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Migratory syndrome in the water strider *Aquarius paludum* (Heteroptera: Gerridae) reared in high versus low nymphal densities

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Gerridae, *Aquarius paludum*, water striders, rearing density, migratory syndrome, flight propensity, indirect flight muscles, reproduction

Abstract. The effect of crowding in nymphal stage on the induction of development of macropterous adults with high flight ability was studied in the laboratory in the water strider *Aquarius paludum*. High density induced a higher proportion of macropterous morphs than low density. No brachypterous adults developed flight muscles in either experimental density. When kept under high density, about 80% of adults kept indirect flight muscles for 25–30 days after adult emergence, whereas only about 50% or 60% of females and males, respectively, retained theirs when grown under low density. The remaining adults histolysed indirect flight muscles in both groups. Development during the fourth and fifth instars only under high density may induce a higher proportion of macropterous adults than those under low density.

INTRODUCTION

Water striders (Heteroptera: Gerridae) inhabit permanent and/or temporary water bodies, and wing polymorphism is common in species living in temperate zones (Andersen, 1973; Vepsäläinen, 1978; Calabrese, 1979; Zera et al., 1983; Spence, 1989). The greater the habitat stability, the higher the proportion of individuals with reduced wings (Vepsäläinen, 1978; Roff, 1986; Spence, 1989; Fujisaki, 1994). *Aquarius paludum* inhabits both permanent and temporary water bodies, and the number of temporary habitats (small streams and puddles) increases after two rainy seasons (mid June to mid July and September) in Kochi, Japan (Harada & Numata, 1993). The size and number of water bodies affects the population density of this species in the field.

High population density is not favourable for nymphal development and reproduction because it leads to a decrease in food supply and habitat area, resulting in serious competition between individuals. Crowding may affect growth, induction of wing morph and allocation of energy between flight and reproduction. Muraji et al. (1989) reported that the wing morph ratio of a semi-aquatic bug, *Microvelia douglasi* is affected by nymphal density: high density induces a high proportion of macropterous morphs. No association between density and morph frequency was observed in samples of over 30 natural populations of *Limnoporus canaliculatus* suggesting that population density does not influence morph determination (Zera et al., 1983). Järvinen & Vepsäläinen (1976) discussed that density is unlikely to influence morph determination in gerrids during any developmental stage. However, no experimental studies have been made on the effects of population density during nymphal stages on dispersal polymorphism and reproduction in Gerridae.

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Density has been estimated by some absolute methods in *Gerris argentatus* (Järvinen et al., 1977: 0.37–3.63 nymphs of 1–4 instars/100 cm^2) and in *G. buenoi* and *G. pingreensis* (Spence, 1980: 0.03–0.6 individuals in all stages/100 cm^2 in *G. buenoi*, 0.008–0.80 individuals in all stages in *G. pingreensis*) in natural populations. However, there have been no data on density-estimation in *A. paludum*.

The present work investigates the effects of nymphal density on nymphal duration and some traits related to "the migratory syndrome" (Dingle, 1985; Fairbairn, 1994) i.e., wing development, flight propensity, development and maintenance of flight musculature, duration of pre-oviposition period and fecundity.

MATERIAL AND METHODS

Adults (nearly all macropterous and ready to overwinter) of *Aquarius paludum* were collected from a pond in Kochi, Japan (33°30′N, 133°35′E) in October, 1994. They were reared in pairs in plastic pots 14 cm in diameter and 5 cm in depth under the photoperiod of 15.5L : 8.5D and 20 ± 2°C (conditions terminating diapause: Harada & Numata, 1993). Newly-hatched nymphs, from eggs which had been laid by more than 12 females, were used for experiments. The first instar nymphs were reared in plastic cases with a surface area of about 800 cm^2.

An experimental condition of high density was used where each nymph is given only a surface area which one adult of *A. paludum* occupies on water bodies. According to this definition, the value of high density was calculated at 4.0 to 5.0 individuals/100 cm^2, and low at 1/4 or 1/5 of it. Two groups of the nymphs were reared either at high or low density through the whole nymphal stage. A third group of nymphs was first reared at low density and transferred to high density at the beginning of fourth instar. Each day, one fly of *Lucilia illustris* was given per five first and second instars, one per three third and fourth instars, and one per two fifth instars. The plastic cases for rearing nymphs were checked for exuviae once a day, at 12:00, to record moulting.

After adult emergence, indices of wing lengths were given by relative lengths according to their abdominal segments (Harada & Taneda, 1989). If the indices of hind wing length are more than 7, the bugs are considered macropterous. The indices less than 3 indicate those brachypterous (Harada, 1993). Immediately after emergence, pairs were formed from males and females belonging to the same density group and having the same wing morph. They were reared to study development of flight muscles and maturation of reproductive organs. One fly of *L. illustris* was supplied to one pair of adults every 2 days. The details of rearing of *A. paludum* were reported in Harada (1992, 1993).

Pre-oviposition period was recorded in some females of the three experimental groups. Some of the other adults were sampled every 8 or 10 days after adult emergence and dissected. The number of mature oocytes was counted, width of testes was measured and conditions of flight muscles were recorded and classified to three ranks. The criteria used by Fairbairn & Desranleau (1987) were simplified to the following: Rank 3: Indirect flight muscles large, fibrous and reddish, corresponding with "normal" in Fairbairn & Desranleau (1987); Rank 2: Flight muscles smaller, soft, white, corresponding with "teneral: advanced" or "histolysed: early" and Rank 1: Muscle fibres not visible, corresponding with "histolysed: advanced or complete" or "teneral: early".

Flight experiment

A white paper was placed on the bottom of a cylindrical transparent box (30 cm in diameter, height 15 cm), and an adult water strider was transferred from the rearing pot into a transparent cylindrical enclosure (5 cm inner diameter) placed at the centre of the box. Infra-red light warmed the bottom of the case to maintain the temperature at 30 ± 2°C. The individual insect was illuminated for 1 min with a beam of blue light (about 3,400 Lx) from a tungsten lamp through a glass filter. The individual was illuminated from the side to trigger the flight. Both high temperature and the blue light were essential stimuli. The enclosure was then picked up and the bug was given two minutes to move. The stimulation by the blue light and the following observation were repeated twice (Fig. 3). In most cases when bugs took off, they flew for less than 0.5 seconds, stopped flying and folded their wings. The number of flights was recorded as an index of "flight propensity".

RESULTS

Duration of development and survival

The duration of the first instar at high density was slightly shorter than at low density [9.3 ± 1.6 days (mean ± S.D.) vs. 9.9 ± 2.2 days; Mann-Whitney U-statistics: $P < 0.05$) (Fig. 1). The difference grew larger as the stage progressed, being about 6 days for the whole nymphal period (41.3 ± 2.0 days vs. 47.5 ± 3.3 days; Mann-Whitney U-statistics: $P < 0.05$) (Fig. 1). More nymphs developed to adults over 50 (or more) days at low density than in the low-to-high density (Fig. 1), although no significant difference was shown between these two groups in whole nymphal duration (Mann-Whitney U-statistics: $P > 0.05$ between low and low-to-high density groups).

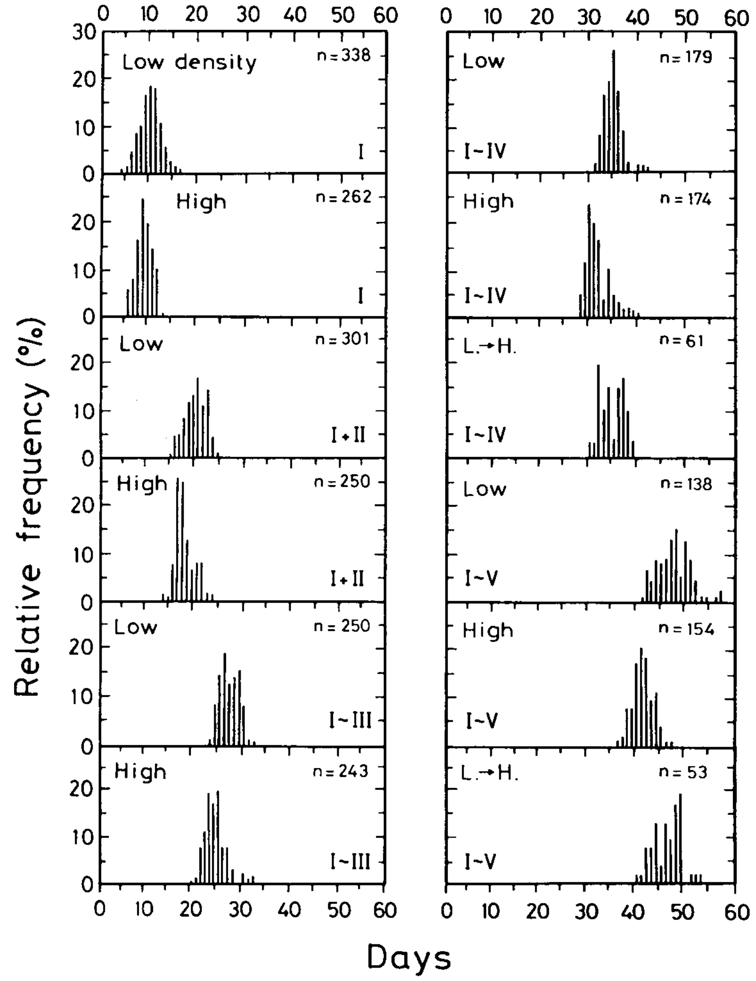

Fig. 1. Duration of the nymphal stage under high, low, and low-to-high (L→H) density at 18 ± 2°C. I, I+II, I–III, I–IV, I–V show duration of nymphal development to the end of first, second, third, fourth and fifth instar, respectively.

During nymphal development, the survival rate was significantly higher under high density than low density: % survival at the beginning of the 3rd instar, 91.9% versus 76.6% (high vs. low density groups); 4th instar, 89.3% vs. 63.6%; 5th instar, 64.0% vs. 45.6%; adult emergence, 56.6% vs. 35.1% (χ^2-test in survival rate at adult emergence: $P < 0.001$).

Proportion of macropterous morphs

The proportion of macropterous morphs in the high density group was significantly higher than in low density (Fisher's Exact Probability test: $P = 0.0118$ between the both groups in females; $P = 0.0091$ in males) (Table 1). Males showed higher proportion of macropteous morphs than females in high and low density groups (Fisher's Exact Probability test: $P = 0.0003$ in high density groups, $P = 0.0023$ in low density group). High density only during the 4th and 5th instars induced a higher proportion of macropterous females than low density (Fisher's Exact Probability test: $P = 0.0153$ in females. $P > 0.05$ in males).

TABLE 1. Incidence of macropterous individuals (%) after rearing at different nymphal densities in *Aquarius paludum*. Number of individuals in parentheses.

	Low density	Low-to-high density	High density
♀	62.0 (57)	90.0 (20)	81.3(80)
♂	87.8 (57)	90.0 (20)	98.7(80)

Duration of pre-oviposition period

The pre-oviposition period of macropterous females was significantly longer in the high density group than that in low density (Mann-Whitney U-statistics: $P < 0.05$) (Table 2). High density only in the 4th and 5th instars also tended to induce longer pre-oviposition period than low density, although there were no statistically significant differences (Mann-Whitney U-statistics: $P > 0.05$) (Table 2).

TABLE 2. Effect of nymphal density on oviposition [mean ± SD (n)] in *Aquarius paludum*.

	High density	Low to high	Low density
Preoviposition period (days)			
Macropterous	21.1 ± 4.2 (34)	21.8 ± 7.6 (13)	16.6 ± 5.3 (19)
Brachypterous	15.8 ± 2.4 (5)	36.5 ± 6.4 (2)	16.1 ± 2.6 (16)
Fecundity for 40 days*			
Macropterous	330.2 ± 111.1 (6)	214.7 ± 55.3 (7)	298.0 ± 44.0 (4)
Brachypterous	—	—	303.5 ± 58.6 (6)

* The number of eggs for 40 days after the onset of oviposition.

Fecundity

There were no significant differences in the total fecundity for 40 reproductive days between the low and high density groups (Mann-Whitney U-statistics: $P > 0.05$). The fecundity of females in the low-to-high density group was significantly lower through the 40 reproductive days than in the other two groups (Mann-Whitney U-statistics: $P < 0.05$).

Most females in the low and high density groups matured oocytes during 10 to 30 days after adult emergence. Testes grew larger gradually during the first 30 imaginal days in both density groups.

Flight muscles

Indirect flight muscles in the mesothorax of macropterous adults developed from Rank 1 to 3 during the first 10 days after emergence in most adults of both density groups (Fig. 2). Only 20% of adults in the high densitgy group histolysed their indirect flight muscles before the adult age of 30 days, whereas 55% of females and 40% of males did so in the low density group (Fisher's Exact Probability Test for equal proportion of adults having muscles histolysed down to Rank 1 or 2 during 25–30 days, females and males pooled: P = 0.052). No brachypterous adults developed indirect flight muscles through the 30 days.

Flight tendency

In flight experiments, individuals induced to show more than 3 flights during 2 min after 8 min for warming up were defined as high-propensity fliers (Fig. 3). There was no significant difference in the proportion of high-propensity fliers between the adults of both density groups (Fisher's Exact Probability Test: P > 0.05).

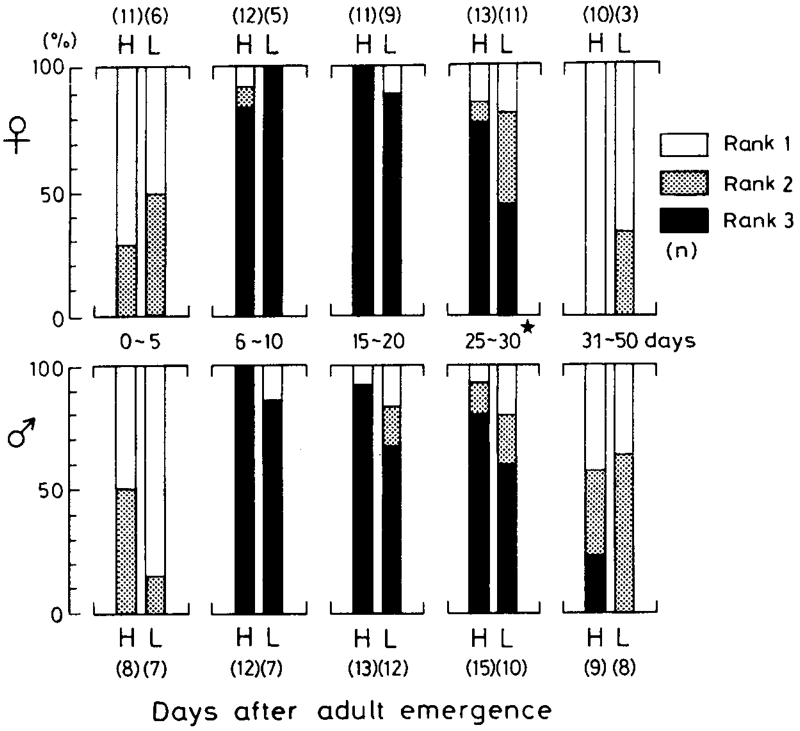

Fig. 2. Conditions of indirect flight muscles in the adults grown under high or low density. H – high density group; L – low density group. ★ – $P < 0.05$, χ^2-test for equal proportion of adults having histolysed muscles. Numbers in parentheses indicate n.

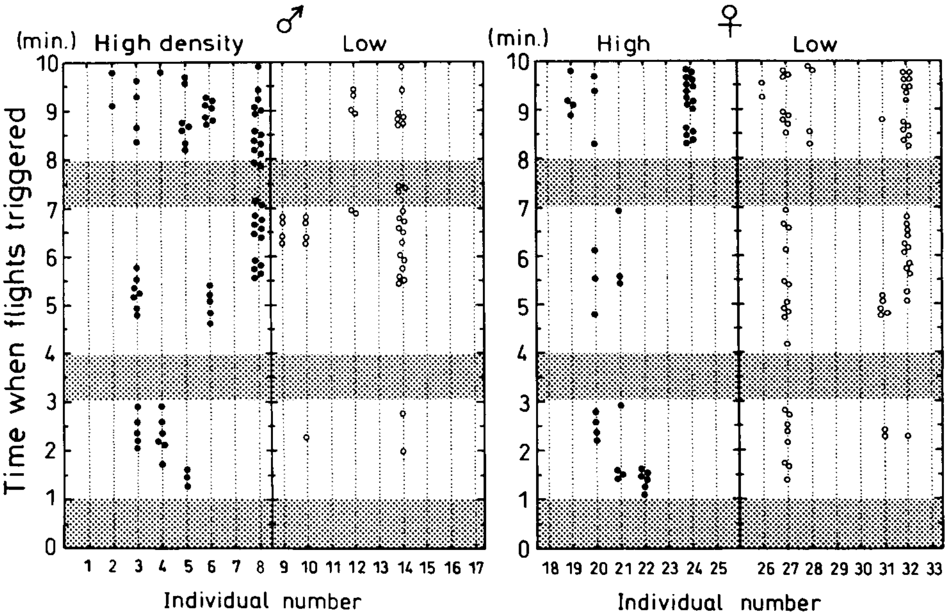

Fig. 3. Flight propensity of adult *Aquarius paludum* (on the 10th day after adult emergence), reared in high vs low nymphal densities. A dot shows one flight triggered. Shaded area shows the duration when a tested adult was exposed to triggering blue light.

DISCUSSION

Crowding accelerated the growth rate in *Aquarius paludum*. Crowded larvae grew faster also in the armyworm *Leucania unipuncta* (Lepidoptera: Noctuidae) (Iwao, 1956, 1959) and the flesh fly *Sarcophaga bullata* (Diptera: Sarcophagidae) (Baxter & Morrison, 1982). However, in most species of higher Diptera examined so far, growth rate is reduced at higher population densities directly e.g., by mechanical stimulus, or indirectly by starvation (Bryan & Sokal, 1967; Bakker, 1969; Beaver, 1974).

The growth rate during the first to third instars was higher in the high density group than that in low density in *A. paludum* (Fig. 1). Crowding only in the fourth and fifth instars may also accelerate the growth rate in *A. paludum*. Therefore, the entire nymphal stage appears sensitive to crowding in *A. paludum*. The mortality of nymphs is possibly caused by desiccation of temporary habitats. The reduction of water surface leads to an increase in population density. The high growth rate caused by crowding appears to permit some nymphs to mature to adults before drying-up of the water body and the death of the nymphs from starvation.

Population density of water striders may be increased owing to the higher number of reproductive females, their higher fecundity and also by the decrease of the area of water surface due to lower precipitation and higher temperature in summer (Vepsäläinen, 1978). A high proportion of macropterous adults (Table 1) and a delay in histolysis of indirect flight muscles (Fig. 2), which may be caused by crowding, are effective for the adults to disperse to other habitats.

Some studies on Gerridae and Gryllidae have shown that the proportion of winged adults, flight propensity, developmental and maintenance of flight muscles, allocation of energy to triglycerides (flight fuel), ovarian development, and fecundity are genetically correlated and this series of correlated traits may be termed "migratory syndrome" (Palmer, 1985; Fairbairn & Desranleau, 1987; Roff, 1990; Roff & Fairbairn, 1991; Fairbairn, 1994). *Aquarius paludum* shows a relatively higher extent of wing reduction in June in the field than other Japanese species of *Aquarius*, *Gerris* and *Limnoporus*, excluding *G. nepalensis* (Andersen, 1990, 1993; Andersen & Chen, 1993; Harada & Taneda, 1989). We suggest that long-winged *A. paludum* have a low dispersal tendency. However, this study suggests that environmental conditions, such as crowding, may shift the correlated traits in the direction to "dispersal" even in a species like *A. paludum* which has a relatively lower tendency to dispersal.

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