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EXPLOITATION OF FOOD BODIES ON *MACARANGA* MYRMECOPHYTES BY LARVAE OF A LYCAENID SPECIES, *ARHOPALA ZYLDA* (LYCAENINAE)

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ABSTRACT. Larvae of *Arhopala zylda* (Lycaenidae) feed on food bodies (FBs) produced by two *Macaranga* (Euphorbiaceae) myrmecophytic species, *M. beccariana* and *M. hypoleuca*. We examined their feeding behavior in detail via field observations and rearing experiments in the field and laboratory. Larvae of *A. zylda* fed only on FBs and not leaves during the first through third instars; during the fourth (final) instar, they ate both FBs and leaves of the host plants. The larvae actively fed on FBs on young leaves, which were always attended by many plant symbiotic ants. These results suggested that *A. zylda* larvae depend entirely on FBs for food, except late in the final instar, and that the FB-feeding habit is associated with special traits that enable the larvae to evade ant aggression, which usually functions as an effective anti-herbivore defense for the host plants.

Additional key words: ant–plant interactions, Borneo, *Crematogaster* ants, larval growth, myrmecoxeny

Myrmecophytes are plants that have symbiotic associations with specific ant species, for which they provide nesting space, called domatia (Davidson & McKey 1993). In return, the symbiotic ants (plant-ants) protect them against herbivores, fungal pathogens, and plant competitors (reviewed by Heil & McKey 2003; Heil 2008). Some myrmecophytes also provide their plant-ants with cellular food bodies (FBs) on the plant surface at leaf tips, stipules, and/or stems (e.g., Janzen 1974; Rickson 1980; O'Dowd 1982; Heil et al. 1997). In addition, some non-myrmecophytic species provide FBs to attract ants to protect them (e.g., Webber et al. 2007; Paiva et al. 2009). FBs contain nutrients for the ants, such as lipids, carbohydrates, and proteins (Janzen 1974; Rickson 1976; Heil et al. 1998, 2004; Hatada et al. 2002). Usually plant-ants on myrmecophytes that produce FBs harvest the FBs as their main food and intensively protect newly-produced FBs (e.g., Rickson 1980; O'Dowd 1982; Fiala & Maschwitz 1990); herbivores that attempt to access the FBs would be aggressively attacked by the ants. Probably because of such anti-herbivore behavior, only a few non-ant FB-feeding insects have been recorded so far (e.g., Letourneau 1990; Jolivet 1996; Itino & Itioka 2001; Roux et al. 2011).

The paleotropical plant genus *Macaranga* Thou. (Euphorbiaceae) includes many myrmecophytic species that produce FBs for their plant-ants (Davidson & McKey 1993; Fiala et al. 1999; Davies et al. 2001). In some *Macaranga* myrmecophytic species, the relationship between the plants and ants are so obligate that neither can survive without the other, and the symbioses are maintained throughout most of both life cycles (Fiala & Maschwitz 1990; Heil et al 2001). In such obligate partnerships, FBs are continuously patrolled and collected by the plant-ants (Fiala & Maschwitz 1990).

On the Malay Peninsula and Borneo, four *Arhopala* lycaenid species were recorded to feed on several *Macaranga* myrmecophytes that have obligate associations with their specific plant-ants (Maschwitz et al. 1984; Okubo et al. 2009). Of the four *Arhopala* species, only larvae of *Arhopala zylda* Corbet, 1941 feeds not only on leaves but also on FBs of two closely-related myrmecophytes, *M. beccariana* Merr. and *M. hypoleuca* (Reichb. f. & Zoll.) Müll. Arg. despite intensive defense for FBs by plant-ants. Larvae of *A. zylda* have myrmecoxenous traits; they can evade anti-herbivore defenses of the plant-ants without being attended by the ants and without providing honeydew

to tame them (Shimizu-kaya et al. 2013). The larval period comprises four instars. For additional details of *A. zylda* development, see Okubo et al. (2009).

The plant-ant of the both *M. beccariana* and *M. hypoleuca* is *Crematogaster decamera* Forel (Fiala et al. 1999; Itino et al. 2001). Plant seedlings are usually colonized by foundress queen ants when they reach approximately 10 cm in height (Murase et al. 2002) and start FB production at almost the same time (Fiala & Maschwitz 1992; Hatada et al. 2002). The leaves of both plant species are three-lobed, and FBs are produced on the abaxial surfaces of developing leaves along the veins and midrib (Fig. 1). Usually, the first, second, and sometimes third leaves from the plant apex bear such FBs. As leaves mature, they produce fewer FBs. Full-sized leaves bear very few FBs, even when they have not fully thickened (hereafter, we refer to these unhardened young leaves as "developed young leaves").

Foundress plant-ant queens brood their workers inside the hollow stems. After the adult workers emerge, they constantly patrol the aboveground plant surfaces, especially leaves at the plant apex (Itioka et al. 2000). The ant colony grows with the host plant (Itino et al. 2001, Handa et al. 2013), but the ratio of ant-to-plant biomass peaks around the time the plant starts branching in *M. beccariana* (Handa et al. 2013), usually when the plant is 2.0–2.5 m tall. Thereafter, the plant-ant worker density on the host-plant surfaces decreases noticeably as the host plant grows (I. T. pers. obs.).

To our knowledge, *A. zylda* is the only known FB-feeding insect species that can feed on myrmecophyte FBs while the plant-ants are present. To better understand the ecology and evolution of this parasitism on myrmecophytism, the characteristics of FB-feeding by *A. zylda* larvae should be elucidated. In this report, we described the FB-feeding behavior of *A. zylda* with special reference to the degree to which the larvae depend on FBs. We observed larval behavior in the field and reared larvae in both the field and laboratory.

MATERIALS AND METHODS

Our study was conducted in the primary lowland mixed dipterocarp forest of Lambir Hills National Park, Sarawak, Malaysia (4°2'N, 113°50'E, 150–200 m asl), from 2006–2012. The main habitats of the two *Macaranga* species were riversides, forest gaps, and forest edges.

We randomly searched for *A. zylda* immatures on *Macaranga* saplings that were 0.5–4.0 m in height. We found 131 larvae and six pupae on approximately 130 saplings of *M. beccariana* and *M. hypoleuca* in the field. For 73 of those saplings, which together hosted 75 larvae and two pupae, we recorded the characteristics of the saplings, such as height and number of leaves; the presence/absence of plant-ants; damage levels, including herbivory to leaves and non-herbivory damage due to tree-fall, litter-fall, and flooding; and the positions of the *A. zylda* larvae on the saplings. For the other saplings, with 56 larvae and four pupae, we recorded only the within-plant positions of the *A. zylda* larvae.

Three second- or third-instar (mid-instar) *A. zylda* larvae were reared in the field until the pupal stage to observe their feeding behavior and development times. These larvae were introduced onto randomly-selected *M. hypoleuca* saplings of about 1.5 m in height. These saplings were unbranched, colonized by plant-ants, and with almost no obvious herbivory damage. Each larva was placed onto the third apical leaf using forceps. After the introduction, we netted the sapling with mesh nylon (#9000 Honeyqueen: Toray Industries, Tokyo, Japan) to exclude other herbivores (Fig. 2). We checked the growth of each introduced larva daily and observed their behavior for 20–60 min at least twice a day. We observed the three larvae a total of 203 times.

In parallel, we reared three similar larvae by feeding them individually with fresh FB-bearing leaves of *M. hypoleuca* in plastic containers (9 × 15 × 7 cm) in the laboratory to estimate their FB consumption during the third and fourth instars. We transplanted *M. hypoleuca* seedlings that were at most 20 cm high and inhabited by plant-ants from the field into a nursery at the study site. These seedlings were cultivated to provide FBs for the laboratory-reared larvae. Larvae of the final instar were reared on FB-bearing and developed young leaves collected from a sapling of approximately 1.5–2.5 m in height in the field or the nursery. We removed all plant-ants from these leaves and inserted the ends of their petioles into wet floral-arrangement sponges (Aquafoam; Matsumura Kogei Co., Osaka, Japan) just before feeding them to the larvae. We replaced each leaf with a fresh one and checked larval growth daily.

To estimate the fresh weight of consumed FBs, we classified FBs into four size classes based on naked-eye assessments of diameter: < 0.2 mm, 0.2–0.4 mm, 0.4–0.5 mm, and > 0.5 mm. We collected 108–213 FBs of each class from seven fresh leaves of five randomly-selected saplings (approximately 1.5–2.5 m in height) in the field and measured the fresh weights of each class. Based on this data, we estimated the mean weight of FB in each class. During the laboratory rearing, we recorded the number of FBs of each size class on each leaf before and after providing them to the larvae. Using the previously estimated mean FB weights, we could thus estimate the fresh weight of FBs that each larva consumed in a day. To estimate the amount of FBs on

FIGS. 1–5. **1.** A new leaf on apical part of a sapling of *Macaranga beccariana* and a third-instar larva of *Arhopala zylda* which rested on the leaf. The leaf bore food bodies, pearl-like particles, on the abaxial side of leaf surface. **2.** A sapling of *Macaranga hypoleuca* enclosed by nylon mesh use to rear a larva of *Arhopala zylda*. **3.** A damaged leaf of *Macaranga beccariana* on which a pupa of *A. zylda* was found. **4.** A fourth-instar larva of *Arhopala zylda* reared on a sapling of *Macaranga hypoleuca*. It was resting along the midrib of a new leaf. **5.** A pupa of *Arhopala zylda* on a sapling of *Macaranga hypoleuca*. It pupated on the petiole of a new leaf after being reared in the field.

leaves of *A. zylda* host plants in the field, we measured the fresh weight of all FBs on the apical parts of each of five randomly-selected saplings of *M. hypoleuca* (approximately 1.5–2.5 m in height).

Each reared pupa was kept in a plastic container (4 × 6 × 1.5 cm) with moistened tissue in the laboratory until adult emergence. The adults have been kept as voucher specimens and deposited at the Forest Research Centre, Sarawak, Malaysia; Kyoto University Museum, Japan; or Tokyo University Museum, Japan.

RESULTS

Field observations. All 73 host plants for which we recorded characteristics were inhabited by plant-ants. There was no damage due to herbivores or accidental disturbances on 86.3% of those plants. There was virtually no leaf loss due to herbivore chewing on any host-plant leaves with either first-, second-, or third-instar larvae (n= 52) nor on some plants hosting fourth-instar larvae (n = 7). On host plants harboring the other fourth-instar larvae or pupae (n = 14), several holes, inferred to be caused by *A. zylda* larvae, were found on one or two apical leaves (Fig. 3). The larvae frequently rested on the abaxial sides of new FB-bearing leaves (Fig. 1), while all pupae were found on petioles of young leaves.

Developmental durations of third- and fourth-instar larvae and pupae. The third and fourth instars of the larvae reared in the field lasted 8 days (n = 1) and 20–29 days (n = 3), respectively, and the pupal period ranged from 12–19 days (n = 3). In the laboratory, the third- and fourth-instar periods of the larvae reared on ant-excluded leaves with FBs were 10–11 days (n = 2) and 17–31 days (n = 3), respectively, and the pupal period lasted 12–21 days (n = 2).

Larval behavior. In the mid-instar stages, larvae that were reared on saplings in the field spent most of their time on the abaxial sides of new leaves along the midrib or veins. Each larva usually remained stationary, but moved from lobe to lobe of the leaf at least once per day. All the larvae that were reared in the laboratory also rested still along the midrib or veins of the provided leaves, except when they ate FBs or leaves, although they moved around the leaves every few hours.

We confirmed at least four times that the larvae reared in the field ate FBs similarly to those in the laboratory. There were no chewing marks on other plant parts, such as leaves, stipules, or stems at mid-instar. Within 1–7 days after they reached the final instar, the larvae first began to eat the developed young leaves. At this time, FBs remained on the saplings. Leaf-feeding was observed only around sunset and at night. Except when they ate leaves, they rested along the midribs or petioles of new leaves (Fig. 4). Both while stationary and while eating, the larvae were neither contacted nor attended by plant-ants on the saplings, even when the plant-ants walked nearby.

Larvae reared in the field ate leaves for a total of 7–11 days before pupation. During the first 3–7 days after initiating leaf feeding, the area of leaf loss to chewing increased daily. This period was followed by a 1–6 day break from leaf-feeding in which no new damage was observed. Then, the larvae resumed leaf-feeding, eating leaves daily until the prepupal stage, which entailed another break of 1–6 days. None of the larvae ate leaves for 1–3 days just before the prepupal stage. Each fourth-instar larva fed on two developed young leaves and consumed an area roughly equivalent to half of such a leaf. Whether they also ate FBs after they began to eating leaves is unknown. They pupated at the base of a petiole of a FB-bearing new leaf or a developed young leaf (Fig. 5).

Larvae reared in the laboratory were also observed to feed on FBs during the third and fourth instars. They preferred more developed FBs that were ≥ 0.4 mm in diameter and ate few small, undeveloped FBs. The fresh weight of FBs consumed per larva varied from day to day (Fig. 6), but was generally being less than the standing crop of FBs on the apical parts of the plant (3.5 ± 0.6 mg, n = 5). The average fresh weights of FBs consumed by a larva were 14.8 ± 1.1 mg (n = 2) and 22.6 ± 9.0 mg (n = 3) in the third and fourth instars, respectively. All three larvae ate only FBs during the initial 9–27 days after reaching the final instar, and they ate only developed young leaves during the 4–10 days just before becoming prepupae. Each larva consumed approximately half of a developed young leaf.

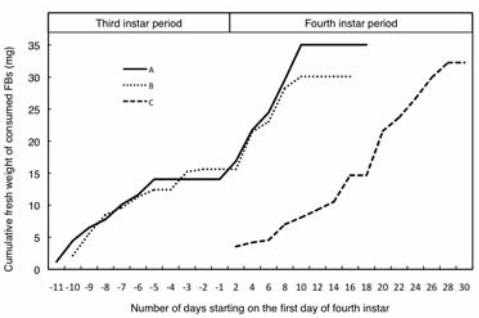

Fig. 6. Cumulative fresh weight of FBs consumed by each of the three *Arhopala zylda* larvae (A, B, C) reared in the laboratory during the third- and fourth- (final) instars. FB consumption of larvae A and B was estimated from the third instar until pupation, while it was estimated from the fourth instar through pupation for larva C. Fourth-instar estimates are plotted every 2 days.

Discussion

Our results for both field- and laboratory-reared larvae strongly suggested that second- and third-instar *A. zylda* rely completely on FBs of their host-plant species for food and that fourth- (final-) instar larvae eat both FBs and young leaves. We inferred that first-instar larvae also rely entirely on FBs, because they were almost always found on FB-bearing leaves with virtually no leaf loss due to herbivore chewing when observed in the field.

In addition to ants, at least five insect species are known to feed on FBs produced by myrmecophytes (Letourneau 1990; Jolivet 1996; Itino & Itioka 2001; Roux et al. 2011), and Ozawa & Yano (2009) reported that a predatory mite species eats the FBs of a non-myrmecophytic species. However, these non-ant arthropods use FBs opportunistically or secondarily and only on plants that have not yet been colonized by ants or when the plant-ant colony declines dramatically due to accidental damage to the host plant. In comparison, the feeding behavior of *A. zylda* larvae is quite remarkable, both because their survival and growth are completely dependent on FBs and because they feed on FBs on intact myrmecophytes harboring active plant-ant colonies that seem able to protect the host plants against other herbivores. The lack of larval interference by plant-ants is probably strongly associated with myrmecoxeny, a peculiar system of evading plant-ants (Fiedler 1991; Pierce et al. 2002) in *A. zylda* (Shimizu-kaya et al. 2013). The other *Arhopala* species that use *Macaranga* myrmecophytes as host plants do not eat FBs or possess myrmecoxenous characteristics.

Our results also suggested that feeding on leaves was necessary to complete larval development and to pupate. Interestingly, larvae late in the final instar tend to shift abruptly from FB to leaf feeding and seem to eat no leaves before the shift. Nutritive components necessary for completing larval growth are presumed to be included in fresh leaves but not in FBs.

Considering that caterpillars tend to prefer nitrogen-rich plants (Pellissier et al. 2012) and that FBs on *M. beccariana* and *M. hypoleuca* are nitrogen rich (Rickson 1980; Hatada et al. 2002), the FBs seem to be an excellent food compared to foliage, so the larval growth rate of *A. zylda* was expected to be higher than that of other *Arhopala* species that eat leaves of other *Macaranga* myrmecophytes. However, contrary to expectation, *A. zylda*'s growth rate was much lower than that of other species (Okubo et al. 2009; U. S. pers. obs.) with a much longer duration especially of the final instar. There are a few plausible explanations. First, FBs may lack nutrients essential for larval growth, as described above. The larval digestive system might also need time to the shift to its new diet during the final instar. Second, the costs of maintaining myrmecoxeny might prolong the growth period, even if FBs provide better nutrients. Of all the *Arhopala* species that feed specifically on *Macaranga* myrmecophytes, only *A. zylda* has a myrmecoxenous association with plant-ants (Shimizu-kaya et al. 2013). Third, *A. zylda* might experience a shortage of FBs throughout the larval period, thereby prolonging development. However, this hypothesis is refuted by our field observation that FBs of the preferred size were never exhausted by larval feeding. Further study is required to elucidate why the larval period is longer in *A. zylda* than in other congeneric species feeding on *Macaranga* myrmecophytes.

Leaf feeding during the final instar was different between larvae reared in the field and in the laboratory; intermittent leaf-feeding with a break was observed only in the field. Two factors could affect this difference. One is a possible reduction in plant chemical defenses under the laboratory conditions, in which the leaves had been cut from saplings. Secretory flow is eliminated when veins are cut, deactivating defensive secondary metabolites in some plant species (Dussourd & Denno 1991). If this were the case in our study, the cut leaves would be more suitable for larval growth than intact leaves in the field and allow the larvae in the laboratory to feed without breaks. Another possible explanation is ant attacks in the field. Because plant-ants of *Macaranga* myrmecophytes show aggressive behavior in response to host-plant volatiles released by leaf damage (Itioka et al. 2000, Inui & Itioka 2007), we can infer that leaf damage by chewing *A. zylda* larvae elicited ant attacks. To avoid or minimize these attacks, the larvae might need to suspend leaf feeding for a few days. Whether either or both factors caused the difference observed is a question to be addressed in future work.

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