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Feeding conditions modify the photoperiodically induced dispersal of the water strider, *Aquarius paludum* (Heteroptera: Gerridae)

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Abstract. Overwintering adults of the water strider, *Aquarius paludum* were collected from the field in fall and kept under short days (12L : 12D) at 20°C for a week. A control group was then kept at 12L : 12D and fed daily, and three experimental groups were transferred to 15.5L : 8.5D and fed at different frequencies: daily or every 2nd or 3rd day. Temperature was kept at 20°C. Flight behaviour of the adults in the four groups was recorded every 10 days up to the end of the 5th week when the adults were dissected. State of the flight muscles and reproductive organs (ovaries and testes) was recorded. Flight ability of the adults fed every 3rd day (Group 3) was higher than that of those fed daily (Group 1). Seventy percent of the females that were fed every 3rd day (Group 3) remained in diapause for 5 weeks, in spite of the reproduction promoting long-days, while none of the females fed every day remained in diapause (Group 1). Flight muscle histolysis, promoted by long-days, was inhibited by poor feeding conditions. Thus, they can migrate and seek more suitable water bodies rich in food. The modifying effect of the availability of food on the trade-off between reproduction and flight is recorded here for the first time for a carnivorous insect.

INTRODUCTION

Control of diapause induction or diapause development may be achieved by integrating photoperiod and food conditions in some insects, including carnivorous insects. Lack of prey or reduced access to prey enhances diapause induction even under "long-days", which promote reproduction in the lacewing, *Chrysopa carnea* (Tauber & Tauber, 1973, 1982) and ladybird, *Semiadalia undecimnotata* (Iperti & Hodek, 1974; Rolley et al., 1974).

Several water striders which inhabit fresh water, use photoperiod to regulate their reproductive and dispersal characteristics, including wing length and flight muscle maturation (Spence & Andersen, 1994; Harada et al., 2000, 2005). In the water strider, *Aquarius paludum*, for example, photoperiod is the main environmental factor regulating several life history traits such as reproduction, wing length, flight muscle condition, flight ability, and resistances to high and low temperatures and drying-out (Harada, 2003a, b). Long days inhibit flight activity and promote flight muscle histolysis (Inoue & Harada, 1997; Harada et al., 2000). Long days promote reproduction, whereas short days induce reproductive diapause or the maturation of flight muscles and flight in *A. paludum* (Inoue & Harada 1997; Harada et al., 2000). Increasing photoperiod, even when shorter than the critical photoperiod for diapause induction, can inhibit flight and promote the histolysis of flight muscles (Inoue & Harada, 1997). As a result of this photoperiodic response, nutritional resources are allocated to reproduction in summer and dispersal to and from overwintering sites in autumn and spring. That is, *A. paludum* shows the so-called "oogenesis flight syndrome" (Johnson, 1969; Harrison, 1980). However, there is no information on whether food availability can modify the photoperiodic control of the trade-off between fllight and reproduction in *A. paludum*. This paper reports the results of a laboratory experiment designed to test this idea.

MATERIAL AND METHODS

Material and rearing conditions

Adults of the water strider, *Aquarius paludum* (Fabricius) which were in reproductive diapause, were collected from two rivers in Kochi (33°N) at the beginning of October, 2003. They were exposed to a low temperature of 7°C for 2 days to promote the development of flight muscles (Harada et al., 2003) and then kept under conditions of 12 h light – 12 h dark (12L : 12D) and 20 ± 2°C for a week, which are similar to those prevailing in the field in late fall at Kochi. Then, they were transferred to one of the following 4 conditions, and kept at 20 ± 2°C.

Group 1: Fed every day, 15.5L : 8.5D,
Group 2: Fed every two days, 15.5L : 8.5D,
Group 3: Fed every three days, 15.5L : 8.5D,
Group 4: Fed every day, 12L : 12D.

Each pair of water striders was fed one adult fly of *Lucilia illustris* per day etc. Each group included 22 pairs of females and males, and all individuals survived for 5 weeks. Flight ability was determined every 10 days after transfer up to the end of the fifth week, when the adults were dissected. Condition of the flight muscles and reproductive organs (ovaries and testes) were observed and recorded.

Flight experiment

Flight ability was determined using the method of Harada et al. (1997). A piece of white paper was placed on the bottom of a large transparent cylinder (30 cm in diameter and 15 cm height), and an adult water strider was transferred from its rearing cage into a small transparent cylinder (5 cm in diameter), which was placed at the center of the piece of paper at the bottom of the large cylinder. Infra-red light warmed the bottom of the large cylinder to a temperature of 32 ± 2°C. The individual insects

TABLE 1. Influence of food supply on the proportion of individuals of the water strider, *Aquarius paludum* that showed wing-opening or flight, and results of χ^2-test of the differences among the 4 experimental groups.

Condition	Proportion of individuals showing wing-opening or flight activity (%)					
	0 W	1 W	2 W	3 W	4 W	5 W
Fed every day, 15.5L : 8.5D						
Males	72.7 (22)	72.7 (22)	45.5 (22)	45.5 (22)	15.0 (20)	5.0 (20)
Females	68.2 (22)	63.6 (22)	36.4 (22)	36.3 (22)	4.5 (22)	9.0 (22)
Fed every 2 days, 15.5L : 8.5D						
Males	90.1 (22)	81.8 (22)	77.3 (22)	63.6 (22)	47.6 (21)	42.9 (21)
Females	72.7 (22)	90.9 (22)	81.0 (21)	60.0 (20)	35.0 (20)	26.3 (19)
Fed every three days, 15.5L : 8.5D						
Males	59.1 (22)	59.1 (22)	50.0 (22)	50.0 (22)	33.3 (21)	28.6 (21)
Females	72.7 (22)	59.1 (22)	63.6 (22)	63.6 (22)	50.0 (22)	36.4 (22)
Fed every day, 12L : 12D						
Males	72.7 (22)	77.3 (22)	72.7 (22)	77.3 (22)	77.3 (22)	36.4 (22)
Females	90.9 (22)	86.4 (22)	95.5 (22)	90.5 (21)	85.7 (21)	66.7 (21)
χ^2 test						
χ^2 value	4.61	10.71	23.35	17.08	44.9	25.12
df	3	3	3	3	3	3
P	0.203	0.013	< 0.001	< 0.001	< 0.001	< 0.001

W = weeks.

were then illuminated from the side for 30 s using a beam of blue light (about 3400 Lx) produced by passing the light from a tungsten lamp through a glassy filter. Administered together, the heat and blue light triggered flight in individuals that were able to fly. The enclosure was then removed and the bug observed for 1 min. After the first observation the bug was again stimulated by exposing it to blue light and observed for an additional minute. Most of the bugs that flew did so for less than 0.5 s and then folded their wings. Flight ability of each insect is indicated by the flight index (FI), which was calculated as follows: Each bug was observed for 3 min, and each wing-opening recorded during this period was assigned "+1" and each flight "+2" and FI was the total of those observations, i.e. FI = (number of wing-openings) + 2 x (number of flights).

Indices of flight muscle development and testis volume

Flight muscle maturation was ranked in one of three grades, according to the criterion proposed by Harada et al. (1997). This is a simplified version of the criterion used by Fairbairn & Desranleau (1987): Rank 3, indirect flight muscles large, fibrous and reddish, which corresponds to "normal" of Fairbairn & Desranleau (1987); Rank 2, flight muscles smaller, soft, white, corresponding to "teneral: advanced" or "histolysed: early"; Rank 1, muscle fibers not visible, corresponding to "histolysed: advanced or complete" or "teneral: early". The volume-index of testes which have a cylindrical shape, was defined as the average of left and right testes volumes, which were calculated using the expression: $(\text{half width})^2 \pi \times (\text{length})\ \text{mm}^3$.

Size of fat body and presence of oil droplets in fat body

The quantity of fat and presence of oil droplets in the fat lining the body wall were estimated as indices, based on the criteria proposed by Kishi et al. (2006).

Fat-body index

Rank 1: no fat, Rank 2: thin layer of fat, body wall visible, Rank 3: thick layer of fat, body wall not visible, Rank 4: extremely thick layer of fat, body wall not visible.

Oil droplets in fat body

Rank 1: no oil droplets, Rank 2: a few small transparent oil droplets, Rank 3: many transparent or yellowish oil droplets, Rank 4: numerous large yellow oil-droplets.

Statistical analysis

Data were analyzed statistically using SSPS 11.0 version for personal computer. Pearson's analysis, Mann-Whitney U-test, Kruskal-Wallis test and χ^2 test were each performed in an appropriate manner.

RESULTS

Flight ability and flight muscles

Significant effects of feeding conditions were not shown on flight during the first 2 weeks (Tables 1, 2). However, after 4–5 weeks significantly more adults fed only every 3 days (Group 3) flew than those fed every day (Group 1) (Kruskal-Wallis test, χ^2 = –5.262 or –4.473, P < 0.001). However, the individuals in Group 3 flew significantly less after 4 and 5 weeks than those kept under 12L : 12D (Mann-Whitney U-test after 4 weeks: z = –3.48, P = 0.001; 5 weeks, z = –2.40, P = 0.017). The high tendency to fly shown by females that were fed less frequently was maintained for 3 weeks, but that of males only 1 week (Table 2)

Many (31.8%) of the adults fed only every 3 days (Group 3) had mature flight muscles of Rank 3, even 5 weeks after transferring then to long-day condition and this was higher than the 4.7% of the adults fed every day (Group 1) (χ^2 test, χ^2 value = 35.89, df = 2, P < 0.001) and 9.1% of those fed every 2 days (Group 2) (χ^2 test, χ^2 value = 13.63, df = 2, P = 0.001) (Table 2).

TABLE 2. Influence of food supply on the incidence of flight in the water strider, *Aquarius paludum* [median (quartiles)] and results of Mann-Whitney U-test of the differences between sexes in each data set.

Condition	Weekly change in flight-index					
	0 W	1 W	2 W	3 W	4 W	5 W
Fed every day, 15.5L : 8.5D						
Males	5.5 (0,21) (22)	4 (0, 7) (22)	0 (0, 9) (22)	0 (0, 5) (22)	0 (0, 0) (19)	0 (0, 0) (19)
Females	11.5 (0, 18) (22)	4.5 (0, 7) (22)	1 (0, 4.5) (22)	0 (0, 3) (22)	0 (0, 0) (22)	0 (0, 0) (22)
Z	–0.578	–0.459	–0.429	–0.086	–0.140	–1.076
P	0.563	0.646	0.668	0.931	0.889	0.282
Fed every 2 days, 15.5L : 8.5D						
Males	18 (7, 27) (22)	23 (11.5, 35) (22)	17 (0.5, 29) (22)	4.5 (0, 13.5) (22)	1 (0, 6) (21)	1 (0, 7) (21)
Females	11 (0, 29) (22)	13 (3, 23) (22)	15 (4, 18) (22)	3 (0.5, 12) (22)	0 (0, 3) (22)	0 (0, 2) (22)
Z	–0.808	–1.761	–1.429	–1.680	–1.871	–0.651
P	0.419	0.078	0.153	0.093	0.062	0.515
Fed every three days, 15.5L : 8.5D						
Males	3 (0, 10.5) (22)	4 (0, 11.5) (22)	1 (0, 9) (22)	1 (0, 10) (22)	0 (0, 7) (22)	0 (0, 2) (21)
Females	5 (0, 23) (22)	3 (0, 20) (22)	3 (0, 12) (22)	5.5 (0, 11) (22)	1 (0, 11) (22)	0 (0, 5) (22)
Z	–0.320	–0.716	–1.834	–1.851	–1.706	–1.616
P	0.749	0.474	0.067	0.064	0.088	0.106
Fed every day, 12L : 12D						
Males	11.5 (0, 27) (22)	12 (2, 20) (22)	15 (0, 17) (22)	15 (1, 21) (22)	5 (1,15) (22)	0 (0, 7) (22)
Females	15.5 (7.5, 29) (22)	21 (3, 27) (22)	19 (8, 27) (22)	21 (12, 29) (22)	14 (6, 22) (22)	9 (1, 22) (22)
Z	–1.422	–0.816	–0.816	–0.513	–1.078	–1.658
P	0.155	0.415	0.476	0.608	0.281	0.097

Reproductive status

Average number of eggs laid per female over the 5 weeks was more than 80 when females were fed every day. However, it was less than 20 in the other three groups (Kruskal-Wallis test: $\chi^2 = -13.08$, P = 0.004). Seventy percent of the females fed every 3 days (Group 3) remained in reproductive diapause, even after 5 weeks under long-days, which promote reproduction (Table 4), while no adults fed every day remained in reproductive diapause (χ^2 test, $\chi^2 = 22.76$, df = 1, P < 0.001). The total number of eggs produced by females fed every 2 or 3 days (Groups 2, 3) was on average 43 or 28 and smaller than the 96 eggs produced by females fed every day (Group 1) (Table 4).

Males fed every 3 days tended to have smaller testes than those fed every day (Mann-Whitney U test: z = –4.01, P < 0.001) or every 2 days (group 2) (z = –1.91, P = 0.056) (Table 4). However, testes of males fed every 3 days, and kept under long days, were larger than those of males kept under the short-days (Mann-Whitney U test: z = –3.50, P < 0.001) (Table 4).

Correlation between reproductive status and flight muscle maturation

There were no significant correlations between the total number of eggs produced and condition of flight muscles

TABLE 3. Effects of food supply on the condition of the flight muscles (after 5 weeks) of the water strider, *Aquarius paludum*, number and (%) and result of χ^2 test of the differences among the 4 experimental groups.

Food given	Photoperiod	Rank of flight muscles			
		1	2	3	Total
Every day	15.5L : 8.5D	29(67.4)	12(27.9)	2(4.7)	43
Every 2 days	15.5L : 8.5D	15(34.1)	25(56.8)	4(9.1)	44
Every 3 days	15.5L : 8.5D	3(6.8)	27(61.4)	14(31.8)	44
Every day	12L : 12D	5(11.4)	29(65.9)	10(22.7)	44

χ^2 test, df = 6, χ^2 cal = 52.711, P < 0.001

TABLE 4. Effect of food supply on reproductive status of females and testes volume of the water strider, *Aquarius paludum* after 5 weeks under each condition (mean ± SD or %) and results of non-parametric tests of differences among the 4 experimental groups.

Food given	Photoperiod	% not in diapause (n)	Total number of eggs produced	Index of testes volume (mm^3) (n)
Every day	15.5L : 8.5D	100.0 (22)	96.5 ± 74.21 (22)	0.117 ± 0.036 (21)
Every 2 days	15.5L : 8.5D	50.0 (22)	43.2 ± 24.4 (11)	0.129 ± 0.016 (21)
Every 3 days	15.5L : 8.5D	31.8 (22)	28.0 ± 26.9 (7)	0.091 ± 0.033 (22)
Every day	12L : 12D	4.5 (22)	17 (1)	0.053 ± 0.014 (22)
		χ^2-test	Kruskal Wallis-test	
	χ^2 cal	42.82	8.21	48.07
	df	3	2	3
	P	< 0.001	0.015	< 0.001

of females kept under long days (Groups 1–3) (Pearson's correlation test: r = –0.14~–0.21, P = 0.37~0.70), or between the total number of eggs produced and flight ability of individuals in both Groups 1 (fed every day, r = –0.14 or –0.28, P = 0.54 or 0.90) and 2 (fed every 2 days, r = 0.01~ –0.17, P = 0.63~0.98).

However, there were significant negative correlations between the flight index and testes volume in males fed every 3 days (Group 3) (after three: r = –0.64, P = 0.001; four: r = –0.59, P = 0.004; and five weeks: r = –0.53, P = 0.01), but not for individuals in Group 1 (fed everyday, r = –0.15~–0.20, P = 0.42~0.51), Group 2 (fed every 2 days, r = 0.09~–0.11, P = 0.64~0.96) or Group 4 (kept under the short days, r = 0.01~–0.17, P = 0.45~0.97).

Size of fat body and presence of oil droplets in fat body

Food supply and photoperiod had no effect on the quantity of fat-body lining the body wall (Table 5). However, there were fewer oil droplets in the fat body of females fed every 3 days (Group 3) than of those in the other three groups (Table 5).

DISCUSSION

Trade-off between reproduction and dispersal characteristics

Strong support for an adaptive trade-off between flight ability and reproduction is provided by comparative studies of wing-polymorphic insects belonging to several orders (Denno et al., 1989; Roff & Fairbairn, 1991; Zera & Denno, 1997). Long-winged forms are significantly less fecund than flightless forms in grasshoppers (Ritchie et al., 1987), crickets (Mole & Zera, 1993; Tanaka & Suzuki, 1998), planthoppers (Denno et al., 1989), aphids (Dixon & Howard, 1986), seed bugs (Solbreck, 1986), water striders and veliids (Zera, 1984; Muraji & Nakasuji, 1988; Harada, 1992).

Response to a low food supply

Even the long-winged adults of the water strider, *Aquarius paludum*, can reproduce in spring after migrating to water bodies from overwintering sites on land (Harada, 1993). The trade-off between flights and reproduction is modified by availability of food. The response to a food shortage depends upon whether the females are on a water surface or not. When water bodies dry out, food shortage promotes the histolysis of flight muscles, and nutritional resources derived from the histolyzed flight muscles enable them to survive until it rains (Harada, 1998). However, when adults on water bodies suffer a food shortage, they retain the ability to fly (Tables 1, 2) and do not histolyse their flight muscles (Table 3). Mechanical stimuli from the substrate (water or land) induce the switch to dispersal; females respond to a shortage of food by adopting " flight" strategy.

TABLE 5. Effect of food supply on size of fat-body and Rank-number of oil-droplets in fat-body (after 5 weeks) of the water strider, *Aquarius paludum*, and results of χ^2 testing of differences in the combined data for both sexes among the 4 experimental groups.

Condition		Rank of fat-body layer				Rank-number of oil-droplets			
		1	2	3	4	1	2	3	4
Fed every day	F	0	5	7	0	0	2	9	1
	M	0	4	4	1	0	1	7	1
	Total	0	9	11	1	0	3	16	2
Fed every 2 day	F	0	3	9	0	0	2	9	1
	M	0	3	7	0	0	0	10	0
	Total	0	6	16	0	0	2	19	1
Fed every 3 days	F	1	4	6	1	4	5	3	0
	M	0	2	8	0	0	1	8	1
	Total	1	6	14	1	4	6	11	1
12L : 12D	F	0	3	9	0	0	1	10	1
	M	0	3	7	0	0	2	7	1
	Total	0	6	16	0	0	3	17	2
		χ^2 test, df = 9, χ^2 cal = 7.67, P = 0.563				χ^2 test, df = 9, χ^2 cal = 16.45, P = 0.058			

The store of fuel in fat body, especially oil droplets are used by the females of *A. paludum,* which mature their flight muscles when short of food (Table 5). Females retain their flight ability for longer than males when starved. Females arriving by chance at a water body, where the feeding conditions are poor, retain their flight ability and seek out food-rich water bodies, utilizing the fuel in their fat bodies, particularly the oil droplets. For a better understanding of the effect of poor nutrition on flight ability, further experiments are needed using individuals that have overwintered or belong to the 1st or 2nd generation, which are present in early spring and summer.

In conclusion, flight muscle histolysis promoted by long-days is inhibited by poor feeding conditions in *A. paludum.* The modifying effect of food supply on the trade-off between reproduction and flight, which is regulated by photoperiod, is reported here for the first time in a carnivorous insect.

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