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The Relation among Emergence Date, Days until First Effective Mating, Fecundity and Adult Longevity in *Isoperla aizuana* and *Sweltsa* sp. (Plecoptera)

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ABSTRACT—The relation between emergence date and the factors concerned in reproduction were studied in the stoneflies *Isoperla aizuana* (Perlodidae) and *Sweltsa* sp. (Chloroperlidae) in the laboratory. Individuals emerging earlier had larger adult size and greater adult longevity. Fecundity was also related to emergence date, adult size, and adult longevity. Furthermore, individuals emerging earlier had more days until first effective mating and tended to mate more effectively than later-emerging individuals. The maturity of the reproductive tissue may differ with emergence date. While most of the later-emerging individuals had a lower rate of effective mating, longer-lived and larger size adults mated more effectively in females of *Sweltsa* sp. The differences in mating character might affect the effectiveness of mating.

Key words: effective mating, adult longevity, adult size, mating behavior, fecundity

INTRODUCTION

In aquatic insects, there is large variation in adult size, which tends to decline with later emergence dates (Scheldon, 1972; Hynes and Hynes, 1975; Vannote and Sweeney, 1980; Michiels and Dhondt, 1989; Takemon, 1990; Dieterich and Anderson, 1995). This variation can be partly explained by the water temperatures to which individuals have been exposed and diet in their nymphal stage (Vannote and Sweeney, 1980; Sweeney and Vannote, 1984; Sweeney *et al.*, 1986). In addition, fecundity is also correlated with adult size; large individuals oviposit more eggs than do small individuals (Vannote and Sweeney, 1980; Sweeney and Vannote, 1984; Honek, 1993).

In stoneflies, there are some reports on the relationship between emergence date and adult size (Scheldon, 1972; Hynes and Hynes, 1975; Dieterich and Anderson, 1995). However, body size is the only parameter for which the relationship with emergence date has been well studied. Little is known of the relationships between adult longevity and fecundity and emergence date, especially in systelognathan species. Moreover, comparative investigations of these relations have not been counted. Only fragmentary and rough information about adult longevity and fecundity has been

reported for *Isoperla* (Perlodidae), *Alloperla* (Chloroperlidae), *Paragnetina*, and *Phasganophora* (Perlidae) species (Harper, 1973a, Jop and Szczytko, 1984). Early emergence, especially for males, might be beneficial for the species that mate immediately after emergence such as *Allocapnia vivipara* (Frison, 1929). Is it also beneficial for the species that need several days until mating? To answer this question, we investigated the relations among emergence date, adult size, adult longevity and fecundity in the systelognathan species *Isoperla aizuana* (Perlodidae) and *Sweltsa* sp. (Chloroperlidae) that need several days until mating. We also examined the interspecific differences of these relations and mating behavior. *Sweltsa* sp. in this report is assigned to *Sweltsa* sp. in Hayashi *et al.* (1997)

MATERIALS AND METHODS

Matured final instar nymphs of *Isoperla aizuana* were collected in the morning on March 21 and 28, 1997, from the Kizu River at Kizu, Kyoto Prefecture (34°44'N, 135°49'E) (Fig. 1), and matured final instar nymphs of *Sweltsa* sp. were collected in the morning on April 12, April 25 and May 4, 1997, from the Shigo River at Aritoshi, Nara Prefecture (34°23'N, 136°00'E) (Fig. 1). The water temperature in both rivers ranged from 10.2 to 15.4°C (at 12:00) when the specimens were collected. The specimens were brought to the laboratory and kept in an aerated aquarium (14×21×13cm) without food. Water temperature in the aquarium ranged from 14.1 to 17.9°C (at 12:00), and the air temperature in the laboratory ranged from 15.8 to 22.3°C (at 12:00) (Fig. 2). We did not collect all the

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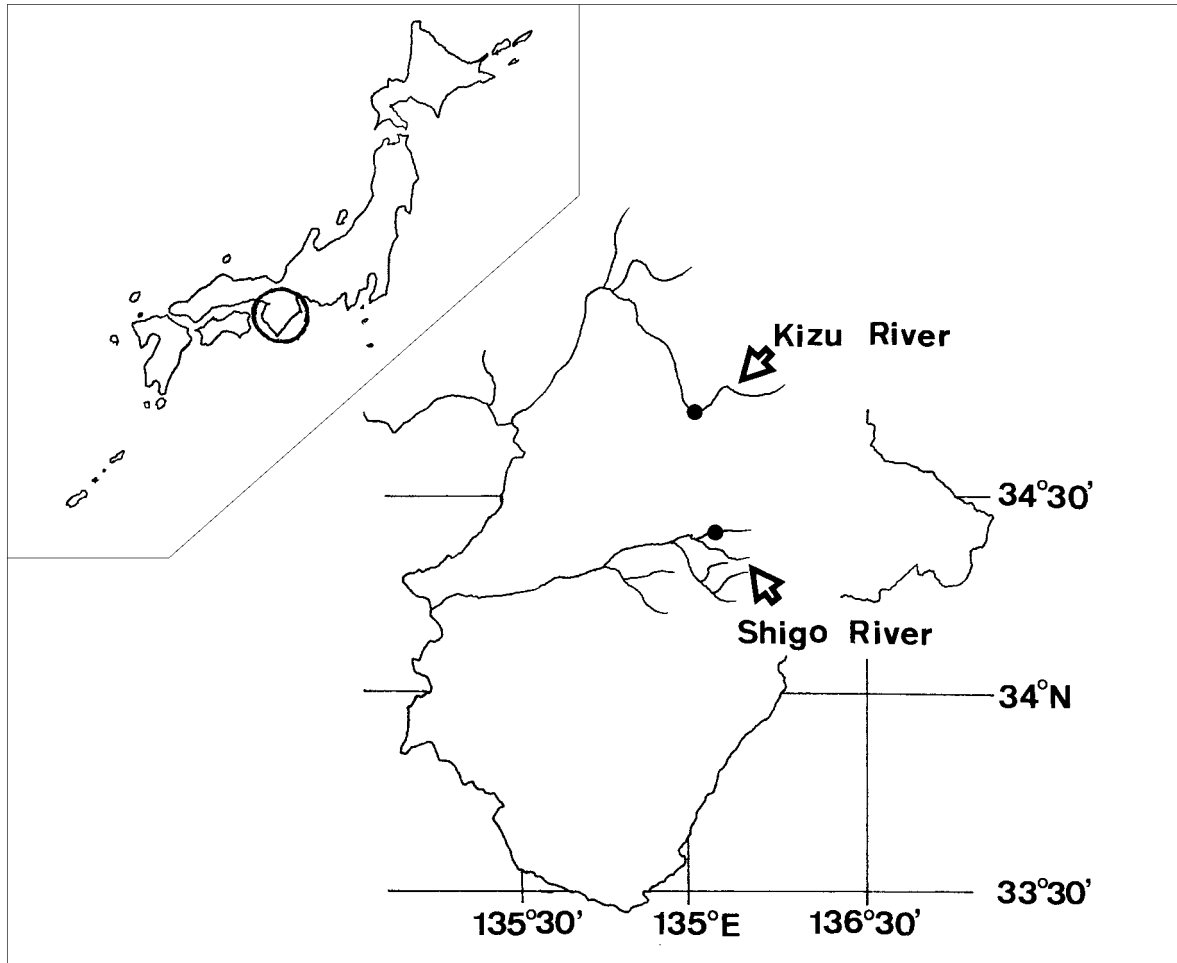


Fig. 1. Collection sites in the Shigo and Kizu Rivers.

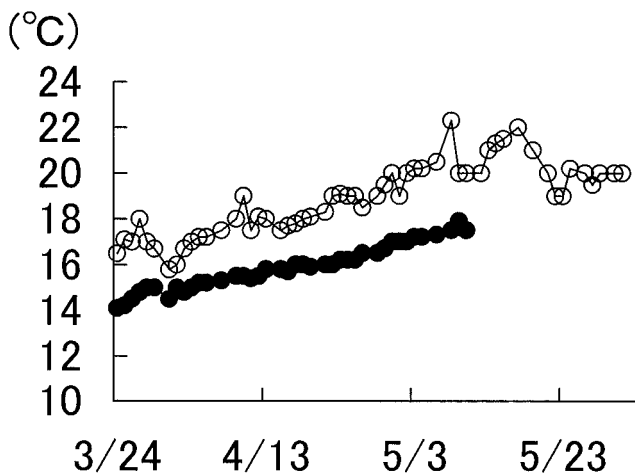


Fig. 2. The change of water temperature (○) in the aquarium and air temperature (●) in the laboratory.

nymphs observed on the collection date in the field, because some were also immature. Even if the nymphs kept in the aquarium could have emerged as adults earlier than they would have in the field, collecting nymphs two or three times in the field would put lag of emergence timing back. Following their emergence, adults were

housed separately in plastic vials ($\phi 3 \times 6.5$ cm). The insects were fed honey diluted with water (1:10) soaked into cotton almost every day.

Two or three days after adult emergence, a female and male were put together in a plastic vial at 11:00 once every two or three days for mating. If they began to mate, their copulation period and mating behavior were observed. If they did not mate, we separated them at 16:00. The females and males that we observed mating had similar adult longevity. Females that had mated once were not used for another mating examination (Fig. 3a), even if the mating was ineffective (Fig. 3b) (we defined effective mating as mating leading to female oviposition) in order to identify which males contributed to oviposition. Females that had not mated were used for another mating examination with another male. Mated males were used in mating examinations several times during their lifetime (Fig. 3c). Therefore, problem with male-female compatibility could be avoided. Each egg mass deposited in a vial after mating was collected until the female died a few days later, and the number of eggs in each egg mass was counted. Dead females were preserved in 80% ethanol, and the widths of their heads were measured.

RESULTS

Emergence period, adult size, and adult longevity

We collected only the final instar nymphs of *Isoperla*

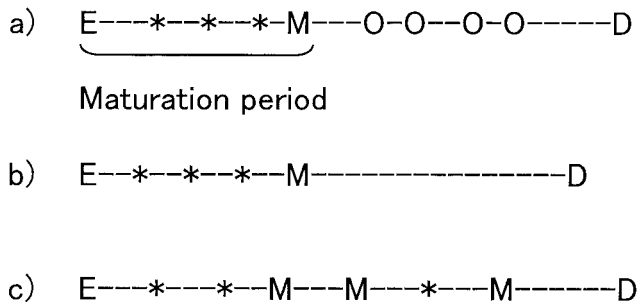


Fig. 3. Example of mating manipulation. a) Females, effective mating. b) Females, not effective mating. c) Males. *: Tried to mate but ended in failure. E: Emergence. M: Mate. O: Oviposition. D: Death.

aizuana on March 21 and 28 and of *Sweltsa* sp. on April 12, April 25 and May 4. On the first collection date, we could observe many immature nymphs of both species in the field, but on the second collection date for *Isoperla aizuana* and on the third collection date for *Sweltsa* sp., most of the observed nymphs were matured ones. Nymphs that we collected on the first collection date had already emerged on the second collection date in the aquarium. On the second and third collection dates (March 28 for *I. aizuana* and April 25, May 4 for *Sweltsa* sp.) no nymphs remained in the aquarium. We tried to collect *I. aizuana* nymphs on April 10 and *Sweltsa* sp. on May 12 (as third and fourth collection

dates) in the field, but were unsuccessful. Emergence occurred from March 24 to April 5 in *Isoperla aizuana* and from April 11 to May 9 in *Sweltsa* sp. in the laboratory.

The head width of *I. aizuana* was from 1.66 to 1.96 mm in females and from 1.48 to 1.72 mm in males. The head width of *Sweltsa* sp. was from 1.08 to 1.40 mm in females and from 1.04 to 1.30 mm in males. In both species, females had larger heads than males (Mann-Whitney U-test: $p < 0.05$). Individual females emerging earlier had a larger head than those emerging later in both species (Fig. 4a, c). *I. aizuana* males tended to have a negative correlation between emergence date and head width, but it was not significant (Fig. 4b). *Sweltsa* sp. males did not show a significant correlation between emergence date and head width because of the small sample size (Fig. 4d).

Adult longevity of *I. aizuana* females was from 3 to 45 days, and that of males was from 14 to 44 days. Adult longevity of *Sweltsa* sp. females was from 2 to 29 days, and that of males was from 4 to 24 days. In *I. aizuana*, adult longevity was greater in individuals emerging earlier compared to those emerging later (Fig. 5a, b). *Sweltsa* sp. females tended to have a negative correlation between emergence date and adult longevity but it was not significant (Fig. 5c). Males of *Sweltsa* sp. did not show a significant correlation between emergence date and adult longevity (Fig. 5d).

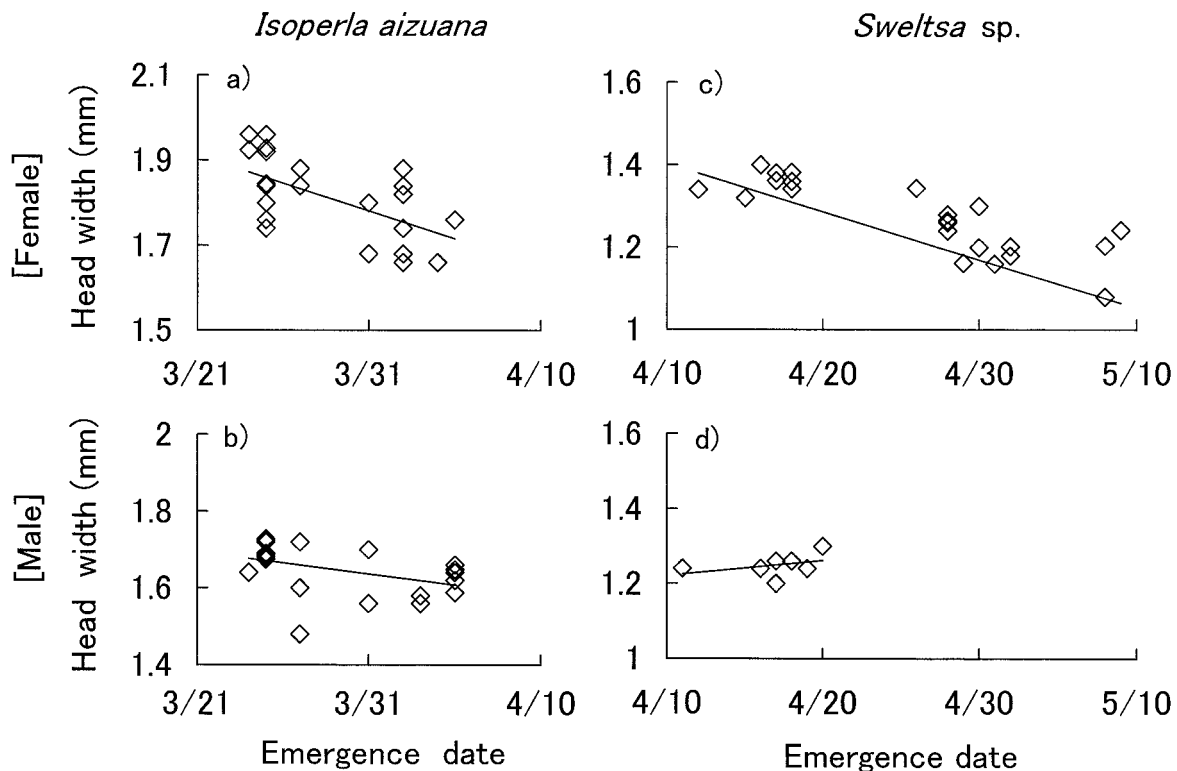


Fig. 4. Relationship between emergence date and head width. a) *Isoperla aizuana*, females: $z = -3.143$, $p < 0.01$, $n = 22$; Kendall test. b) *Isoperla aizuana*, males: $z = -1.809$, $p < 0.07$, $n = 20$; Kendall test. c) *Sweltsa* sp. females: $z = -4.22$, $p < 0.01$, $n = 23$; Kendall test. d) *Sweltsa* sp. males: N.S., $n = 8$; Kendall test.

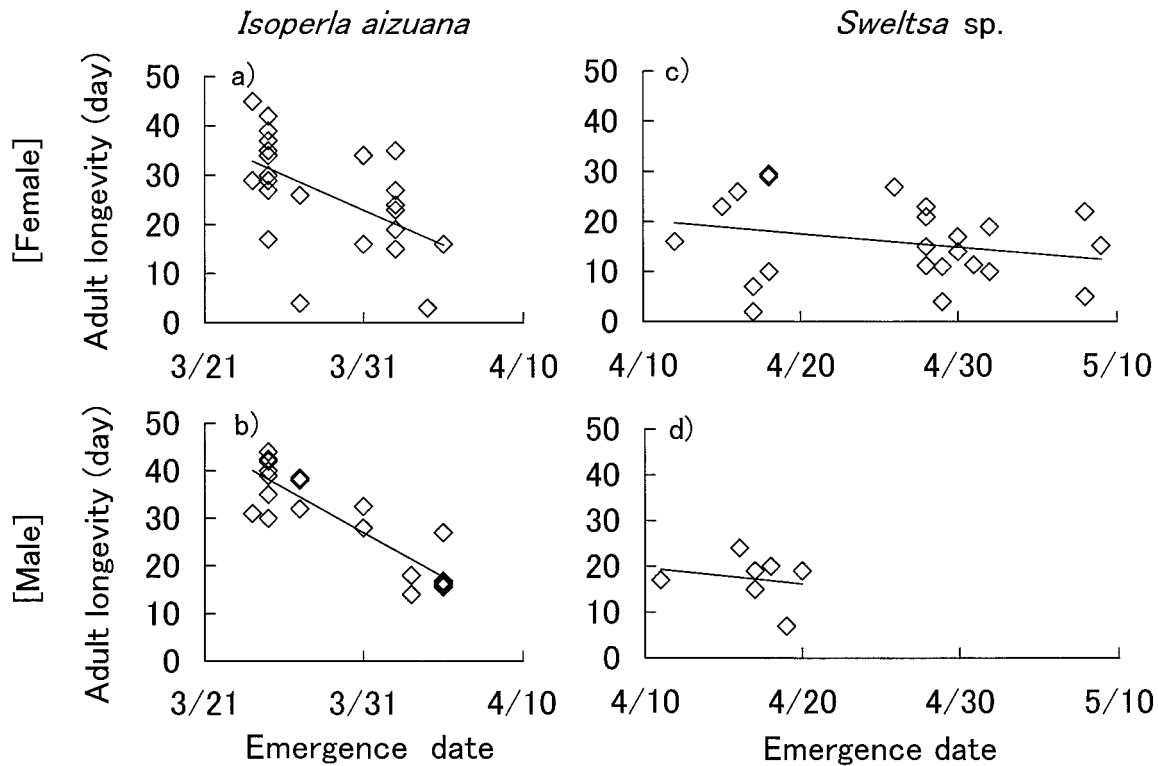


Fig. 5. Relationship between emergence date and adult longevity. a) *Isoperla aizuana*, females: $z = -3.269$, $p < 0.01$, $n = 22$; Kendall test. b) *Isoperla aizuana*, males: $z = -3.99$, $p < 0.01$, $n = 20$; Kendall test. c) *Sweltsa* sp. females: $z = -1.805$, $p < 0.07$, $n = 23$; Kendall test. d) *Sweltsa* sp. males: N.S., $n = 8$; Kendall test.

Days until first effective mating and emergence date

Isoperla aizuana females required 7 to 26 days until their first effective mating, and males required 7 to 16 days. Individuals emerging earlier required significantly more days than those emerging later (Fig. 6a, b). The number of days until first effective mating did not differ significantly between females and males (Mann-Whitney U-test: $p > 0.05$).

Sweltsa sp. females required 2 to 7 days until their first effective mating and males required 3 to 12 days, and individuals emerging earlier tended to need more days until their first effective mating compared with those emerging later (Fig. 6c, d). The number of days until first effective mating was not significantly different between females and males (Mann-Whitney U-test: $p > 0.05$).

Effective mating and emergence date

All the individuals were divided into two groups: individuals that emerged before March 29 or after March 28 for *Isoperla aizuana*, and individuals that emerged before April 22 or after April 21 for *Sweltsa* sp. In each group, all the individuals were subdivided into effectively mated ones, only mated ones and others. Then, the rate of mating (the ratio of all the mating ones to all the individuals of each group) and the rate of effective mating (the ratio of effective mating to all the mating individuals of each group) in the two groups was compared (Fig. 7). Two *I. aizuana* and three *Sweltsa*

sp. did not have a chance to mate because of their short adult life and the lack of a partner. There was a possibility that ineffective mating of females was due to specific males, but it was not observed in this study. And ineffective mating could be observed in both the early and late emerging groups.

In *Isoperla aizuana*, the rate of mating in females in the early-emerging group (Fig. 7a) tended to be higher (Fisher's exact test, $p > 0.05$) than that in the late-emerging group, but it was not significant. And the early-emerging group of females tended to mate more effectively (Fisher's exact test, $p > 0.05$) than the late-emerging ones, but it was not significant. In *Isoperla aizuana* males, the rate of mating in the early-emerging group (Fig. 7b) tended to be higher (Fisher's exact test, $p < 0.076$) than that in the late-emerging group, but it was not significant. And the early-emerging group of individuals tended to mate more effectively (Fisher's exact test, $p > 0.05$) than the late-emerging ones, but it was also not significant. In *Sweltsa* sp., the rate of mating in females in the early-emerging group (Fig. 7c) was significantly higher (Fisher's exact test, $p < 0.03$) than that in the late-emerging group. But the late-emerging group of females tended to mate more effectively (Fisher's exact test, $p < 0.051$) than the early-emerging ones, but it was not significant. Males could not be compared because no individuals emerged after April 23.

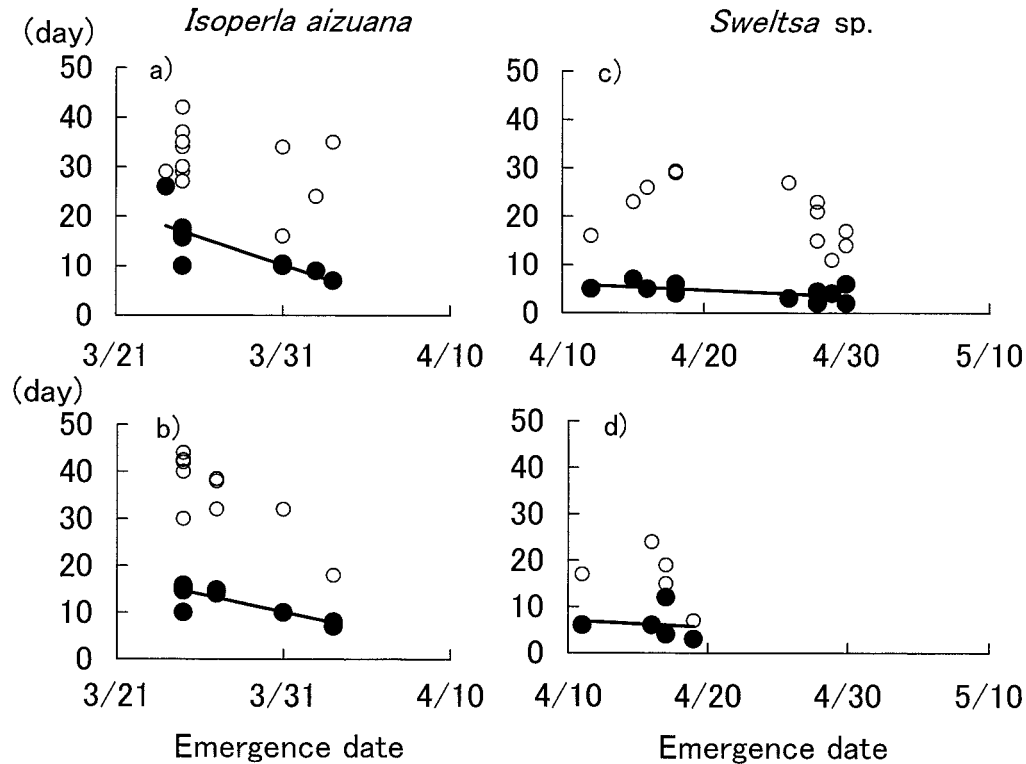


Fig. 6. Relationship between emergence date and days until first effective mating (●). Adult longevity (○) is also shown. a) *Isoperla aizwana*, females: $z = -3.73$, $p < 0.01$, $n = 12$; Kendall test. b) *Isoperla aizwana*, males: $z = -2.7$, $p < 0.01$, $n = 12$; Kendall test. c) *Sweltsa* sp., females: $z = -1.76$, $p < 0.07$, $n = 12$; Kendall test. d) *Sweltsa* sp., males: $z = -1.089$, $p < 0.27$, $n = 5$; Kendall test.

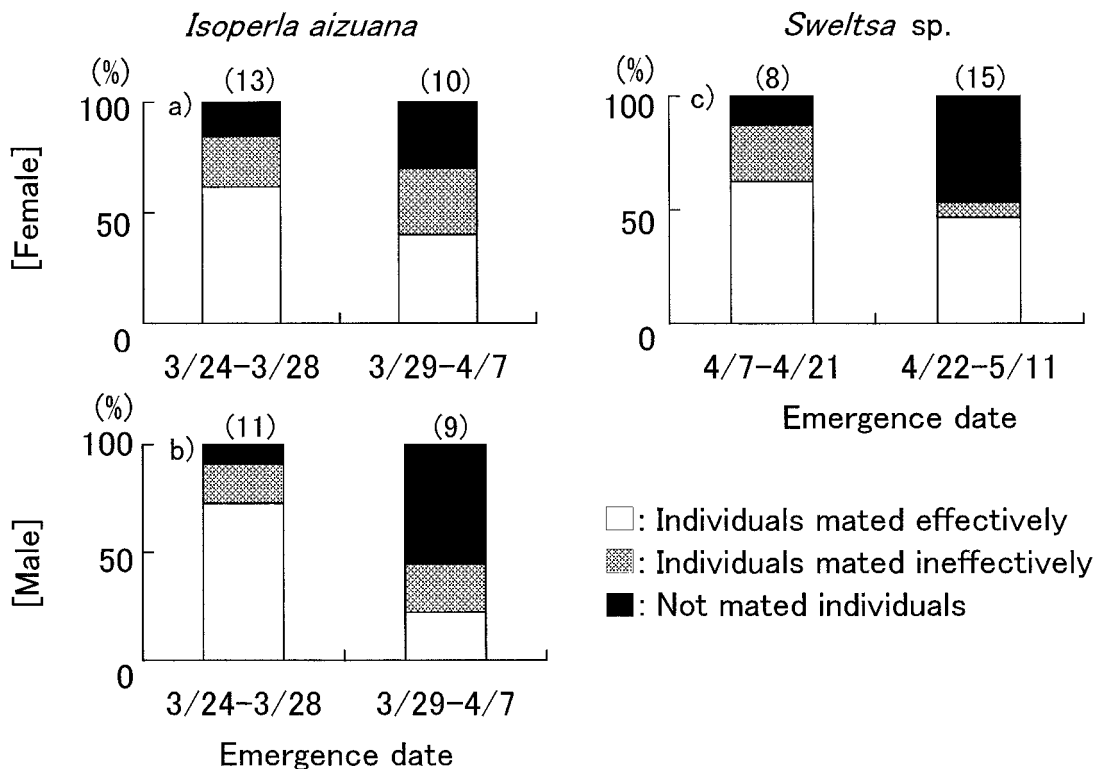


Fig. 7. The rate of effectively mated individuals, ineffectively mated individuals and not mated individuals between the early-emerging group and late-emerging group. (Number) shows the total individual number. We defined effective mating as mating leading to female oviposition. a) *Isoperla aizwana*, females. b) *Isoperla aizwana*, males. c) *Sweltsa* sp., females.

Mating behavior and copulation period

When a male found a female, the male approached the female and tried to mount her back. In most cases, she refused to be mounted. When mounting occurred successfully, the male bent his body in an S-shape and they mated.

In *Isoperla aizuana*, when a male found a female, the male tried to catch the female immediately, and tried again if he failed. Many failures were observed, but once a male caught a female he never released her. The copulation period of effective mating ranged from 1 hr 35 min to 3 hr 15 min (2 hr 13 min \pm 34 min, Mean \pm S.D., n=12). Females that only mated for 15 to 40 min did not oviposit, probably because the mating duration was insufficient or because the

mating date was too early for the individuals to mate effectively. Spermatophore-like objects could not be observed during and after mating.

In *Sweltsa* sp., even if a male found a female, the male did not try to catch her immediately in most cases, but he examined her with his antenna. Failure to catch a female was rarely observed, and when a male did fail to catch a female, he stopped trying to catch her. Sometimes, a male could not mate, even if he mounted a female, because she was walking around. The copulation period of effective mating ranged from 2 hr 20 min to 5 hr (3 hr 36 min \pm 50 min, Mean \pm S.D., n=11) and was significantly longer than that of *I. aizuana* (Mann-Whitney U-test: $p<0.05$). Spermatophore-

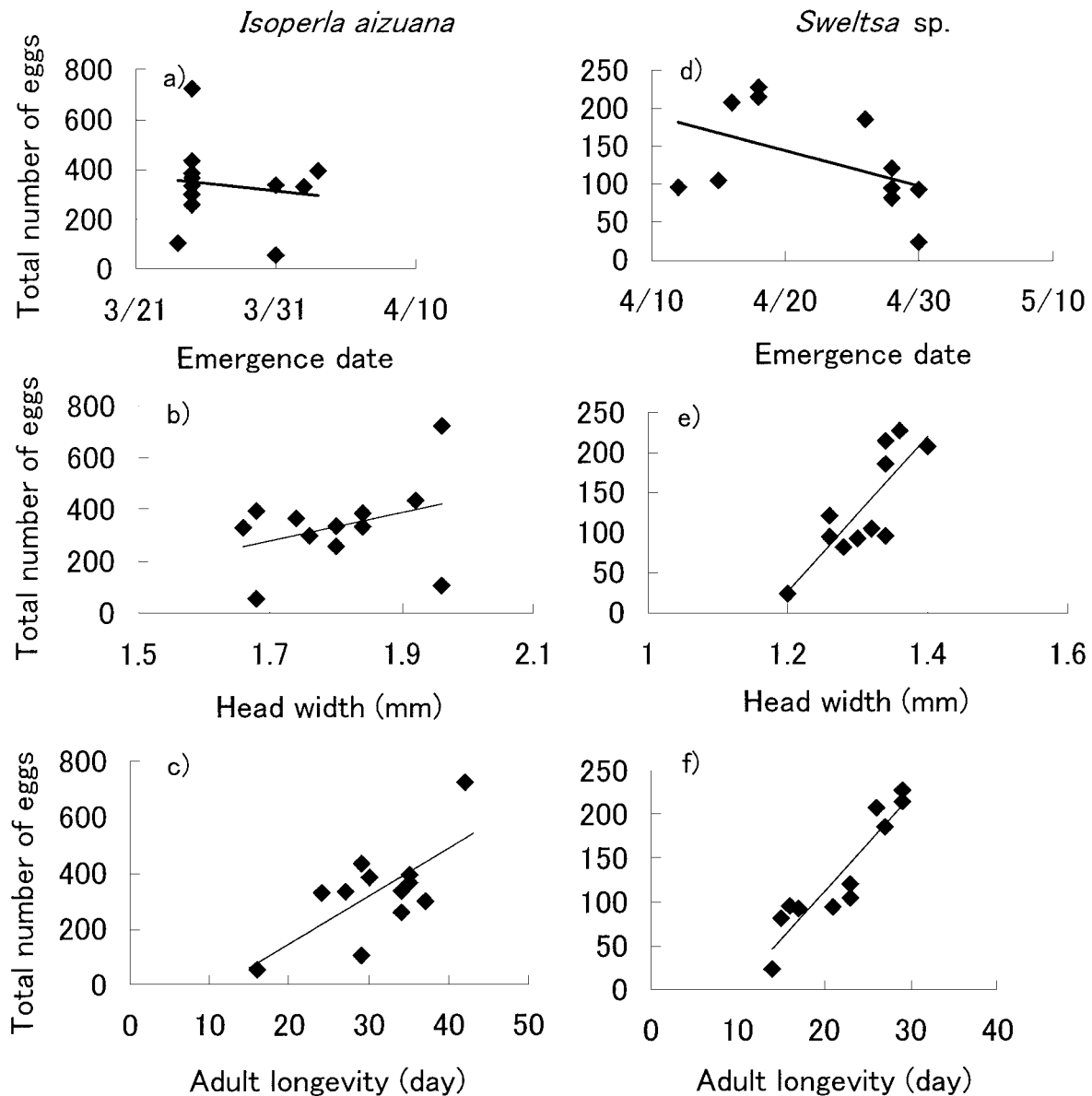


Fig. 8. The relation between emergence date (a, d), head width (b, e) adult longevity (c, f) and total number of egg. a) *Isoperla aizuana*, females: $z=0.255$, $p>0.05$, $n=12$; Kendall test. b) *Isoperla aizuana*, females: $z=0.99$, $p>0.05$, $n=12$; Kendall test. c) *Isoperla aizuana*, females: $z=1.755$, $p>0.05$, $n=12$; Kendall test. d) *Sweltsa* sp., females: $z=-1.796$, $p<0.07$, $n=12$; Kendall test. e) *Sweltsa* sp., females: $z=2.67$, $p<0.01$, $n=12$; Kendall test. f) *Sweltsa* sp., females: $z=3.72$, $p<0.01$, $n=12$; Kendall test.

Table 1. The difference of adult longevity and head width in term of effective mating in the early and late emerged groups.

		Earlier				Later			
<i>Isoperla aizuana</i>		Max.	Min.	Mean±S.D. (n)		Max.	Min.	Mean±S.D. (n)	
Head width (mm)	Mate	1.96	1.74	1.85±0.09 (8)	NS	1.80	1.68	1.71± 0.06 (4)	NS
	Not mate	1.92	1.76	1.86±0.07 (5)		1.88	1.66	1.78± 0.08 (6)	
Adult longevity (day)	Mate	42	27	32.88± 5.06 (8)	NS	35	16	27.25± 9.00 (4)	NS
	Not mate	45	4	26.20±16.54 (5)		27	3	17.17± 8.26 (6)	
Head width (mm)	Mate	1.72	1.48	1.66±0.08 (8)	NS	1.70	1.58	1.57± 0.01 (2)	NS
	Not mate	1.72	1.64	1.68±0.04 (3)		1.66	1.56	1.62± 0.04 (7)	
Adult longevity (day)	Mate	44	30	38.25±4.95 (8)	NS	32	18	25.00± 9.90 (2)	NS
	Not mate	39	31	35.00±4.00 (3)		28	14	19.00± 5.86 (7)	
<i>Sweltsa</i> sp.									
Head width (mm)	Mate	1.40	1.32	1.35±0.03 (5)	NS	1.30	1.20	1.26± 0.04 (7)	***
	Not mate	1.38	1.36	1.37±0.01 (3)		1.26	1.08	1.20± 0.06 (8)	
Adult longevity (day)	Mate	29	16	25.00±4.94 (5)	**	23	11	16.83± 4.49 (7)	**
	Not mate	10	2	6.33±4.04 (3)		22	4	12.13± 6.29 (8)	
Head width (mm)	Mate	1.26	1.20	1.24±0.02 (7)		1.30	1.04	1.17± 0.18 (2)	
	Not mate								
Adult longevity (day)	Mate	24	7	17.00±5.76 (7)		19	4	11.5±10.60 (2)	
	Not mate								

NS: $p>0.05$, **: $p<0.05$, ***: $p<0.01$; Mann-Whitney U-Test

Mate: effectively mated ones, Not mate: others

like objects were observed during and after mating. Females that mated for 1 hr 45 min and 6 hr did not oviposit, because the mating duration was too short or because the female dropped the spermatophore-like objects after mating.

In both species, the copulation period had no correlation with head width, adult longevity, or fecundity.

Fecundity

Female *Isoperla aizuana* oviposited 1 to 6 egg masses (2.96 ± 1.56 , Mean±S.D., $n=12$). Each egg mass contained 15 to 365 eggs (111.38 ± 81.43 , Mean±S.D., $n=12$), and they oviposited 55 to 723 eggs in total (333.50 ± 166.50 , Mean±S.D., $n=12$). Female *Sweltsa* sp. oviposited 1 to 4 egg masses (2.00 ± 1.04 , Mean±S.D., $n=12$). Each egg mass contained 11 to 146 eggs (57.58 ± 33.50 , Mean±S.D., $n=12$), and they oviposited 20 to 228 eggs in total (122.75 ± 71.00 , Mean±S.D., $n=12$).

In *I. aizuana*, the total number of eggs per female was not significantly correlated with emergence date (Fig. 8a), head width (Fig. 8b), or adult longevity (Fig. 8c). By contrast, in *Sweltsa* sp., although the total number of eggs was not correlated with emergence date (Fig. 8d), it was significantly correlated with head width (Fig. 8e) and adult longevity (Fig. 8f).

The factors related with effective mating

In the early-emerging females of *Isoperla aizuana*, greater head width and/or adult longevity had no relation with effective mating, while in later-emerging females of *I. aizuana*, individuals that had longer adult lives tended to mate more effectively, although the difference was not significant (Mann-Whitney U-test: $p=0.077$). In *I. aizuana*

males, effective mating had no relation with the factors discussed above.

In the early-emerging females of *Sweltsa* sp., individuals with greater adult longevity mated more effectively (Mann-Whitney U-test: $p<0.05$). In later-emerging females of *Sweltsa* sp., individuals with a greater head width (Mann-Whitney U-test: $p<0.01$) or adult longevity (Mann-Whitney U-test: $p<0.05$) mated more effectively. In *Sweltsa* sp. males, these factors were not correlated (Table 1).

DISCUSSION

In several species of aquatic insects, adult size and adult longevity are closely related; larger individuals live longer than smaller ones (Banks and Thompson, 1987; Michiels and Dhondt, 1989; Neems *et al.*, 1990). In stoneflies, although the relationship between emergence date and adult size has been investigated (Scheldon, 1972; Hynes and Hynes, 1975), the relationship with adult longevity has not been well studied. Only in a dragonfly, *Sympetrum danae*, is adult longevity reported to shorten with later emergence date (Michiels and Dhondt, 1989). In this study, we obtained a similar result; individuals that emerged earlier had greater adult longevity needless to say of the relation with body size in *I. aizuana* or *Sweltsa* sp. In *I. signata*, many laboratory-reared adults live over 2 weeks although averaged adult longevity is 7 days (Harper, 1973a). Adult longevity in *I. aizuana* is not noticeably different from that of *I. signata*. Individuals emerging later in spring are exposed to higher water temperatures in the nymph stage and higher air temperatures in the adult stage than earlier-emerging individuals. Nebeker (1971) reports that average adult lon-

evity of *Pteronarcys dorsata* kept under 10°C in their nymphal stage is 36 days, under 15°C is 31 days, and under 20°C is 17.5 days, but more period was needed to emerge at the lower temperatures. And he concluded that adult longevity is determined partly by the water temperature to which the individuals are exposed in the immature stage, and by the air temperature encountered after emergence.

There are two groups of stoneflies with respect to the days until mating: individuals that can mate immediately after emergence (Brink, 1949; Hanada *et al.*, 1992) and individuals that need at least a few days before mating (Harper, 1973ab; Sephton and Hynes, 1983; Jop and Szczytko, 1984; Hanada *et al.*, 1992). The species that we investigated were the latter type; *Isoperla aizwana* required 7 to 26 days in females and 7 to 16 days in males before mating, and *Sweltsa* sp. required 2 to 7 days and 3 to 12 days, respectively. Furthermore, in both species studied, adults emerging earlier required more days until first effective mating. Michiels and Dhondt (1989) reported that in dragonflies, the number of days until mating is negatively correlated with emergence date, and attributed the shortened maturation period with emergence date in dragonflies to photoperiod, although they could not rule out the possibility that an unknown genetic difference plays a role.

The stonefly emergence period is not as long as in dragonflies. Environmental factors, such as water and air temperature, would affect the maturation period and adult longevity more than photoperiod. In mayflies, although higher temperatures initiate maturation of adult tissues, they reduce the overall potential for growth of the body, so later-emerging individuals tend to be smaller (Vannote and Sweeney, 1980; Sweeney *et al.*, 1995). Small adults also have less reproductive tissue (Sweeney *et al.*, 1995). Therefore, later-emerging stoneflies might have a smaller amount of mature reproductive tissue. And although fecundity is reduced in later-emerging stoneflies, fewer days are required until effective mating.

The period required for individuals to reach maturation following emergence might depend on two factors. First, the reproductive tissue of late-emerging individuals is more mature at the time of emergence, and therefore the maturation period was shorter for the later emerging ones. Second, development of adult reproductive tissue is influenced by air temperature, with higher temperatures causing rapid maturation. Further study would be needed to understand the factors associated with the length of time between emergence and mating.

Michiels and Dhondt (1989) reported that large and early-emerging dragonflies live longer; consequently, large individuals might gain a higher lifetime mating success. Banks and Thompson (1985) revealed that in damselflies, lifetime mating success is positively related to adult longevity. In the stoneflies that we studied, when individuals emerged late, the rate of effective mating tended to decrease. Khoo (1968) also suggested that in stoneflies, the stimulus for emergence causes small nymphs to accelerate

to be adult late in the season, so they cannot attain their full size and they develop poorly. The accelerated maturation of reproductive tissue might lead to fewer days until mating, but it might also lead to inferior maturation of the tissue. Therefore, later-emerging individuals would mate less effectively than early-emerging ones.

However, adult size is correlated positively with adult longevity (Banks and Thompson, 1987; Michiels and Dhondt, 1989; Neems *et al.*, 1990), and adult size or adult longevity is correlated positively with fecundity (Nebeker, 1971; Vannote and Sweeney, 1980; Sweeney and Vannote, 1984; Banks and Thompson, 1987). Therefore, even among later-emerging individuals, we believe that longer-lived and larger females tend to mate more effectively. In *Isoperla aizwana*, however, adult size and adult longevity were not significant factors for effective mating among later-emerging individuals, although they were significant in *Sweltsa* sp.

We observed inserted spermatophore-like objects in the females of *Sweltsa* sp. In Odonata, the females that get a spermatophore by mating can use it as energy for egg maturation and their adult longevity is long (Watanabe and Sato, 1995). Though there are several reports of no correlation between male nutrients and female fecundity (Boggs, 1990), Boggs (1990) suggests when the food resources for adult females are limited, the significance of male nutrient donation will increase. It might be also possible for stoneflies to use spermatophores to increase adult longevity, especially in later-emerging individuals.

The copulation period was longer in *Sweltsa* sp. than in *I. aizwana*, though, mating duration had no correlation to fecundity, adult longevity and adult size. The results of long mating duration might be related with other factors such as sperm competition. In one study on butterflies, for example, the sperm giving was finished in the first half of mating (about 70 min) and the second half of mating was used for guarding females (Watanabe and Sato, 1995). This suggests that long mating duration plays an important role in female guarding.

A longer copulation period in *Sweltsa* sp. may be also related with their behavior. *Isoperla aizwana* males tried to mate immediately after finding a female. By contrast, *Sweltsa* sp. males tried to mate after examining the females. These differences in mating character might affect the relationships with effective mating, so that adult size and adult longevity might not be significantly related to fecundity in *Isoperla aizwana*, while they are related to fecundity in *Sweltsa* sp.

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