Effects of host pupal age on host preference and host suitability in *Brachymeria lasus* (Walker) (Hymenoptera: Chalcididae)

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Abstract

The influence of host pupal age on host preference and host suitability in *Brachymeria lasus* (Walker) was examined. Rice armyworm, *Mythimma separata* (Walker), pupae of different ages, i.e., 0–1, 2–3, 4–5, 6–7 and 8–9 d old were used as hosts. The females accepted the host pupae equally for oviposition among 5 age groups, suggesting that female *B. lasus* does not discriminate hosts of different ages. However, the rate of progeny emergence was lower in old (6 to 9 d old) hosts. The adult parasitoid progeny produced from young (0 to 5 d old) hosts were heavier in body weight than those from old hosts. The developmental time of the immature stages of progeny was not significantly affected by host pupal age. Adult progeny with heavier body weight emerged earlier than lighter ones when reared on 0- to 5-d-old hosts. However, there was no correlation between the progeny body weight and developmental time of the immature stages when reared on 6- to 9-d-old hosts. Most of the progeny were females and no effect of host age was found on progeny sex ratio, which may be due to the low oviposition rate they experienced.

Key words: Host age, host suitability, *Brachymeria lasus*, Chalcididae, *Mythimna separata*

INTRODUCTION

Host factors such as age, size and physical defenses of the host interact with the reproductive ability of female parasitoids (e.g., Wylie, 1962, 1963, 1964; Chabora and Pimentel, 1966; Rotheray and Barbosa, 1984). Among these factors, host age affects host preference and host suitability of parasitoids (Vinson, 1976; Vinson and Iwantisch, 1980). Also, some species of parasitoids can control the sex ratio of their progeny in response to host age (e.g., Singh and Pandey, 1986; Islam, 1994; Ueno, 1997, 1999).

For idiobiont parasitoids, which paralyze the host permanently at oviposition, host age was shown to have a significant effect on offspring size compared to the koinobiont species (Ueno, 1997). Also, host age can have a greater effect on sex allocation by idiobiont than by koinobiont parasitoids, because host age is more important to the fitness of offspring in idiobionts (King, 1987, 1989).

*Brachymeria lasus* (Walker) is an idiobiont species and a polyphagous pupal parasitoid. Habu (1962) reported that *B. lasus* has a host range of more than 100 species of Lepidoptera, Hymenoptera and Diptera. *B. lasus* is widely distributed throughout the Pacific area, including Japan, Taiwan, China, the Philippines, Vietnam, India, Fiji and Hawaii (Husain and Agarwal, 1982). In Japan, *B. lasus* was reported as a potential biocontrol agent for the oriental tea tortrix, *Homona magnanima* Diakonoff (Mao and Kunimi, 1991, 1994).

Mao and Kunimi (1994) reported the longevity and fecundity of *B. lasus* and also showed that progeny sex ratio changed depending on maternal age, but the effects of host age on behavioral and developmental aspects were not examined. This study was performed to determine the effect of host pupal age on host preference and host suitability in *B. lasus*.

MATERIALS AND METHODS

Insects. *B. lasus* was originally obtained from pupae of the fall webworm, *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae) which were collected from the field, and reared continuously in our laboratory for more than six years on rice armyworm, *Mythimna separata* (Walker) (Lepidoptera: Noctuidae) pupae. Emerged adult para-

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sitoids were kept in a container (28×16×17 cm) at a density of 20 to 30 pairs and honey and water were provided. In this study, mated females (10–30 d old) which had experienced oviposition at arbitrary host density were used. At this age range, there was no significant change in fecundity and sex ratio (Husni and Kainoh, unpublished data), and also the longevity of females was ca. 130 days under similar rearing conditions (Mao and Kunimi, 1994). The host (M. separata) pupae were obtained from a stock culture and reared continuously on an artificial diet (Silk Mate®, Nihon Nosan Kogyo Inc.) according to the method of Kanda (1991). Both B. lasus and M. separata cultures were kept at 25±1°C, 60±20% RH and 16L:8D photoperiod. In order to obtain different ages of host pupae, newly pupated M. separata were collected daily and kept separately according to the following ages: 0–1, 2–3, 4–5, 6–7 and 8–9 d. Under these conditions, the developmental time of M. separata from pupation to adult emergence was 9–10 d.

**Host preference.** The preference of female wasps for host pupae of different ages was examined. A single female was released into the center of a cylindrical plastic container (15 cm in dia., 9 cm high) into which host pupae, one from each age group, were placed along the circumference, and the first and second attacks (= ovipositor drilling) by the wasp to host pupae were observed for 5 min, which was long enough for at least two attacks to occur. Fifty-three females were used for this experiment. Although we did not confirm the presence of eggs by dissection after the attack behavior, in a preliminary experiment, females attacked the hosts with their ovipositor and in most cases, even with 9-d-old pupae, oviposited in them.

**Host suitability.** The effect of host pupal age on the development of B. lasus progeny was evaluated. A host pupa of each age group was offered singly to a single female wasp in a plastic cup (7 cm in dia., 4 cm high). If the wasp did not attack the pupa within 5 min, the wasp was replaced with a new one. Each wasp used for a single oviposition to prevent superparasitism, and the pupae were kept individually in plastic cups until the progeny emerged. Forty female wasps were used for each treatment. The percentage of adult progeny emergence, sex ratio and developmental time of immature stage of progeny (from oviposition to adult emergence) were recorded. After anesthetizing with CO₂, each adult progeny emerged was weighed to clarify the correlation between developmental time of immature stage and adult body weight.

### RESULTS

**Host preference**

When a female B. lasus was released into the bottom of a container, she started walking randomly and, if she encountered a host pupa, she antennated and mounted the pupa, then walked on it before she started probing and drilling with the ovipositor. After probing and drilling for ca. 30 s, she left the pupa and started searching for a 2nd pupa.

The female B. lasus mounted and attacked (= with ovipositor drilling) host pupae of the 5 age groups equally, both at the first and second oviposition sequence (p>0.05, Table 1), suggesting that, at this stage of host selection, they did not discriminate among hosts of different ages.

**Host suitability**

The percentage progeny offspring was 70%, 68%, 50%, 44% and 40% for 0–1, 2–3, 4–5, 6–7 and 8–9 d host pupal ages, respectively (Fig. 1), decreasing gradually with increasing host pupal age (χ²=12.18, df=4, p<0.05). Twenty percent of 8- to 9-d-old pupae produced adult moths (Table 2) which escaped parasitism. Most progeny (88–100%) produced from all age groups of host pupae were females and there was no significant difference in the sex ratio between host pupal age groups (χ²=2.87, df=4, p>0.05; Table 2).

The developmental time of immature stages of

### Table 1. The percentages of first and second attacks on host pupae of different age groups by female B. lasus

<table>
<thead>
<tr>
<th>Pupal age (day)</th>
<th>First attack</th>
<th>Second attack</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–1</td>
<td>18.9</td>
<td>11.8</td>
</tr>
<tr>
<td>2–3</td>
<td>22.6</td>
<td>14.7</td>
</tr>
<tr>
<td>4–5</td>
<td>18.9</td>
<td>20.6</td>
</tr>
<tr>
<td>6–7</td>
<td>17.0</td>
<td>32.4</td>
</tr>
<tr>
<td>8–9</td>
<td>22.6</td>
<td>20.6</td>
</tr>
</tbody>
</table>

* Each host pupa of different age groups was offered to a single female in a choice test (n=53).

**Table 2**

<table>
<thead>
<tr>
<th>Pupal age (day)</th>
<th>Developmental time (d)</th>
<th>Proportion of pupae with parasitism (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–1</td>
<td>24</td>
<td>2.6</td>
</tr>
<tr>
<td>2–3</td>
<td>24</td>
<td>2.0</td>
</tr>
<tr>
<td>4–5</td>
<td>24</td>
<td>1.6</td>
</tr>
<tr>
<td>6–7</td>
<td>24</td>
<td>1.6</td>
</tr>
<tr>
<td>8–9</td>
<td>24</td>
<td>1.6</td>
</tr>
</tbody>
</table>

* Each host pupa of different age groups was offered to a single female in a choice test (n=53).
progeny was not significantly affected by host pupal age (Table 2, *p* > 0.05). The developmental time of female progeny was about 17 days, regardless of the age of the pupal host in which they were reared (Table 2). The data for developmental time of male progeny were excluded because only a few male progeny emerged.

On the other hand, there was a significant difference in body weight of adult progeny, which were produced from different age groups of hosts (Fig. 2, *p* < 0.01). The progeny produced from 6- to 9-d-old host pupae were significantly lighter in body weight than those produced from 0- to 5-d-old hosts. There was a correlation between the developmental time of immature stages of progeny and adult progeny body weight when the progeny were reared on 0- to 5-d-old hosts (Fig. 3; $r^2$ = 0.57; *p* < 0.001). However, there was no correlation between the adult body weight and developmental time of progeny reared on 6- to 9-d-old host pupae (Fig. 3; $r^2$ = 0.03). Progeny with heavier body weights emerged earlier than lighter ones when they were reared on 0- to 5-d-old host pupae.
DISCUSSION

The choice test showed that female *B. lasus* exhibited no preference for host pupal age groups, both at the first and the second oviposition sequence (Table 1). *B. lasus*, however, produced more offspring from younger (0 to 5 d old) hosts than from older (6 to 9 d old) ones (Fig. 1). These data showed that there were no cues which allowed the female wasps to discriminate hosts of different ages from a distance. Other parasite species, i.e., *Microcharophis anticarsiae*, a larval parasite of *Anticarsia gemmatalis* (Patel and Habib, 1993) and *Microplitis croceipes*, a larval parasite of soybean and corn pests (Harrison et al., 1993) also showed no preference for hosts of particular age and no host-age effect on host suitability.

In our preliminary experiments, one parasitoid larva was found from each host pupa, when the 0- or 9-d-old pupa was attacked by the female wasp (*n*-12) and those pupae were dissected 3 days later (Husni and Kainoh, unpublished). These results indicated that all the wasps laid eggs even into 9-d-old host pupae when they attacked, but some of the hatched larvae died (Fig. 1). Therefore, the adult wasp cannot discriminate between higher quality (young) hosts and lower quality (old) hosts and lays an egg each time it attacks. This behavior may appear disadvantageous, but the inability to discriminate may be adaptive in consideration of the low host densities in the field compared with egg or larval stages, since the acceptance of even a poor-quality host is always optimal under natural conditions when host encounter rate is low (Godfray, 1994).

Another possibility is that the females we used might have been limited to those that had only experienced hosts in low density. In our rearing conditions, *B. lasus* was given hosts at arbitrary intervals before the choice tests, which meant that they experienced low host density. The low host density experienced might influence host-age-specific preference of *B. lasus* and increase the threshold for detecting differences in host age, which resulted in an even rate of attack (Table 1). Similar choice tests with *B. lasus* experiencing higher host density should be carried out.

Lashomb et al. (1983) reported that old gypsy moth pupae were not preferred and not suitable for development of *Brachymeria intermedia*. Minot and Leonard (1976) considered that the reduced offspring emergence of *B. intermedia* from old wax moth pupae is due to the advanced development of host pupae. Our data also showed that 20% of 8- to 9-d-old *M. separata* pupae produced adult moths (Table 2), and parasitoid progeny emerged from only 40% of those hosts (Fig. 1). Chabora and Pimentel (1966) reported that *Nasonia vitripennis*, a pupal parasitoid of *Musca domestica*, produced more progeny on 2- to 5-d-old hosts while the older hosts had a high percentage of yielding neither fly nor parasitoid.

The offspring produced from young (0 to 5 d old) *M. separata* pupae were significantly heavier in body weight than those produced from old (6 to 9 d old) hosts (Fig. 2). The heaviest weight of a progeny wasp was 21 mg and the lightest was 5 mg; these were produced from 2-3- and 8-9-d-old hosts, respectively. Presumably, host age has an effect on nutrition supply for development of the parasitoid progeny, and old host pupae are not suitable for development of *B. lasus* progeny. Wylie (1963) reported that parasitoid *N. vitripennis* reared on old hosts were smaller, and that relatively fewer emerged, probably because of unsuitability of the food provided by old hosts. Wylie (1964) mentioned that the food was sucked from the young hosts more easily and thereby it was ingested at a greater rate than food in old hosts. Other parasitoid species, i.e., *Spalangia cameroni*, a parasitoid of house fly pupa (King, 1998); and *Pimpla nipponica* (Ueno, 1999) also developed to larger size when they were reared on younger hosts.

There are many advantages to the female wasps having a larger body size. For example, Ellers et al. (1998) reported that the larger females of a braconid, *Asobara tabida*, had higher fecundity, having more fat reserves, living longer and dispersing over larger distances than smaller females. In *B. lasus*, females with a larger body size derived from young hosts should also be favored during reproduction.

The developmental time of immature progeny of *B. lasus* showed no significant difference when they were reared on different ages of *M. separata* pupae (Table 2). The similar developmental time of *B. lasus* emerged from the young hosts of high quality and old ones of low quality may be due to...
the different developmental rate depending on the host quality. The larvae in young hosts grew faster and larger, whereas those in old hosts grew slower and smaller (Figs. 2 and 3). Consequently, the developmental times in the two conditions were similar. *B. lasus* larvae in old hosts with slow developmental rate that might prohibit completion of development within this period may die. In some of the idiobiont parasitoid species, i.e., *N. vitripennis* (Wylie, 1964), and *Dinarmus basalis* (Islam, 1994), it has been reported that the developmental time of the progeny varied with host age or host stadium.

Adult *B. lasus* progeny with heavier body weights emerged earlier than smaller ones when they were reared on young (0 to 5 d old) host pupae (Fig. 3). Similarly, larger progeny emerged earlier than smaller ones in several parasitoid species, i.e., *Aphidius sonchi* (Liu, 1985), *N. vitripennis* (Wylie, 1964), and *D. basalis* (Islam, 1994). Liu (1985) mentioned that variations in developmental time among *A. sonchi* progeny reared from the same host stadium might be caused by variations in host size. However, in the case of *B. lasus*, we used host pupae of similar size to exclude the effect of host size. We suspect that other characteristics of the hosts, e.g., nutritional condition, might affect the variation of developmental time and body weight of *B. lasus* progeny. Alternatively, variation in the developmental rate of *B. lasus* larvae might cause the difference, i.e., fast-growing larvae become larger in a shorter time and slow-growing larvae become smaller in a longer time. In *B. lasus*, further experiments are needed to clarify the host nutritional effect on parasitoid development.

The observations of sex ratio of *B. lasus* offspring showed no significant differences among different pupal age groups (Table 2). This result contradicts findings for some other pupal parasitoids, i.e., *Itoplectis naranae* (Ueno, 1997) and *P. nipponica* (Ueno, 1999), which change offspring sex ratio in response to host age. In the present study, we exposed each female wasp to a host pupa for oviposition only once a day, which was a low oviposition rate compared with the maximum number of progeny (ca. 6) they can produce in a day (Mao and Kunimi, 1994). The result that most of the progeny were females (Table 2) suggests that under the condition of low oviposition rate, *B. lasus* may produce a female-biased sex ratio and may not change the sex ratio of their progeny in response to the variation of host pupal ages. In a preliminary experiment with higher oviposition rate, the *B. lasus* progeny sex ratio was 56% (females, *n*=112). In *B. intermedia*, sex ratio was affected by some other factors, i.e., host size (Barbosa and Frongillo, 1979); age of parent parasitoid (Barbosa and Frongillo, 1979; Barbosa et al., 1986); parental sex ratio (Mohamed and Coppel, 1986). Studies on other biological aspects, such as the effect of host size and host species on progeny production and sex ratio in *B. lasus* are necessary.

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**REFERENCES**


