A Preliminary Study on Effects of Nymphal Density on Nymphal Duration and Reproduction in the Water Strider *Aquarius paludum**

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ABSTRACT

The reduction of water surface by dessication is dangerous for water striders especially for nymphs. This study aims at clarifying whether the water strider *Aquarius paludum* uses increasing population density as signal of the reduction of their habitat. It took a slightly shorter time for nymphs to grow up at high density (14.4-4.4 nymphs / 100cm²) than at low density (7.8-1.3 nymphs / 100 cm²). High density during nymphal stage caused lower fecundity than was seen under low density. These results suggest that *Aquarius paludum* uses high density as signal of reduction of their habitat in the field.

Key words: Nymphal density, nymphal duration, reproduction, wing dimorphism, water strider

INTRODUCTION

Water strider (Heteroptera, Gerridae) inhabit permanent and / or temporary water surfaces, and wing polymorphism is common in species living in temperate zones (Andersen 1973, Vepsäläinen 1978, Carabrese 1979, Zera 1983, Spence 1989). The greater the habitat-stability is, the higher the proportion of wing-reduced individuals is (Vepsäläinen 1978). The size of permanent, and the number of temporary, water surfaces vary with seasonal changes in temperature, solar radiation, precipitation, etc., and with non-seasonal aspects of weather (Vepsäläinen 1978). Drying of ponds or streams is very dangerous for the nymphs of water striders, because they have a soft cuticle and seem to suffer a greater loss of water than do adults. Nymphs may use increasing density as one signal of reducing water surfaces. Population density during the nymphal stage may affect growth, wing form and allocation of nutritional source between flight and reproduction after adult

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emergence. Muraji (1989) reported that the wing morph ratio of a semi-aquatic bug, *Microvelia douglasi* is affected by nymphal density: high density induces high proportion of macropterous form. Among Gerridae, however, no reports have been made on the effects of population density during the nymphal stage on the physiological and morphological characters described above. The present work aims at investigating the effects of nymphal density on nymphal duration and adult oviposition in the water strider *Aquarius paludum*.

MATERIALS AND METHODS

Overwintering adults (nearly all macropterous) of *Aquarius paludum* collected from a water way in Kochi, Japan (33° 30' N, 133° 35' E) in late April, 1989 were reared in pairs in plastic pots 14 cm in dia and 5 cm in depth. Photoperiod and temperature were maintained at 15.5h light-8.5h dark and 25 ± 2℃ throughout the rearing. For the experiments, the first newly-hatched instar nymphs were used. They derived from the eggs which had been laid by the 12 overwintering females. Nymphs were reared under high or low density during the nymphal stage (Table 1), and the plastic pots were checked for exuviae once a day, at 12:00, to determine whether or not moulting had occurred. After adult emergence, one male and one female showing the same wing form were reared in a single plastic pot. The preoviposition period was examined in each pair, and the number of eggs counted every 1-2 days.

Table 1. Percentage of survival in high and low densities for the immature and adult stages in *Aquarius paludum*.

		Instar					Adult
		1	2	3	4	5	
High density (48 [a])	Density [b]	21.6	16.4	12.1	9.8	6.8	2
	Percentage [c]	100	58.3	41.7	33.3	29.2	27.1
Low density (128 [a])	Density [b]	12.0	8.2	6.5	4.5	2.0	2
	Percentage [c]	100	57.0	39.1	31.3	29.7	26.6

a Number of nymphs at the beginning of 1st instar stage
b Number of nymphs / 1 pot (water surface: 153.9 cm²)
c Percentages are derived from the number of nymphs entering each instar stage.

RESULTS

During the nymphal stage, the process of percentage survival at high density was similar to that at low density (Table 1). The duration of the first instar at high density was slightly longer than that seen at low density [high density: 5.2 ± 1.2 days (mean $\pm$ S.D.), low density: 4.7 ± 1.0 days; Mann-Whitney U-test : $z = 1.67$, $P = 0.048$] (Fig. 1).

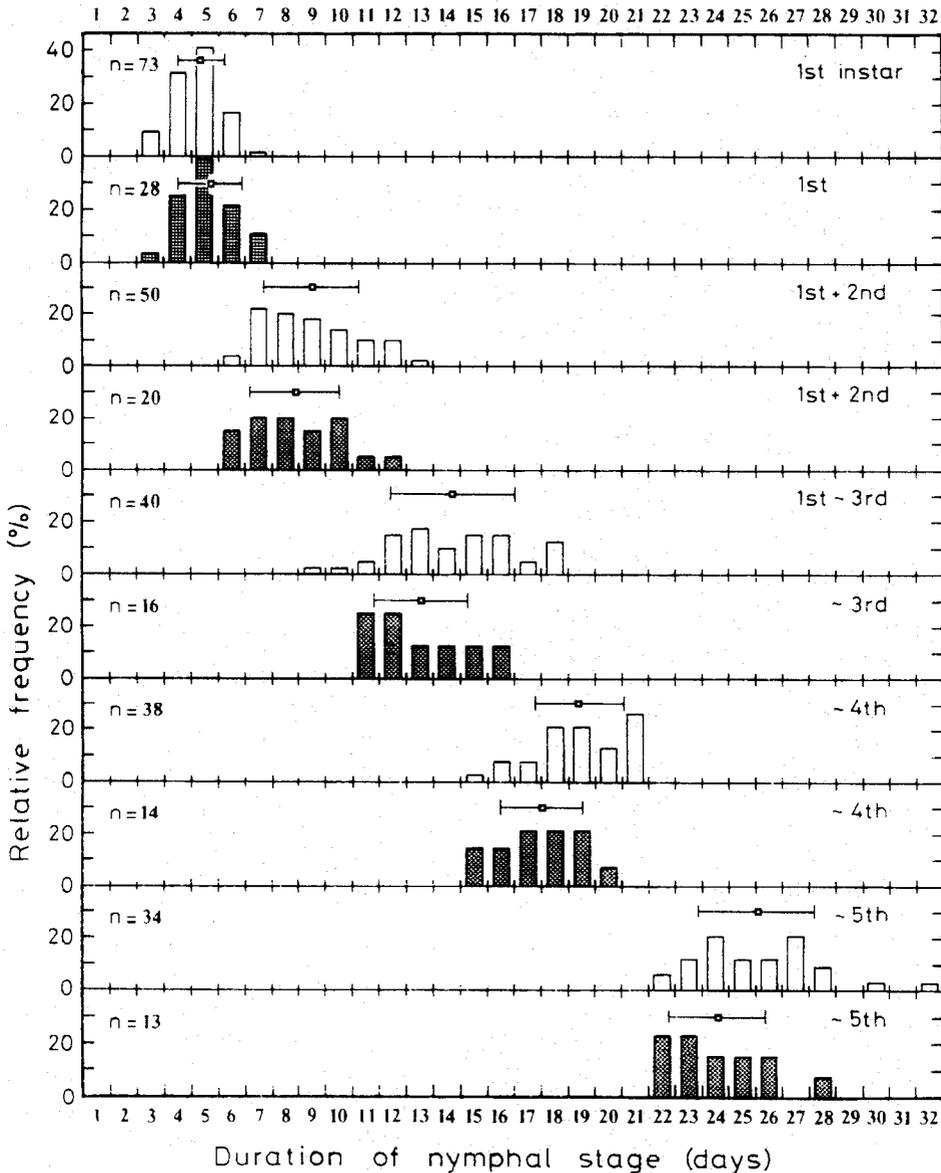Fig.1. Duration of the nymphal stage of high (▨) and low (☐) density groups under 15.5h light-8.5h dark and at $25 \pm 2°C$. Circles and bars show means and S.D. respectively.

However, the duration of the second to fourth instars at high density was significantly shorter than that seen at low density [the first two instars: 8.4 ± 1.7 days (high density), 9.0 ± 1.8 days (low density); the first three instars: 13.0 ± 1.8 days (high), 14.3 ± 2.4 days (low); the first four instars: 17.4 ± 1.6 days (high), 19.0 ± 1.7 days (low), Mann-Whitney U-test, z = 2.6, $P < 0.01$] (Fig. 1). The difference in duration of the entire nymphal period (1.5 days) between the two density groups was similar to that of the first four instars (1.6 days) [the whole nymphal stage: 24.1 ± 1.9 days (high), 25.6 ± 2.3 days (low)] (Fig. 1). No difference between the density groups in duration of the last (5th) instar was observed. Although the deviation from the mean of the duration increased over the course of nymphal development in the low density group, it remained low in the high density group [F-test between the duration of the first instar and that of the whole nymphal stage: $P < 0.01$ (low density), $P > 0.05$ (high density)].

Thirteen adults (4 females, 9 males) and 34 adults (22 females. 12 males) emerged in the high and low density groups respectively. The proportion of macropterous forms in the high density group (92.3 %) was thought to be higher than in the low density group (73.5 %), although the difference could not be inferred statistically because of an insufficient number of samples within the high density group. Three macropterous pairs were set up using individuals from the high density group while seven macropterous and four brachypterous pairs were set up using low density individuals. The preoviposition period shown by macropterous females was slightly longer in the high density group than in the low density group (Table 2). Macropterous females in the high density group were less fecund than either macropterous or brachypterous females of the low density group throughout the entire reproductive period (Table 2). Total fecundity in the high density group was about half that of the low density group. The rate of oviposition by brachypterous females peaked during the first ten days (Randomization test between the first 10 days and the 10-20 days: $P < 0.05$). On the other hand, the rate of oviposition by macropterous females was significantly higher in the days 10-20 than it had been before, or was after, in both density groups (Randomization test between days 10-20 and each of the first 10 days and days 20-30: $P < 0.05$). In the low density group, total fecundity by macropterous females was similar to that of brachypterous females (Mann-Whitney U-test: $P > 0.05$) (Table 2).

DISCUSSION

In *Aquarius paludum*, high population density in the nymphal stage accelerates the growth rate in the second through fourth instars (Fig. 1). Crowded larvae grow faster than do uncrowded larvae in the armyworm *Leucania unipuncta* (Lepidoptera) (Iwao 1956, 1959) and the flesh fly *Sarcophaga bullata* (Diptera) (Baxter and Morrison 1982). In most of the species of higher Diptera examined so far, however, growth rate is reduced at higher population densities (Bryant 1969, Bakker 1969, Beaver 1974). In *Leucania unipuncta*, population density during the second half of larval stage is effective on the growth rate

Table 2. Effect of density in the nymphal stage on oviposition process
[mean ± S.D. (n)] under 15.5h light-8.5h dark at 25±2℃.

	High density	Low density	
	Macropterous	Macropterous	Brachypterous
Preoviposition period (days)	13.3±6.1 (3)	9.9±1.9 (7)	10.8±1.9 (4)
Number of eggs*			
0−10	39.3±27.6 (3)	71.3±26.7 (7)	151.8±42.8#(4)
10−20	84.0±67.2 (3)	130.0±33.2 (6)	119.0±31.2 (4)
20−30	34.3±18.5#(3)	83.5±33.4 (6)	58.8±43.4 (4)
30−40	40.3±35.5#(3)	81.4±10.5 (5)	86.5±15.0 (4)
40−50	51.1±46.1 (3)	84.0±33.8 (5)	76.8±20.3 (4)
Total fecundity**	249.0±58.6#(3)	478.4±83.2 (5)	492.8±98.8 (4)

* The number of eggs for every 10 days after the onset of oviposition
** The total number of eggs for 50 days after the onset of oviposition
\# P<0.05 on Mann-Whitney U-statistics for difference between macropterous females grown in high and low densities, or between macropterous and brachypterous females in the low density group.

(Iwao 1959). The sensitive stage seems to be included in the first to fourth instars in the case of *Aquarius paludum* (Fig. 1).

High population density may induce a high proportion of macropterous forms in *Aquarius paludum* (Table 2), as it does in some species of Aphididae, Delphacidae (Homoptera)(Harrison 1980). It has, however, brachypterizing effect in *Gryllus rubens* (Orthoptera)(Zera and Tiebel 1988). Crowding or high population-density in the larval stage induces or enhances the level of photoperiodically controlled diapause in some lepidopterous and coleopterous species (Danks 1987). In *Aquarius paludum*, high density during the nymphal stage cannot induce reproductive diapause (Table 2). However, it can reduce the number of eggs (Table 2). The means by which the density effects operate cannot be defined on the growth rate, wing form and reproduction by *Aquarius paludum*. But we can eliminate the state or amount of food as an indirect cue in this study, differing from the case of *Cydia pomonella* by Brown *et al.* (1979). Mechanical stimuli and / or chemical cues may be the means by which density elicits its effect.

Shortage of temporary habitats as a result of deciccasion is possible after the rainy season of June and the first ten days of July in Kochi. Therefore, in temporary habitats where only macropterous parents are present after dispersal, the mortality of nymphs due to dried up habitats is possible [the second generation nymphs of *A. paludum*: Harada (1992)]. The reduction of water surface leads to an increase in population density. In this

type of dry season, the growth rate rises higher because of the high density (Fig. 1), and more nymphs can grow up before the water surface dries up.

Macropterous adults grown under high-density conditions show lower fecundity than do either macropterous or brachypterous females grown under low density (Table 2). In some insect species, adults allocate the available resources to flight capability versus reproduction (Tauber *et al.* 1986). Macropterous adults in *Aquarius paludum* grown at high population densities seem to spend more resources on flight capability than do those grown in low density. The longwinged water strider *Gerris thoracicus* has two morphs, fliers and non-fliers, with regard to maintaining flight ability during the reproductive period. Fliers maintain flight muscles throughout the reproductive period and lay fewer eggs than do non-fliers, which histolyze their flight muscles (Kaitala 1988). High density in nymphal stage may produce "flier" macropterous adults and low density promoting "non-flier" in *Aquarius paludum*, although no experimental evidence is available on the ability of these macropterous adults to fly.

During the first ten days of reproduction, the fecundity of brachypterous females is higher than that of macropterous females in the low density group (Table 2). No significant difference is, however, seen between the two wing forms over the first 50 reproductive days, which accords with the data Harada (1992) has presented on individuals grown under 15.5h light-8.5h dark and at 20 ± 2°C through the nymphal and adult stages. This difference shown by *A. paludum* between the two wing forms in the oviposition process has been also reported in *G. buenoi* and *G. pingreensis* (Spence 1989). In view of the oögenesis-flight syndrome (Johnson 1969, Harrison 1980), macropterous adults grown in low population density may supply some part of the restricted resources to flight only in the prereproductive and early reproductive period before the hystolysis of flight muscles occurs (Table 2).

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