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Adult Diapause Induced by the Loss of Water Surface in the Water Strider, *Aquarius paludum* (Fabricius)

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ABSTRACT—Adults of *Aquarius paludum* collected in autumn were reared on a water surface or, alternatively, on a wet-paper surface under 10L-14D at 20±2°C. After the photoperiod was changed to 15.5L-8.5D terminating reproductive diapause, the percent of individuals adopting diapause posture decreased from more than 50% to 20% on the water surface, while more than 50% of the individuals on the wet paper continued to show diapause posture for 35 days. Moreover the adults placed on the wet paper surface were less fecund than those on the water surface.

INTRODUCTION

Water striders of the genera *Aquarius, Limnoporus*, and *Gerris* are predatory bugs living on the surface of the bodies of fresh water [18]. In general, they survive winter as adults at overwintering sites on land, appear and reproduce on the water surface in spring and summer [18]. Loss of water surface by desiccation in spring and summer means loss of habitat for water striders and that situation seems to make them choose for flying to other water surfaces or for entering diapause behaviorally and reproductively at the site without water surface until water returns. Wilcox and Maier [20] reported that adults of a water strider, *Aquarius remigis* estivated facultatively with diapause posture during summer in damp area underneath stream bed-rocks when a pool in a small stream became dry. Estivation is common among insects and can be induced by relatively predictable factors of environment, such as photoperiod and temperature, or by unpredictable factors, such as wet or dry condition [1, 2, 13, 19]. Wilcox and Maier [20] showed the evidence for behavioral association with a damp-microhabitat, but not for specific cues that instigated the striders' diapause behavior in *Aquarius remigis*. In the case of water striders, the loss of water surface may be an important cue to induce estivation including diapause behavior and reproductive diapause. However, this point has not been studied so far.

Overwintered (long-winged) adults of *Aquarius paludum* kept under outdoor conditions laid eggs shortly after they were moved from fallen leaves to the water surface at the beginning of March, although the transfer to water surfaces was earlier than in nature [8]. This earlier reproduction suggests that the water surface is a cue that induces the maturation of the reproductive system. Conversely, the lack of water surface in reproductive season might be a causal factor of reproductive suppression or diapause.

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The present work aims at examining the effects of loss of water surface on diapause posture by adults and reproduction.

MATERIALS AND METHODS

Fifth instar nymphs destined to overwinter as adults were collected from a pond in Sakurai (34°31'N, 135°22'E), Nara Prefecture, Japan in the middle of October, 1992, and allowed to complete development under outdoor conditions. Males and females with the same wing form were paired just after emergence and held in individual plastic pots. Adults grown under short-days enter diapause, and the diapause is kept under short-days and terminated by long-days [7, 10]. Pairs were kept on water under a short-day (10L-14D) at 20±2°C for 20 days to remain diapause.

After that, some of them were moved onto wet paper. The rest was maintained on the water surface. Five days later, the photoperiod was changed to 15.5L-8.5D terminating reproductive diapause. Adults were checked every 1–2 days at 13:00 to see if they had adopted a diapause-posture (positioning of all six legs along the body to resemble a stick). In this study, the preoviposition period, which was defined as the days after the change to the long-day, and the number of eggs were examined evey 1–2 days.

The plastick pots, 14 cm in diameter and 5 cm in depth, were used for the rearing of adults and filled with water to a depth of 5–10 mm or with wet-paper on the bottom, and each pot was provided with a wooden stick, about 1 cm in diameter and 12 cm long, for oviposition or resting site. Water striders could walk on the wet paper and the stick was kept wet. Therefore the main difference between the two conditions was that in mechanical stimulus on the tarsa of the legs. The water and wet paper were exchanged every day and the striders were fed on flies *Fannia canicularis* L. every day at the rate of one per one pair.

RESULTS AND DISCUSSION

On the water surface, females began to lay eggs at 14–16 days after the change to the long-day photoperiod (Table 1). On the other hand, some of the females on the wet paper began to lay eggs as much as 10 days later, though the rest began to do so at the same time as those on the water surface. The number of eggs per female on the wet paper was similar

TABLE 1. Influence of shortage of water surface on the oviposition process

	On wet paper	On water surface
Preoviposition period (days)*	19.6±8.1 (7)	15.7±1.9 (6)
Number of eggs**		
0–5 days	29.3±14.7 (7)	40.0±13.0 (6)
5–10	48.6±26.9 (7)	52.0±22.2 (6)
10–15	36.3±21.8 (7)#	79.2±30.2 (6)
15–20	31.4±17.9 (7)#	55.2±18.2 (5)
20–25	23.0±22.8 (7)#	91.6±15.5 (5)
25–30	6.0±4.7 (4)#	67.8±23.5 (5)
Total fecundity***	180.4±105.8 (5)#	398.4±80.4 (5)

Values are mean±S.D. (n).
* Days after the change to the long-day photoperiod.
** Number every 5th day after the onset of oviposition.
*** Total number of eggs for 30 days after the onset of oviposition.
# $P<0.05$ on Mann-Whitney U-statistics for differences between the two conditions.

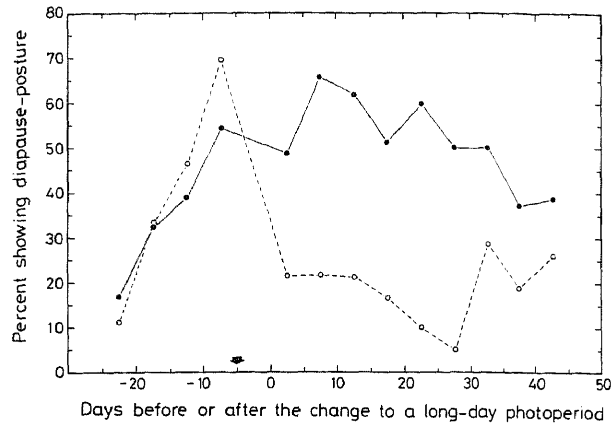

FIG. 1. Effect of a shortage of water surface on diapause-posture under 15.5L-8.5D at 20±2°C. Symbols are based on data obtained for 5 days. Open and solid circles are for the adults maintained on the water surface and wet paper, respectively. The day when adults were transferred onto the wet paper is shown with an arrow. n=28–96 for each 5 days in the wet-paper-group; n=16–72 in the water-surface-group.

to that on the water surface over the first 10 reproductive days (Table 1). After that, females on the water surface continued to lay 50–95 eggs per female and per 5 days over days 10–52 after which time they died (Table 1). However, on the wet paper, the number of eggs decreased (Table 1) and four of seven females finally stopped laying eggs 20–30 days after the onset of oviposition. The four females had no or only a few matured oocytes in their ovaries at the time they died, while the females on water surface had matured ones more than 20. In addition to seven females in Table 1, two females survived for 23 or 33 days after the change to the long-day without laying eggs and died on the wet paper.

Under the short-day photoperiod, the percent adopting diapause posture increased up to more than 50% on both the water surface and the wet paper (Fig. 1). On the water surface, the high number of individuals showing diapause posture decreased to 20% after the change to the long-day photoperiod. On the wet paper, however, diapause posture was mostly maintained for 35 days. The number was significantly higher on the wet paper than on the water surface through the 35th day after the change to the long-day photoperiod (χ^2-test: $P<0.05$). The number of females adopting diapause behavior was similar to that of males in both groups throughout the entire rearing period.

The loss of water surface induces the prolonged preoviposition period by some females and makes the adults take a diapause posture even under the photoperiod terminating adult diapause. These results suggest that the unpredictable loss of water surface is a factor delaying the termination of winter-diapause in spring. Moreover the dramatical decrease in fecundity and the following reproductive diapause which are caused by water loss imply the adopting of summer diapause in the case of dessication during reproductive season.

Polymorphism for dispersal ability or tendency is wide spread among insect species [3, 4, 11, 12]. Some studies on Gerridae and Gryllidae show that the proportion of winged adults, flight propensity or performance, development and maintainance of flight muscle, allocation of energy to triglycerides (flight fuel), ovarian development, and fecundity are genetically correlated and this series of correlatd traits can be called the migratory syndrome [5, 6, 14, 15, 16, 17]. *Aquarius remigis* of which the estivating adults were observed [20] show these traits with low dispersal tendency [6]. *A. paludum* also show relatively higher extent of wing reduction than other Japanese *Aquarius* and *Gerris* species excluding *G. amembo* [9, 10]. Therefore, when water in habitats goes dry, the adopting of diapause, which can be induced by the loss of water surface in *A. paludum*, is proposed to be also another negatively correlated trait for dispersal tendency.

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