Effect of Stationary and Changing Photoperiods on Nymphal Development in *Carbula humerigera* (Heteroptera: Pentatomidae)¹

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At 25°C, the nymphal diapause of *Carbula humerigera* was induced in the second to fifth instars by short stationary photoperiods of 10 to 13 hr and averted by long ones of 14 to 16 hr. In a photoperiod of 13.5 hr, the nymphal development was transitional. At 20°C, the nymphal diapause was induced by a photoperiod of 14 hr or shorter and averted by photoperiods of 15 to 16 hr. The critical daylength lies between 14 and 15 hr. Therefore, temperature exerted a modifying effect on the critical photoperiod. The nymphal development was affected by changes in photoperiod and the adult emergence tended to be more synchronized by increasing photoperiod.

INTRODUCTION

Most heteropteran bugs enter diapause in the adult stage. However, some species enter diapause in the nymphal or egg stage. The examples are *Poecilocoris lewisi* and *Urochela leteovaria* (NOSAWA, 1980) entering diapause in the nymphal stage and *Urostylis striicornis*, *U. westwoodi* (NOSAWA, 1980) and *Cavelerius saccharivorus* (HOKYO et al., 1983) entering diapause in the egg stage. However, the photoperiodic responses in these insects have not been reported.

In the temperate areas, the life cycles of insects are mainly controlled by daylength. The photoperiodic responses are mainly divided into two types, the long- and short-day types. In long-day responses, insects develop or reproduce in summer and diapause before the winter, such as *Laspeyresia molesta* (DICKSON, 1949), *Acronycta rumicis* (DANILEVSKII, 1948) and *Aelia acuminata* (HODEK, 1969). In the short-day type, insects enter summer diapause and reproduce in the fall and/or winter. MASAKI (1956, 1959) found a short-day response in a geometrid moth, *Abraxas miranda*. The larvae of the first generation occur in early spring, mature in early summer and the pupae enter aestivation. When the temperature falls, the pupae emerge as adults and reproduce.

In nature, daylengths change day by day. An increasing daylength indicates the approach of summer and a decreasing one the approach of winter. Some insects, such as *Crysopa carnea* (TAUBER and TAUBER, 1973), maintain diapause in decreasing daylengths and terminate it in increasing ones. The larvae of *Acalolepta luxuriosa* mature in an increasing daylength, while they fail to do so in stationary short or long photoperiods as well as in a decreasing one (HONDA, 1981). This kind of photoperiods response has

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been reported for several univoltine species.

Carbula humerigera is a rice paddy pest and occurs throughout the northern parts of Japan. In Hirosaki, this bug is univoltine and overwinters in the nymphal stage (KIRITANI, 1985). In the natural conditions at a constant temperature (25°C), oviposition by the female of *C. humerigera* was suppressed in increasing daylengths and promoted in decreasing daylengths in June–July. Nymphs also responded to decreasing photoperiods in fall and winter and would not mature until the winter solstice (KIRITANI, 1985). The present study examines the effect of stationary and changing photoperiods on nymphal development, and analyses the seasonal life cycle of *C. humerigera*.

MATERIALS AND METHODS

Nymphs and adults of *Carbula humerigera* were collected at Nakatomarisawa and Shinzansawa near Hirosaki in the summer of 1981 and 1982. They were reared under natural daylengths at 25°C. Adults laid eggs on pieces of cotton wool from early August and these eggs were used for the experiments. Bugs were usually reared in plastic containers (7 cm high and 13 cm in diameter). The bottom was lined with sheets of filter paper and the top was covered with a ventilated lid. Water was provided in vials with cotton plugs and renewed about once a week. Bugs were fed on dry soybeans and foxtail millet seeds, *Setaria italica*. The number of eggs laid on the cotton wool was counted. The newly hatched nymphs were provided with rice seedlings (*Oryza sativa*). When adults emerged, each pair of female and male was kept separately.

The temperature was maintained at 20 ± 1 and $25 \pm 1^\circ\text{C}$ incubators each fitted with a 6 W white fluorescent lamp. The light periods were controlled by automatic time switches. Further details about the experimental methods will be described in appropriate sections.

RESULTS

Effect of stationary photoperiod

The nymphal development times in various stationary photoperiods at 25°C are shown in Fig. 1. The shortest development time from hatching to adult emergence was found in a photoperiod of 16 hr or constant darkness (DD), where all nymphs emerged by day 61 after hatching. In all photoperiods longer than 13.5 hr, most nymphs emerged as adults by day 70 and a few showed delayed development. The nymphal development time was long and its variance was large in short photoperiods of 12 and 13 hr. The development time in 10 or 13.5 hr photoperiod was intermediate between the typical and short-day values and the variance was the greatest in the 10 hr photoperiod (Table 1). The variance in development time under the long-day was smaller than those in the short days.

In photoperiods longer than 14 hr, few nymphs delayed development at various instars (Fig. 1). In a photoperiod of 13.5 hr, the nymphal development was mainly retarded at the fourth or fifth instar. In a 13 hr photoperiod, development was delayed in the third to fifth instars, and in 12 or 10 hr photoperiods, in the second or third. As the photoperiod decreased, the nymphal development was retarded at younger instars. After nymphs resumed development, they developed without further delay.

Fig. 1. Nymphal development of *Carbula humerigera* under stationary photoperiods at 25°C.

: first instar, : second instar,
 : third instar, : fourth instar,
 : fifth instar, : adult.

Fig. 2. Effects of increasing photoperiod on nymphal development in *C. humerigera* at 25°C. Solid circle indicates the mean nymphal development time. Arrow indicates the time of transfer. Number on the arrow indicates weeks from hatching before transfer.

Table 1. The duration of nymphal development of *C. humerigera* under various stationary photoperiods at 25°C

Photoperiod (light-dark)	Total number of individuals	No. emerged as adults	Development time (days)	
			$\bar{X} \pm \text{S.D.}$	Range
16 - 8	82	75	48.0 ± 5.0	38- 61
15 - 9	46	19	59.1 ± 8.9	49- 75
14.5- 9.5	27	24	55.0 ± 4.9	48- 67
14 -10	43	30	57.4 ± 10.5	44- 97
13.5-10.5	32	13	80.1 ± 11.8	57- 97
13 -11	52	39	99.6 ± 13.7	78-119
12 -12	44	30	93.9 ± 10.9	75-119
10 -14	48	45	74.2 ± 15.1	47-119
0 -24	36	28	50.6 ± 3.7	45- 58

At 20°C, the nymphal development time was generally longer than at 25°C (Table 2). In long photoperiods of 15 and 16 hr, nymphs began to emerge from day 53 after hatching. In a photoperiod of 14 hr, however, nymphs needed on the average about 110 days to mature. The development time almost doubled in 14 hr as compared with that in 15 hr. In photoperiods shorter than 14 hr, the adult emergence was never com-

Table 2. The duration of nymphal development of *C. humerigera* under various stationary photoperiods at 20°C^a

Photoperiod (light-dark)	No. emerged as adults	Development time (days)		No. surviving as nymphs ^b
		$\bar{X} \pm \text{S.D.}$	Range	
16 - 8	35	59.3 $\pm$ 4.7	53- 69	—
15 - 9	26	66.8 $\pm$ 8.7	55- 85	—
14 -10	25	110.6 $\pm$ 6.9	101-127	—
13.5-10.5	9	134.3 $\pm$ 7.2	120-147	7
13 -11	5	136.2 $\pm$ 4.0	131-141	3
12 -12	0	— —	—	21

^a The number of individuals used in each treatment ranged from 30 to 40.^b Number surviving as nymphs on day 150 after hatching.Table 3. Effect of increasing photoperiods on the duration of nymphal development in *C. humerigera* at 25°C^a

a) Transfer from 10 to 12 hr photoperiods

Photoperiod (light-dark)		Days before transfer to 12L-12D	No. emerged as adults	Development time (days)	
1st	2nd			$\bar{X} \pm \text{S.D.}$	Range
12-12	12-12	—	44	93.9 $\pm$ 10.9	75-119
10-14	12-12	21	19	86.5 $\pm$ 6.3	74- 94
10-14	12-12	35	35	83.2 $\pm$ 7.1	69-100
10-14	12-12	49	23	83.5 $\pm$ 4.1	76- 90
10-14	10-14	—	58	74.2 $\pm$ 15.1	49-119

b) Transfer from 10 to 13 hr photoperiods

Photoperiod (light-dark)		Days before transfer to 13L-11D	No. emerged as adults	Development time (days)	
1st	2nd			$\bar{X} \pm \text{S.D.}$	Range
13-11	13-11	—	24	99.6 $\pm$ 13.7	61-119
10-14	13-11	21	11	78.3 $\pm$ 6.5	66- 86
10-14	13-11	35	15	84.1 $\pm$ 8.4	75- 98
10-14	13-11	49	22	90.5 $\pm$ 9.0	77-106
10-14	10-14	—	58	74.2 $\pm$ 15.1	49-119

c) Transfer from 10 to 14 hr photoperiods

Photoperiod (light-dark)		Days before transfer to 14L-10D	No. emerged as adults	Development time (days)	
1st	2nd			$\bar{X} \pm \text{S.D.}$	Range
14-10	14-10	—	30	57.4 $\pm$ 10.5	44-100
10-14	14-10	21	12	57.1 $\pm$ 2.0	55- 62
10-14	14-10	35	24	78.6 $\pm$ 9.6	72-107
10-14	14-10	49	15	80.4 $\pm$ 4.2	72- 87
10-14	10-14	—	58	74.2 $\pm$ 15.1	49-119

d) Transfer from 12 to 13 hr photoperiods

Photoperiod (light-dark)		Days before transfer to 13L-11D	No. emerged as adults	Development time (days)	
1st	2nd			$\bar{X} \pm \text{S.D.}$	Range
13-11	13-11	—	29	99.6 $\pm$ 13.7	61-119
12-12	13-11	21	12	85.1 $\pm$ 7.8	70- 98
12-12	13-11	35	27	88.3 $\pm$ 6.5	75-104
12-12	13-11	49	25	84.4 $\pm$ 6.6	71-102
12-12	13-11	56	13	76.5 $\pm$ 7.5	65- 86
12-12	12-12	—	44	93.9 $\pm$ 10.9	75-119

e) Transfer from 12 to 14 hr photoperiods

Photoperiod (light-dark)		Days before transfer to 14L-10D	No. emerged as adults	Development time (days)	
1st	2nd			$\bar{X} \pm \text{S.D.}$	Range
14-10	14-10	—	30	57.4 $\pm$ 10.5	44-100
12-12	14-10	35	16	71.6 $\pm$ 3.3	66- 79
12-12	14-10	49	18	75.1 $\pm$ 4.7	69- 83
12-12	14-10	56	12	82.3 $\pm$ 6.2	67- 90
12-12	12-12	—	44	93.9 $\pm$ 10.9	75-119

^a The number of individuals used in each treatment ranged from 30 to 40.

pleted by day 150 after hatching. In particular, at the 12 hr photoperiod all individuals persisted as nymphs for more than 150 days.

Thus *C. humerigera* enters a facultative diapause at the second to fifth instars in short daylengths. When the nymph is exposed to a low temperature, its development is retarded by a longer photoperiod than at a high temperature.

Effect of changing photoperiod

Newly hatched nymphs were first kept in a photoperiod of 10 or 12 hr and transferred to a longer one of 12, 13 or 14 hr at week 3, 5, 7 or 9 after hatching. The cumulative percentages of adult emergence, average nymphal development time and variance in development time in the changing photoperiods at 25°C are shown in Fig. 2 and Table 3. In stationary photoperiods of 10, 12, 13 and 14 hr, adults emerged sporadically, and variances were large, ranging from 10.5 to 15.1 days (Table 3). In the transfer from a photoperiod of 10 to 14 hr at week 3, acceleration of development and synchronous adult emergence were most conspicuous. In the same transfer at week 5, a few individuals showed delayed development and this made the variance very large. At week 7, however, the adult emergence was synchronized without any acceleration of development. Among the others with different times of transfer, the mean development times were not significantly different from one another, being about 78 to 90 days.

DISCUSSION

Heteropteran bugs generally overwinter at the adult stage. In bugs entering diapause at the adult stage, however, nymphs are somewhat sensitive to photoperiod.

Riptortus clavatus is sensitive at the fourth or fifth instar (NUMATA and HIDAKA, 1982; KIRITANI, unpublished), *Eysarcoris lewisi* at the fifth instar (KIRITANI, unpublished) and *Lygus hesperus* at the nymphal stage (BEARD and STRONG, 1966). Therefore, heteropteran bugs overwintering as adults might be generally sensitive to photoperiod at the nymphal stage like the nymph-overwintering species, *C. humerigera*.

C. humerigera enters diapause at the nymphal stage, from the second to fifth instars (Fig. 1). Nymphs enter diapause at the younger stages with shortening photoperiod. In natural daylengths, they enter diapause at third, fourth or fifth instar (KIRITANI, 1985). The nymphs hatching in early date entered diapause at the older stages and those in late date did so at the younger stages. The second instar nymph entering diapause was observed in the stationary photoperiod of 12 or 10 hr but not in the natural daylengths at Hirosaki. It is inferred that nymphs hatched in October and later, when photoperiod becomes 12 hr or shorter, will enter diapause at the second instar. This situation may be encountered in the southern localities.

The nymphal diapause is induced by a short photoperiod and averted by a long one. In a stationary photoperiod of 13.5 hr at 25°C, the nymphal development shows a transitional state (Fig. 1). In the natural daylengths at about 25°C, nymphs entered diapause in photoperiods between 13.5 and 15 hr (KIRITANI, 1985). Half of the nymphs that had hatched in late July emerged in mid-September and the rest entered diapause at the fifth instar. In this case, the daylength during the nymphal development decreased from 15 to 13.5 hr. At 20°C, the nymphal growth was decelerated and the critical daylength was longer than that at 25°C (Table 2). Therefore, low temperature increases the tendency toward diapause.

When nymphs were transferred from photoperiods of 10 or 12 hr to longer ones, adult emergence was synchronized (Fig. 2 and Table 3). Even in an increasing daylength below the critical level, the synchronization effect was observed. An accelerating effect on the nymphal development was also detected, but the increasing daylength was effective in synchronization rather than acceleration. It is already reported that the nymphal diapause is maintained by decreasing daylength (KIRITANI, 1985). Although the nymphal diapause was induced by stationary short-photoperiods, it was terminated within 60 days after diapause induction without any change in photoperiod. The nymphs of *C. humerigera* respond to the increase and decrease in daylength, and such responses are important to control their development.

TANAKA (1978, 1979) studied the univoltine ground cricket, *Pteronemobius nitidus*, which enters diapause mainly at the penultimate nymphal stage. The diapause instar is influenced by photoperiod, temperature or interaction of these two factors. When nymphs were exposed to increasing photoperiods, the adult emergence was accelerated and synchronized, while there was a great variance of the adult emergence time in stationary photoperiods. A decreasing photoperiod was also effective on deceleration of nymphal development. He concluded that the effects of changing daylengths were determined by the absolute level, magnitude and direction of change in photoperiod. In the semivoltine ant lion, *Hagenomyia micans*, larvae enter diapause at any instar (FURUNISHI and MASAKI, 1981). The final-stage larvae are accelerated to mature by the increasing daylengths in spring, when there is enough food supply.

The nymphs of *Carbula humerigera* respond to both stationary and changing photoperiods. Based on these responses, the life cycle of this species can be inferred as follows. The nymphs enter diapause in the short photoperiod of 13.5 or shorter. Their diapause

is maintained by decreasing photoperiod. Although the nymphs may be released from diapause as the decreasing rate of photoperiod becomes small at around the winter solstice, they remain in a dormant state because of the low temperature. The overwintering nymphs resume development under the increasing daylength from late spring to early summer. Together with the rising temperature, such conditions favor synchronized emergence of adults to occur from late June to early July.

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