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Seasonal and Daily Flight Timing of Oviposition in Several Stonefly Species (Plecoptera) in the Field

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ABSTRACT—Peak preovipositional flight season and peak preovipositional flight time of day were compared among 12 species of Nemouridae, Chloroperlidae, Perlodidae and Perlidae. Species with a later peak date of preovipositional flight were found to have a later peak preovipositional flight time of day than species with an earlier peak in preovipositional flight season. A later peak preovipositional flight season correlated with a lower light intensity. Similarly, a later peak preovipositional flight time of day correlated with a lower light intensity and a later sunset. Individuals of one species (*Sweltsa* sp.), whose preovipositional flight date was later, flew over the stream at a later time of day. Species differences in peak preovipositional flight season and peak preovipositional flight time of day may be driven by species specific sensitivity for different light intensities.

Key words: preovipositional flight timing, light intensity, air temperature, photoperiod, stoneflies

INTRODUCTION

Stoneflies fly up into the trees after emergence. Compared to other aquatic insects, they have a less definitive upstream flight. They move far from the stream before returning for oviposition (Hynes, 1976). Some species walk on snow after emergence towards objects on the horizon, a behavior considered to be controlled by the direction of light (Butz, 1973). Although some stoneflies deposit their eggs on stones and in leaf litter, most species deposit their eggs amongst riffles (Komatsu, 1956; Hynes, 1976). Females glide down to the water surface where their egg mass is washed from their ovipositor by the stream (Hynes, 1974). Most females oviposit several times over several days (Hynes, 1976).

The onset of insect oviposition is often driven by photoperiod (Beck, 1980). Furthermore, insects show species-specific preferences for different light intensities during which to oviposit (Hinton, 1981). Stoneflies oviposit under a range of light conditions, depending on species (Hynes, 1974). Although the daily flight behavior of *Calineuria californica* (Poulton and Stewart, 1988) and stonefly oviposition season and timing have been described (Harper and Hynes, 1972; Harper, 1973a), to date a comparative study of oviposition behaviour in stoneflies has not been conducted. It is likely that oviposition season will relate to emergence period. The environmental factors that determine oviposition timing, however, are not clear. A comparison of oviposition timing among stonefly species may reveal the environmental factors that drive the timing of oviposition.

In this study, we determined peak preovipositional flight season and time of day for twelve stonefly species, Nemouridae (*Amphinemura* sp.), Chloroperlidae (*Sweltsa* sp.), Perlodidae (*Stavsolus* sp.1, *Stavsolus* sp.2, *Stavsolus japonicus*, *Isoperla nipponica*, and *Ostrovus* sp.) and Perlidae (*Kiotina pictetti*, *Kamimuria tibialis*, *Kamimuria uenoi*, *Oyamia* sp., and *Oyamia lugubris*) by capturing adult females as they engaged in preovipositional flights above a stream riffle. We discuss the implications of species and individual differences in the timing of oviposition and investigate the hypothesis that light intensity and air temperature are major factors in determining the timing of oviposition.

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MATERIALS AND METHODS

Adult stoneflies were collected at Omata (34°22´N136°05´E) on the Shigo River, Nara Prefecture, Japan, on April 28, May 12, May 28, May 29, June 9, June 22, and July 23, 1999. On May 28, only *Sweltsa* sp. was collected. The stream was approximately 5 m wide, with a surface flow velocity of approximately 1 m/s and the riffle used by the female stoneflies for oviposition contained large rocks. The southern bank was covered with vegetation, and the northern bank was a three meter wide 'beach' of stones and sand (Fig. 1). Mountains covered with Japanese cedars and broad-leaved trees surrounded the collection point. The weather was fair for the duration of the study, with the exception of June 22nd when it rained.

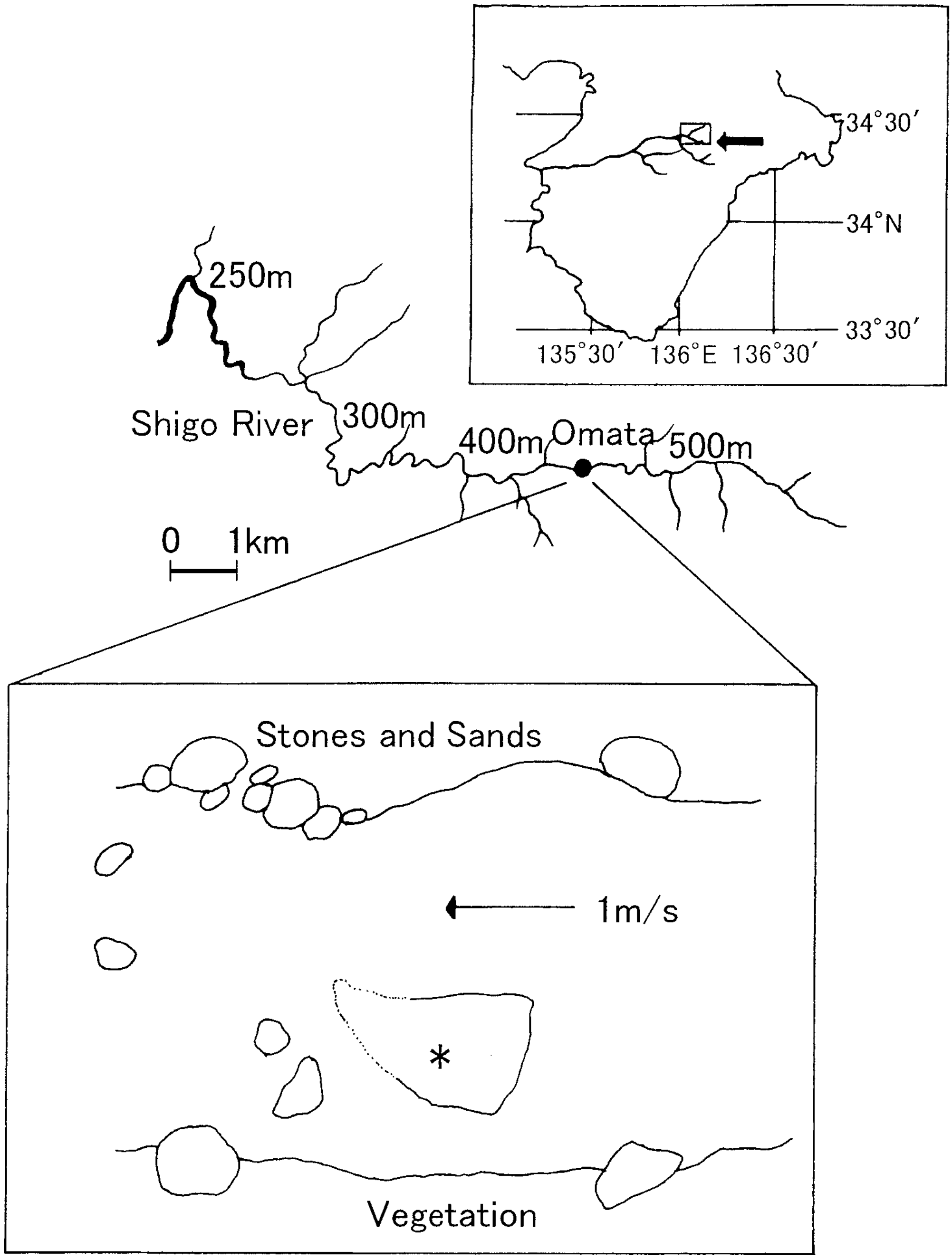

Fig. 1. A map of the collection site and the position (*) where individuals were collected

Time interval collections of female stoneflies were made to determine peak preovipositional flight season and peak preovipositional flight time of day. On each day, preovipositional flight was observed from one point (*) on a large rock, which was positioned just beside the oviposition riffle. All females flying within a 2 m radius of the observation rock and within 1.5 m of the stream surface were captured using a sweep net. Net sweeps were conducted for 10-min periods and were followed by a 5-min interval during which captured individuals were fixed in 80% ethanol. The sequence of 10-min net sweeps followed by a 5-min interval was continued throughout the 14:25 to 18:50 capture period. Water and air temperature were measured and a lux meter (Handy Lumi, SEKONIC) was used to measure light intensity.

The peak in preovipositional flight season was taken to be the day when most individuals of a species were captured above the riffle. Similarly, the peak preovipositional flight time of day was considered to be the mean time when most individuals of one species came to the riffle during a 10-min sweep. For example, if the sweep conducted at 2:55–3:05 captured most individuals, then peak preovipositional flight time of day was taken as 3:00.

The differences in the peak preovipositional flight season were statistically examined using a Kolomogorov-Smirnov two-sample test with Bonferroni correction to identify the species with a difference in seasonal timing. The three species where only one adult was captured during the study were excluded from this analysis. The statistical analysis of interspecific differences in preovipositional flight time of day was done using a Kolmogorov-Smirnov two-sample test with Bonferroni correction among all the collected species on each collection date.

The *Sweltsa* sp. investigated in the present study is the same as the *Sweltsa* sp. recorded by Hayashi *et al*. (1997). *Stavsolus* sp.1 and *Stavsolus* sp.2 were defined by habitat and head and abdomen pattern according to Inada (1996).

RESULTS

Preovipositional flight season

There were two types of preovipositional flight behavior. Individuals of *Kiotina pictetti*, *Stavsolus* sp.1, *Stavsolus* sp.2, *Stavsolus japonicus* and *Ostrovus* sp. flew from the trees beside the stream straight to the stream surface to release their egg mass. Individuals of *Amphinemura* sp., *Sweltsa* sp., *Kamimuria tibialis*, *Kamimuria uenoi*, *Isoperla nipponica*, *Oyamia lugubris* and *Oyamia* sp. flew from the trees and glided for a while, before descending to the stream and releasing their egg mass. The peak preovipositional flight season for the twelve species is shown in Table 1. The significance level of the Kolmogorov-Smirnov two-sample test with Bonferroni correction was P=0.0014. There was an interspecific difference in peak preovipositional flight season among nine species.

The peak preovipositional flight season of *Amphinemura* sp. was April 28th. A Kolmogorov-Smirnov two-sample test with Bonferroni correction showed that the flight season of *Amphinemura* sp. was significantly earlier than that of *Sweltsa* sp. (D_{mn}=0.77, P<0.001), *Isoperla nipponica* (D_{mn}=0.86, P<0.001), *Stavsolus* sp.2 (D_{mn}=0.89, P<0.001), *Kamimuria uenoi* (D_{mn}=0.89, P<0.001) and *Oyamia lugubris* (D_{mn}=1, P<0.001). The peak in preovipositional flight season of *Sweltsa* sp. was on May 12th and that of *Isoperla nipponica*, *Stavsolus* sp.2, *Ostrovus* sp. and *Kamimuria uenoi* on May 29th. The flight season of *Sweltsa* sp. tended to be earlier than that of *Isoperla nipponica*, *Stavsolus* sp.2 and *Ostrovus* sp.. *Kamimuria uenoi* tended to fly around in the same season as *Isoperla nipponica*, *Stavsolus* sp.2 and *Ostrovus* sp.. The peak in preovipositional flight season of another perlid species, *Oyamia lugubris*, was on June 9th. A Kolmogorov-Smirnov two-sample test with Bonferroni correction showed that *Oyamia lugubris* came to the stream for preovipositional flight significantly later than *Sweltsa* sp. (D_{mn}=0.69, P<0.001), *Isoperla nipponica* (D_{mn}=0.79, P<0.001), *Stavsolus* sp.2 (D_{mn}=0.79, P<0.001) and *Kamimuria uenoi* (D_{mn}=0.73, P<0.001). No stoneflies visited the oviposition riffle on June 22nd because of rain. Similarly, individuals were not observed on July 23rd until after the capture period and so again none were captured.

Preovipositional flight time of day

On April 28th (Fig. 2a), water temperature was 11°C and air temperature was 16°C at 15:00. The peak preovipositional flight time of day was 14:55 to 15:05 in *Amphinemura* sp. and 15:25 to 15:35 in *Sweltsa* sp. The significance level of the Kolmogorov-Smirnov two-sample test with Bonferroni correction was p=0.016. Interspecific differences in preovipositional flight time of day among the three species captured were not statistically significant. However, *Amphinemura* sp. tended to fly over the stream earlier in the day than *Sweltsa* sp.

On May 12th (Fig. 2b), water temperature was 12.5°C and air temperature was 20°C at 15:00. The peak preovipositional flight time of day was 17:10 to 17:20 in *Sweltsa* sp., 17:55 to 18:05 in *Isoperla nipponica* and 17:25 to 17:35 in *Stavsolus* sp.1. The significance level of the Kolmogorov-Smirnov two-sample test with Bonferroni correction was p=0.0014. Although, not significant using a Kolmogorov-Smirnov two-sample test with Bonferroni correction, the preovipositional flight time of *Isoperla nipponica* tended to be later than that of *Sweltsa* sp. and *Stavsolus* sp.1.

On May 29th (Fig. 2c), water temperature was 13°C

Table 1. Number of females of each stonefly species caught on each of the preovipositional flight days.

		Preovipositional flight date					
		4/28	5/12	5/29	6/9	6/22	7/23
Nemouridae	*Amphinemura* sp.	**8**	1	0	0	0	0
Chloroperlidae	*Sweltsa* sp.	16	**75**	25	15	0	0
Perlodidae	*Isoperla nipponica*	1	12	**18**	0	0	0
	Stavsolus sp.1	0	**5**	4	0	0	0
	Stavsolus sp.2	0	3	**9**	0	0	0
	Stavsolus japonicus	0	**3**	2	1	0	0
	Ostrovus sp.	0	1	**7**	1	0	0
Perlidae	*Kiotina pictetti*	0	0	1	0	0	0
	Kamimuria uenoi	0	7	**9**	1	0	0
	Kamimuria tibialis	0	1	0	0	0	0
	Oyamia lugubris	0	0	3	**11**	0	0
	Oyamia sp.	0	0	1	0	0	0

Bold number indicates the peak preovipositional flight date of the season.

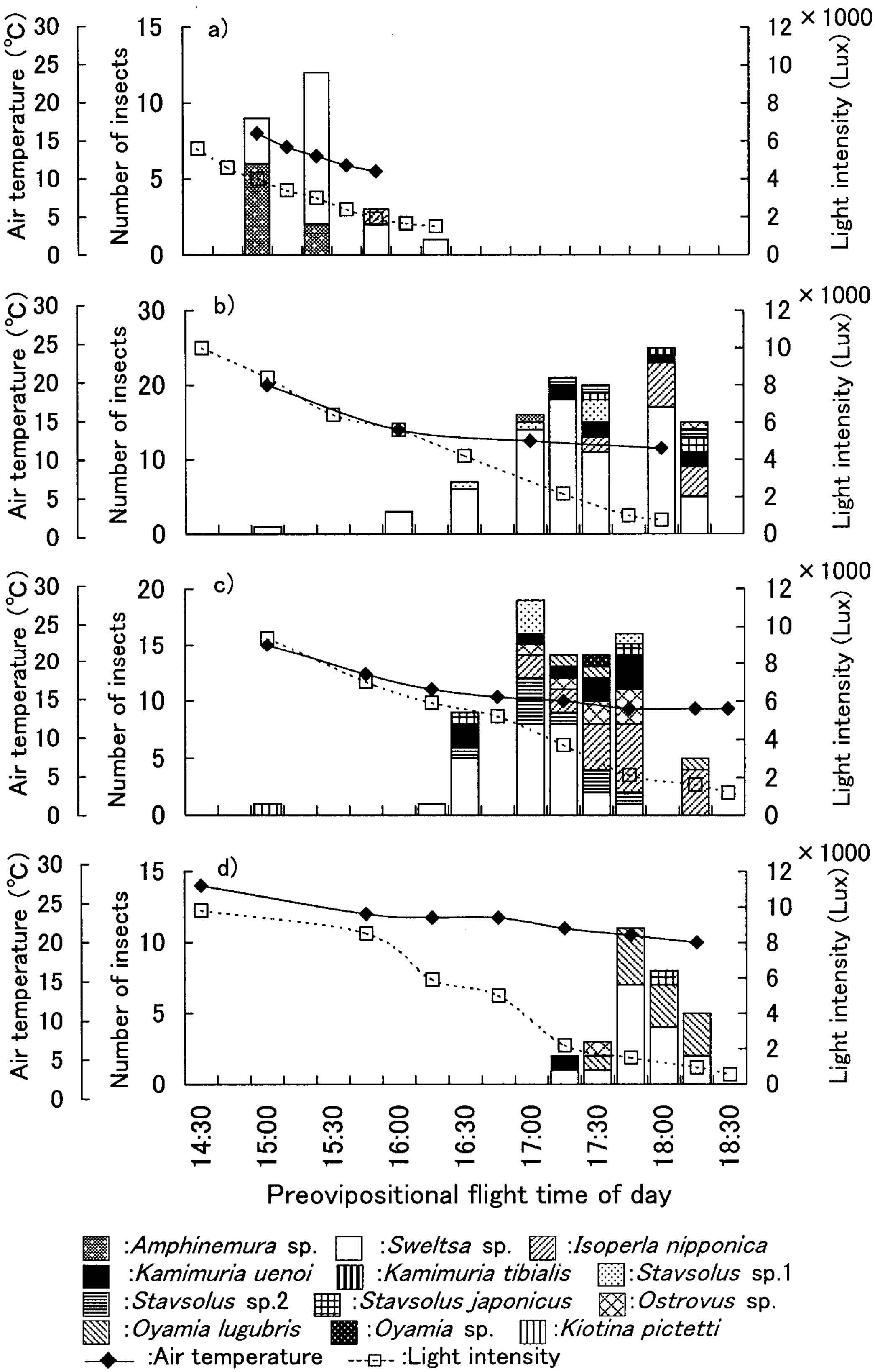

Fig. 2. Daily periodicity of preovipositional flight. Broken line: Light intensity. Solid line: Air temperature. a) April 28, b) May 12, c) May 29, d) June 9.

and air temperature was 22.5°C at 15:00. The peak preovipositional flight time of day was 16:55 to 17:05 in *Sweltsa* sp. and *Stavsolus* sp.2, and 17:40 to 17:50 in *Isoperla nipponica, Ostrovus* sp. and *Kamimuria uenoi*. The significance level of the Kolmogorov-Smirnov two-sample test with Bonferroni correction was *p*=0.0011. Preovipositional flight time of day was significantly earlier for *Sweltsa* sp. than *Isoperla nipponica* (D_{mn}=0.66, *P*<0.001, Kolmogorov-Smirnov two-sample test with Bonferroni correction). The preovipositional flight time of *Ostrovus* sp. tended to be later than that of *Sweltsa* sp., but the trend was not significant.

On June 9th (Fig. 2d), water temperature was 14°C and air temperature was 24°C at 15:40. The peak preovipositional flight time of day was 17:40 to 17:50 in both *Sweltsa* sp. and *Oyamia lugubris*. The significance level of the Kolmogorov-Smirnov two-sample test with Bonferroni correction was *p*=0.005. A significant difference in preovipositional flight time could not be found.

The relationship between preovipositional flight season and time of day

Peak preovipositional flight season and peak time of day could not be estimated for *Stavsolus japonicus, Kiotina pictetti*, *Kamimuria tibialis* and *Oyamia* sp. because of small sample sizes at Omata. In the remaining eight species of Nemouridae (*Amphinemura* sp.), Chloroperlidae (*Sweltsa* sp.), Perlodidae (*Stavsolus* sp.1, *Stavsolus* sp.2, *Isoperla nipponica* and *Ostrovus* sp.) and Perlidae (*Kamimuria uenoi* and *Oyamia lugubris*), the relationship between peak preovipositional flight season and peak time of day was examined. A significant positive relationship (τ=0.651, z=0.2256, n=8, *P*<0.05, Kendall-test, Fig. 3a) was found between date of peak preovipositional flight season and peak flight time of day *i.e.* the later in the season the peak in preovipositional flight season the later the peak flight time of day.

Species whose peak preovipositional flight date was later in the season flew over the stream under significantly lower light intensities at the peak time of the peak day (τ=–0.713, z=–2.469, n=8, *P*<0.05, Kendall-test) than the species whose peak flight date was earlier (Fig. 3b). Air temperatures at the peak time of the peak day tended to be higher for the species whose peak preovipositional flight day was later in the season (Fig. 3b). In addition, a later peak preovipositional flight time of day coincided with a significantly lower (τ=–0.914, z=–3.166, n=8, *P*<0.005, Kendall-test) light intensity (Fig. 3c). The peak preovipositional flight time on the peak day was also correlated with time of sunset (τ=–0.651, z=–0.2256, n=8, *P*<0.05, Kendall-test, Fig. 3c), but it was not significantly correlated with air temperature (Fig. 3c).

Although the trend was not significant, the peak preovipositional flight time of day of *Sweltsa* sp. appeared to get later as the flight season progressed (Fig. 4a). Individuals of *Sweltsa* sp. whose flight date was later in the season tended to fly over the stream under lower light intensities and higher air temperatures at the peak preoviopositional flight time of day than the population whose peak flight date was earlier (Fig. 4b).

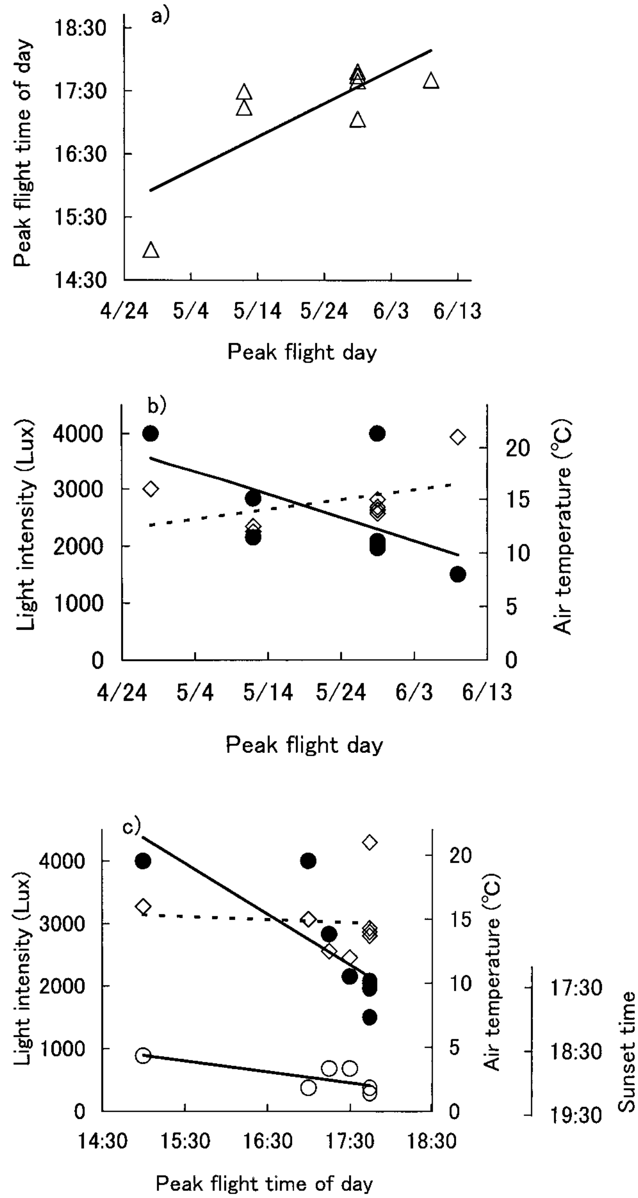

Fig. 3. The relation between peak preovipositional flight date in the season and peak preovipositional flight time on that day in eight species, and their relation to light intensity, air temperature and sunset timing. a) the relation between peak preovipositional flight date in the season and peak preovipositional flight time of day in eight species, b) the relation between peak preovipositional flight date in the season and light intensity and air temperature at the peak preovipositional flight time of that day in eight species, c) the relation between peak preovipositional flight time of day and its light intensity, air temperature and sunset timing, ●: light intensity, ◇: air temperature, ○: sunset timing, Solid lines: significant relation, Broken lines: not significant.

Individuals of *Sweltsa* sp. whose peak preovipositional flight time was on a later collection date flew over the stream under significantly lower light intensities (τ=–0.8, z=–1.96, n=5, *P*<0.05, Kendall-test) (Fig. 4c) than the population whose peak flight time was earlier. However, time of sunset

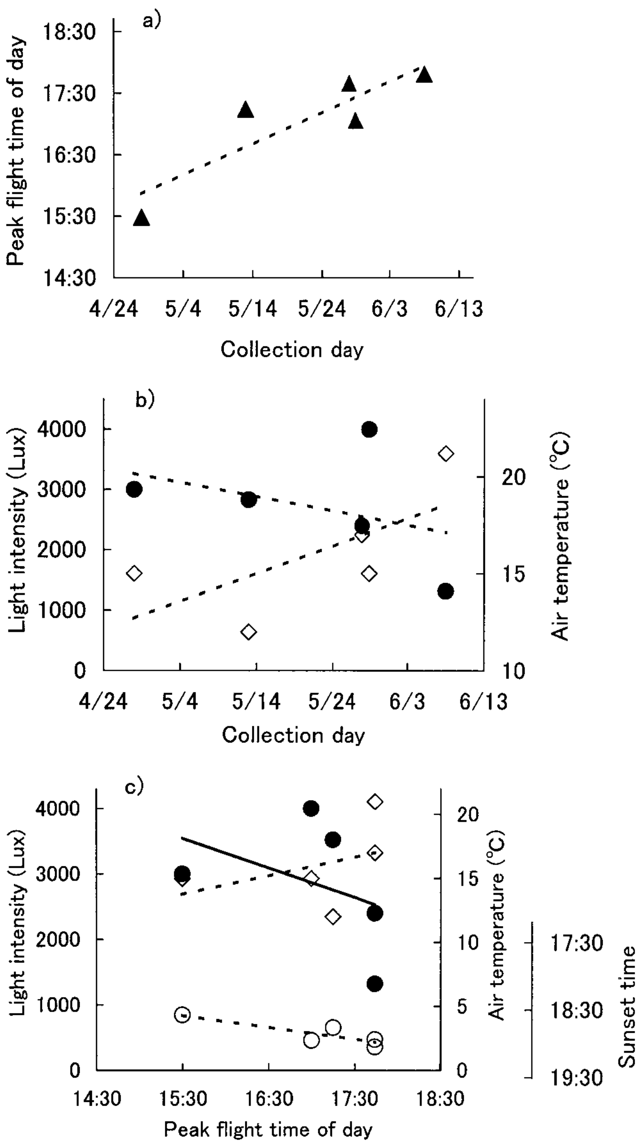

Fig. 4. The relation between collection date and peak preovipositional flight time on that day, and their relation to light intensity, air temperature and sunset timing in *Sweltsa* sp. a) the relation between collection date and peak preovipositional flight time of day, b) the relation between collection date and light intensity and air temperature at the peak preovipositional flight time of that day, c) the relation between peak preovipositional flight time of day and its light intensity, air temperature and sunset timing, ●: light intensity, ◇ : air temperature, ○: sunset timing, Solid lines: significant relation, Broken lines: not significant.

and air temperature could not explain the finding that peak preovipositional flight time of day got later as the season advanced (Fig. 4c).

DISCUSSION

In stoneflies, the egg-laying season differs from spring to autumn among species, even within the same genus (Harper and Hynes, 1972; Harper, 1973a, b; Komatsu, 1956, 1971). The species investigated in this study emerge in spring and oviposit in spring and early summer. In order to oviposit their egg mass, they fly over the stream and glide down to the water surface. The egg mass is washed from their abdomen tip by the current. The peak in preovipositional flight season of *Amphinemura* sp. was earliest followed by *Sweltsa* sp., *Stavsolus* sp., *Isoperla nipponica, Ostrovus* sp. and *Oyamia lugubris* respectively. Differences in peak preovipositional flight season among species can be explained by differences in emergence season.

Mori and Matsutani (1953) studied the daily swarming behavior of lentic caddisflies and concluded that swarming place and time is different depending on the species. Oviposition timing in stoneflies also varies among species. For example, oviposition of *Neoperla clymene* living in Texas occurs at night (Vaught and Stewart, 1974), although most species of stonefly oviposit during the day (Harper, 1973a, b; Hynes, 1974; Poulton and Stewart, 1988). This current study also showed that peak preovipositional flight time of day in stoneflies was different depending on the species. *Amphinemura* sp. tended to fly over the stream earlier in the day than *Sweltsa* sp., and *Isoperla nipponica* later than *Sweltsa* sp.. The preference of *Amphinemura* sp. for ovipositing early in the day is consistent with a previous study which showed them to favor oviposition under bright conditions (Harper, 1973b).

Generally, Nemouridae emerge in colder seasons. Perlidae emerge in warmer seasons and live in warm areas (Illies, 1964). In this study, nemourid species flew over the stream earlier in the season and at an earlier time of day than Perlid species. Light phase and air temperature experienced through adult life might differ between the two families. These factors might partly explain the differences in adult preovipositional flight time of day.

Species with later peak preovipositional flight dates had later peak preovipositional flight times of day than species with earlier peak preovipositional flight dates. Sunset occurs progressively later throughout spring; so light intensity at any given hour of the afternoon becomes stronger as the season progresses. Therefore, for preovipositional flight to occur under similar light conditions, flight time of day must be delayed. Species flying later in the season delayed their flight time of day long enough to experience a lower light intensity than they did earlier in the season. The peak preovipositional flight time on the peak day was also related to light intensity and time of sunset. Light intensity is related to day-length and fixed by sunset timing, but air temperature is more changeable and dependent upon the weather. Light intensity for preovipositional flight might be roughly fixed for each species.

The individuals that have later peak preovipositional flight dates experience higher air temperatures throughout their adult stage. Kon (1984) reports that higher temperatures allow Chironomidae to fly more easily and that swarming occurs after sunset in summer, whereas swarming occurs before sunset when temperatures are low, because low temperatures impair flight ability. Swarming after sunset

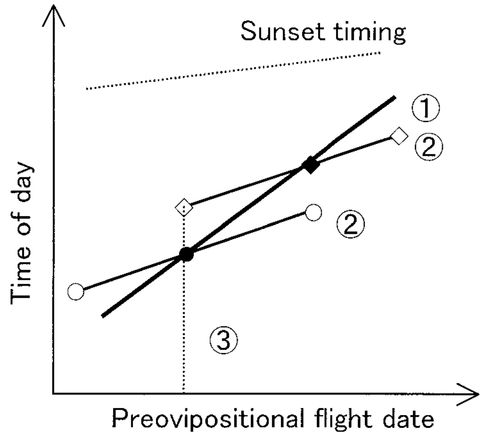

Fig. 5. The concept of preovipositional flight timing. ①: Comparison among species: Species whose preovipositional flight season is later fly later during the day. ②: Comparison among individuals of one species: Individuals whose preovipositional flight date in the season is later fly later in the day. ③: One day observation: Species whose preovipositional flight season is later fly later in the day.

may be advantageous in terms of predator avoidance. A buprestid beetle, *Nascioides enysi*, oviposits in shaded areas when temperatures are high, and in bright areas when temperatures are low (Hinton, 1981). In this study, however, air temperatures during peak preovipositional flight time of day were not related to preovipositional flight season and time of day. Poulton and Stewart (1988) reported the female flight periodicity relating to flight behavior in *Calineuria californica.* They concluded that female flight in *Calineuria californica* occurred between 19:30 and 21:00. Air temperature and percent relative humidity were partly responsible for female flight periodicity. However, the greatest determinant of female flight periodicity in *Calineuria californica* was light condition.

Individuals that flew at a later date in the season tended to fly preovipositionally over the stream later in the day than individuals that flew at an earlier date. Species flying at a later date in the season flew over the stream later in the day than species that flew at an earlier date. A model of this relationship can be drawn as in Fig. 5. The intraspecific difference in preovipositional flight time of day was only related to light intensity. However, the interspecific difference in preovipositional flight season was related to light intensity and interspecific differences in flight time of day were related to light intensity and sunset timing. It might be considered that every species has a fundamentally determined light intensity for preovipositional flight. Light intensity influenced preovipositional flight time of day in individuals, but other environmental factors such as air temperature might also be weakly related to intraspecific differences in preovipositional flight.

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