of an effective population size. Long term analysis of the effect of early and delayed rainfall and food availability to post dormancy beetles are necessary to understand the patterns of female biased sex ratio of *M. villiger* populations.

5.2. Host plants and host plant preferences

Feeding Preference towards Tender and Senescent Leaves of host plants: *Mesomorphus villiger* showed feeding preferences among the 14 leaf types studied and also between the tender and senescent categories of each leaf type. Beetles preferred tender leaves of both evergreen (Jackfruit, Mango, Wild jack, Cashew, Cocoa and Tamarind) and deciduous trees (Rubber, Flowering murdah, Rain tree, Cassia, Indian beech, and Macaranga) and displayed equal preference towards the tender and mature leaves of Mexican lilac and Indian kino (deciduous). Preference for tender leaves of 12 out of 14 host plants highlights the importance of leaf age in determining the food selection and food preference of *M. villiger*. High nutritional value could be the reason for the high preference towards tender leaves (Bernays and Chapman 1994) of most host plants, because plant nutritional quality decreases with age (Scheirs *et al.*, 2002) and leaf maturation is accompanied by a decline in the concentrations of proteins and other nutrients (and perhaps also secondary defence chemicals), and an increase in sugars and also leaf toughness (Bernays and Chapman 1994).

Feeding of *Mesomorphus villiger* on the tender leaves of many host plants indicates that *M. villiger* has many leaf resources and is not a specialist on particular host plant and is polyphagous (involving several host plant families). Though not strictly herbivorous as *M. villiger* were feeding only fallen and wilted leaves, as like other herbivorous insects, they show a pronounced variability in food plant preferences, representing a continuum from strict monophony (feeding on a single host plant species) to pronounced polyphony (Blu[¬]thgen and Metzner 2007).

Mesomorphus villiger preferred tender leaves of most host plants except Mexican lilac and Indian kino. Beetles preferred tender leaves than senescent leaves of other leaf types (Jackfruit, Mango, Wild jack, Cashew, Cocoa, Tamarind, Rubber, Flowering murdah, Rain tree, Cassia, Indian beech, and Macaranga) with variation in preferences. Preference for tender leaves of most host plants highlights the importance of leaf age in determining the food selection and food preference of *M. villiger*. High nutritional value could be the reason for the high preference towards tender leaves (Bernays and Chapman 1994). Analysis of the feeding preference towards tender leaves of common plants revealed that Rubber and Jackfruit were the most preferred host plants for *M. villiger* in tender leaf category. Rubber was preferred as its tender leaves are with high leaf nutrient levels resulting from nutrient resorption in deciduous trees (Aerts 1996; Wright and Westoby 2003; Vergutz *et al.*, 2012), the regular fertiliser treatment in Rubber plantations which increases the nutrient quality of Rubber leaves (Sabu *et al.*, 2014) compared to most other host plants except Cocoa which are not plantation crops. Studies on the reproductive performance of *L. tristis* showed that nutrient rich tender leaves of Rubber is essential for attaining reproductive maturity, egg production, longevity and storage of fat reserves for the prolonged dormancy phase (Sabu *et al.*, 2014; Vinod and Sabu 2010). It is obvious that the most preferred host plant (leaf type) status of Rubber and its wide occurrence close to residential buildings aids in the population build up *M. villiger* in such places.

Jackfruit leaves are another major host plant selected by *M*. *villiger*. Jackfruit is a common tree in Rubber and non-Rubber belts, availability of nutrients from annual fertiliser treatment in agribetls and the nutrients available from the decomposition of its fallen fruits and seeds could be making its leaves nutrient rich. As an evergreen tree, there is no annual leaf fall and annual leaf sprouting and no record of premature leaf fall (personal observations), availability of sufficient quantity of its tender leaves regularly as food source is limited. However the test results established that tender Jackfruit leaves are major host plant of the beetles.

Cocoa, Flowering murdah, Mexican lilac, Cashew, Cassia, Wild jack, Rain tree, Tamarind and Mango were the moderately preferred host plants while considering tender leaves. Cocoa was a major plantation crop in the locality. These plantations were also subjected to regular use of fertilisers, and making its leaves nutrient rich. As the beetle prefer its tender leaves, periodic pruning in Cocoa plantations makes it tender leaves available to the beetles. Presence as a monoculture plantation of evergreen tree, leads to the round the year presence of thick leaf litter in plantations which will be providing a good breeding and feeding habitat for the beetles. Periodical pruning of mature and tender shoots of Cocoa and pruning and application of mature leaves of Mexican lilac as green manure (Bah and Rahman 2001; Sabu *et al.*, 2012; Kwesiga *et al.*, 2003) are common agricultural practices in the region. Pruning makes tender and senescent leaves of Cocoa and senescent leaves of Mexican lilac available to the beetles

Flowering murdah is a dominant tree in the natural forests of the Western Ghats (Sundarapandian *et al.*, 2005; Nanda *et al.*, 2011) and it is common in the agribetls in the moist south Western Ghats. Annual leaf fall of Flowering murdah during pre-summer period and widespread use of its senescent and tender leaves as green manure during summer lead to availability of its litter as food resource and breeding habitat for *M. villiger*. Rain tree is another common evergreen tree across south India and it is noted as a promising agroforestry species (Duke 1983; National tropical botanical garden 2013 b). Its presence as a shade tree in the campuses of many institutions, where *M. villiger* aggregate during dormancy period. Being evergreen, its tender leaf availability is also limited.

Availability of fallen senescent leaves during all seasons and the presence of Rain trees in the premises of old buildings as a shade tree, makes it a major host plant of *M. villiger*, though the reasons for its preference are not known. Preference towards tender Cashew leaves and presence of Cashew monoculture plantations with occasional premature leaf fall due to powdery mildew disease and defoliation by the caterpillar, *Nudaurelia bellina* (Lepidoptera: Saturniidae) (Orwa *et al.*, 2009d) leads to tender leaf availability for *M.villiger* and the Cashew plantation belts becoming breeding habitat for *M.villiger*.

Mango is widely present in south India. Multiple leaf flushings of Mango tree (Bally 2010) and tender leaf fall greatly due to wind action and also due to leaf-cutting weevil *Deporaus marginatus* Pascoe (Singh 2014), which ensures availability of its tender leaves are likely to contribute towards higher incidence of *M.villiger* in Mango belts.

Tamarind and Cassia are common trees in south India and Wild jack common in Rubber belts and moderate preference of beetles towards their leaves indicate, *M. villiger* must be sustaining on these leaves when the preferred leaf types are not available. Macaranga, Indian beech and Indian kino are the low preferred leaf types. Leaf toughness of Macaranga could be the reason for low feeding on these plants and data on the chemical traits nonexistent. Low preference towards. Macaranga, a common shade tree, in the agriculture belts would not aid in the population build up of *M. villiger* in any region. Jacobson (1975) reported that root, leaf and seed extracts of *Pongamia glabra*, a related species of Indian-beech (*Pongamia pinnata*) show insecticidal activity against *M. villiger*. So it cannot be

considered as a host plant of the *M. villiger*. Indian kino, a dominant tree in the deciduous forests of south India (Sundarapandian *et al.*, 2005; Nanda *et al.*, 2011) is of least importance as a host plant leading to population builds up of *M. villiger* as it comes under least preferred host plants.

Feeding on senescent leaves, even when tender leaves were available during no choice tests, logically raises questions about the possible reasons for feeding on mixed diets and the advantages it provides as in L. tristis (Sabu and Vinod 2009). Avoidance of overspecialization on tender leaves enables switching over between the more readily available but nutritionally inferior senescent leaves and seasonal but nutritionally superior tender leaves, irrespective of their innate preferences towards the former. Among senescent leaves, Mexican lilac Flowering murdah and Rain tree are the major host plants, their distributional pattern makes them important host plants for M. villiger. Annual leaf fall of Flowering murdah during pre-summer period and widespread use of its senescent and tender leaves as green manure during summer lead to availability of its litter as food resource and breeding habitat for M. villiger. Rain tree is a common evergreen tree across south India and is a shade tree in the campuses of many institutions with its fallen senescent leaves available during all seasons. As beetle aggregation noticed in regions where Rain tree present (personal observations) and availability of its senescent leaves make it as a host plant of *M.villiger*.

Reasons for the preference hierarchy in its food selection and non differentiation of tender and senescent leaves of Mexican lilac leaves are not understood. Among the various alternate host plants, feeding pattern on Mexican

53

lilac requires special attention. *Mesomorphus villiger* equally preferred its tender as well as senescent leaves and as a common tree its leaf resources are readily available to the beetles. It is a host plant for many insect orders (Banjo *et al.*, 2006). It is a most common hedge plant in agri-belts because of its ability for fast growth and utilisation of its leaves as fodder and green manure. High N content in senescent leaves of nitrogen fixing plants due to reduced nutrient resorption might be the reason for the preference of *M. villiger* towards the senescent leaves like that of its tender leaves.

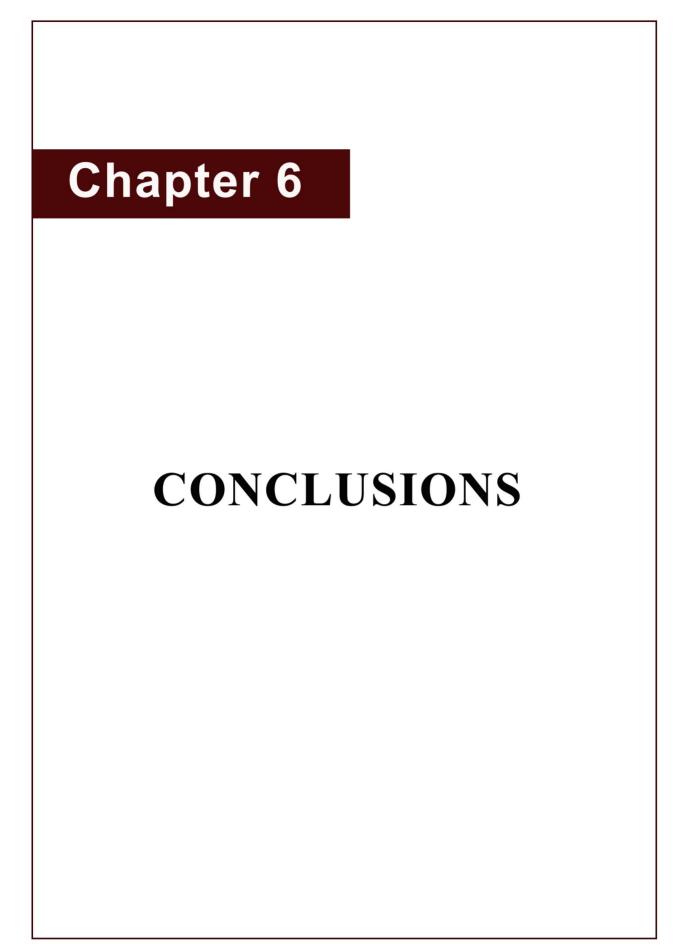
5.3. Reproductive performance on preferred host plants

Analysis of the reproductive performance of *Mesomorphus villiger* on Rubber and Jackfruit host plants indicated that *M. villiger* complete their life cycle on both Rubber and Jackfruit. Analysis of the influence of leaf age classes showed that tender leaves are important for the completion of the life cycle on both the host plants. Results indicated that Jackfruit is an inferior quality host for *M. villiger* compared to Rubber and this in turn negatively influences the survival of individuals in pre adult and adult stages

Though longevity on Rubber is longer compared to Jackfruit as the adults could tide over the dormancy phase and enter into reproductive phases during the post dormancy, it becomes clear that *M. villiger* can sustain with low reproductive performance on Jackfruit. Additionally, it shows that jackfruit is another major host plant of *M. villiger* and as Jackfruit is a common tree in the Rubber and non-Rubber agribelts in the region, *M. villiger* can sustain well on utilising the fallen Jackfruit leaves. Total larval period is a crucial time in the development of any insect as the time spent for larval development is important to Darwinian fitness because of increased vulnerability to weather and natural enemies that increases mortality (Campos *et al.*, 2003; Ishihara and Ohgushi 2006). Prolongation of larval period was observed with Jackfruit as host plant for *M. villiger* and prolongation of larval period affects the time available for the active feeding during pre dormancy and time available for preparation of dormancy as observed in *L. tristis* (Sabu *et al.*, 2014). Presented results are similar to the prolongation of developmental phase recorded in another tenebrionid beetle, *L. tristis* fed with Rubber and Jackfruit in the same region (Campos *et al.*, 2003; Nirdev 2016).

Host plant quality components, such as levels of carbon, nitrogen, and defensive metabolites, positively or negatively affect the performance of herbivorous insects, including survivorship, development time, and fecundity (Scriber and Slansky 1981; Bernays and Chapman 1994; Schoonhoven *et a.l.*, 1998; Awmack and Leather 2002). Egg size and quality, the allocation of resources to eggs, the choice of oviposition sites and insect reproductive strategies may all be influenced by plant quality, as may egg or embryo resorption on poorquality hosts. This difference is attributed to the presence of nutritional, phagostimulant factors (such as carbon and nitrogen) as well as defensive metabolites that directly affect potential and achieved herbivore development and fecundity (Awmack and Leather 2002)

Low fecundity on Jackfruit leaves when compared to Rubber indicates the low nutritional quality of Jackfruit leaves. Low fecundity is attributed to the low nutritional quality of Jackfruit leaves as a female insect encountering a poor-quality host plant may modify her oviposition behavior either by reducing the number of eggs she lays on each plant or, in some cases, adjusting the size or nutritional content of the eggs (Leather and Bernad 1987). If host plant quality is poor, many insects resorb eggs or embryos to provide nutrients and allow the survival of the mother. Sabu et al. (2014) provided nutrient levels (N, Na, K, Ca, Mg and P) and moisture content for Rubber leaves of different age group and a better survival and reproductive performance of L. tristis on tender Rubber leaves were explained on the basis of elevated levels of nitrogen and moisture content in tender leaves over senescent and dry leaves. Such data on the nutrient contents of Jackfruit leaves is lacking, however as the feeding on Jackfruit leaves negatively influenced vital parameters of insect performance like fecundity, egg and larval duration and mortality, it becomes clear that the host quality of Jackfruit is inferior to Rubber and it resulted in the lower performance of the beetle on Jackfruit leaves.



CONCLUSIONS

6.1. Biology and habits

- Life cycle of *Mesomorphus villiger* involves egg, larval, pupal and adult stages and is univoltine
- Distinct seasonality in life cycle was present with breeding in the region takes place only once during the summer season (February, March and April)
- 3) As monsoon rains starts in the region before the beetles could enter into reproductive phase, the new generation adults started home invasion and dormancy by the month of June.
- 4) Number of larval instars in *Mesomorphus villiger*, ranges between seven and nine and further empirical analysis are needed to understand the exact factors behind the intra specific variability in the number of instars.
- 5) Adult stage was 398.8 ± 19.92 days and the involved three distinct phases:pre-dormancy (30.8 ± 2.1), dormancy (184.5 ± 5.06) and post-dormancy (193.7 ± 12.32) with reproductive activities confined to the post dormancy.
- 6) Along with high egg and larval mortalities, higher mortality of adults during dormancy is reported and the higher mortality during dormancy becomes the reason for their lower abundance and population build up of *M. villiger* compared to *Luprops* exists.
- 7) Sexual dimorphic morphological differences, in the form of a pair of papillae on ventral region of 8th abdominal sternite of the female pupae and

presence of no such structures on the male pupae, aids in the early sexing of beetles.

- 8) Mass entry of *M. villiger* in to shelters in response to the onset of monsoon rains and total absence of the beetles in the litter stands indicate that wetness of the habitat conditions induced migration of towards shelters and into dormancy in the region.
- 9) Female biased sex ratio exists in *Mesomorphus villiger* and further studies are needed to understand the reasons.

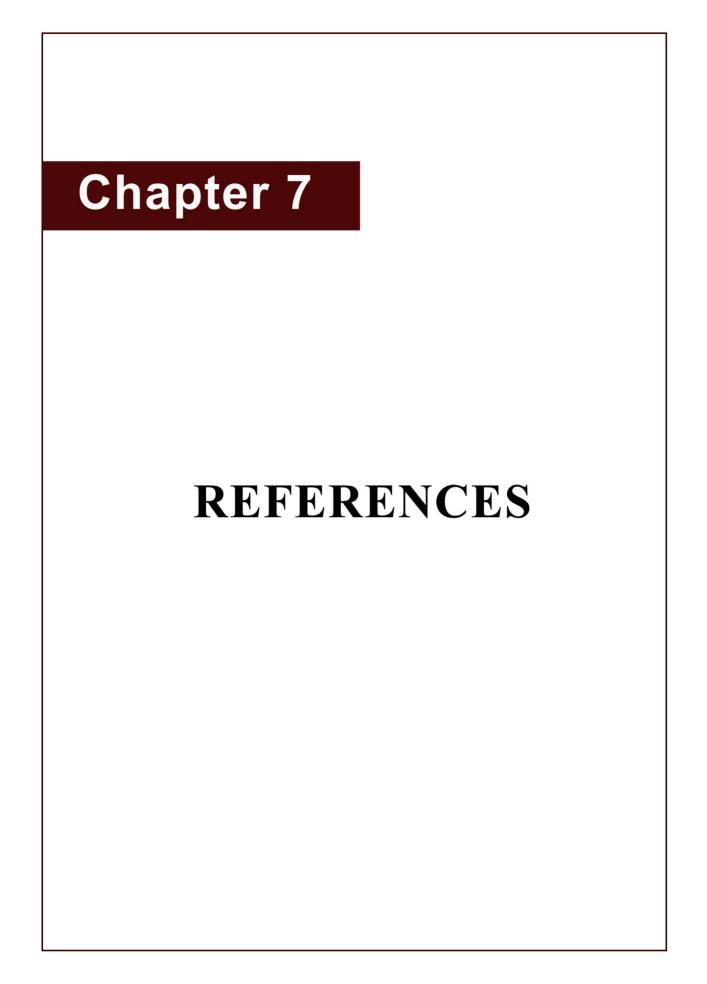
6.2. Host plants and host plant preferences

- 1) Best host plants based on tender leaf preference: In addition to the feeding preference, tender leaf availability during summer months and its wide presence in the region as plantations makes, Rubber as the best host plant for *M.villiger*.
- 2) Best host plants based on senescent leaf preference and leaf availability in the study region: High preference towards the senescent leaves of Flowering murdah, and Mexican lilac together with their wide presence in agribetls either as a shade tree or a tree for green manure makes Flowering murdah, and Mexican lilac as important host plant of *M. villiger*.

6.3. Reproductive performance on preferred host plants

1) *Mesomorphus villiger* can complete their life cycle on both Rubber and Jackfruit leaves. Tender leaves of the host plants, rubber and jackfruit are essential for the completion of the life cycle of *M. villiger* on both the host plants.

2) Jackfruit is an inferior quality host plant for *M. villiger* compared to Rubber as the survival of pre adult and adult stages are low on Jackfruit leaves.



REFERENCES

- Adachi I. 1981. Comparison of the effects of larval aggregation between gregarious and solitary species of sawflies, *Arge nigrinodosa* Motschulsky and *Arge nipponensis* Rohwer (Hymenoptera: Argidae). *Applied Entomology and Zoology*, 16: 477–486.
- Adachi I. 1994. Development and life cycle of *Anoplophora malasiaca* (Thomson)
 (Coleoptera: Cerambycidae) on citrus trees under fluctuating and constant
 temperature regimes. *Applied Entomology and Zoology*, 29: 485–497.
- Aerts R. 1996. Nutrient resorption from senescing leaves of perennials: Are there general patterns?. *Journal of Ecology*, 84: 597–608.
- Allsopp P.G. and Adams G.D. 1979. Difficulties in separating larval instars of *Pterohelaeus darlingensis*, Carter (Coleoptera: Tenebrionidae). *Journal of the Australian Entomological Society*, 18: 373–375.
- Alonso C., Ruohomaeki K., Rippi M. and Henriksson J. 2001. Testing for prerequisites of local adaptation in an insect herbivore, *Epirrita autumnata*. *Ecoscience*, 8: 26–31.
- Arunraj C. 2013. Studies on the systematic and diversity of epigeal tenebrionid beetles of south India, *Ph.D thesis*. University of Calicut. 188 pp.
- Arunraj C. and Sabu T.K. 2012. Sexing of the home invading darkling beetle Mesomorphus villiger (Coleoptera: Tenebrionidae: Opatrini). Entomon, 37(1–4): 71–75.

- Aswathi 2013. Host plants, arthropod predators and insecticide susceptibility of nuisance pest *Luprops tristis* (Coleoptera: Tenebrionidae). *Ph. D Thesis*. University of Calicut. 104 pp.
- Awmack C.S. and Leather S.R. 2002. Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology*, 47: 817–844.
- Bah R.A. and Rahman Z.A. 2001. *Gliricidia (Gliricidia sepium)* green manures as a potential source of N for maize production in the tropics; optimizing nitrogen management in food and energy production and environmental protection. Proceedings of the 2nd International nitrogen conference on science and policy. *The Scientific World*, 1(S2): 90–95.
- Ballmer G.R. and Pratt G.F. 1989. Instar number and larval development in Lycaenaphlaeas hypophlaeas (Boisduval) (Lycaenidae). Journal Lepidopterist's Society, 43: 59–65.
- Bally I.S.E. 2010. Mangifera indica (Mango), ver. 3.1. In Species Profiles for Pacific Island Agroforestry, C.R. Elevitch, Eds., Permanent Agriculture Resources (PAR), Holualoa, Hawaii, USA.
- Banjo A.D., Lawal O.A. and Songonuga E.A. 2006. The nutritional value of fourteen species of edible insects in southwestern Nigeria. *African Journal* of Biotechnology, 5 (3): 298–301.
- Beckett S.J. and Evans D.E. 1994. The demography of *Oryzaephilus surinamensis*(L.) (Coleoptera: Silvanidae) on kibbled wheat. *Journal of Stored Products Research*, 30: 121–137.

- Bernays E.A. and Chapman R.F. 1994. *Host-Plant Selection by Phytophagous Insects.* Chapman and Hall, New York. 313 pp.
- Blüthgen N. and Metzner A. 2007. Contrasting leaf age preferences of specialist and generalist phasmids. *Oikos*, 116: 1853–1862.
- Bonal R., Hernández M., Espelta J.M., Muñoz A. and Aparicio J.M. 2015. Unexpected consequences of a drier world: evidence that delay in late summer rains biases the population sex ratio of an insect. *Royal Society Open Science*, 2: 150–198.
- Breniere J. 1960. Note on Gonocephalum simplex Fabr. (Coleoptera: Tenebrionidae) harmful to tobacco Madagascar. Agronomia Tropical Maracay, 15: 414–433.
- Burley N. 1981. Mate choice by multiple criteria in a monogamous species. *The American Naturalist*, 117: 515–528.
- Calvert P.P. 1929. Different rates of growth among animals with special reference to the Odonata. *Proceedings of the American Philosophical Society*, 68: 227– 274.
- Campos W.G., Schoereder J.H. and Sperber C.F. 2003. Does the age of host plant modulate migratory activity of *Plutella xylostella?*. *Entomological Science*, 7: 323–329.
- Charnov E.L., Los-den Hartogh R.L., Jones W.T. and Van den Assem J. 1981. Sex ratio evolution in a variable environment. *Nature*, 289: 27–33.
- Clark A.B. 1978. Sex ratio and local resource competition in a prosimian primate. *Science*, 201:163–165.

- Collins P.J., Mulder J.C. and Wilson D. 1989. Variation in life history parameters of Oryzaephilus surinamensis (L.) (Coleoptera: Silvanidae). Journal of Stored Products Research, 25:193–199.
- Corbet P.S. 1999. *Dragonflies: Behaviour and ecology of Odonata*. Cornell University Press, Ithaca, United States. 829 pp.
- Danks H.V. 1987. Insect Dormancy: An Ecological Perspective. Biological survey of Canada (Terrestrial Arthropods), Ottawa. 433 pp.
- Danks H.V. 2003. Studying insect photoperiodism and rhythmicity: Components, approaches and lessons. *European Journal of Entomology*, 100: 209–221.
- Database on State of Environment 2010. Kerala Symbols. Government of Kerala. http://www.kerenvis.nic.in/isbeid/kerala-symbols.html. Accessed on 10 August 2010.
- Denlinger D.L. 1986. Dormancy in tropical insects. *Annual Review of Entomology*, 31: 239–264.
- Duke J.A. 1983. Handbook of Energy Crops. http://www.hort.purdue.edu/newcrop%20/duke_energy/dukeindex.html. Accessed on 12 October 2013.
- Elevitch C.R. and Francis J.K. 2006. *Gliricidia sepium* (Gliricidia), Ver. 2.1. In *Species Profiles for Pacific Island Agroforestry*, Elevitch C.R. (Ed.). Holualoa, Hawaii, USA.
- Elevitch C.R. and Manner H.I. 2010. Artocarpus heterophyllus (Jackfruit), ver. 1.1v. In Species Profiles for Pacific Island Agroforestry, C.R. Elevitch, Eds., Permanent Agriculture Resources (PAR), Holualoa, Hawaii, USA.

- Endrody-Younga S. and Tschinkel W. 1993. Estimation of population size and dispersal in *Anomalipus mastodon* Fahraeus, 1870 (Coleoptera, Tenebrionidae, Platynotini). *Annals of the Transvaal museum*, 36: 21–30.
- Esperk T., Tammaru T. and Nylin S. 2007. Intraespecific variability in number of larval instars in insects. *Journal of Economic Entomology*, 100: 627–645.
- Ferrer J. 1996. Contributions to the knowledge of the Tenebrionidae of Kenya (Insecta: Coleoptera). *Frustula Entomologica*, 19: 51–109.
- Ferrer J. 2000. Les especes Africaines appartenant au genre Mesomorphus Seidlitz 1893 (Coleoptera, Tenebrionidae, Opatrini). Linzer biologische beitrage, 32(1): 463–527.
- Ferrer J. 2002a. Revision of the Oriental species of the genus *Mesomorphus* Seidlitz
 1893 (Coleoptera: Tenebrionidae: Opatrinae: Opatrini). *Annales Zoologici*, 52(4): 533–557.
- Ferrer J. 2002b. Nouvelles donnees sur la repartition de *Pheugonius borneesis* Fairmaire 1899 (Coleoptera, Tenebrionidae, Lagriinae, Pycnocerini). *Nouvelle Revue d' Entomologie*, 19: 55–56.
- Ferrer J. 2008. Australian species of the genus *Mesomorphus* Miedel, 1880, and description of a new species from South Africa (Coleoptera, Tenebrionidae, Opatrini). *Bulletin de la Société Entomologique de France*. 113(3): 287–300.
- Fracknath S. 2005. Leaf age and life history variables of a leafminer: the case of *Liriomyza trifolii* on potato leaves. *Entomologia Experimentalis et Applicata*, 115: 79–87.

- Frankis M. and Schulz K. 2010. *Theobroma cacao L*. Encyclopedia of Life. http://www.eol.org/pages/484592>. Accessed on 21 September 2010.
- Ghahari H., Havaskary M., Tabari M., Ostovan H., Sakenin H. and Satar A. 2009. An annotated catalogue of Orthoptera (Insecta) and their natural enemies from Iranian rice fields and surrounding grasslands. *Linzer Biologische Beitrage*, 41(1): 639–672.
- Goettel M.S. and Philogene B.G.R. 1978. Effects of photoperiod and temperature on the development of a univoltine population of the banded woolly bear, *Pyrrharctia (Isia) isabella. Journal of Insect Physiology*, 24: 523–527.
- Groom A. 2012. Pongamia pinnata. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. < www.iucnredlist.org>. Accessed on 05 October 2013.
- Hamilton W.D. 1967. Extraordinary sex ratios. Science, 156: 477–488.
- Hanks L.M. 1999. Influence of the larval host plant on reproductive strategies of cerambycid beetles. *Annual Review of Entomology*, 44:483–505.
- Hegde V.D., Lal B. and Kushwaha R.K. 2013. Darkling beetles (Tenebrionidae: Coleoptera) of Dudhwa National Park, Uttar Pradesh. *India Journal on New Biological Reports*, 2(2): 130–141.
- Ishihara M. and Ohgushi T. 2006. Reproductive Inactivity and Prolonged Developmental Time Induced by Seasonal Decline in Host Plant Quality in the Willow Leaf Beetle *Plagiodera versicolora* (Coleoptera: Chrysomelidae). *Environmenal Entomology*, 35(2): 524–530.

- Jacobson M. 1975. Insecticides from plants: A review of the literature, 1954–1971. Agriculture Hand Book 461, U.S.D.A, Washington, D.C. 138 pp.
- Jolivet P. 1998. Inter relationship between insects and plants. CRC press, Washington, D.C. 208 pp.
- Jones D., Jones G. and Bhaskaran G. 1980. Induction of supernumerary moulting by starvation in *Manduca sexta* larvae. *Entomologica Experimentalis et Applicata*, 28: 259–267.
- Joshi B.G. 1962. Laboratory studies on the biology of tobacco ground beetle Mesomorphus villiger Blanch. Indian Journal of Entomology, 24 (3): 205– 210.
- Joshi B.G. and Pavate M.V. 1963. Studies on the biology of Tobacco ground beetle Mesomorphus villiger, Blanch, by periodic regression analysis. Indian Journal of Entomology, 25 (1):1–8.
- Kaszab Z. 1963. Angaben zur Kenntnis der Tenebrioniden des Tschadsee-Gebietes,
 nebst einer Revision der afrikanischen *Mesomorphus*-Arten (Coleoptera).
 Revue de Zoologie et de Botanique Africaines, 68: 341– 385.
- Kaszab Z. 1979. Faunistik der Tenibrioniden von Sri Lanka (Coleoptera). Folia Entomologica Hungarica, Rovartani Kozlemenyek (Series Nova), 32(2): 43–128.
- Kwesiga F., Akinnifesi F.K., Mafongoya P.L., McDermott M.H. and Agumya A.
 2003. Agroforestry research and development in southern Africa during the 1990s: review and challenges ahead. *Agroforestry Systems*, 59: 173–186.

- Leather S.R. and Burnand A.C. 1987. Factors affecting life-history parameters of the pine beauty moth, *Panolis flammea* (D&S): the hidden costs of reproduction. *Functional Ecology*, 1: 331–338.
- Leather S.R., Walters K.F.A. and Bale J.S. 1995. *The ecology of insect over wintering*. Cambridge University Press, Cambridge. 268 pp.
- Leonard D.E. 1968. Effects of density of larvae on the biology of the gypsy moth, Porthetria dispar. Entomologica Experimentalis et Applicata, 11: 291– 304.
- Lobl I. and Smetana A. 2008. *Catalogue of Palaearctic Coleopteran. Vol 5. Tenebrionoidea*. Apollo books, Stenstrup. 670 pp.
- Ludwig D. 1956. Effects of temperature and parental age on the life cycle of the mealworm, *Tenebrio molitor* Linnaeus (Coleoptera: Tenebrionidae). *Annals of the Entomological Society of America*, 49: 12–15.
- Ludwig D. and Fiore C. 1960. Further studies on the relationship between parental age and the life cycle of the mealworm *Tenebrio molitor*. *Annals of the Entomological Society of America*, 53: 595–600.
- Mansingh A. 1971. Physiological classification of dormancies in insects. *Canadian Entomologist*, 103: 983–1009.

Masaki S. 1980. Summer diapauses. Annual review of Entomology, 25: 1-25.

Menezes Jr.A.O., Mikami A.Y., Ide A.K. and Ventura M.U. 2005. Feeding preferences of *Microtheca punctigera* (Achard) (Coleoptera: Chrysomelidae) for some Brassicaceae plants in multiple-choice assays. *Scientia Agricola*, 62 (1): 72–75.

Michitaka C. 1978. Tenebrionidae of The Nansei Islands III (Coleoptera). *Esakia*, 11: 63–80.

Minitab Inc. 2010. MINITAB Statistical Software. Release 16 for Windows.

- Mishra R.K., Upadhyay V.P., Bal S., Mohapatra P.K. and Mohanty R.C. 2006. Phenology of species of moist deciduous forest sites of Similipal biosphere reserve. *Lyonia journal of ecology and application*. http://www.lyonia .org/downloadPDF.php?pdfID=2.465.1pp>. Accessed on 05 February 2013.
- Mopper S. 1996. Adaptive genetic structure in phytophagous insect populations. *Trends in Ecology and Evolution*, 11: 235–238.
- Morita M. and Tojo S. 1985. Relationship between starvation and supernumerary ecdysis and recognition of the penultimate-larval instar in the common cutworm, *Spodoptera litura, Journal of Insect Physiology*, 31: 307–313.
- Morton J. 1987. *Tamarind*. In *Fruits of warm climates*. Julia F. Morton (Ed.), Miami, FL. 115–121 pp.
- Nadgauda R., Jayasankar S. and Litz R.E. 2005. Anacardium occidentale Cashew. In Biotechnology of Fruit and Nut Crops. R.E. Litz, Eds., CABI Publishing, UK. 707pp.
- Nair P.N. and Nair C.S. 1999. *Forest plants of Kerala*. State Institute of languages, Trivandrum, Kerala. 495pp.
- Nanda A., Prakash H.M., Murthy L.K. and Suresh H.S. 2011. Phenology of leaf flushing, flower initiation and fruit maturation in dry deciduous and

evergreen forests of Bhadra Wildlife Sanctuary, Karnataka, Southern India. *Our Nature*, 9: 89–99.

- National tropical botanical garden. 2013. Meet the Plants: *Tamarindus indica*. http://www.ntbg.org/plants/plant_details.php?plantid=10971>. Accessed on 04 October 2013.
- National tropical botanical garden. 2013b. Meet the Plants: Samanea saman. <http://www.ntbg.org/ plants/plant_details.php>. Accessed on 4 October 2013.
- Natural resources data bank Thrissur 2014 Kerala state land use board. <http://kslub. kerala.gov.in/ images/ pdf/ natural_resources/ 8 Thrissur>. Accessed on September 2016.
- Nijhout H.F. 1975. A threshold size for metamorphosis in the tobacco hornworm, Manduca sexta (L.). Biological Bulletin, 149: 214–225.
- Nirdev 2016. Identification of aggregation pheromones of *Luprops tristis* beetles and analysis of maternal host plant influence on reproductive potential and longevity. Ph.D thesis, *University of Calicut*, 118pp.
- Orwa C., Mutua A., Kindt R., Jamnadas R. and Simons A. 2009b. *Gliricidia sepium*. Agroforestree Database: a tree reference and selection guide version 4.0 <http://www.worldagroforestry.org/sites/treedbs/treedatabases.asp>. Accessed on 07 September 2013.
- Orwa C., Mutua A., Kindt R., Jamnadas R. and Simons A. 2009c. Pongamia pinnata. Agroforestree Database: a tree reference and selection guide

version 4.0 <http://www.world agroforestry .org/af/treedb/asp>. Accessed on 07 September 2013.

- Orwa C., Mutua A., Kindt R., Jamnadass R. and Simons A. 2009a. *Cassia fistula*. Agroforestry Database: a tree reference and selection guide version 4.0. < http://www.worldagroforestry.org/af/ treedb>. Accessed on 07 September 2013.
- Orwa C., Mutua A., Kindt R., Jamnadass R. and Simons A. 2009d. Anacardium occidentale. Agroforestree Database: a tree reference and selection guide version 4.0. http://www.worldagro forestry.org/af/treedb/>. Accessed on 07 September 2013.
- Palaniswamy P. and Lamb R.J. 1992. Host preferences of the flea beetles *Phyllotreta cruciferae* and *P. striolata* (Coleoptera: Chrysomelidae) for crucifer seedlings. *Journal of Economic Entomology*, 85 (3): 743–752.
- Pillai P.K.C. and Chandrashekara U.M. 2011. Regeneration study of selected Terminalias in Kerala. KFRI Project report No. 471/2005, Kerala Forest Research Institute, 67pp.
- Quennedey A., Aribi N., Everaerts C. and Delbecque J.P. 1995. Postembryonic development of *Zophobas atratus* Fab. (Coleoptera: Tenebrionidae) under crowded or isolated conditions and effects of juvenile hormone analogue applications. *Journal of Insect Physiology*, 41: 143–152.
- Ramesh B.R., Pascal J.P. and Nouguier C. 1997. Atlas of endemics of the Western Ghats (India): distribution of tree species in the evergreen and semi-

evergreen forests, vol. 38 of Publications du Departement d' Ecologie, Institut Francais de Pondichery. 403pp.

- Rao E.V.V.B., Swamy K.R.M. and Bhat M.G. 1998. Status of cashew breeding and future priorities. *Journal of Plantation Crops*, 26: 103–114.
- Rico-Gray V., Chemas A. and Mandujano S. 1991. Uses of tropical deciduous forest species by the Yucatan Maya. *Agroforestry Systems*, 14: 149–161.
- Rodrigues D. and Moriera G.R.P. 1999. Feeding preference of *Heliconius erato* (Lepidoptera, Nymphalidae) in relation to leaf age and consequences for larval performance. *Journal of Lepidopterists's society*, 53 (3): 108–113.
- Sabu T.K. and Vinod K.V. 2009. Population dynamics of the rubber plantation litter beetle *Luprops tristis*, in relation to annual cycle of foliage phenology of its host, the para rubber tree, *Hevea brasiliensis*. *Journal of Insect Science*, 9 (56): 1–10.
- Sabu T.K., Greeshma M. and Aswathi P. 2012. Host plant and leaf-age preference of *Luprops tristis* (Coleoptera: Tenebrionidae: Lagriinae: Lupropini): a home invading nuisance pest in rubber plantation belts. *Psyche*, 1–7.
- Sabu T.K., Nirdev P.M. and Aswathi, P. 2014. Reproductive performance of Mupli beetle, *Luprops tristis* (Coleoptera: Tenebrionidae: Lagriinae: Lupropini): in relation to leaf age of the para rubber tree, *Hevea brasiliensis. Journal* of Insect Science, 14 (12): 1–11.
- Sabu T.K., Vinod K.V. and Jobi M.C. 2008. Life history, aggregation and dormancy of the rubber plantation litter beetle, *Luprops tristis*, from the rubber

plantations of moist South Western Ghats. *Journal Insect Science*, 8 (01): 1–17.

- Saminathan J. and Vetrichelvan T. 2012. Anti-secretory properties of *Macaranga peltata* Roxb. in various experimental models. *International journal of Pharmacology Research*, 2 (1): 22–28.
- Sangwan S., Rao D.V. and Sharma R.A. 2010. A Review on *Pongamia pinnata* (L.) Pierre: A great versatile leguminous plant. *Nature and Science*, 8 (11): 130–139.
- Sanker S. and Chandrshekara U.M. 2002. Development and testing of sustainable agroforestry in different agroclimatic zones of Kerala with emphasis on socio-cultural, economic, technical and institutional factors effecting this sector. KFRI Research Report No.234, Kerala Forest Research Institute. 85pp.
- Sato T. 2003. Effect of photoperiod and temperature on development and larval diapauses of *Dacne picta* (Coleoptera: Erotylidae). *The Japanese Journal of Applied Entomology and Zoology*, 38: 1117–1123.
- Schawaller W. 2000. The genus Mesomorphus Seidlitz in Nepal. Faunistische Abhandlungen Staatliches Museum fur Tierkunde, 22(4): 39–48.
- Scheirs J., Debruyn L. and Verhagen R. 2002. Seasonal changes in leaf nutritional quality influence grass miner performance. *Ecological Entomology*, 27: 84–93.

- Schmidt F.H. and Lauer W.L. 1977. Developmental polymorphism in *Choristoneura* spp. (Lepidoptera: Tortricidae). *Annals of the Entomological Society of America*. 70: 112–118.
- Schoonhoven L.M., Jermy T. and van Loon J.J.A. 1998. Host-plant selection: Why insects do not behave normally, pp. 195–220. In. L.M. Schoonhoven., T. Jermy., J.J.A. van Loon (eds.) Insect -plant biology: from physiology to evolution. Chapman and Hall. New York.
- Scott P.T., Pregelj L., Chen N., Hadler J.S., Djordjevic M.A. and Gresshoff P.M. 2008. *Pongamia pinnata*: an untapped resource for the biofuels industry of the future. *Bio Energy Research*, 1 (1): 2–11.
- Scriber J.M. and Slansky F. 1981. The nutritional ecology of immature insects. Annual Review of Entomology, 26:183–211.
- Seena C.M. and Sabu T.K. 2013. Defensive Glands of the Darkling Beetle
 Mesomorphus villiger Blanchard (Coleoptera: Tenebrionidae). Psyche, 1–
 3.
- Shahout H.A., Xu J.X., Yao X.M. and Jia Q.D. 2011. Influence and mechanism of different host plants on the growth, development and fecundity of reproductive system of common cutworm *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae). *Asian Journal of Agricultural Science*, 3 (4): 291–300.
- Shintani Y. and Ishikawa Y. 1997. Temperature dependency of photoperiodic response and its geographic variation in the yellow-spotted longicorn

beetle, *Psacothea hilaris* (Pascoe) (Coleoptera: Cerambycidae). *Applied Entomology and Zoology*, 32: 347–354.

- Simons A.J. and Stewart J.L. 1994. *Gliricidia sepium*: a multipurpose forage tree legume, In: Gutteridge R.C., Shelton H.M. (Eds). *Forage tree legumes in tropical agriculture*. Wallingford: CAB International, 30–48.
- Singh H.S. 2014. Management of fresh leaf-cutting weevil, *Deporaus marginatus* (Pascoe) in mango. *Insect Environment*, 20 (1): 19–21.
- Sitaramaiah S., Rama Prasad G. and Sreedhar U. 1999. Management of tobacco ground beetle, *Mesomorphus villiger* with insecticide baits on flue cured Virginia tobacco. *Indian Journal of Agricultural Sciences*, 69 (9): 660– 663.
- Sundarapandian S.M., Chandrasekaran S. and Swamy P.S. 2005. Phenological behaviour of selected tree species in tropical forests at Kodayar in the Western Ghats, Tamil Nadu, India. *Current Science*, 88 (5): 805–810.
- Tauber M.J. and Tauber C.A. 1976. Insect seasonality: Diapause maintenance, termination and post diapause development. Annual Review of Entomology, 21: 81–107.
- Trivers R.L. and Willard D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science*, 179: 90–92.
- Tschinkel W.R. and Wilson C.D. 1971. Inhibition of population due to crowding in some tenebrionid beetles. *Journal of experimental Zoology*, 176 :137–146.

- Urs, K.C.D. and Hopkins T.L. 1973. Effect of moisture on growth rate and development of two strains of *Tenebrio molitor* L. (Coleoptera, Tenebrionidae). *Journal of Stored Products Research*, 8: 291–297.
- Uvarov B.P. 1966. *Grasshoppers and locusts*. A handbook of general acridology.vol.1. Cambridge University Press, Cambridge, United Kingdom. 613pp.
- Varghese E. 1996. A case study among the Kharias of central India. Deep publication, New Delhi. 164pp.
- Vergutz L., Manzoni S., Porporato A., Novais R.F. and Jackson R.B. 2012. Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. *Ecological Monographs*, 82 (2): 205–220.
- Via S., Gomulkiewicz R., de Jong G., Scheiner S. M., Schlichting C.D. and Van Tienderen P.H. 1995. Adaptive phenotypic plasticity: consensus and controversy. *Trends in Ecology and Evolution*, 10: 212–217.
- Viet Nam Net. 2013. Black bean beetles disturb Kon Tum people '.<http://english.vietnamnet.vn/fms/society/76773/black-bean-beetlesdisturb-kon-tum-people.html > . Accessed on 9 July 2015.
- Vinod K.V. and Sabu T.K. 2010. Dormancy-inducing factors of rubber litter beetle, *Luprops tristis* (Coleoptera: Tenebrionidae). *Insect Science*, 17: 47–51.
- Vinod K.V., Sabu T.K. and Benny T.M. 2008. Sex determination of the live rubber plantation litter beetle, *Luprops tristis*: a novel method. *Journal of Insect Science*, 8 (12): 1–6.

- Wang X., Feng G.E. and Xue F. 2006. Host plant mediation of diapauses induction in the large cabbage-beetle, *Colaphellus bowringi* Baly (Coleoptera: Chrysomelidae). *Insect Science*, 13: 189–193.
- Watt J.C. 1992. Fauna of New Zealand, No.26: Tenebrionidae, 7–11. DSIR Auckand.
- Weiss N.A. 2007. *Introductory Statistics*. Dorling Kindersley, India, 7th edition. 960 pp.
- Wigglesworth V.B. 1972. *The principles of insect physiology*. Chapman & Hall, London, United Kingdom. 763pp.
- Wolda h. and Denlinger D.L. 1984. Diapause in alarge aggregation of a tropical beetle. *Ecological Entomology*, 9: 217–30.
- World Conservation Monitoring Centre. 1998. Pterocarpus marsupium. IUCN
 2013. IUCN Red List of Threatened Species. Version 2013.1.
 <www.iucnredlist.org>. Accessed on 05 October 2013.
- Wright I.J. and Westoby M. 2003. Nutrient concentration, resorption and lifespan: leaf traits of Australian sclerophyll species. *Functional Ecology*, 17: 10– 19.
- Wu K. and Li M. 1992. Nutritional Ecology of the cotton ballworm, *Heliothis armigera* (Hubner): effects of dietary sugar concentration on development and reproduction. *Acta Entomologica Sinica*, 35: 47–52.
- Xue M., PangY.H., Wang H.T., Li Q.L. and Liu T.X. 2010. Effects of four host plants on biology and food utilization of the cutworm, *Spodoptera litura*. *Journal of Insect Science*, 10 (22): 1–5.

- Yan X., Zhou H., Shen Z., Li W., Guo D., Song Y., Lan S. and Zhang J. 2010. National investigations of stored grain arthropods in China .10th International working conference on stored product protection. Chengdu Grain Storage Research Institute, No.95 Huapaifang Street, Chengdu. 425: 212–216.
- Yin C.M. and Chippendale G.M. 1974. Juvenile hormone and the induction of larval polymorphism and diapause of the southwestern corn borer, *Diatrea grandiosella*. *Journal of Insect Physiology*, 20: 1833–1847.
- Yoichi S. and Haruo K. 1999. Host plants of the phytophagous ladybird beetle, *Epilachna vigintioctopunctata* (Coleoptera: Coccinellidae), in Southeast Asia and Japan. *Applied Entomology and Zoology*, 34 (1): 75–83.
- Zhou H.Z. and Topp W. 2000. Diapause and polyphenism of life-history of *Lagria hirta*. *Entomologica Experimentalis et Applicata*, 94: 201–210.