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Oviposition Patterns of Asian Phytophagous Ladybird Beetles (Coleoptera, Coccinellidae, Epilachninae)

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ABSTRACT The oviposition patterns of seven *"Epilachna"*, one *Afidenta* and three *"Henosepilachna"* species from Indonesia and Japan were examined and compared with those of 10 Asian species of epilachnines previously documented. The 21 species were divided into two groups based on the patterns. The first group consisted of twelve *"Henosepilachna"* species and *Afidenta misera*, and the other one consisted of eight *"Epilachna"* species. The former group laid several to dozens of eggs in an erect position and in mass on the underside of host leaves. On the other hand, the oviposition pattern of the latter group was diverse. They laid eggs singly, or up to ten plus eggs together, on the leaf surface or in tendrils of host plants. Eggs were usually not erect, but flat on host leaves, or were attached to or inserted into tendrils. The possible relevance between the oviposition patterns and the abundance of epilachnine species in the field was briefly discussed.

Key words: Epilachninae / Asia / oviposition pattern / *Epilachna* / *Henosepilachna* / *Afidenta*

Phytophagous ladybird beetles of the subfamily Epilachninae (Coleoptera, Coccinellidae) are diversified in the tropics and subtropics worldwide (Dieke, 1947; Li & Cook, 1961; Liu, 1965; Gordon, 1975; Pang & Mao, 1979; Fürsch, 1990, 1991). Indonesia is one of many countries with a rich fauna of Epilachninae (Dieke, 1947; Bielawski, 1959; Fürsch, 1959; Gunst, 1957). We collected 26 species from only West Sumatra and West and East Java from 1981 to 1998 (Katakura *et al.*, 2001). Such diversity enables comparative studies of both taxonomic and ecological characters that contribute to clarify phylogenetic relationships. Katakura *et al.* (1994) divided 22 Asian species into three groups based on the conditions of bursa copulatrix and spermatheca, and modes of sperm transfer, and suggested that their group 2 (*Epilachna admirabilis*, *E. decipiens* and related species) and group 3 (*E. orthofasciata*, *E. gedeensis* and their relatives) are phylogenetically more closely related to each other than they are to group 1 (the species belonging to *"Henosepilachna"*). As a

succession to Katakura *et al.* (1994), we will herewith describe the oviposition patterns of eleven species of epilachnines distributed in Indonesia and Japan.

Oviposition patterns have already been reported for 14 species of Asian Epilachninae (Takahashi, 1932; Katakura, 1976, 1981, 1988; Nakamura, 1983; Nakamura *et al.*, 1984, 1995; Abbas *et al.*, 1985; Nakano *et al.*, 2001). Except for *Epilachna admirabilis* reported by Takahashi (1932), however, all the above species belong to *"Henosepilachna"* (for the classification system and species codes used in the present paper, see Katakura *et al.* (2001)). In the present study, we newly examine the oviposition patterns of seven *"Epilachna"* (*Epilachna alternans*, *E.* sp. G, *E. orthofasciata*, *E.* sp. K, *E. chinensis*, *E. gedeensis*, and *E. incauta*), one *Afidenta* (*A. misera*) and three *"Henosepilachna"* species (*E. boisduvali*, *E.* sp. 5, and *E. pytho*), and compared them with those of previously reported species. Furthermore, we will briefly discuss the possible relevance between oviposition patterns and the abundance of epilachnine species in the field.

MATERIALS AND METHODS

The oviposition patterns of eleven species were examined from 1993 to 1999 in the field and/or by maintaining adults with their host plants in the laboratory. When the taxonomic identity of eggs or larvae observed under field conditions was ambiguous, we reared them to adulthood for identification. Rearing was carried out at the Guest House of the Bogor Botanical Gardens for Javanese species, the laboratory of Andalas University for Sumatran species, and the laboratory of Hiroshima Shudo University for Japanese species. Rearing of Indonesian species was done under a relatively constant temperature (27-30°C) and natural day length (12L12D) from 1996 to 1998, and under a constant temperature (23.5°C) and 12L12D conditions in 1999, while that of Japanese species was performed under a constant temperature (23.0°C) and 16L8D conditions.

RESULTS

1) *Epilachna boisduvali* (*"Henosepilachna"*)

This species lays eggs in an erect position and in mass on the underside of host leaves (cf. Fig. 1).

Six first instar larvae were collected next to the hatched shells of an egg mass on a leaf of *Mukia javanica* (Cucurbitaceae) at Sukarami, about 20 km south of Solok, West Sumatra on August 18, 1998. Also, an egg mass consisting of 27 eggs was collected on another host plant, *Diplocyclos palmatus* (Cucurbitaceae) on Amami Island, Kagoshima Pref., southern Japan on May 2, 1993. Under laboratory conditions, one female kept together with one male laid 26, 33, 14 and 15 eggs in mass on August 21, 23, 25 and 27, 1993, respectively.

2) *Epilachna* sp. 5 (*"Henosepilachna"*)

This species also lays eggs in an erect position and in mass on the underside of host leaves.

One egg mass consisting of 20 eggs and one adult female were collected on the same individual of a host plant (unidentified species of Acanthaceae) at Mt. Rasam, 40 km southeast of Padang, West Sumatra on May 8, 1999. The female subsequently laid three egg masses consisting of 22, 8 and 9 eggs on May 10, 18 and 28, respectively, in the laboratory.

Figs. 1-4. Eggs of four *Epilachna* species (scales not settled). 1: egg mass of *Epilachna boisduvali* (*"Henosepilachna"*) on the underside of a leaf of the blue cohosh, *Caulophyllum robustum*; 2: eggs of *Epilachna orthofasciata* (*"Epilachna"* Group 3) along the midrib on the underside of a leaf of *Saurauia* sp.; 3: eggs of *Epilachna alternans* (*"Epilachna"* Group 1) inserted into a tendril of a cucurbit, *Schizopepon bryoniaefolius*; 4: eggs of *Epilachna* sp. G (*"Epilachna"* Group 2) scattered on the underside of a leaf of *Clematis* sp. (three of the eggs are indicated by arrows).

3) *Epilachna pytho* (*"Henosepilachna"*)

This species, too, lays eggs in an erect position and in mass on the underside of host leaves.

Hatched shells of an egg mass and 21 first instar larvae feeding near the egg shells were collected on *Gynostemma pentaphyllum* (Cucurbitaceae) at Air Sirah, a suburb of Padang, West Sumatra on April 27, 1999. Furthermore, one adult female, which was collected on *Trichosanthes tricuspidata* (Cucurbitaceae) at Air Sirah on April 27, 1999, laid 27, 22, 24, and 15 eggs in mass on April 30, May 11, 18, and 23, respectively, under laboratory conditions.

4) *Epilachna alternans* (*"Epilachna"* Group 1)

This species lays eggs singly, or in a loose mass consisting of only a few eggs, usually in tendrils (cf. Fig. 3) but rarely on leaves. Eggs do not take an erect position, but lie flat on host leaves or are attached to or inserted into the tendrils of host plants.

Six eggs were collected on *Mukia javanica* (Cucurbitaceae) at Sukarami, West Sumatra on August 18 and 21, 1998, together with three larvae near the eggs and an adult. The eggs were laid at tendrils singly (one case), or in small groups consisting of two or three eggs (one case each).

Five adults (sex not confirmed) were collected on *Gynostemma pentaphyllum* (Cucurbitaceae) at Mt. Rasam, West Sumatra on August 31, 1997, and were kept in a group in the laboratory. They laid three, two, and six eggs in small masses in three different tendrils, and one egg lying flat on the underside of a leaf on September, 3. One egg, and four and two eggs in a group in tendrils, and one egg lying flat on the underside of a leaf, were also found on September 10, 1997.

One egg lying flat on the upside of a leaf of *G. pentaphyllum* was collected at Mt. Rasam on October 20, 1999. Although we did not succeed in rearing this individual to adulthood, it was probably *E. alternans* since only this species had been collected on *G. pentaphyllum* from this location.

5) *Epilachna* sp. G (*"Epilachna"* Group 2)

The oviposition pattern of this species is diverse. The female usually lays eggs singly (Fig. 4), or in a loose mass consisting of a few eggs, on host leaves. Eggs take an inclined position or lie flat on host leaves, but rarely take an erect position.

One female adult collected on *Clematis* sp. (Ranunculaceae) at Cibodas, a suburb of Bogor, West Java on September 6, 1997, laid twelve eggs on the underside of two *Clematis* leaves on September 6-8, and four, three, and two eggs on the underside of leaves on September 10, 12-13, 14-15, respectively. Eggs were scattered and did not form a mass.

Eggs were collected from nine leaves of *Clematis* sp. at Situ Gunung, a suburb of Bogor, West Java, on July 11, 1999. The number, positions and sites of eggs on each of the nine leaves were as follows (except for eggs on the upside of a leaf No.1, all eggs were on the underside of leaves): 1) one egg lying flat beside the midrib; 2) one hatched egg shell standing beside the midrib; 3) two hatched egg shells attached to each other lying flat beside the vein; 4) six eggs attached to each other and two eggs attached to each other both lying flat near the apex of a blade; 5) one egg in an inclined position between veins; 6) two hatched egg shells, close but not attached to each other, in an inclined position near the midrib; 7) one hatched egg shell lying flat beside the midrib; 8) one hatched egg shell in an inclined position beside the vein; 9) one egg in an inclined position at the leaf edge. We unfortunately failed to rear hatched larvae to adulthood, but it is likely that these eggs were also laid by *E.* sp. G, because three pupae collected near the above nine leaves grew to *Epilachna* sp. G adults.

6) *Epilachna orthofasciata* (*"Epilachna"* Group 3)

This species lays eggs singly (Fig. 2), in a line, or in a loose mass of a few eggs on host leaves. Eggs lie flat on host leaves or are attached to or inserted into the tendrils of host plants.

Eggs were collected on seven leaves of *Saurauia* sp. (Actinidiaceae) at Sukarami, West Sumatra on August 19, 1998. They were laid at the edges of leaves or along the veins, and they lay flat at the leaves. The number of eggs laid on each leaf was two (close together at the edge on the underside of a leaf), six (lined along the leaf edge, underside), one (at the edge, underside), two (close together beside the midrib, underside), one (along the midrib, underside), one (at the edge, underside), and one (at the edge, upside).

Egg shells and the first to fourth instar larvae were collected on an unidentified species of Vitaceae at Pinang Pinang, Ulu Gadut in Padang, West Sumatra on August 26, 1998. Shells were laid in tendrils. The numbers of eggs laid in respective tendrils were five (two and three in each winch), four, eight (one, three, two, one, and one in each winch), and four.

7) *Epilachna* sp. K (*"Epilachna"* Group 3)

This species laid eggs in a line or singly on the host leaves under laboratory conditions. No information was available for the oviposition of this species in the field.

Three females collected on *Cissus modesta* (Vitaceae) in Bogor, West Java on October 10, 1999, laid eggs in the laboratory. All the eggs were laid on minute slits formed between sheets of tissue paper placed in the rearing cage, and lay flat on the tissue paper. Female no. 1 laid fifteen and two eggs on October 16, and two eggs on October 24. Eggs laid during the first oviposition were close together and lined up, while those in the second one were scattered. Female no. 2 laid fourteen and four eggs on October 24, and these eggs were also close together. Female no. 3 laid one egg each on October 18 and 22.

8) *Epilachna chinensis* (*"Epilachna"* Group 3)

This species also lays eggs in a line or singly.

Adults were collected on *Paederia scandens* (Rubiaceae) at Izuhara, Tsushima Island, Nagasaki Pref., Western Japan in early September, 1993. Under laboratory conditions, eleven females laid a total of 611 eggs (8.1 eggs/female/day) in minute spaces between stipules and leaf axils of *P. scandens,* or between sheets of tissue paper placed in the rearing cage. Of these, 18 eggs were laid singly, while the others were lined in small groups consisting of up to 19 eggs (90.6 % of these egg groups consisted of two to ten eggs, and the rest had between 11 to 19 eggs) (Nakano, unpubl.). All eggs lay flat on the substrate.

9) *Epilachna gedeensis* (*"Epilachna"* Group 4)

This species scattered single eggs on the underside of host leaves and in flowers under laboratory conditions.

Several adults were collected on *Elatostema acuminata* (Urticaceae) at the foot of Mt. Gede, a suburb of Bogor, West Java in early September, 1997. They laid one or two eggs everyday on the underside of leaves and in the flowers of their host plants.

10) *Epilachna incauta* (*"Epilachna"* Group 4)

This species scattered single eggs on the underside of host leaves. It feeds on several species of Urticaceae, including *Boehmeria macrophylla*, *Villebrunea* sp., *Debregeasia wallichiana*, Urticaceae sp. 1, and sp. 2. (Katakura *et al.*, 2001; Nakano, unpubl.).

Four eggs laid on the underside of a leaf of *Boehmeria macrophylla* were collected at Air Sirah, West Sumatra on May 11, 1999. Eggs were scattered and lay flat on the underside of the leaf.

One egg each from two leaves of *Debregeasia wallichiana* was collected at Sukarami, West Sumatra on August 17, 1998. Both eggs lay flat along the midrib of the underside of the leaves.

In the case of Urticaceae sp. 1, one egg was deposited along the vein of the underside of a leaf at Sukarami on August 17, 1998.

Eggs were observed on the underside of five leaves of Urticaceae sp. 2 at Sukarami on August 17, 1998. The number of eggs and the oviposition sites on respective leaves were one (at the edge of leaf), one (at the edge), one (between veins), two (one at the edge and another along the midrib), and one (along the midrib).

Table 1. Oviposition patterns of 20 species of Asian *Epilachna* and one species of *Afidenta*.

Species [1]	Taxonomic group [2]	Distr.[3]	Oviposition			Ref. [6]
			Type [4]	Site [5]	Egg position	
*E. vigintioctopunctata**	H	I, J	Mass	Leaf (UD)	Erect	a, b
*E. pusillanima**	H	I, J	Mass	Leaf (UD)	Erect	c, d
*E. septima**	H	I	Mass	Leaf (UD)	Erect	c
E. sp. 3	H	I	Mass	Leaf (UD)	Erect	e
E. sp. 5	H	I	Mass	Leaf (UD)	Erect	PS
E. pytho	H	I	Mass	Leaf (UD)	Erect	PS, f
E. boisduvali	H	I, J	Mass	Leaf (UD)	Erect	PS
*E. enneasticta**	H	I	Mass	Leaf (UD)	Erect	e
*E. pustulosa**	H	J	Mass	Leaf (UD)	Erect	g
*E. niponica**	H	J	Mass	Leaf (UD)	Erect	h
*E. yasutomii**	H	J	Mass	Leaf (UD)	Erect	i
*E. vigintioctomaculata**	H	J	Mass	Leaf (UD)	Erect	b
E. alternans	E(1)	I	Single/loose mass	Tendril/leaf (UP,UD)	Lying flat/inclined	PS
E. admirabilis	E(1)	J	Single/loose mass	Tendril/leaf (UD)	Inclined	b
E. sp. G	E(2)	I	Single/loose mass	Leaf (UD, UP)	Erect/lying flat/inclined	PS
E. orthofasciata (S)	E(3)	I	Single/loose mass	Leaf (UD, UP)	Lying flat	PS
E. orthofasciata (V)	E(3)	I	Single	Tendril	Inclined	PS
E. sp. K	E(3)	I	Single/on a line+	Minute space	Lying flat	PS
E. chinensis	E(3)	J	Single/on a line+	Minute space	Lying flat	PS
E. gedeensis	E(4)	I	Single+	Leaf (UD)/in flower	Lying flat	PS
E. incauta	E(4)	I	Single	Leaf (UD)	Lying flat	PS
*Afidenta misera**	AF	I	Mass	Leaf (UD)	Erect	PS

1) * Pest species; S, population on *Saurauia*; V, population on Vitaceae.

2) H, "*Henosepilachna*" ; E(1), "*Epilachna*" Group 1; E(2), "*Epilachna*" Group 2; E(3), "*Epilachna*" Group 3; E(4), "*Epilachna*" Group 4; AF, *Afidenta*.

3) Distribution: I, Indonesia; J, Japan.

4) + observed in laboratory.

5) UD, underside of leaf; UP, upside of leaf.

6) PS, present study; a, Abbas *et al.* (1985); b, Takahashi (1932); c, Nakamura *et al.* (1984); d, Nakano & Katakura (1999); e, Nakamura *et al.* (1995); f, Nakano *et al.* (2001); g, Katakura (1976); h, Nakamura (1983); i, Katakura (1981).

11) *Afidenta misera*

This species lays eggs in an erect position and in mass on the underside of host leaves.

Egg masses, consisting of a few dozens of eggs, were collected on *Desmodium* sp. (Leguminosae) in Bogor, West Java on September 4, 1996.

DISCUSSION

Table 1 summarizes the oviposition patterns of 21 Asian epilachnine species clarified by the present and previous studies. These species are divided into two groups on the basis of oviposition patterns. The first group consists of twelve *"Henosepilachna"* species and *Afidenta misera*, and the other one consists of eight *"Epilachna"* species. The former group lays several to dozens of eggs in an erect position and in mass on the underside of host leaves (Fig. 1). Two other species of *"Henosepilachna"* (*Epilachna cucurbitae* and *E. vigintisexpunctata*) also belong to this group judging from their oviposition patterns reported for Australian populations (Richards & Filewood, 1988, 1990). On the other hand, the oviposition pattern of the latter group is diverse. They lay eggs singly (Fig. 4), or lay a

few to ten plus eggs together (Figs. 2, 3), on the leaf surface (Figs. 2, 4) or in tendrils (Fig. 3) of host plants. Eggs usually do not take an erect position, but lie flat on host leaves or are attached to or inserted into tendrils. They also lay eggs in minute spaces of tissue papers under laboratory conditions.

Except for *E. orthofasciata* and *E. alternans*, all the species listed in Table 1 seemed to have species-specific oviposition sites. However, the case of *E. alternans* described above indicates that at least some *"Epilachna"* species can change oviposition sites according to the morphology of their host plants. Oviposition sites of *E. orthofasciata* are also different between populations on *Saurauia* (Actinidiaceae) and those on Vitaceae, but these two populations may represent two closely related species (Katakura *et al.*, 2001), and thus the observed difference might be species-specific characteristics.

Oviposition in tendrils was observed in *E. admirabilis* and *E. alternans* (*"Epilachna"* Group 1) on Cucurbitaceae, and *E. orthofasciata* (*"Epilachna"* Group 3) on Vitaceae. This suggests a parallel evolution of this oviposition habit in the two different lineage of epilachnines. On the other hand, the fact that 12 *"Henosepilachna"* and one *Afidenta* species showed the same oviposition pattern could be interpreted as either an independent parallelism, or the sharing of an apomorphic trait.

Based on the conditions of bursa copulatrix and spermatheca, and modes of sperm transfer, Katakura *et al.* (1994) divided 22 Indonesian and Japanese species into three groups. They suggested that groups 2 (species originally referred as belonging to the *Epilachna admirabilis* species-group and *E. chapini* group; corresponding to *"Epilachna"* Groups 1 and 2 in the present study, see Katakura *et al.*, 2001 and Table 1) and 3 (referred to the *E. flavicollis* group and *E. fallax* group; corresponding to *"Epilachna"* Groups 3 and 4 in the present study) are phylogenetically more closely related to each other than they are to group 1 (*"Henosepilachna"*). The results of the present study are consistent with this view, because overall difference of oviposition patterns is much larger between *"Henosepilachna"* and *"Epilachna"* species than among the species-groups of *"Epilachna"*.

The results of the present study may explain why some species of epilachnines are extremely abundant while others are rather rare. Eight out of 12 species of *"Henosepilachna"* in Table 1 and *Afidenta misera* are pests of crops or have high density local pest populations in the field (Katakura, 1981; Nakamura, 1983; Katakura *et al.*, 1988, 2001; Shirai, 1990; Shirai & Morimoto, 1997; Nakano & Katakura, 1999). The information available suggested that laying eggs in mass results in higher fecundity. Pest and non-pest species of "*Henosepilachna*" laid much larger numbers of eggs than "*Epilachna*" in a given time under laboratory conditions as follows (the number of eggs laid per female per week; Nakano, unpubl.; Mitsuyama & Katakura, unpubl.):

"Henosepilachna": *E. vigintioctopunctata,* 151.3 (N=2); *E. enneasticta,* 72.5 (N=16); *E.* sp. 3, 80.4 (N=3); *E. pytho* 55.5 (N=18).

"Epilachna": *E. admirabilis*, 38.5 (N=7); *E. chinensis*, 34.0 (N=1); *E. incauta,* 11.1 (N=1).

In addition to the condition that many *"Henosepilachna"* species occur on the two plant families Solanaceae and Cucurbitaceae, which include various important crops and weeds (Katakura *et al.*, 2001), therefore, laying eggs in mass seems to be an important factor in maintaining high population density. Furthermore, low fecundity coupled with scattered egg laying and preferences for particular sites (such as tendrils) for oviposition may partly explain the extremely low density of immature individuals under field conditions in some Indonesian *Epilachna* (Katakura *et al.*, 2001).

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中野　進，片倉晴雄，Idrus Abbas, Sih Kahono，中村浩二　　アジア産食植性テントウムシ（甲虫目，テントウムシ科，マダラテントウ亜科）の産卵パターン

インドネシアと日本産の11種のマダラテントウの産卵パターン（卵の数と産み方，産卵場所，卵の付着場所）を調べ，これまで報告されている10種のマダラテントウの結果とあわせて検討を行った。

合計21種（"*Henosepilachna*" 12種，"*Epilachna*" 8種，*Afidenta* 1種）のマダラテントウは卵数と産み方により，以下の２グループに分かれた。すなわち，"*Henosepilachna*" の12種と *Afidenta* の1種は全てが直立した卵を十数個から数十個，卵塊として食草の葉の裏に産みつける。一方，"*Epilachna*" ８種の産卵パターンは多様であり，一個一個別々か，数個から十数個の卵をまとめて葉の表面に寝かせたり傾けて産卵するか，あるいは，食草の巻きひげのコイルの内側に付着させた。"*Epilachna*"は飼育条件下では二枚重ねのティッシュペーパーのせまい隙間にも産卵した。

これらの21種には9種の農作物害虫が含まれるが，そのうち８種は "*Henosepilachna*" である。"*Henosepilachna*" の多くの種の食草が重要作物を含むウリ科とナス科であることに加え，卵塊産卵であるために "*Epilachna*" と比較して単位時間あたりの産卵数が多いことが，"*Henosepilachna*" が頻繁に害虫をうみだしている理由の一つであると考えられる。