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Natural History and Leaf Shelter Construction of the Asian Rice Leptispa Beetle *Leptispa pygmaea* Baly (Coleoptera: Chrysomelidae: Cassidinae: Leptispini)

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Kaniyarikkal Divakaran Prathapan, Caroline S. Chaboo, and Kolandaivelu Karthikeyan (2009) Natural history and leaf shelter construction of the Asian rice leptispa beetle, *Leptispa pygmaea* Baly (Coleoptera: Chrysomelidae: Cassidinae: Leptispini). *Zoological Studies* **48**(5): 625-631. The leaf-roll construction by the Asian rice leptispa beetle *Leptispa pygmaea* Baly (Cassidinae: Leptispini) was studied. Consistent adult feeding on the adaxial side of tender rice leaves *Oryza sativa* Linnaeus (Poaceae) induces partial upward rolling of the leaf lamina. Adult leaf rolls are ephemeral and not apparent, and they unfurl once the beetle leaves the leaf. Females oviposit clutches of up to 8 eggs mostly on the adaxial side of the leaf within such rolls. Neonate larvae migrate to the base of the leaf axil and feed by scraping, which induces formation of leaf rolls from the base where the leaf is already curled up. All 5 larval instars feed in this manner, migrating to new leaves and forming new leaf rolls. Pupation occurs within the leaf roll of the 5th instar. Adult leaf rolls are partial and ephemeral, and therefore offer only limited protection to eggs and adults. In contrast, larval leaf rolls are well formed and cohesive compared to those of adults. This is probably due to the sedentary nature and active feeding of the larvae resulting in a greater reduction in leaf turgidity. The host plant, leaf curling, and leaf-roll architecture of *Leptispa* Baly differ from the leaf 'sandwiches' built by some Neotropical cassidines, of the Imatidiini, that glue together *Inga* leaves (Fabaceae). Two terms, leaf rolls for Leptispini and leaf case shelters for Imatidiini, are proposed to reflect the lack of homology of these structures, although both function as shelters. We also propose that *Leptispa* feeding probably induces loss of turgor pressure that in turn induces inward curling of the leaf to produce an elongated leaf roll. This may be regarded as an ideal example of cost-effective shelter building by an insect. http://zoolstud.sinica.edu.tw/Journals/48.5/625.pdf

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Animal constructions can convey a wealth of information about the biology and behavior of the architect. The topic can be broadly appealing to both scientists and laypeople, as evidenced by several popular books (von Frisch 1974, Hansell 1984 2005 2007, Gould and Gould 2007). Birds, spiders, and Hymenoptera (ants, bees, and wasps) are the best-known builders whose constructions serve as domiciles (e.g., bird nests), traps (e.g., spider webs), and displays (e.g., nests of bower birds). Constructions of many animals, particularly invertebrates, remain obscure. Among beetles, the most spectacular radiation of insects, architects are rare, yet in the leaf beetle

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family Chrysomelidae (with ca. 40,000 species), domiciles and defensive shields built from feces and exuvial skins are becoming better understood as a common phenomenon (Chaboo et al. 2007 2008 and citations therein). In this paper, we report on the unique construction of leaf shelters in 1 chrysomelid species, *Leptispa pygmaea* Baly, commonly called the Asian rice leptispa or blue beetle, which is better known as a pest of rice (e.g., Burlow 1899, Maxwell-Lefroy 1906 1909, Maulik 1913 1919, Anand 1989, Karthikeyan 2007, Karthikeyan and Jacob 2008).

Animal constructions indicate many aspects of the ecology and evolution of the builder, and can affect other taxa in a community. Animals invest considerable expenses of time, energy, and secretions in making constructions (Hansell 1984), so one can hypothesize that such constructions might improve the survivorship of individuals in ecological time and perhaps of clades over evolutionary time. Other insects build leaf shelters, e.g., some pyralid moths (Solís 2007) and some weevils (Horváth 1988, Vogt 1992); leaf shelters were shown to be ideal microenvironments, simultaneously providing domiciles, herbivorous feeding sites, and concealment from enemies (e.g., Cappuccino 1993). They even offer secondary habitats for other animals thereby enhancing species diversity on a given host (Vogt 1992, Martinsen et al. 2000). Within the Chrysomelidae, leaf shelter building occurs in 2 clades of the Cassidinae (tortoise beetles): the Neotropical tribe Imatidiini Hincks (Gilbert et al. 2001) and the Old World tribe Leptispini Weise 1911 (Maulik 1919, Voronova and Zaitsev 1982).

The Leptispini comprises 2 genera, *Leptispa* Baly and *Ovotispa* Medvedev (Medvedev 1992). *Ovotispa* contains a single species, *O. atricolor* Pic, whereas *Leptispa* comprises 71 known species that are found only in the Old World (Maulik 1939, Uhmann 1958, Würmli 1975, Jolivet and Hawkeswood 1995, Chaboo 2007). They are known to use host plants in the families Cyperaceae and Poaceae (Maulik 1939, Jolivet and Hawkeswood 1995). Their biology is poorly known, with limited reports available for only 8 species. Voronova and Zaitsev (1982) described *L. bambusae* Voronova and Zaitsev, *L. bicoloripennis* Voronova and Zaitsev, *L. conicicollis* Voronova and Zaitsev, and *L. medvedevi* Voronova and Zaitsev as pests of bamboo in Vietnam. Brief notes are available for *L. pici* Uhmann (Chen 1973, Chen et al. 1986, Kimoto and Takizawa 1994 1997), *L. filiformis* (Germar) (Vela and de Ferrer 1994, Bordoni 1998), *L. godwini* Baly (Liao and Shen 1981), and *L. pygmaea* Baly (Maxwell-Lefroy 1906, Fletcher 1914, Maulik 1919, Kalshoven 1951).

Burlow (1899) first reported *L. pygmaea* as a pest of rice. Its life history was supposed to be similar to that of the rice hispa, *Dicladispa armigera* (Olivier), the larvae of which are leaf miners (Maxwell-Lefroy 1906, Ramakrishna Ayyar 1932 1940). A brief remark by Fletcher (1914: 314) is the first accurate clue to its natural history: “The eggs are laid on paddy leaves and the grubs also feed on the upper surface of the leaves, the attacked leaves usually folding over so as to hide the enclosed grub. The grub, when full-fed, pupates on the leaf, the beetles emerging after about 4 days”. A leaflet published by the Department of Agriculture, Madras, India (Anonymous 1931) states that “The grub, however, is not flattened and does not mine in the leaves but feeds from the surface of the leaf”. Fletcher (1917) illustrated the adult and immature stages. Dalvi et al. (1985a b), Patel and Shah (1985a), Karthikeyan (2007) and Karthikeyan and Jacob (2008) studied its life history and reported the durations of various life stages as 3-7 d for eggs, 6-14 d for larval instars, 2-5 d for pupae, and 12-24 d for the total life cycle. Later researchers examined the natural enemies (Fletcher 1917, Patel and Shah 1985 a b, Karthikeyan 2007) and grasses (Poaceae) as alternate hosts in India (Cotes 1896, Maxwell-Lefroy 1906 1909, Maulik 1919, Khanvilkar et al. 1983, Dalvi et al. 1985a, Dale 1994, Karthikeyan 2007). Anand (1984 1986 1989) also indicated *L. pygmaea* as a pest of sweet potato (Convolvulaceae: *Ipomoea batatas* (L.) Lam) and sugarcane (Poaceae: *Saccharum officinarum* L.). Today, *L. pygmaea* is regarded as a pest of rice on the Indian subcontinent that often reaches serious levels, thereby necessitating chemical control measures (Swamiappan et al. 1990, Nadarajan 1996, Karthikeyan 2007).

Since Fletcher’s (1914) description, no further information has been added to our knowledge of leaf roll construction by *Leptispa*. We were stimulated to more deeply analyze the interesting natural history of *Leptispa* in an effort to improve our understanding of evolutionary patterns within the subfamily Cassidinae. This is the first report on our study of *Leptispa*. Morphological descriptions of immature stages are provided elsewhere.

MATERIALS AND METHODS

The study was carried out in rice fields at the Farming Systems Research Station, Karamana, Trivandrum, Kerala, India (Fig. 1). Living *L. pygmaea* was studied by one of us [PKD] on several visits during the period of Jan. to Oct. 2007, which includes the south-east and north-west monsoon seasons and intermittent dry spells. Experimental plots of rice at different growth stages in the station provided an ample scope for observing the insect, except during the hot summer. Here, rice is grown as a transplanted crop in wetlands with the application of chemical fertilizers and pesticides. *Lepstipa* activity was easily noted by the presence of leaf rolls containing eggs, larvae, pupae, adults and feeding scars (Figs. 2-9).

Laboratory Study

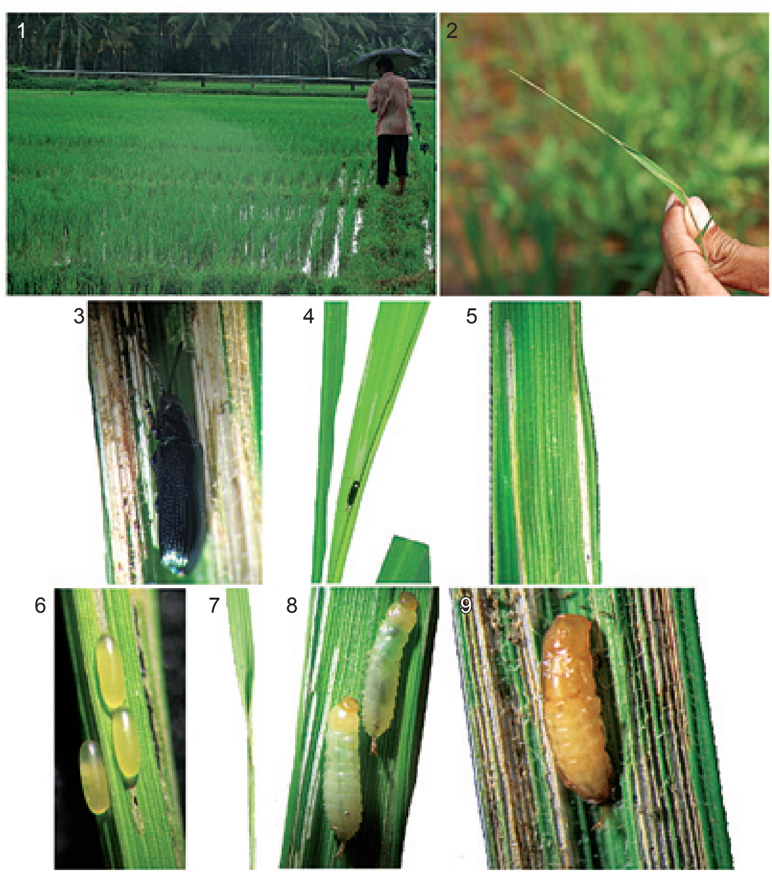
Data on behavior associated with the formation of leaf rolls were collected through a series of observations using field-collected specimens and untreated potted rice plants at the College of Agriculture, Vellayani, India. Plants were of 2 ages in the tillering stage: 39 d (leaf width of 7.0-9.0 mm) and 52 d (leaf width 8.5-10.1 mm) after sowing.

Observation 1: Many gravid females were confined to plants in cages so that they would oviposit. Emerging neonate larvae hatching out of these eggs were observed.

Observation 2: A pair of larvae (instars 2-4) were each placed medially on the adaxial side of 20 fully emerged leaves of 39-d-old seedlings, and the time required to form a leaf-roll was recorded.

Observation 3: Single larvae (instars 2-4) were each placed medially on the adaxial side of 30 leaves of 52-d-old seedlings, and the time required to form a leaf roll was recorded.

Specimen vouchers were collected into 70% ethanol and are deposited in the Travancore Collection, Kerala Agricultural Univ., Vellayani,



Figs. 1-9. **1.** Field site with cultivated rice, Trivandrum, India. **2.** Leaf roll made by *Leptispa pygmaea* larva. **3.** Blue-black Asian rice hispa adult. **4.** Adult feeding in leaf roll. **5.** Linear feeding scars made by adult scraping. **6.** Leaf roll with eggs *in situ*. **7.** Leaf roll with larvae *in situ*. **8.** Larvae feeding *in situ*. **9.** Pupa *in situ*.

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RESULTS

The rice leaf comprises a sheath and a lamina without a narrow petiole. The sheath tightly covers the stem, and the lamina is semi-vertical. In young leaves, the base of the lamina is inwardly curled.

The life cycle of *L. pygmaea* is comprised of solitary adults (Fig. 3), clustered or loosely clustered naked eggs (Fig. 6), 5 larval instars (Fig. 8), and naked pupae in leaf rolls (Fig. 9). All stages occur on shoots of rice plants, not in the roots or soil. Since rice is grown in flooded fields, all stages may experience flooding from time to time. Larvae and pupae do not retain exuvio-fecal shields as do many tortoise beetles (Chaboo 2007). Both adults and larvae are leaf scrapers, leaving long feeding scars on the leaf lamina (Figs. 3-9).

Adult leaf rolls: Adult feeding, especially on tender leaves, results in the partial upward rolling of the leaf lamina (Fig. 4). Adults prefer to feed on the dorsal surface of the leaf by scraping linear streaks (they also feed on the ventral leaf surface, although not as frequently) (Fig. 5). These rolls are incomplete, ephemeral, not apparent, and unfurl once the beetles depart the leaf. Courtship and oviposition often occur in such leaf shelters. No special leaf rolls for egg are formed, but the solitary gravid female apparently provides some protection for herself and her offspring by ovipositing up to 8 eggs in rows or loose clusters within a leaf roll where she feeds (Fig. 6). No additional egg coverings are provided. Less frequently, eggs were found on both the ventral and dorsal surfaces of leaves not eaten by adults or used as pupal leaf rolls. Only 6 of 21 observed clutches were on the ventral leaf surface. This finding contrasts with previous reports of oviposition mostly on the leaf venter (Dalvi et al. 1985a) or of no surface preference (Karthikeyan 2007). Apparently those researchers did not observe the partially rolled up leaves formed by adult feeding and which are used as oviposition sites.

Larval leaf rolls: (a) Larval movement: *Leptispa pygmaea* has 5 larval instars (Karthikeyan 2007). Newly hatched larvae migrate to the base of the leaf axil where the lamina is still curled up. A neonate displays a characteristic movement on the edge of the leaf: on reaching the margin of the leaf blade, it aligns its body longitudinally on the edge, keeping its legs on both the abaxial and adaxial sides of the blade so that it is ‘hugging’ the edge, and then it crawls down along the edge. After crawling down to the base of the leaf on which the eggs were laid, neonates may crawl up and migrate into the uppermost leaf that is yet to unfurl when such a leaf is available. After settling down on the leaf, older larvae released on the lamina begin moving down towards the base where the leaf lamina is partially curled, and they start feeding on the adaxial surface. When the leaf lamina is not unfurled at the base, the larvae disappear into the curled basal region of the leaf. Unlike neonate larvae, older instars were not observed crawling along or hugging the edge of the leaf blade. (b) Leaf roll construction: The leaf base provides a concealed microclimate for the neonate. Generally, all active larvae settle down on the lamina on 1 side of the midrib, one after the other, and begin feeding between the midrib and lateral margin. This results in further upward curling of the lamina from the base to the apex, extending the initial curling at the leaf base. Such leaves never unfurl as long as larvae are inside. Multiple larvae occupy the same leaf roll (Fig. 8). Formation of the larval leaf roll always occurred from the base to the apex.

Neonate larvae migrate to the base of the same leaf or into new tender leaves for feeding, and thus initiate new leaf rolls but they never appear to exploit the adult leaf rolls. Both neonate and older larvae form similar leaf shelters. The laminar side on which larva feed initially curls upwards from the base, gradually forming a longitudinal leaf roll. The opposite side of the lamina may also fold up, thus closing the roll.

When a larva makes use of more than 1 leaf for feeding, it exits the leaf roll and migrates to a younger leaf that is yet to unfurl. Larval feeding does not generally completely damage the leaves, as deserted leaf rolls lose their integrity, and the undamaged portion tends to unfurl. Pupation occurs within the last leaf roll of the 5th larval instar (Fig. 9). In general, all larvae feeding on a leaf pupate on that leaf.

Timing of shelter construction: After a pair of larvae was introduced onto intact leaf lamina and began feeding (n = 20), leaf rolls formed over several hours: 2 rolls within 6 h, 12 rolls within 12 h, 17 rolls within 24 h, and 20 rolls within 48 h. The minimum time taken for the formation of a fully formed leaf roll was about 4.75 h. In the 2nd set of observations with 1 larva each placed on 30 leaves, the formation of leaf rolls occurred as follows: 2 leaf rolls in 5 h, 4 leaf rolls in 6 h, 18 leaf rolls in 12 h, 20 leaf rolls in 24 h, and 24 leaf rolls in 48 h. One leaf roll remained incomplete, and 5 larvae failed to become established on the leaf surface and were lost. Single larvae failed to successfully construct a leaf roll in six of 30 instances (20%), while all larvae in pairs successfully constructed a leaf roll within 48 h. Group feeding probably hastens the formation of a leaf roll through increased loss of turgidity of the leaf, in addition to enhancing its size and cohesiveness. Even though age and size of the leaves of the plants used in observations 2 and 3 were not the same, it was evident that single larva often failed to establish themselves on a leaf, while the release of a pair invariably led to formation of a leaf roll.

Pupal rolls: Voronova and Zaitsev (1982) first mentioned pupal rolls in other *Leptispa* species. In *L. pygmaea*, larvae pupate in the middle of a leaf more or less in a line. Up to 3-5 pupae were found in a single leaf roll.

DISCUSSION

Leptispa pygmaea adults form leaf rolls that are incomplete, loose, ephemeral, and not apparent. These may offer limited shelter for both eggs and adults. The adult rolls are formed anywhere along the length of the leaf on the adaxial surface and are only rarely formed near the base. In contrast, larvae avoid adult leaf rolls and instead construct their own rolls, invariably starting from the base of the leaf. Since this roll is complete and cohesive, it appears to offer great protection for larvae from abiotic and biotic factors. Not every feeding adult was seen in the rolls, as only prolonged feeding results in rolling, but larvae were invariably observed only in leaf rolls. We observed that single larvae could complete the formation of a leaf roll, but generally many individuals (up to 7-9) live together and pupate on the same leaf, apparently with little interaction.

Application of insecticides is reported to be effective against *L. pygmaea* (Thondadarya and Devaiah 1975, Dalvi et al. 1985b, Singh and Rana 2004, Karthikeyan 2007), however leaf rolls may have some implications for such control measures. The case of the rice leaf folder, *Cnaphalocrocis medinalis* Guen (Lepidoptera: Pyralidae) illustrates this: the animals are hidden and are not directly exposed to the chemicals, and it was advised that leaf folds be opened up with the help of a thorny twig prior to pesticide application (Sheela et al. 2007).

While most imatidiines are exposed feeders (Bondar 1940), adults of the 2 *Imatidium* Fabricius species reported by Gilbert et al. (2001) partially overlap and glue together leaves of their host, *Inga marginata* Willd. (Fabaceae). The source of the glue is unclear. *Imatidium* larvae and pupae occur on exposed surfaces of leaves. In contrast, *Leptispa* larvae and pupae are invariably hidden inside the leaf rolls that form naturally in response to feeding. The differences in construction modes, life stages involved, host plants, and end-product architecture suggest that shelters produced by the Imatidiini and Leptispini are not related by a common ancestry, i.e., they are not homologous. The 2 tribes are only distantly related (Chaboo 2007). We propose different terminology - leaf rolls for the Leptispini and leaf-case shelters for the Imatidiini - that reflects this lack of homology between leaf usage by imatidiines and leptispines. The active construction of leaf shelters is also distinct from the use of cocoa-leaf debris (Sterculiaceae: *Theobroma cacao* Linnaeus) as shelters on *Heliconia* Linnaeus plants (McCoy 1984 1985) or the better-known cassidine invasion of rolled leaves of the plant order Zingiberales (e.g., Maulik 1937, Seifert 1975, Seifert and Seifert 1976, Strong 1977, Chaboo 2007 and citations therein).

Leptispa pygmaea appears to take advantage of a particular property of rice leaves. Rice is highly sensitive to water stress and is one of the few agricultural crops cultivated under water-logged conditions. Rice leaf blades begin rolling up immediately on excision or under conditions of water stress, and the rolled-up excised leaves unfurl when immersed in water. *Leptispa* larvae and adults feed by scraping, producing linear scars on the leaves (Figs. 3-9). We propose that this damage and consequent loss of water on the adaxial surface of the leaf lamina is the plausible driving force that leads to leaf rolling. Adult leaf rolls are insignificant compared to that of the larvae. Successful larval feeding invariably leads to the formation of leaf rolls while adult feeding, especially brief feeding by solitary individuals, does not always result in the rolling of leaves. The sedentary nature coupled with an active feeding habit might explain the success of larvae in leaf rolling compared to adults. Another probable reason is the difference in behavior: larvae always begin feeding from the base of the lamina, where the leaf is already curled, while adults have no such preference. Insects that feed on the abaxial surface (e.g., Lepidoptera: Pyralidae: rice case worm, *Nymphula depunctalis* Guen.) or by cutting the leaf lamina (e.g., Lepidoptera: Satyridae: *Melanitis* sp.) generally do not induce rolling in rice. On the other hand, the rice thrips, *Baliothrips biformis* (Bagnall) (Thysanoptera: Thripidae), which feeds on the adaxial surface, does induce dorsad curling of the rice leaf; in young infested plants, leaf tips roll up after feeding damage and form leaf rolls in which all stages live (Nair 1970 1978, Nugaliyadde and Heinrichs 1984). *Leptispa* apparently expends little energy on cutting, bending, and tying rice leaves, or on glue or silk to hold the leaves together. The shelters on rice follow naturally from *Leptispa*'s feeding action. Thus, *Leptispa* leaf rolls appear to be an ideal example of cost-effective shelter building.

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