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Sensitive Stages in the Photoperiodic Determination of Wing Forms and Reproduction in the Water Strider, *Aquarius paludum* (Fabricius)

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ABSTRACT—The present work was performed to clarify the photosensitive stage for wing-form determination and reproduction in *Aquarius paludum*. Only 40–60% of the adults were long winged when they were reared under 12 hr light–12 hr dark (12L–12D) during the first two instars and under 15.5L–8.5D during the rest of nymphal stage. However, all became long-winged, when they were exposed to 12L–12D until the end of the third instar. The exposure to 15.5L–8.5D till the end of the third instar induced short-winged adults of less than 15%, but long days until the fourth instar promoted about 40%. The exposure to long days either during the third, fourth or fifth instar promoted brachyptery, whereas all became long-winged when they were reared under long days either during the first or second instar. The exposure during the fifth instar induced maturing oocytes. The results indicate that the photosensitive stage for brachyptery occurs from the third to the beginning of the fifth instar, whereas that for oocyte maturation occurs during the fifth instar. Such a difference may refute the supposition of the oogenesis-flight syndrome that the two factors are tightly linked.

INTRODUCTION

Water striders belonging to *Aquarius*, *Gerris* and *Limnoporus* frequently exhibit wing dimorphism (Andersen, 1993; Spence and Andersen, 1994). *Aquarius paludum* (Fabricius) produces both brachypterous and macropterous morphs, which are under photoperiodic control: long days throughout the development induce brachyptery and reproduction, whereas short days throughout induce macroptery and diapause (Harada and Numata, 1993). The critical day length for the determination of wing forms was, however, longer by about 45 min than that for the induction of adult diapause for the populations in Kochi, Japan. The nymphs of the first generation in Kochi develop in May and early June when the natural day length is longer than either of the two critical day lengths for wing-form and reproduction. The majority (60%) become brachypterous and promptly begin to reproduce. The nymphs of the third generation develop in late September and October when the natural day length is shorter than the either of the two critical day lengths. Most of them become macropterous adults and enter diapause. The nymphs of the second generation develop in August and early September when the natural day length is between the two critical day lengths. Therefore, most of them become macropterous and promptly begin to reproduce, and a linkage between wing form and reproduction (short winged,

reproductive; long winged, diapause), supposed by oogenesis-flight syndrome (Johnson, 1969; Harrison, 1980) is not seen for the second generation. However, a tight linkage between the photosensitive stages for wing form and reproduction has not been established.

The present study investigates the sensitive stages for the two photoperiodic phenomena in *A. paludum* to elucidate this linkage.

MATERIALS AND METHODS

Macropterous adults (Exp 1, 2 and 4) of the second and third generations or brachypterous adults (Exp 3) of the first generation were collected from a pond or a waterway in Kochi, and they were reared under 15.5L–8.5D at $20 \pm 2^\circ\text{C}$ which promotes reproduction. Eggs laid by these females were kept under the same conditions. The first instar nymphs hatching from the eggs were used for the experiments. Fifteen to twenty individuals were reared in a plastic case ($34 \times 23.5 \times 4.5 \text{ cm}^3$) under different photoperiods at $20 \pm 2^\circ\text{C}$.

A group of nymphs derived from the above females were reared under 15.5L–8.5D until a specific instar and then transferred to 12L–12D, or vice versa (Exp 1 and 2). Another group of nymphs were exposed to 15.5L–8.5D during one specific instar and to 12.5L–11.5D (value close to the critical daylengths: 13L–11D for reproduction and 13.75L–10.25D for wing forms) during the other four instars (Exp 3). Still another group of nymphs were reared under 15.5L–8.5D only during one or two specific instars and under 9.5L–14.5D (far from the two critical daylengths) during the rest of the nymphal period (Exp 4).

At adult emergence, wing lengths were presented by relative lengths (wing index) to abdominal segments (Harada and Taneda, 1989), and classified as long-winged [females: (fore wing index, hind wing index) = (11,9); males: (12,11)], semi-long winged [females: (10,8), (11,8) or (10,9); males: (12,10) (12,9) or (11,10)], or short

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winged [females: (7-4,1-2); males: (9-7,5-1)].

After adult emergence, a single male and female pair was transferred to a plastic pot (14 cm diameter; 5 cm depth) and reared either under 9.5L-14.5D (Exp 4), 12L-12D (Exp 1 and 2) or 12.5L-11.5D (Exp 3). The detailed rearing method has been reported (Harada, 1992, 1993). Oviposition was observed for the first 30 days of adult life (Exp 3 and 4). Adults were dissected at 30 days after adult emergence to determine the presence and number of mature oocytes (Exp 1-4). Adults which had more than one mature oocyte were judged as non-diapause adults, while those having no mature oocytes as diapause ones (Exp 3,4).

RESULTS

The exposure to 12L-12D throughout the nymphal stage produced 100% long-wings, as did 15.5L-8.5D in the first instar, only (Fig. 1a,b). The exposure to 15.5L-8.5D until the second or third instar also induced a low percentage of short-wings, but caused a small percentage of adults to develop semi-long wings (Fig. 1c,d). The same exposure till the fourth instar, or later, produced many short-winged adults (Fig. 1e,f).

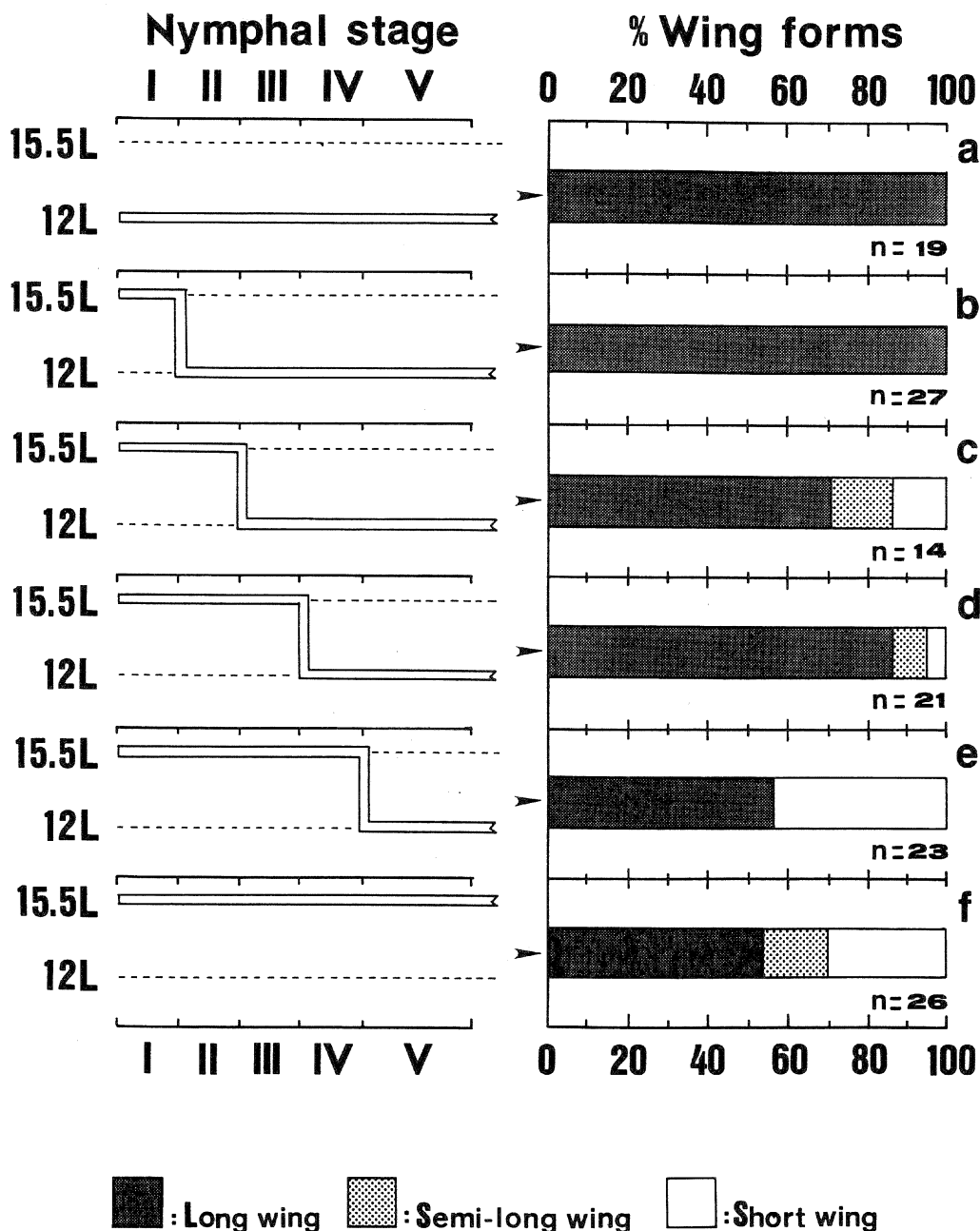


Fig. 1. Effect of transfer from 15.5L-8.5D to 12L-12D photoperiod during various instars on the induction of three wing-forms in *A. paludum*. Nymphs were transferred on the first day of new instars. Results of Fisher's exact probability test for the proportion of wing-forms: a versus b, c or d, $P > 0.05$; a versus e or f, $P < 0.05$.

Only 50% to 60% of the nymphs developed into the long-winged when they were placed under 12L-12D for the first one or two instars only, or under 15.5L-8.5D throughout nymphal stage (Fig. 2a,b,c). All became long-winged adults, when they had been grown under 12L-12D until the end of the third instar or later (Fig. 2d,e).

The exposure to 15.5L-8.5D during the first or the second instar produced no semi-longed or short-winged adults (Fig. 3b,c) as did 12.5L-11.5D through the whole nymphal stage

(Fig. 3a). The exposure to 15.5L-8.5D during the third (Fig. 3d) or fourth (Fig. 3e) instar induced small percentages of short-winged or semi-long winged adults. The exposure to 15.5L-8.5D during the fifth instar slightly increased the proportion of short-winged form (not significant of $P=0.051$). 15.5L-8.5D during one of the first to fourth instars failed to induce oocyte maturation in the majority of females (Fig. 3a-e). However, about 80% of females, when the fifth instar nymphs had been exposed to 15.5L-8.5D, produced mature

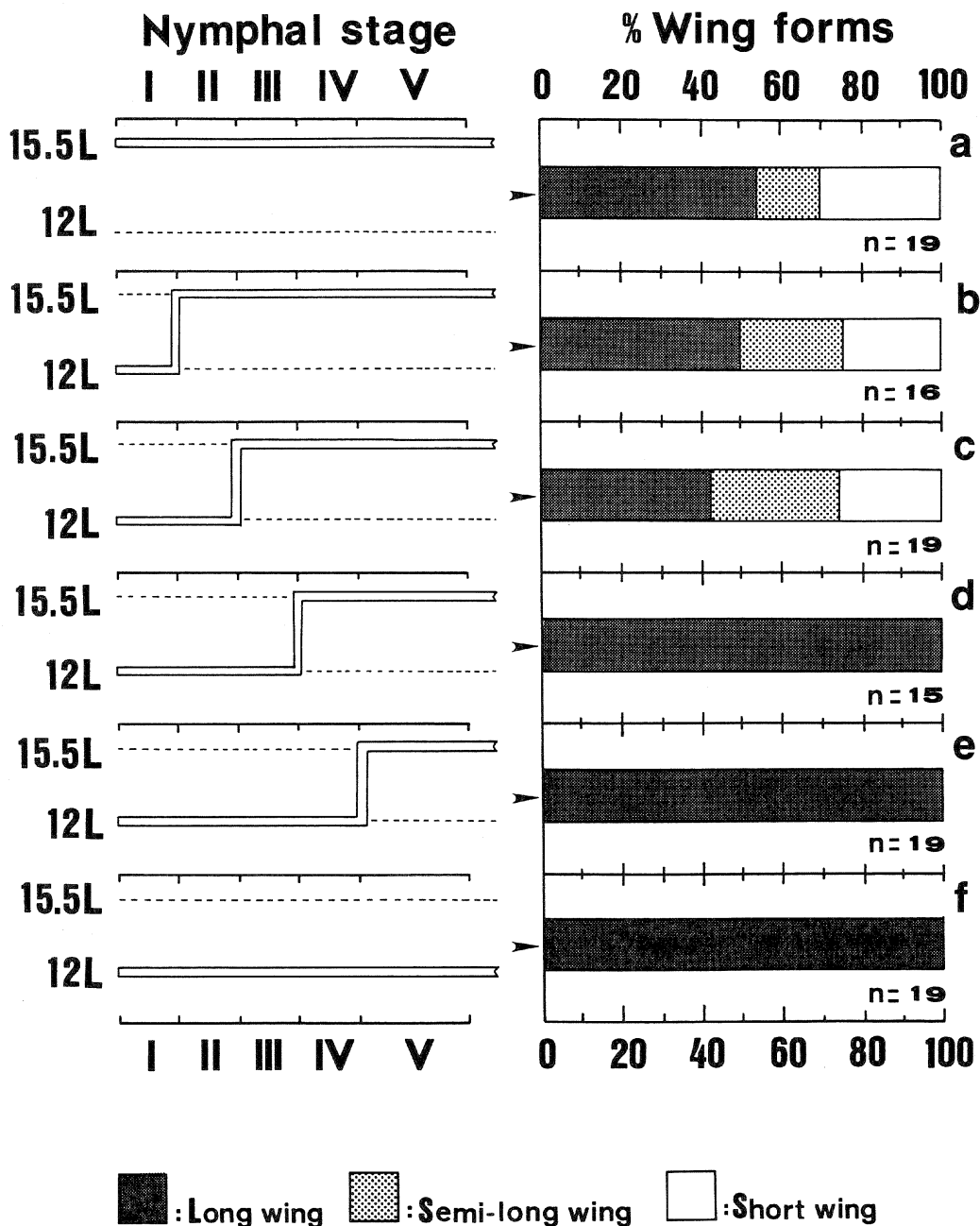


Fig. 2. Effect of transfer from 12L-12D to 15.5L-8.5D photoperiod during various instars on the induction of three wing-forms in *A. paludum*. Nymphs were transferred on the first day of new instars. Results of Fisher's exact probability test for the proportion of wing-forms: a versus b or c, $P>0.05$; a versus d, e or f, $P<0.05$.

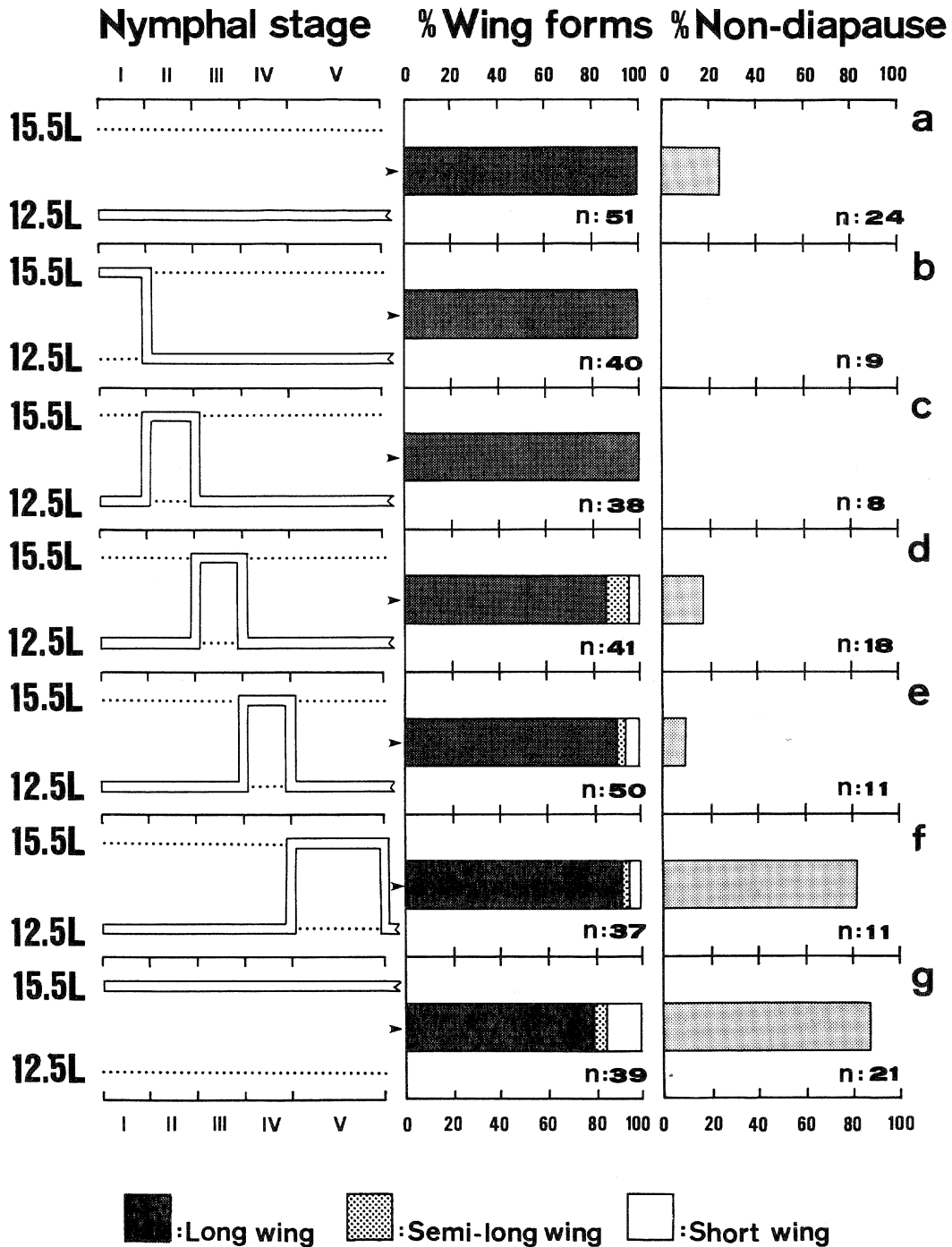


Fig. 3. Development into adults with each wing-form and reproductive maturation in Experiment 2 when the short-day photoperiod was set at 12.5L-11.5D in *A. paludum*. Results of Fisher's exact probability test for the proportion of wing-forms: a versus b, c or f, $P > 0.05$, a versus d, e, or g, $P < 0.05$.

oocytes (Fig. 3f). The mean number of mature oocytes in the females of this group was $8.6 (\pm 7.7; \text{SD})$, similar to that (10.1 ± 11.8) of the group exposed to 15.5L-8.5D throughout maturation. Although only 27% of the females oviposited within 30 days after adult emergence, 60.7% of the females did so in the 15.5L-8.5D control group. When nymphs were reared under 15.5L-8.5D only during the first two instars (Fig. 4b),

the next two instars (Fig. 4c), or the fifth instar (Fig. 4d), most of the nymphs became long-winged adults, unlike the results of Experiment 3. This difference is due to the fact that the short day in Experiment 4 was 9.5 hr, shorter by 3 hr than that in Experiment 3 (12.5 hr). Half of the nymphs became short-winged adults in the 15.5L-8.5D control group (Fig. 4e). 15.5L-8.5D during the first two or the next two instars failed to induce

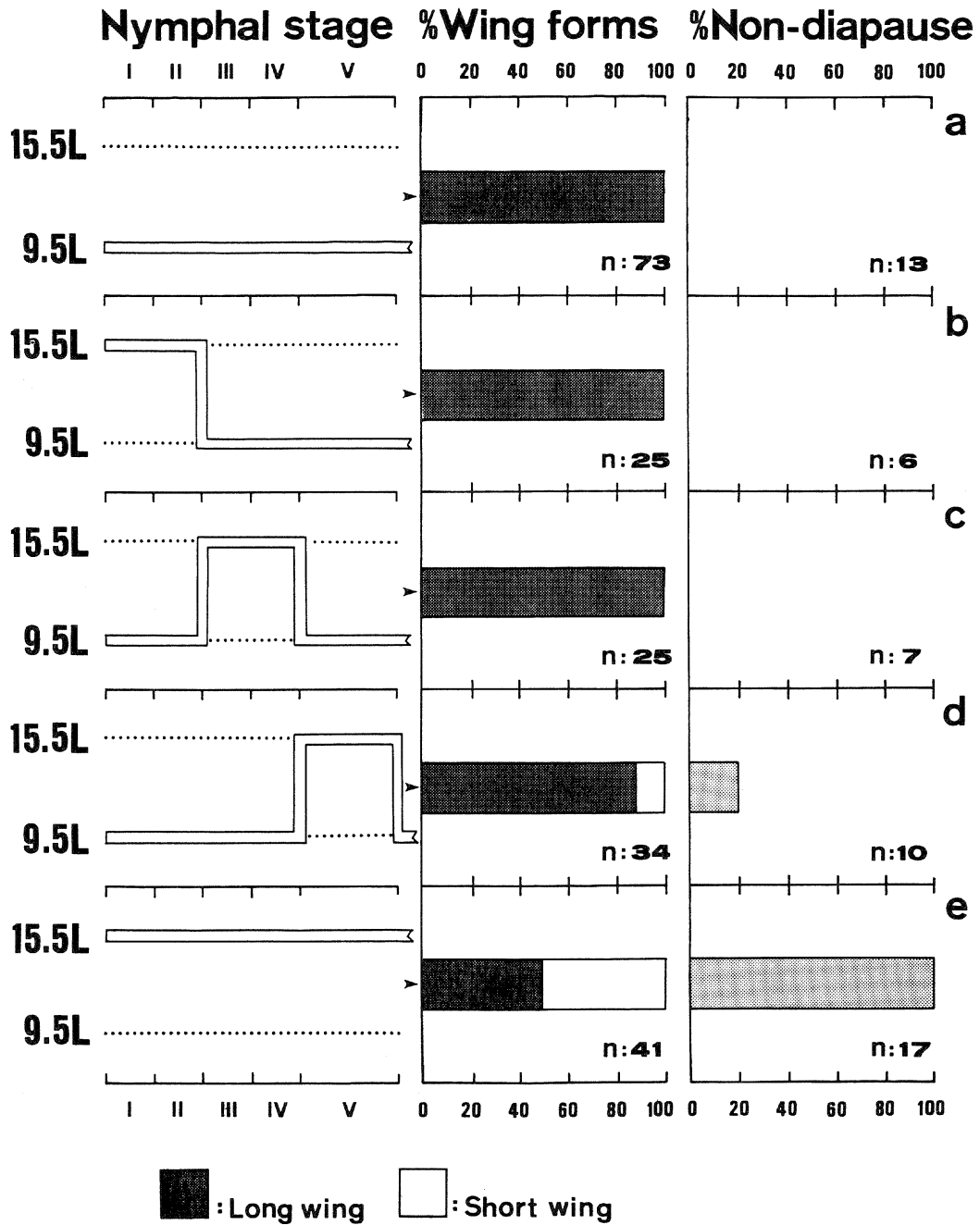


Fig. 4. Development into adults with each wing-form and reproductive maturation in Experiment 3 when 9.5L-14.5D was used in *A. paludum*. Results of Fisher's exact probability test: a versus b, c or d, $P > 0.05$; a versus e, $P < 0.05$.

maturation of oocytes (Fig. 4b,c). Only two of the ten females had mature oocytes when they had been exposed to 15.5L-8.5D during the fifth instar (Fig. 4d), unlike the results in Exp. 3. All of the females had, however, mature oocytes in the 15.5L-8.5D control-group (Fig. 4e).

DISCUSSION

In *Aquarius paludum*, the photosensitive stages for the determination of wing-form are mainly the third and fourth

instars, because:

1. Long days until the end of the fourth instar or later induced many short-winged adults in Experiment 1 (Fig. 1).
2. Short days until the end of the third instar or later caused all the individuals to become long-winged adults in Experiment 2 (Fig. 2).
3. Long days at a specific stage of the third or fourth instar had a significant wing-shortening effect (Fig. 3).

Zera and Tiebel (1991) reported that the sensitive stage for the determination of wing-forms was restricted to the second

instar in *Limnopus canaliculatus*: 16L-8D and 12L-12D induced apterous and macropterous adults, respectively. Wing-pad development was strikingly different between the two wing forms in *L. canaliculatus*. This difference appears earlier in *L. canaliculatus* (at the beginning of the third instar or earlier) than in *A. paludum* (during the fifth instar) [Fig. 546 in Andersen (1982); Harada, unpublished]. In both species, the sensitive stage occurs mainly just before the stage at which the morphology of wing pads differentiates between the two wing-forms.

Aquarius paludum is the most sensitive in the last instar with respect to reproduction, as in other water striders, *Gerris odontogaster* (Kopfli *et al.*, 1987) and *G. comatus* (Spence, 1989), and in other insects, such as *Anopheles maculipennis* (Vinogradova, 1960), *Oncopeltus fasciatus* (Dingle, 1974), and *Anthocoris nemorum* (Parker, 1975). However, relatively long durations of sensitivity were suggested in water striders *Gerris buenoi* and *Limnopus dissortis* (Spence, 1989). The long sensitive stage for reproduction corresponds to that for wing form determination in these species and this correspondence fits to the Vepsäläinen's model (Vepsäläinen, 1978) that brachyptery and direct breeding (macroptery and diapause) are tightly linked according to the oogenesis-flight syndrome (Johnson, 1969) and that wing-form and reproduction are controlled by photoperiod in the same way. However, the present investigation revealed different sensitive stages for wing-form determination (the third and fourth instars) and reproduction (the fifth instar) in *A. paludum*, which suggests the tight linkage between wing-form and reproduction is not always the case.

In the present study, a long day photoperiod during either the third or fourth instar produced some short-winged adults, even when nymphs were reared during the rest of their nymphal stage under 12.5L-11.5D, a photoperiod near the critical one that is 13.75L-10.25D for the populations in Kochi (Harada and Numata, 1993) (Fig. 3). This effect of long day photoperiod was, however, suppressed by the exposure to 9.5L-14.5D, which is much below the critical value, during the first and second instars (Fig. 4). Moreover, reproductive maturation caused by long days during the fifth instar was also inhibited by exposure during the rest of nymphal and adult stages to 9.5L-14.5D, but not by 12.5L-11.5D (Figs. 3,4). The results suggest that various photoperiods are not detected merely as 'long days' or 'short days'. Both wing-form determination and reproductive diapause appear to be based on the quantitative assessment of photoperiodic information. *Pieris brassicae* (Lepidoptera) and *Plautia stali* (Heteroptera) also assess photoperiod quantitatively for the induction of diapause (Spieth and Sauer, 1991) and nymphal body coloration (Numata and Kobayashi, 1994), respectively. Also in the case of *A. paludum*, quantitative assessment is performed and this quantitative information is converted to 'all-or-none' responses as diapause vs non-diapause or long-wing vs short-wing. However, it is not known where the quantitative information is converted to 'all-or-none' information in the effector system as described by Beck (1980), which

could be at a photoperiod-accumulation-level, a neurosecretion level, an ecdysteroid or juvenile hormone level, or a hormone sensitivity level with respect to the effects on wing pads and the ovary. The conversion from the quantitative information to 'all-or-none' information should be clarified by future studies.

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