一亚热带蜚蠊(*Periplaneta japanna*)两地理种群间相异的光周期反应模式

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摘要: 为弄清光周期对一种亚热带蜚蠊(*Periplaneta japanna*)若虫发育的控制机理,检测了光周期对冲绳(26°N)和八丈岛(33°N)两个地理种群若虫发育的影响。结果表明,光周期显著影响两地理种群的若虫发育,然而,冲绳和八丈岛种群间显示不同的光周期反应模式。冲绳种群在长日条件下(LD 16:8h)若虫发育显著快于中间日长(LD 14:10h)和短日条件下(LD 12:12h)的若虫发育,孵化后 60d 或 120d 将若虫自 LD 16:8h 向 LD 12:12h 转移,若虫发育受到抑制,而自 LD 12:12h 向 LD 16:8h 转移,则促进若虫发育。八丈岛种群的若虫在短日条件下发育最快,其次是中间日长,长日条件下若虫发育最慢,孵化后 60d 或 120d 将若虫自 LD 16:8h 向 LD 12:12h 转移抑制若虫发育,反方向转移的若虫快速发育。两地理种群间不同的光周期反应模式可以认为是趋异进化的结果。

关键词: 蜚蠊; 光周期; 地理变异; 滞育; 亚热带; *Periplaneta japanna*

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Different photoperiodic responses in two geographic populations of a subtropical cockroach, *Periplaneta japanna* Asahina

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Abstract: Effects of photoperiod on nymphal development were investigated in two subtropical populations of *Periplaneta japanna* living on Naha, Okinawa Islands (26 N) and Hachijo island (N33 N), Japan. Nymphal development was greatly influenced by photoperiod with different photoperiodic response pattern occurring between Okinawa and Hachijo population. In the Okinawa population, nymphs developed faster under LD 16:8h and LD 14:10h than under LD 12:12h at constant photoperiods. When photoperiodic shifts from long days (LD 16:8h) to short days (LD 12:12h) at 60 and 120 days restrain nymphal development, while photoperiodic shifts from short days to long days accelerate the nymphal development. However in Hachijo population, nymphal development was the fastest under LD 12:12h, followed by LD 14:10h and the slowest

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under LD 16:8h. Nymphal growth is restrained when the nymphs are transferred from LD 16:8h to LD 12:12h at 60 and 120 days after hatching, rapid development is observed when nymphs were transferred in the opposite direction in Hachijo population. The different photoperiodic response pattern in nymphal development between the two parapatric geographical populations might be regarded as the result of divergent evolution.

Key Words: cockroach, photoperiod, geographic variation, diapause, subtropics, *Periplaneta japanna*

Photoperiodic response for diapause induction is an important life history trait for temperate insects in regulating their seasonal life cycles, because photoperiod is the most regular and therefore most reliable long-term cue to future conditions in the temperate zone [1,2]. Furthermore, as climatic conditions such as temperature and daylength have clear latitudinal gradients, many insects occurring over wide geographic ranges usually show clinal variation in life history traits as a result of adaptation. Even in the same species, life history traits are often quite different between northern and southern populations [1-3]. For example, geographic variation in the critical photoperiod for diapause induction occurs because photoperiod changes consistently with latitude [1,2,4]. The adaptation of geographical populations is dominantly manifested in voltinism, displaying a great plasticity in the number of generations [5-7]. In addition, different photoperiodic response curves among different geographical populations also have been reported in some insect species [8,9]. Cockroaches usually require a relatively long time to complete development and photoperiod often plays an important role in the control of nymphal diapause [10,11].

Periplaneta japanna Asahina is a field-dwelling cockroach distributing from Okinawa Islands to the south of Kyushu Island and Hachijo island, Japan. Both adults and nymphs are dark black, and newly emerged adults weigh 0.3 —1.3 g and their head width is 4.1 —5.4 mm. Adults and nymphs usually occur under stones, wooden boards and so on [12]. Little information is available about the seasonal life cycle and its control in this subtropical species. In the current study, we compared the photoperiodic response pattern and their variation between two subtropical populations of *Periplaneta japanna* to understand the role of photoperiod in controlling nymphal devolopment. The two subtropical populations, collected from Okinawa Islands and Hachijo island, showed markedly different photoperiodic response pattern.

1 Materials and methods

1.1 Insects and rearing methods

Nymphs of Hachijo population were collected on Hachijo island (33.06 N, 139.47 E), a small Pacific island (about 60 km in perimeter) located 290 km south of Tokyo, in March 2001. Nymphs of Okinawa population were donated by Dr. K. Hirai (Division of Insect and Animal Sciences, Independent Administrative Institution) collected on Naha, Okinawa Islands, Japan, in November 2001 (26.15 N, 127.40 E).

In the laboratory, the collected nymphs were fed Insect Feed (Oriental Yeast Co., Japan) and slices of carrot in plastic containers (5 cm in diameter; 9 cm in height) in groups at 25℃ ±1℃ and LD 16:8 h. The container had a lid with a hole (5 cm in diameter) covered with nylon mesh. Carrot was refreshed every other day. Corrugated filter paper (1 cm in diameter) was placed in each container to increase available shelters for the insects. A waterish plastic vial (diameter 2 cm; length 9 cm) with a cotton plug was placed in each container to supply water. Oothecae deposited on cotton plugs were collected and used in the experiments.

1.2 Effect of constant photoperiods on nymphal development

To examine effects of photoperiod on the nymph development, newly-hatched nymphs of each population were exposed to LD 16:8, 14:10 or 12:12 h at 25℃ ±1℃ in incubators (FLC-750S, Fuji Medical Science Industry, Japan). Cockroaches were weighed with an electronic balance (0.1 mg accuracy; Mettler, AT201, Switzerland) every month until most individuals matured. Adult emergence was checked every other day. All newly-emerged adults were removed from the container.

1.3 Effect of changes in photoperiod on nymphal development

To test effects of changes photoperiod on the nymphal development, newly-hatched nymphs of each population were first reared at LD 16:8 h and 25℃ and then transferred to LD 12:12 h at day 60 or 120 after hatching, and vice versa at day 60 or 120. Nymphs were weighed every month and adult emergence was checked every other day.

2 Results

2.1 Okinawa population

2.1.1 Effect of constant photoperiods on nymphal development

Newly-hatched nymphs were reared in long days (LD 16:8 h), intermediate days (LD 14:10 h) and short days (LD 12:12 h) at 25℃ (Fig. 1A). Nymphal development was faster at LD 16:8 h and LD 14:10 h, duration of nymphal development was 229.7 ± 32.9 (mean SD, $n = 24$) and 225.5 ± 27.4 ($n = 19$) days, respectively, showed no significant difference (t-test, $t = 0.4503$, $p > 0.05$). However, nymphal development was obviously slower at LD 12:12 h (349.2 ± 57.7 days, $n = 15$) (t-test, 16L *vs* 12L, $t = 8.2823$; 14L *vs* 12L, $t = 8.2906$, $p < 0.001$, respectively). Changes in body weight indicated that nymphal development was slow under short-day condition (Fig. 1B). These results indicated that nymphal diapause was induced at LD 12:12h.

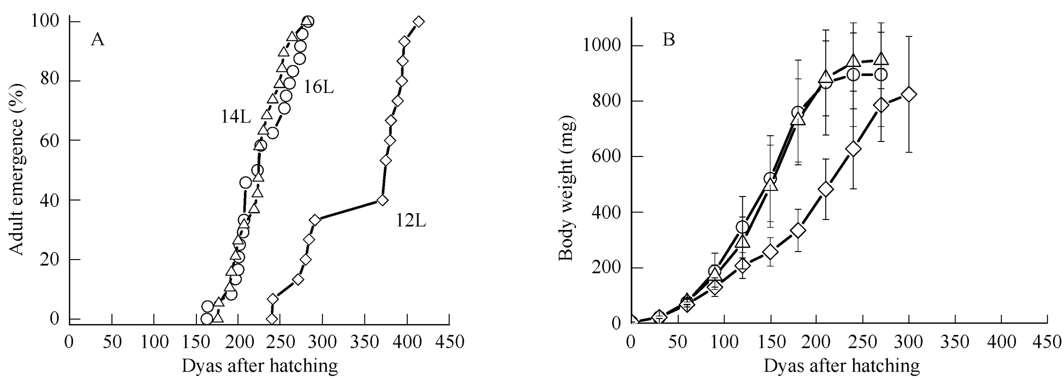

Fig. 1 Cumulative percentages of adult emergence (A) and changes in body weight (B) of Okinawa population reared at different photoperiods and 25℃ ($n = 15 - 24$); Error bars indicate SD

2.1.2 Effect of changes in photoperiod on nymphal development

Nymphs were first kept at LD 16:8h and then transferred to LD 12:12h at day 60 or 120 after hatching. Adults emerged later than those reared continuously at LD 16:8h (t-test, 16L *vs* day 60, $t = 6.2790$; 16L *vs* day 120, $t = 4.1329$, $p < 0.001$, respectively; Fig. 1A and Fig. 2A). At constant LD 16:8h, the mean durations of nymphal development were 229.7 ± 32.9 days (Fig. 1A), in cockroaches transferred at 60 and 120 days, the mean durations of nymphal development were 317.9 ± 51.1 ($n = 12$) and 294.6 ± 66.5 ($n = 18$) days, respectively (Fig. 2A). After transferring, body weight increased slowly (Fig. 2B).

The reverse transfer, i.e. from LD 12:12 to LD 16:8 at day 60 or 120 after hatching, nymphal development remarkably faster than which reared at constant LD 12:12h (t-test, 12L *vs* day 60, $t = 8.9844$; 12L *vs* day 120, $t = 4.3411$, $p < 0.001$, respectively; Fig. 1A and Fig. 3A). The mean duration of nymphal development which nymphs transferred at day 60 and 120 after hatching were 233.0 ± 28.8 ($n = 29$) and 273.6 ± 38.3 ($n = 16$) days, respectively, particularly in cockroaches transferred at day 60, nymphal development even fast as those reared

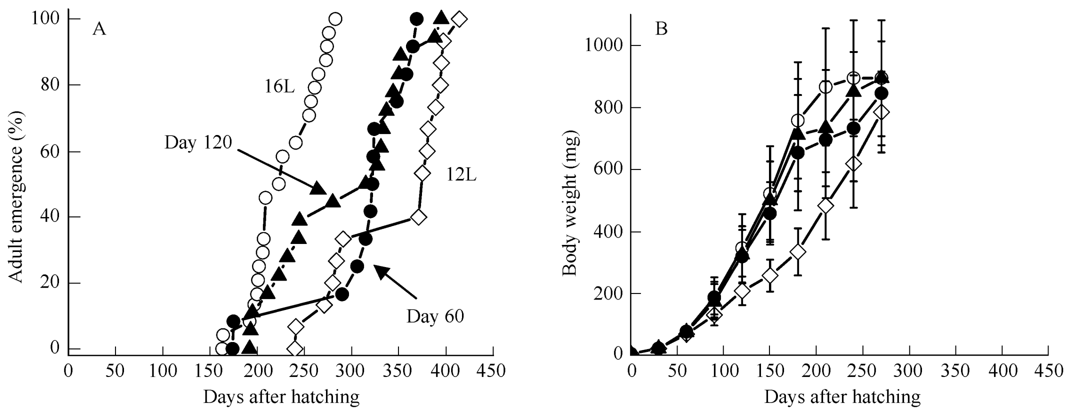

Fig. 2 Effect of photoperiodic shift from LD 16:8 to LD 12:12 at 25℃ at day 60 ($n = 12$) or day 120 ($n = 18$) on adult emergence (A) and body weight (B) of Okinawa population; The data for constant LD 16:8 ($n = 24$) and LD 12:12 ($n = 15$)

continuously at LD 16:8h (t-test, $t = 0.6995$, $p > 0.05$). Obvious increase in body weight was observed after transfer to LD 16:8h (Fig. 3B).

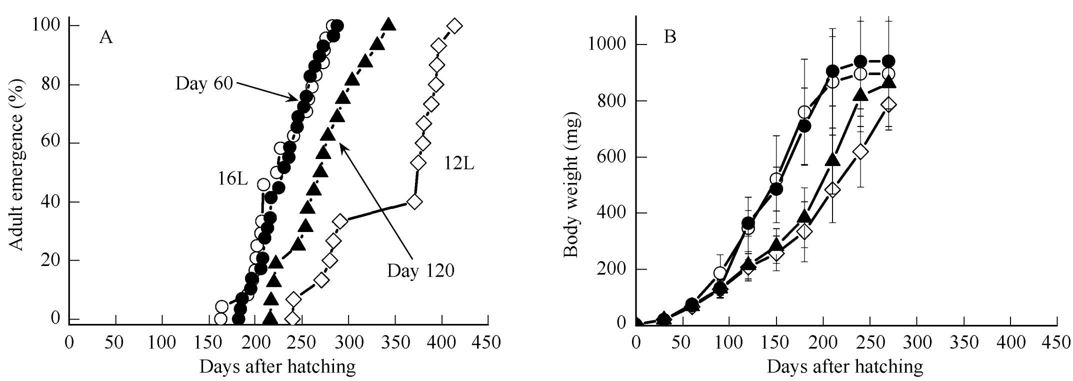

Fig. 3 Effect of photoperiodic shift from LD 12:12 to LD 16:8 at 25℃ at day 60 ($n = 29$) or day 120 ($n = 16$) on adult emergence (A) and body weight (B) of Okinawa population. The data for constant LD 16:8 ($n = 24$) and LD 12:12 ($n = 15$)

These results indicated that the photoperiodic responses of Okinawa population of *P. japanna* is simplicity, nymphal diapause is induced and maintained by short days and terminated by long days, belong to long-day type population.

2.2 Hachijo population

2.2.1 Effect of constant photoperiods on nymphal development

Newly-hatched nymphs were kept at LD 16:8, LD 14:10 and LD 12:12 h and 25℃ (Fig. 4). Nymphal development was the fastest at LD 12:12 h (254.3 ± 28.7 days, $n = 20$), followed by LD 14:10 h (284.4 ± 45.2 days, $n = 31$), and the slowest at LD 16:8h (352.6 ± 30.0 days, $n = 22$) (Fig. 4A). It is likely that nymphal diapause was induced at LD 16:8h. Although adults emerged most rapidly at LD 12:12h, changed in body weight indicated that nymphal weight increased slower at LD 12:12 h than at LD 14:10 h and LD 16:8 h, particularly during the early stage (Fig. 4B).

2.2.2 Effect of changes in photoperiod on nymphal development

Nymphs wear exposed to a photoperiodic shift from long days (LD 16:8h) to short days (LD 12:12h) at 60 or 120 days after hatching (Fig. 5). After transferring, nymphal development tended to slowness, body weight increased markedly slowly (Fig. 5B). Those transferred at day 60 after hatching, the mean duration of nymphal

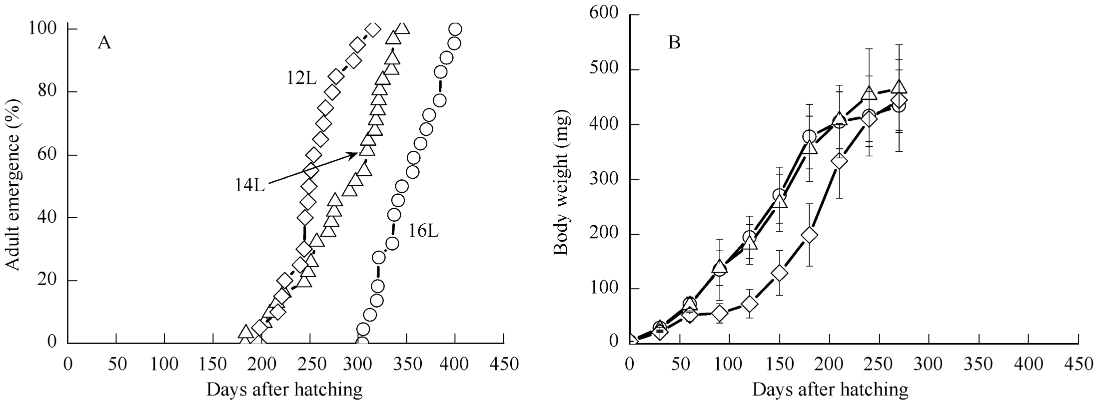

Fig. 4　Cumulative percentages of adult emergence (A) and changes in body weight (B) of Hachijo Island population reared at different photoperiods and 25℃ (n = 20 – 31); Error bars indicate SD

development was 386.7 ± 33.2 days (n = 17), longer than cockroaches reared continuously at LD 16:8h (352.6 ± 30.0) (t-test, $t = 3.1640$, $p < 0.01$). In cockroaches transferred at day 120 after hatching, the mean duration of nymphal development was 336.6 ± 23.8 days (n = 33), no significant difference between those and nymphs reared continuously at LD 16:8h (t-test, $t = 1.9114$, $p > 0.05$; Fig. 4A and Fig. 5A).

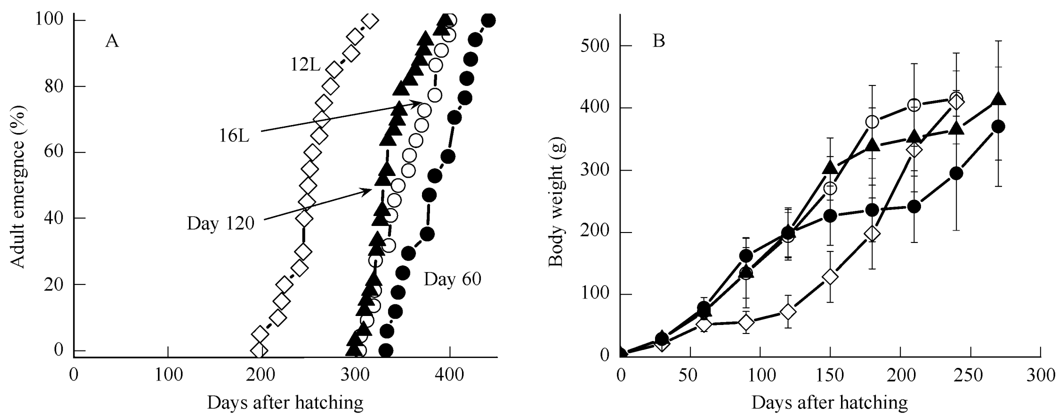

Fig. 5　Effect of photoperiodic shift from LD 16:8 to LD 12:12 at 25℃ at day 60 (n = 17) or day 120 (n = 33) on adult emergence (A) and body weight (B) of Hachijo Island population. The data for constant LD 16:8 (n = 22) and LD 12:12 (n = 20) are derived form Fig. 3

The reverse transfer, i.e. from short days to long days at day 60 or 120 after hatching, nymphal development faster than those reared at constant LD 12:12h (t-test, $t = 8.0416$, $p < 0.001$, at day 60; $t = 2.5386$, $p < 0.05$, at day 120; Fig. 4A and Fig. 6A). The mean duration of nymphal development were 208.7 ± 15.5 (n = 42) and 234.9 ± 19.8 (n = 21) days in cockroaches transferred at 60 and 120 days, respectively. Obvious increase in body weight was observed after transfer to LD 16:8h (Fig. 6B).

These results indicated that changed photoperiods affect nymphal development, photoperiodic shifts from short days to long days shorten the duration of nymphal development, photoperiodic shifts from long days to short days restrain nymphal development as cockroaches reared at constant long-day condition.

3　Discussion

Cockroaches generally require a relatively long time to complete development [0]. For example, a British small cockroach, *Ectobius panzeri*, has a univoltine life cycle, and overwinters as diapause eggs within an ootheca [3]. Two other British cockroach species, *Ectobius lapponicus* and *Ectobius pallidus*, have semivoltine life cycles, passing the

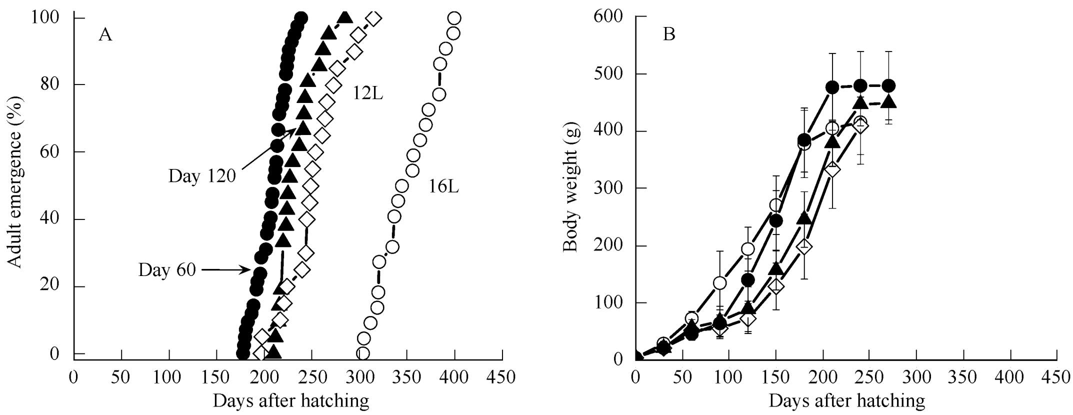

Fig. 6 Effect of photoperiodic shift from LD 12:12 to LD 16:8 at 25℃ at day 60 (n = 42) or day 120 (n = 21) on adult emergence (A) and body weight (B) of Hachijo Island population. The data for constant LD 16:8 (n = 22) and LD 12:12 (n = 20) are derived form Fig. 3

first winter as diapause eggs and the second winter as diapause nymphs [3-15]. The Yamato cockroach, *Periplaneta japonica*, occurring in Japan, is also semivoltine, and overwinters twice as diapause nymphs [6-18]. In recent studies, two cockroach species, *Symploce japonica* [9] and *Opisoplatia orientalis* [1], have benn found to be semivoltine and another cockroach species, *Margattea satsumana* [20], has a univoltine life cycle, on the subtropical island, Hachijo island, Japan. In this study, a subtropical cockroach species, both Okinawa and Hachijo population of *Periplaneta japanna*, nymphs developed slowly, not only at long-day conditions but also at short-day conditions, duration of nymphal development were over 220 days at 25℃ (Fig. 1 and Fig. 4).

The present results indicated that nymphal development of *Periplaneta japanna* was greatly influenced by photoperiod, but shown different photoperiodic response pattern between Okinawa and Hachijo population. In Okinawa population, at constant photoperiods, nymphal development was faster under LD 16:8h and LD 14:10h, slower under LD 12:12h (Fig. 1). When photoperiodic shifts from long days to short days restrain nymphal development, photoperiodic shifts from short days to long days shorten the duration of nymphal development (Fig. 2 and Fig. 3). Those results suggested that the photoperiodic responses of Okinawa population of *Periplaneta japanna* is simplicity, nymphal diapause is induced and maintained by short days and terminated by long days, belong to long-day type insect population and maybe suggesting adults emerge in spring or summer, as Zhuzhou population of *Blattella germanica* [21]. In Hachijo population of *Periplaneta japanna*, at constant photoperiods, nymphal development was the fastest under LD 12:12h, followed by LD 14:10h, the slowest under LD 16:8h (Fig. 4), the shorter the day-length, the faster the nymphal development. However, when photoperiodic shifts from long days to short days restrain nymphal development, while photoperiodic shifts from short days to long days shorten the duration of nymphal development (Fig. 5 and Fig. 6). Furthermore, although Nymphs matured most rapidly at LD 12:12h, nymphal weight increased slower at LD 12:12h than at LD 14:10h and LD 16:8h, particularly during the early stage (Fig. 4B). Those results suggested that the cockroach of Hachijo population shows a complicated response to photoperiod over different developmental stages, as another cockroach species, *S. japonica*, on the same subtropical island with three types of diapause in its semivoltine life cycle [9]. In *Periplaneta japanna*, more experiments involving various photoperiodic changes are necessary to compare the underlying control mechanism of life cycles. *M. satsumana*, a univoltine cockroach species, on the same subtropical island, nymphs grow slower at constant LD 16:8h than that at LD 12:12h. But nymphal development was further prolonged when the nymphs were transferred from short days to long days, rapid development was observed when nymphs were transferred from long days to short days, suggested that nymphs of *M. satsumana* matured to adults before winter [20]. In Hachijo population of

Periplaneta japanna, adult emergence was accelerated when daylength increased, should suggesting adults emerge in spring or summer.

Periplaneta japanna is known to be distributed from Okinawa Islands to the south of Kyushu Island and Hachijo island, Japan [2]. Although their distribution is continuous from Okinawa Islands to the south of Kyushu, but it is an independent distributed zone on Hachijo island. The different photoperiodic response pattern in nymphal development between the two parapatric geographical populations at constant photoperiods, might be regarded as the result of divergent evolution.

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