Change in Photoperiodic Sensitivity during Hibernation in a Semi-Aquatic Bug, *Microvelia douglasi* (Heteroptera: Veliidae)¹

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Timing of induction of reproductive diapause of *Microvelia douglasi* were investigated. Diapausing females began to appear in early September in field population. Under laboratory condition at 24°C, reproductive diapause was induced by photoperiods shorter than 12.5 hr of light, which coincides with the daylength in early September. Seasonal changes in the pattern of egg production of overwintering females incubated under laboratory conditions at 24°C were also examined. When the insects were incubated under 16L–8D photoperiod, almost all the females began to lay eggs irrespective of the sampling date. When incubated under 12L–12D and 8L–16D, the percentage of females which laid eggs was low in samples collected before December, but it became as high as 100 percent in samples collected after December. The preoviposition period from the date of the collection increased until the end of October, decreased to 5 to 6 days in late December and stayed at a constant level thereafter. Although females incubated under 16L–8D continued to lay eggs throughout experimental period, some females, which were incubated under 12L–12D and 8L–16D, stopped laying eggs soon after beginning of incubation. However, under 12L–12D, the percentage of such females decreased in samples collected later in the winter.

INTRODUCTION

Microvelia douglasi occurs on various kinds of water surfaces including paddy fields. Several authors have shown that *M. douglasi* is a predator of homopteran insect pests (OHO and MIYAHARA, 1957; NAKASUJI and DYCK, 1984) and larvae of vector mosquitoes (KURIHARA, 1974) in rice fields. We reported earlier that this bug occurred from late April to mid-October and produced 3 or 4 generations in this period in south western Japan (MURAJI et al., 1989). However, little is known about the mechanism controlling the seasonal life cycle of this species.

In the present study, in order to elucidate the timing of induction and termination of reproductive diapause in *M. douglasi*, we examined the seasonal occurrence of dia-

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pausing females in natural populations, the critical day length for diapause induction, and the responses of hibernating females to the different photoperiods under laboratory conditions.

MATERIALS AND METHODS

Adults of *M. douglasi* were collected in ponds around Matsue City, southwestern Japan, in 1983; more than 90% of individuals were apterous. They were reared in a group of 30–50 individuals in a container (15 cm in diameter and 6.5 cm in height) filled to 2 cm with dechlorinated tap water, and kept at 24°C and under 16L–8D photoperiod. Two or three pieces of filter paper (2 cm × 7.5 cm) were placed on the side wall of the container for oviposition and resting of insects. They were fed with a mixture of various kinds of frozen arthropods (0.5–1.0 g/day) which were collected from grass fields and stored in a freezer. Food and water were changed daily.

First-instar nymphs obtained from the insect culture were introduced into plastic containers in groups of 30–50 individuals, and were reared under 8L–16D, 12L–12D, 12.5L–11.5D, 13L–11D, 14L–10D or 16L–8D at 25°C until adult emergence. Females and males, which emerged on the same day, were paired in plastic cups (5 cm in diameter and 4 cm in height) and were maintained under the same conditions as they were reared under until 20 days after the emergence. They were fed about 0.1–0.2 g of food every day. Oviposition was recorded daily. The females that did not oviposit were dissected and the development of ovary was examined.

Field sampling was carried out at 10-day intervals from mid-April to mid-October in 1982 and 1984 in paddy fields and ponds around Matsue City. Adults were collected by sweeping with an aquatic net. The developmental stage of the ovaries of apterous females was examined by dissection.

Hibernating adults were collected from ponds around Matsue City. Nine samples were collected from mid-November, 1983, to late March, 1984, and six samples were collected from mid-September, 1984, to late February, 1985. A few macropterous adults were collected in this period, but the number was too small to be analyzed. Apterous females and male adults were paired in plastic cups within 24-hr after collection and were reared under 16L–8D, 12L–12D or 8L–16D photoperiod at 24°C. The number of eggs laid was observed daily for 30 days after sampling. Females which stopped ovipositing under 12L–12D and 8L–16D were transferred to 16L–8D on the 40th day and subsequent oviposition was recorded.

RESULTS

Critical daylength for induction of reproductive diapause

Figure 1 shows the photoperiodic response curve of *M. douglasi*. Reproductive diapause was induced under daylengths shorter than 12.5 hr at 24°C.

The timing of initiation and termination of the reproduction

The seasonal trend in the percent of females which have mature ovaries is shown in Fig. 2. The trends in both years were similar. The percent rapidly increased from mid- to late April, and decreased from early to mid-September.

Fig. 1. Photoperiodic response curve for reproductive diapause in *M. douglasi* at 24°C. Percent of diapause is the proportion of females which did not lay eggs within 20 days after emergence as an adult. Each point represents 21 females.

Fig. 2. Seasonal change in the percent of females which have mature ovaries. Each point is based on more than 20 females.

Fig. 3. Seasonal change in the percent of females which began to lay eggs within 25 days after transfer to 16L-8D, 12L-12D and 8L-16D at 24°C from the hibernating sites.

Fig. 4. Seasonal change in the number of days to the beginning of oviposition after collection of overwintering females under 16L-8D, 12L-12D and 8L-16D at 24°C. Vertical line and square indicate the range and standard error, respectively.

Fig. 5. Seasonal change in the number of eggs laid within 25 days after beginning of oviposition under 16L-8D, 12L-12D and 8L-16D at 24°C. Vertical line and square indicate the range and standard error, respectively.

Response of hibernating females to different photoperiods

Photoperiod sensitivity changed during the hibernation period. When hibernating adults were incubated at 24°C under 16L-8D photoperiod, nearly all the females began to lay eggs irrespective of the sampling date (Fig. 3). When the insects were incubated at 24°C under 12L-12D or 8L-16D, the percentage of females which laid eggs was low in samples collected before December, but all females collected after December oviposited.

Fig. 6. Oviposition pattern of females collected from hibernating sites on January 15, February 16 and March 28, 1984 and incubated at 24°C under 16L-8D, 12L-12D and 8L-16D.

Table 1. Percentage of females stopped oviposition within 15 and 30 days after transfer from field to 16L-8D, 12L-12D and 8L-16D photoperiod at 24°C

Date of collection		16L-8D		12L-12D		8L-16D	
		15 days	30 days	15 days	30 days	15 days	30 days
January	5	0 (11)	0 (11)	0 (11)	54.5 (11)	—	—
	15	0 (11)	0 (11)	7.1 (14)	28.6 (14)	25.0 (12)	83.3 (12)
February	2	—	—	0 (12)	8.3 (12)	16.7 (12)	58.3 (12)
	16	0 (11)	9.1 (11)	8.3 (12)	33.3 (12)	15.4 (13)	100 (13)
March	2	—	—	0 (13)	7.7 (13)	12.5 (8)	50.0 (8)
	28	0 (16)	0 (16)	0 (15)	6.7 (13)	0 (10)	80.0 (10)

Numerals in parentheses indicate the number of pairs examined.

The preoviposition period from the day of collection under 8L-16D, 12L-12D and 16L-8D at 24°C is shown in Fig. 4. Females which did not lay eggs within 25 days after collection were excluded from the calculation of the period. All the females collected on early October, 1984, did not lay eggs under 12L-12D. The period increased until the end of October and decreased thereafter irrespective of the rearing conditions. The change was more obvious under 12L-12D and 8L-16D than that under 16L-8D. The period decreased to 5 to 6 days in late December and stayed at a constant level thereafter under all treatments; the variation among individuals was small during this time.

Seasonal change in the number of eggs laid within 25 days after beginning oviposition is shown in Fig. 5. The number of eggs laid was similar among the different collecting dates under 16L-8D and was greater than 100 eggs. Under 12L-12D and

8L-16D photoperiods, the total number of eggs laid increased during the period. The change was greater under 12L-12D than that under 8L-16D. Although the change was similar in the both years, it occurred earlier in 1984/1985 than 1983/1984.

The fecundity schedules of the females, which were collected from the fields, on January 15, February 16 and March 28, 1984, are shown in Fig. 6. Table 1 shows the percentage of females which stopped oviposition within 15 and 30 days under different conditions after collection.

Under a 16L-8D photoperiod, all females began to lay eggs within 4 or 5 days after collection and the number of eggs oviposited increased to 8 eggs around the 10th day and remained at 7 to 8 eggs/day throughout the experimental period.

On the other hand, under a 8L-16D photoperiod, the number of eggs laid decreased after the 10th day. Under this condition more than 50% of females ceased oviposition within 30 days (Table 1). Under a 12L-12D photoperiod, the fecundity patterns of females collected in mid-January and mid-February were similar to those under 8L-16D condition, however, the pattern in late March was similar to that under 16L-8D photoperiod. Under this photoperiodic condition the percentage of females which stopped oviposition decreased as they were collected later in the winter (Table 1).

The females which ceased oviposition under 12L-12D and 8L-16D photoperiods were transferred to 16L-8D photoperiod on the 40th day. All of them began to lay eggs again within 4.7 days (Range: 2-10, S.E.=0.22, $n=26$) and 7.2 days on average (Range: 1-11, S.E.=0.31, $n=49$) after the transfer from 12L-12D and 8L-16D to 16L-8D, respectively.

DISCUSSION

Reproduction of *M. douglasi* adults occurred from mid-April to early September in Matsue (Fig. 2). When insects were reared under laboratory conditions, reproductive diapause was induced by a photoperiod shorter than 12.5 hr at 24°C (Fig. 1). The daylength in early to middle September in Matsue coincided well with the critical daylength when twilight time was taken into account. Reproductive diapause in natural populations is probably induced by the daylength in this period.

Many authors have reported that physiological changes occur in hibernating insects as diapause development proceeds (TAUBER and TAUBER, 1976; HODEK, 1983). In many insects, in which autumnal and hibernal reproductive diapause is induced by photoperiod, the photoperiodic sensitivity is lost until mid-winter. In such insects, the diapause-inducing photoperiods do not inhibit the termination of diapause and the onset of reproduction, and the onset of reproduction depends only on the thermal accumulation during the postdiapause quiescent stage in early spring (TAUBER et al., 1986).

In *M. douglasi*, the percentage of females that laid eggs under diapause-promoting photoperiods, i.e., 12L-12D and 8L-16D, gradually increased from early to mid winter and it was 100 percent in late December to spring. The preoviposition period after collection from the field was shortest from late December to spring. These results indicate that a major change in physiological states of diapausing insects have occurred until late December.

The beginning of oviposition of hibernating females under diapause-promoting photoperiods has been considered to indicate the completion of diapause (TAUBER and

TAUBER, 1976). However, this is not true for *M. douglasi* and the results of this study show that completion of reproductive diapause of this bug is more complicated process. In this bug, considerable number of females which began oviposition under such conditions stopped it within a few weeks even in the samples collected after late December. The fact that these females began ovipositing again when they were transferred to 16L–8D indicates that they did not completely lose sensitivity to diapause-promoting photoperiods.

The resumption of sensitivity to diapause inducing photoperiods soon after beginning oviposition was reported for some Hemipteran insects such as *Pyrrhocoris apterus* (HODEK, 1974) and *Riptortus clavatus* (NUMATA, 1987). Such a temporal oviposition under diapause promoting photoperiod was considered to be caused by a weakened diapause activated by increasing of temperatures when diapause development is not far advanced (HODEK, 1983). In fact, the proportion of females that retained photoperiodic sensitivity to 12L–12D decreased as they were collected later in the winter, although most females retained sensitivity to 8L–16D irrespective of the sampling date. Therefore the potential for diapause development of this bug lasts even after late December when diapause development should be complete. If the complete loss of sensitivity to 12L–12D, which coincides the daylength in early spring, is considered to be a criterion of the end of diapause, this bug ends reproductive diapause as late as late winter to early spring.

In order to explain the endogeneous mechanisms of diapause completion, HODEK (1983) proposed the interlocking two processes, “horotelic” and “tachytelic” processes. The former means the diapause development under diapause promoting conditions, and the latter means prompt completion of diapause activated by diapause averting conditions. The duration needed for diapause completion by “tachytelic” process becomes shorter as “horotelic” process advances. In *Pyrrhocoris apterus* (HODEK, 1974), completion of “horotelic” process leads to the completion of a change in both reproductive delay and the photoperiodic sensitivity. However, in *M. douglasi*, the temporal pattern in the change of the both traits did not coincide with each other. Therefore, “horotelic” process in this species may have more complicated physiological basis. Further studies are needed in this point.

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