Oviposition behaviour of *Sympetrum frequens* (Selys) (Odonata: Libellulidae)

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Oviposition behaviour by *Sympetrum frequens*, a species endemic to Japan, has been observed throughout its entire breeding season, which extended for about one month after the harvest of rice. Approximately 50% of oviposition events occurred during the first week of the reproduction period. Sunny oviposition sites were preferentially selected by ovipositing pairs. The starting time of oviposition was highly correlated with the ambient temperature (Ta), the days elapsed since the beginning of the oviposition period, and the weather of the day. The mean duration of oviposition (DO) was 325.0 ± 194.7 s in tandem oviposition (TO) and 152.5 ± 101.8 s in oviposition of the female alone (single oviposition; SO), and DO was poorly correlated with Ta. Dip rate (DR) was constant throughout the oviposition bout; however, wing-stroke frequency (WSF) of the tandem male declined from the start of oviposition to its end. The WSF of males in TO was 39.4 ± 2.8 Hz, significantly higher than that of tandem females (34.5 ± 3.0 Hz, $p < 0.0001$), but that of females in SO was as high as that of tandem males (39.7 ± 3.7 Hz). WSF was negatively correlated with Ta. In TO the male expends more energy than the female and it controls flight direction, so for the female TO is energetically less costly than SO. Furthermore, flying-oviposition into mud is more effective than non-contact flying-oviposition as the number of eggs per dip in the former exceeds one and more eggs are deposited per time unit than in the latter.

Keywords: Odonata; dragonfly; *Sympetrum frequens*; oviposition; dip rate; wing-stroke frequency; number of deposited eggs

Introduction

Oviposition in *Sympetrum* spp., typically performed by pairs in flight in tandem position and sometimes by females alone, has been studied under various aspects (e.g. Jurzitza, 1965; Koch, 2005; Koch & Suhling, 2005; Rehfeldt, 1992; Schenk et al., 2004; Taguchi & Watanabe, 1995). One of the species in which oviposition behaviour has been investigated is *Sympetrum frequens* Selys (Arai, 1978, 1994; Ishizawa, 1998, 2006, 2008b). However, these studies mostly concern thermoregulation during reproductive activity, based on sparse observations only and not encompassing the entire reproductive period. Therefore, more information is desirable, especially on the flight behaviour during oviposition related to ecological factors.

Sympetrum frequens is a well-known endemic dragonfly in Japan (Ishida et. al., 1989), ranging from Hokkaido across Honshu to Kyushu. The species is considered the insular vicariant of

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the continental *S. depressiusculum* (Selys), which is widely distributed from the Korean Peninsular through north-eastern China and southern Siberia to Europe. It is believed that the latter species extended its range far into the Japanese Archipelago during the early Quaternary. After the archipelago became detached from the continent in the third glacial period, the now isolated population of *S. depressiusculum* evolved to a separate species with a larger body size, known as *S. frequens* (Asahina, 1984). A recent study by Sawabe et al. (2004) revealed no genetic difference between the two species.

Sympetrum frequens breeds in paddy fields, often in great numbers. Adults emerge in the middle of the rainy season in summer, and migrate to highlands, where they aestivate for the hot period (Uéda, 1988). They descend to lowlands at the end of summer and early autumn (Baba, 1953; Tanaka, 1985) and appear in paddy fields where they reproduce (Arai, 1994; Uéda, 1988). As the species undergoes prereproductive diapause by aestivating in highlands and reproduces in autumn, Uéda (1990) defined it as an "autumnal species". Females usually oviposit at paddy fields or muddy places at bogs or puddles after rain, typically employing flying-oviposition in tandem into mud (TO), although sometimes unaccompanied females similarly oviposit into mud (SO) (Eda, 1975). They rarely oviposit into open water of swimming pools at schools (Shimoyamada et al., 2003), but usually only in urban areas, where no more suitable spot for oviposition exists. As to the thermoregulation during their reproductive behaviour, it was reported that the body temperature (T_b) was the highest at the end of copulation and gradually declined as oviposition proceeded (Ishizawa, 1998, 2006). The dip rate is reported to be $c.1.7\,s^{-1}$, and the oviposition bout lasts $c.5$ min (Arai, 1978; Ishizawa, 1998, 2006, 2010).

To complete the present knowledge on the oviposition behaviour of *S. frequens* I observed this species in paddy fields over the entire breeding season. The observations were focused on the frequency of oviposition events in the course of the reproduction period and the daily beginning of oviposition with respect to ambient temperature and as the reproduction period proceeded. Furthermore, I collected data on the duration of oviposition bouts and on the dip rate and wing-stroke frequencies of tandems and single females. Due to recent technical advances in high-speed digital video cameras that allow computer-based analyses of the films, it was possible to define the wing stroke frequencies.

Study sites and methods

Observations were made at two localities on Honshu, Japan. Locality 1 included two observation spots (A and B) of paddy fields situated at Bodaigi, Yamaguchi, Tokorozawa City, Saitama Prefecture (35°46′21″ N, 139°25′5″ E; Figure 1). Spot A was bordered on the west side by a mountain ridge that separated it by a distance of 400 m from Spot B. Locality 2 was at paddy fields at Nishikubo (35°47′10″ N, 139°22′41″ E), Iruma City, Saitima Prefecture, 4 km west of Bodaigi. Each locality was open to the north, with the remaining three sides bordered by ridges, thus morning sunshine first hit the north-western part of the paddy and gradually reached its southeastern part.

The duration of oviposition bouts (DO) was studied in October and November from 2007 to 2010 using a stopwatch, supplemented by a high-speed digital video camera from 2008 to 2011, including, during 2009, a 23-day period without precipitation, thus extending almost over the entire oviposition period from 19 October to 25 November of that year.

Observations were made mostly from 09:00 h to 12:00 h local time and sometimes from 08:50 h onwards. Ambient temperature (Ta) was measured at 10 min intervals with a digital thermistor thermometer, and the wing-stroke frequency (WSF) was video-recorded with a high-speed digital video camera (CASIO EX-F1) at 300 frames per second (fps). At the end of each video recording Ta was measured. Wing-stroke frequency was analysed based on pictures that were converted from the movie at 300 fps to 1200 fps by the application of Apple i-Movie™.
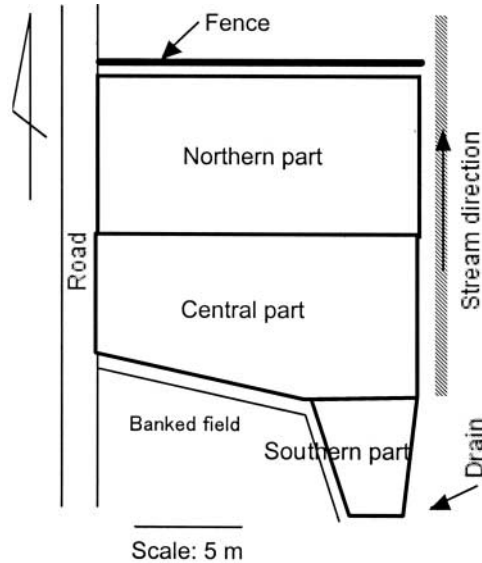
Figure 1. A schematic map of the paddy fields at study site 1A (Bodaigi, Tokorozawa City, Saitama Prefecture, Japan).

The number of eggs deposited per dip was determined using a modification of the method of Wildermuth (1998) who used dark brown Perspex plates for confirmation of recognition of oviposition sites by polarized light in Odonata. My experiments were as follows: in the field, sheets of brown satin lining, black polyester gauze and translucent polyethylene were placed on the mud at a paddy field. Oviposition was monitored by a digital compact camera, Finepix F300EXR and the eggs per dip were calculated by dividing the total eggs deposited by the number of dips; indoors I used translucent plastic cups filled with water, and I forced females of *S. frequens* to deposit eggs in the cups, either continuously by holding the end of the abdomen under the surface or, alternatively, by dipping the abdomen at various intervals. Deposition of eggs was monitored by the Finepix camera, and egg numbers per second was counted on the display of the camera.

Also, the number of eggs that could be deposited by randomly collected females during one bout was estimated by experiments in 1989. Adult females of *S. frequens* were collected near my house at Tokorozawa City, at some distance from any oviposition site. Their body weights were measured before and after forced oviposition into a translucent plastic cup, as described above, and the deposition was video-recorded with an 8 mm video-camera SONY CCDV90. The number of deposited eggs per bout was counted based upon the pictures replayed on the TV display frame by frame. The weight per egg was estimated by dividing the change in body weight before and after deposition by the number of eggs deposited.

Differences between means were statistically analysed by t-test and categorical distributions by χ^2 test. For the data among three groups ANOVA was applied. The correlation among factors was analyzed by regression analysis.

Results

Seasonal progression of oviposition

The first oviposition in 2009 was observed on 9 October at site B of locality 1. However, the paddy fields dried up soon afterwards. Therefore, observations were continued at site A for 23 days from 19 October to 25 November. The total number of recorded tandem pairs and single females that
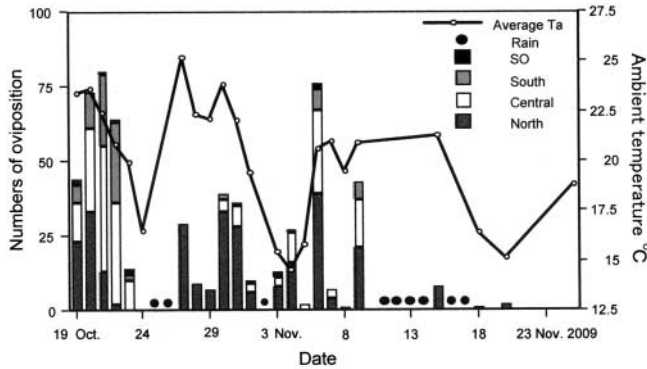
Figure 2.   Numbers of ovipositing females (TO and SO) of *Sympetrum frequens* at study site 1A during the observation period from 19 October 2009 to 25 November 2009.

appeared at site A during this period was 1130, of which 575 successfully engaged in tandem oviposition (TO) and 10 in single oviposition (SO), i.e. a total of 51.8% of female visits resulted in oviposition (Figure 2). Oviposition was observed until 20 November. Two pairs appeared on 25 November but both left the site without egg deposition. TO was observed 281 times at the northern part of the paddy, 205 times at the central paddy, and 89 times at the southern paddy (Figure 1). The numbers expected if TO events were evenly distributed by area are approximately 270, 259 and 46, respectively, which is significantly different from the observed distribution ($\chi^2 = 51.9$, $p < 0.001$), with a deficiency of ovipositions in the central paddy and an excess in the southern paddy.

The average water temperature of the puddles at paddies at early times in the morning was $19.3 \pm 3.3°C$ at the north section, $18.8 \pm 3.0°C$ at the central section and $17.5 \pm 3.2°C$ at the south section and after about one hour was $22.9 \pm 2.8°C$, $22.2 \pm 2.0°C$ and $21.8 \pm 1.8°C$, respectively; in neither case were the differences significant. Water temperature did increase significantly (t-test, $p = 7.4E-08$) in all sections over the course of the day.

Figure 2 shows that the proportion of oviposition events was highest during the first week of observation (47%). Thereafter, the number decreased gradually except for a burst of oviposition on 6 November, the first warm day after a period of low Ta. Rains were recorded on 25–26 October and 2, 11–14 and 16–17 November. However, number of pairs in oviposition did not always increase on fine days after rain.

Daily course of oviposition

On 20 October, 2009 oviposition started at the northern part of site A at 09:00 h at Ta of 20°C, and reached the peak at 10:30 h at Ta of 25°C, and finished at 11:54 h (Figure 3). The number of ovipositions was 33 at the northern part, 28 at the central and 12 at the southern part. The difference among the numbers of the events by the area in comparison with the expected distribution was significant ($\chi^2 = 7.4$, $p < 0.01$).

Early in the season oviposition started soon in the morning, and as the days passed it began progressively later (Figure 4). However, the starting time was influenced by the weather. On sunny days the starting time tended to be earlier than that on cloudy days. The mean Ta at the start of oviposition was $19.7 \pm 2.8°C$ in TO ($11.9–23.3°C$, $n = 25$), and $20.8 \pm 2.4°C$ in SO ($15–24°C$, $n = 11$). This difference is not significant ($p > 0.3$).

Multiple regression analysis including several environmental factors may reveal which environmental variables most strongly influence the starting time of oviposition (y). Three such factors were included, i.e. the days elapsed from 9 October (x_2), cloud cover (x_3 discerning
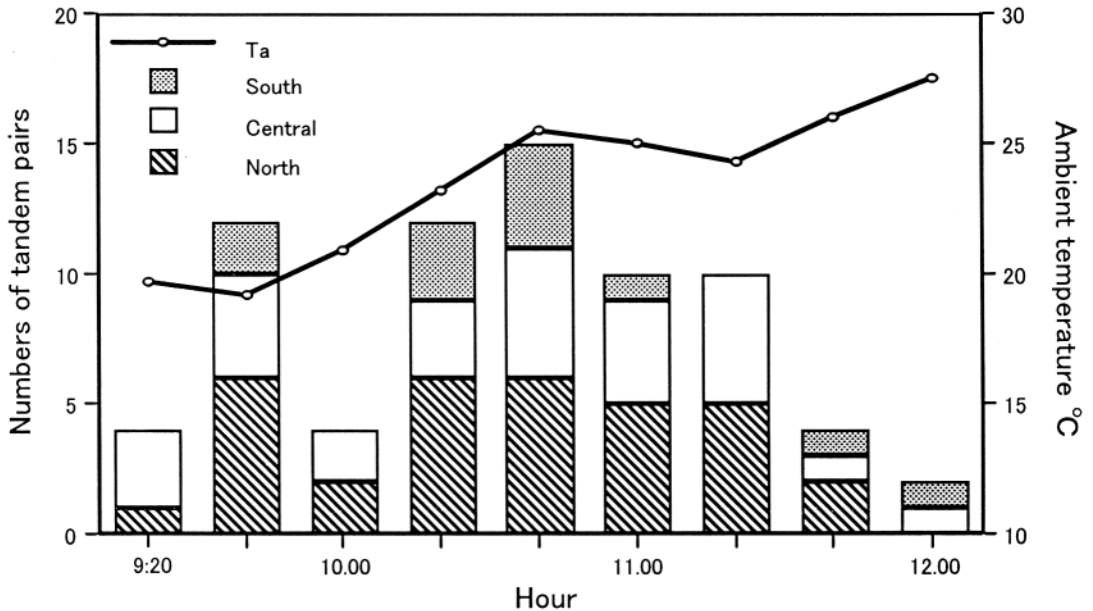
Figure 3. Numbers of ovipositing pairs of *Sympetrum frequens* at study site 1A in the course of a single morning on 20 October 2009.
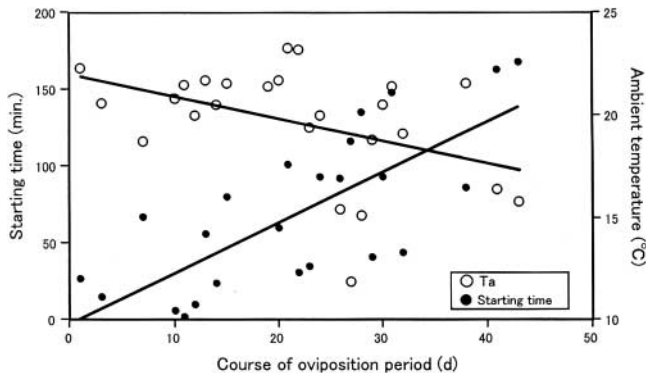

Figure 4. Relationship between the starting time (y_1) of tandem oviposition or the ambient temperature (y_2) at the starting time during the course of the seasonal oviposition period (x) in *Sympetrum frequens* at Bodaigi in 2009. The first day of the observation was 9 October 2009. Starting time versus days after 9 October: $y_1 = 3.271x - 2.616$, $n = 25$, $r = 0.728$, $p < 0.001$; Ta versus days after 9 October: $y_2 = -0.109x - 22.070$, $n = 25$, $r = 0.438$, $p < 0.05$.

four categories: 1 cloudy, 2 slightly cloudy, 3 clear, 4 fine) and Ta (x_1). A linear combination of these variables did, in fact, explain much of the variation in the time of onset of oviposition ($r = 0.858$, $p = 2.800E-6$, $n = 25$). The most important factor delaying the onset of oviposition was cloud cover (−26.4 min.), whereas Ta had only a moderate effect (−7.5 min.), and the impact of the daily progress of the reproductive period was minimal (2.2 min.). Cloud cover and Ta were negatively correlated to the onset of oviposition ($y = -7.545x_1 + 2.193x_2 - 26.410x_3 + 238.037$).

Oviposition peaked in late forenoon. The peak time inclined toward a delay as the days elapsed, shifting in October from 10:30 h to 11:30 h. The mean Ta at the peak was $21.0 \pm 3.2°C$ (14.4–25.3°C, $n = 24$), and was not significantly ($p > 0.3$) higher than the average of the entire

oviposition period ($20.5 \pm 3.0°C$, range $14.5–25.2°C$, $n = 24$). Oviposition was mostly finished by noon, with only a few pairs present at the site thereafter.

Duration of oviposition (DO)

The mean duration of an oviposition bout was 325.0 ± 194.7 s in TO ($50–1770$ s, $n = 370$) and 152.5 ± 101.8 s ($30–373$ s, $n = 21$) in SO. This difference was highly significant ($p < 0.0001$). Some pairs oviposited for more than 30 min, and pairs frequently alternated between oviposition and copulation, thus extending the duration of the procedure. Also interference with ovipositing pairs by males of other species such as *Sympetrum eroticum eroticum* and *Orthetrum albistylum speciosum* that patrolled frequently over the paddies extended DO. However, interference by conspecific lone males was rare. In one case, on 12 November 2010, a pair copulated 15 times during their tandem oviposition from 10:59 h to 11:08 h (Ta, $16.8°C$), hence, the real DO was shorter. DO was poorly correlated with Ta. It was significant and negative for TO (TO: $r = -0.182$, $p < 0.001$) but not for SO ($r = 0.145$, $p > 0.5$; Figure 5). Slightly stronger correlations existed between DO and the starting time of oviposition, both in TO and in SO (TO: $r = 0.220$, $p = 1.9E\text{-}05$; SO: $r = 0.499$, $p < 0.05$).

Dip rate (DR) and wing-stroke frequency (WSF)

During 1702.7 s of observation of TO, the time between two consecutive dips during oviposition averaged 0.7 ± 0.1 s, i.e. mean DR (the number of dips per second) was $1.4 \pm 0.2 \, s^{-1}$ (range $0.9–2.0 \, s^{-1}$ at $20.9 \pm 2.7°C$, $n = 169$) and during 152.1 s of SO mean DR was $1.2 \pm 0.3 \, s^{-1}$ in SO (range $0.7–2.0$ at $22.3 \pm 2.2°C$, $n = 35$). The difference in means is highly significant ($p < 0.0001$). DR was nearly constant throughout an oviposition bout in TO (ANOVA: d.f. $= 2$, F $= 4.737E\text{-}03$, $p = 1.0$, Table 1).

The mean values for WSF during oviposition (Ta records were the same as for DR) was 39.4 ± 2.8 Hz in the male during TO (range $32.8–44.9$ Hz, $n = 124$) and 34.5 ± 3.0 Hz (range $23.1–41.2$ Hz, $n = 124$) in the female. The difference between sexes was highly significant ($p < 0.0001$). Mean WSF of the female in SO was 39.7 ± 3.7 Hz (range $31.9–45.7$ Hz, $n = 35$) and not significantly different from that of the male in TO ($p > 0.4$) but highly significantly different from that of the tandem female ($p < 0.0001$). In males of the same pairs for which DR
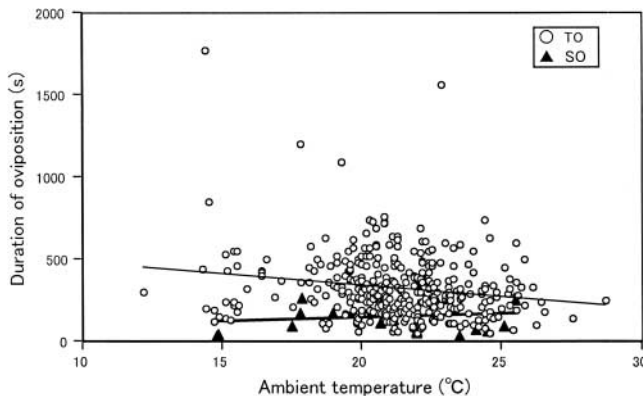

Figure 5. Relationship between duration of oviposition (y) and ambient temperature (x) of tandem oviposition (TO) as well as single oviposition (SO) in *Sympetrum frequens*. Data were collected at study sites 1A and 1B (Bodaigi) and 2 (Nishikubo) from 2007 to 2010. TO: $y = -13.928x + 620.032$ $n = 370$, $r = 0.182$, $p < 0.001$; SO: $y = 4.830x + 51.453$, $n = 35$, $r = 0.145$, $p > 0.5$.

Table 1. Wing-stroke frequency (WSF) and dip rate (DR) during one bout of tandem oviposition in *Sympetrum frequens* (Selys) one, three and five minutes after the start of oviposition.

Phase	Wing-stroke frequency (Hz)			Dip rate (s^{-1})	Ambient temperature (°C)
	Male	Female	p, by sex[a]		
1 min	41.7 ± 2.2	35.5 ± 3.0	5.53E-07	1.56 ± 0.21	19.4 ± 1.8
range	(37.0–48.4)	(30.2–40.4)		(1.11–2.13)	(15.7–22.9)
3 min	40.8 ± 2.4	36.4 ± 3.3	3.67E-09	1.57 ± 0.22	19.5 ± 1.8
range	(34.3–46.1)	(28.2–42.4)		(1.22–2.02)	(15.1–23.5)
5 min	39.1 ± 3.4	34.1 ± 3.6	2.99E-09	1.56 ± 0.23	19.7 ± 1.6
range	(30.1–45.3)	(27.4–42.8)		(1.15–2.17)	(15.8–22.0)
p, by time[b]	< 0.01	< 0.05		= 1.0	= 0.81

[a]Probability of H_z = difference between male and female at each time (phase).
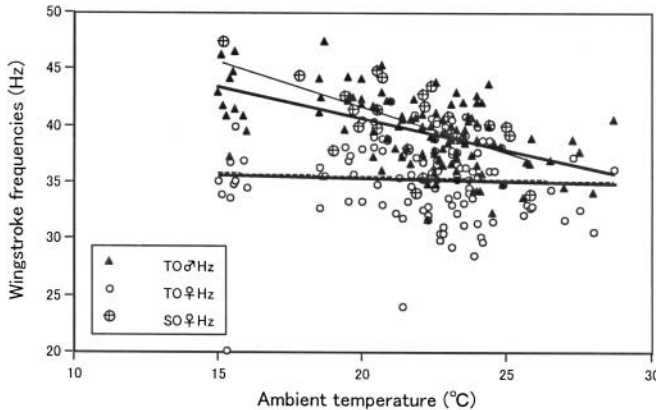[b]Probability of H_z, DR and ambient temperature = difference among times after initiation of oviposition.

Figure 6. Correlation between wing-stroke frequency (y) and ambient temperature (x) in ovipositing *Sympetrum frequens*. Data for tandem pairs were collected at study sites 1B (Bodaigi) from September to November 2011 and those of females in SO were collected at the same area in the same season of 2008 and 2009. TO male: y = −0.415 x + 47.827, n = 124, r = 0.408, p < 0.0001; TO female: y = −0.265x + 39.977, n = 124, r = 0.242, p < 0.01; SO female: y = −0.766x + 56.739, n = 35, r = 0.442, p < 0.01.

was measured (Table 1), WSF declined significantly during the oviposition bout ($p < 0.01$). In the female it rose between one and three min., then declined ($p < 0.05$).

The correlation between DR and Ta was not significant during either TO ($r = 0.036$, $p > 0.5$) or SO ($r = 0.184$, $p > 0.1$). The correlation between WSF and Ta during TO was negative in each case, i.e. $r = -0.408$ ($p < 0.0001$) in the tandem-male, $r = -0.242$ ($p < 0.01$) in the tandem-female, and during SO $r = -0.442$ ($p < 0.01$) in the female (Figure 6). No significant correlations were found between DR and WSF for either sex ($r = 0.003$, $p > 0.9$ in the male, and $r = 0.012$, $p > 0.8$ in the female). The mean WSF of hovering males in search of females at the oviposition site was very high, 42.8 ± 3.9 Hz (range 34.0–49.4 Hz, Ta 19.1 ± 4.1°C, $n = 19$) and the correlation with Ta was not significant ($r = 0.277$, $p > 0.2$).

Numbers of eggs per dip, rate of egg deposition and numbers of deposited eggs per bout

The mean number of eggs per dip in the field was 4.2 ± 2.1 (range 1.7–6.3, $n = 4$, DR $= 1.26 \pm 0.14$ s^{-1}) and the mean number per second was 6.4 ± 3.6 (range 4.0–10.5, total measuring time, 93.9 s). In the indoor experiment mean number of eggs per second during continuous deposition of eggs was 4.7 ± 1.5 (range 1.6–6.7, $n = 34$ trials, total measuring time, 370.3 s, and mean
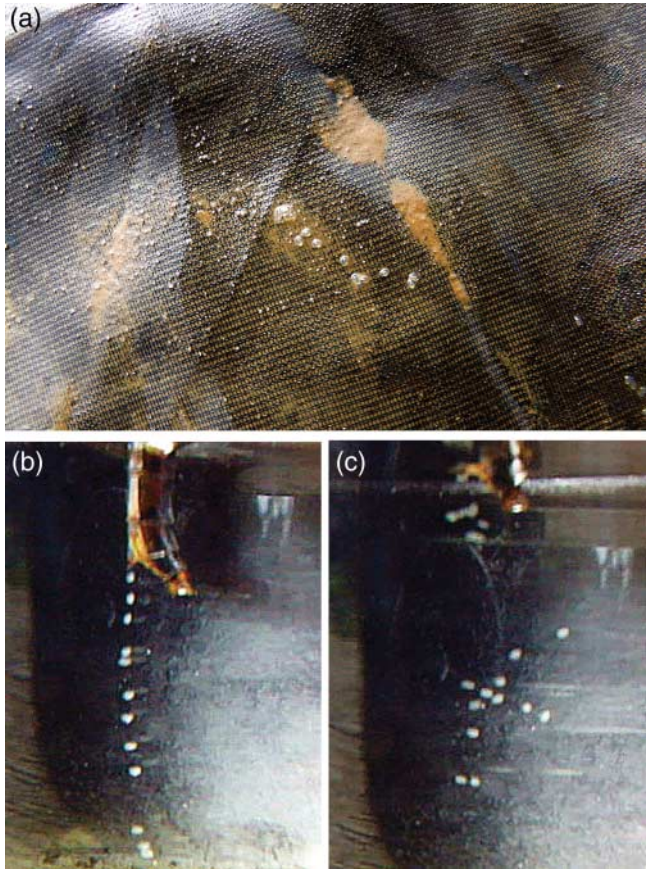
Figure 7.   Pictures of deposited eggs of *Sympetrum frequens*: (a) eggs deposited on a sheet of black polyester gauze in the field, dip direction is downward to the right; (b) eggs continuously deposited in the indoor experiment; (c) eggs intermittently deposited.
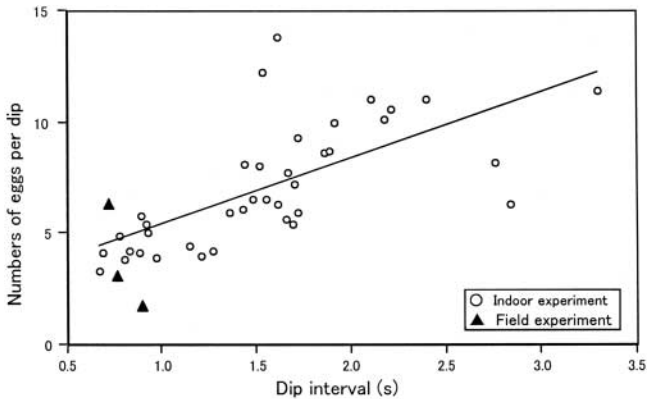

Figure 8.   Relationship between numbers of eggs deposited per dip (y) and dip interval (x); i.e. 1/DR. Data were collected during experiments at study site 1B (Bodaigi) and indoors at Tokorozawa City from late September to mid October 2011. y = 2.981x + 2.399, $n = 38$, $r = 0.677$, $p < 0.00001$.

number of eggs per second at various intervals of dip was 4.7 ± 1.3 (range 2.2–8.6, $n = 38$ trials, total measuring time, 631.6 s with mean DR of $1.6 \pm 0.6 \, \text{s}^{-1}$; range, 0.7–$3.3 \, \text{s}^{-1}$); there was no significant difference in the number of eggs between the former and the latter ($p > 0.9$, Figure 7a, b, c). Figure 8 shows the relationship of the number of deposited eggs to dip interval ($= 1/\text{DR}$), and shows that the number of eggs per dip is proportional to interval (number of eggs per dip (y) = $2.981 \times$ dip interval (x) $+ 2.399$, $r = 0.677$, $p < 0.00001$).

In the field, oviposition on the artificial sheets occurred only when there was no suitable oviposition site at paddy fields except the sheets, and pairs of *S. frequens* never oviposited on the polyethylene sheet.

The number of deposited eggs per bout of oviposition, as determined in the 1989 experiments, was 1103.6 ± 535.8 (196–1806, $n = 17$) and females deposited eggs of $15.6 \pm 8.1\%$ (2.4–32.3%, $n = 17$) of their own body weight. The weight per egg was 0.040 ± 0.008 mg (0.026–0.060 mg, $n = 17$).

Discussion

Oviposition of *Sympetrum frequens* usually started immediately after rice harvest, because the harvest removed obstructions to oviposition due to dense rice stems, and because the water surface of the paddies became visible and the reflected polarized light elicited oviposition (Wildermuth, 1998). Nearly 50% of oviposition events occurred within the first week, and oviposition was largely finished by early November. *Sympetrum frequens* typically oviposits initially at paddies on which the morning sun shines first, and where the water temperature is higher than other parts of the paddies (Ishizawa, 2010). Michiels and Dhondt (1990; cited by Corbet, 1999) found that *Sympetrum danae* adjusts the orientation of oviposition flights according to ambient temperature. The preference for the southern part at site 1A in this study might have occurred because a bank $c.1$ m high near the west side of the paddy might have warmed the southern part. Other factors also may influence oviposition micro-site preference, including, for example, the distribution of suitable oviposition substrates.

Arai (1978) noted that among tandem pairs that arrived at an oviposition site, 35.2% oviposited there and the rest flew away without oviposition. In contrast, during this study over 50% oviposited when they first appeared at an observation site, although the proportion varied from day to day.

At the beginning of the reproduction season oviposition starts about at 09:00 h, and as the days pass oviposition tends to be delayed, but this tendency is strongly influenced by Ta and the weather of the day. Both higher temperature and sunny weather result in earlier oviposition. Ambient temperature at the starting time was about 20°C for both TO and SO. The frequency of oviposition peaks at 10:30 h in the beginning of the reproduction period and shifts towards 11:30 h as the season progresses. If oviposition occurs in the end of the summer or beginning of autumn the daily peak of oviposition is reached earlier in the forenoon (Ishizawa, 1998, 2008b). Oviposition usually ends at about noon, although a few individuals are occasionally sighted in the early afternoon. H. Naraoka (pers. comm., September 1, 2009) has observed oviposition in the mid-afternoon only once, soon after rain.

The duration of an oviposition bout lasts $c.5$ min in TO and over 2 min in SO and was not influenced by Ta. The shortening of DO in the course of the day may at least partly be due to the fact that some females ovipositing later had deposited part of the clutch earlier on the same day and accepted a second copulation in order to gain access to the oviposition site.

The dip rate (DR) in *S. frequens* is $1.4 \, \text{s}^{-1}$ in TO and $1.1 \, \text{s}^{-1}$ in SO, i.e. DR is faster in the former than in the latter, as previously reported by Ishizawa (1998, 2008b). This time it was confirmed that each dip of the species results in deposition of several eggs (mean number 4.2), as known

from other species of libellulids (Ottolenghi, 1987; Robert, 1959) and corduliids (Ubukata, 1975). This was also shown in the TV film "Super flight techniques of dragonflies" broadcast by NHK (Japan Broadcasting Corporation) on 27 November 2011. Oviposition of *S. frequens* was filmed with an endoscope camera that was immersed in a puddle at a paddy.

The number of eggs deposited in one oviposition bout in *S. frequens* was calculated by multiplying DO by $1.4 \times 4.2 \times 325$ in TO or by $1.1 \times 4.2 \times 152.5$ in SO. The results are 1911 and 702 eggs per bout, respectively. Dipping was sometimes interrupted by site changing or interference by syntopic species, as in *Sympetrum vicinum* in North America (McMillan, 1996) or in other libellulids (Koch, 2005), so the actual number of deposited eggs may be fewer than calculated here, because DO includes the duration of these interruptions. In *S. darwinianum* (Taguchi & Watanabe, 1995), which performs guarded non-contact flying-oviposition (Eda, 1975), DO was 461.3 s and the dip rate was $0.5\,\mathrm{s}^{-1}$ in TO; in *Sympetrum maculatum* (Ishizawa, unpublished), with the same oviposition mode, corresponding values are 404.2 s and $0.83\,\mathrm{s}^{-1}$ in TO and 75 s and $0.67\,\mathrm{s}^{-1}$ in SO, respectively. Therefore, the numbers of eggs deposited per bout are 230.7 in TO for *S. darwinianum* and 336.8 in TO and 50 in SO for *S. maculatum*. In spite of longer DO in both species the number of eggs deposited in non-contact-flying oviposition may be fewer than in tandem flying-oviposition in to mud by *S. frequens*.

Mizuta (1978) noted that the volume of the egg of *S. frequens* was $0.03–0.04\,\mathrm{mm}^3$, and this is consistent with the estimated weight of one egg in my experiments, assuming they are slightly denser than water.

Neither DR nor DO was correlated with Ta, and DR also was not correlated with WSF. As Ta rose, metabolic rate and dip rate might be expected to increase, but, in fact, the opposite occurred. Therefore, other factors must come into play; for example, I did not measure the dip height from the surface of the puddle, however, the dip height may be lowered as the oviposition progresses due to energy expenditure.

Throughout oviposition DR is nearly constant, but WSF of the male declines significantly as the oviposition bout progresses. This may reflect a decrease in the rate of investment by the male in TO, as the short-term reproductive value of the female must decline towards the end of an oviposition bout. Flight during oviposition is probably energetically demanding because it requires much hovering and relatively complex manoeuvres. Dragonflies usually fly against the wind while ovipositing. This is probably because lifting power increases as the relative wind velocity increases, so this behaviour may reduce the energy demand on the ovipositing insects and hence may prolong DO (Ishizawa, 1987, 2008a). Flight effort, body temperature and WSF are closely correlated during flight (May, 1995). In *S. frequens*, WSF during TO is 40 Hz in males and 35 Hz in females, and over 40 Hz in SO, which is as high as that of males in TO. This pattern corresponds to the propensity to thermoregulate during oviposition (Ishizawa, 1998). The correlation of WSF with Ta was rather high in males during TO and in females in SO, but was low in females during TO. This may be related to the fact that females during tandem flight probably do not have to generate lift equal to their full body weight. This supposition is consistent with the fact that during TO in *S. frequens* the females' body temperature is about 3°C lower than that of the male partner. On the other hand, during SO it is higher than that of females in TO and close to that of males in TO (Ishizawa, 1998, 2006). According to Taguchi and Watanabe (1995), in *S. darwinianum* the difference in body temperature between the sexes in TO is *c*.1°C. Pairs of the species usually make slight up and down movements in non-contact flying-oviposition ("contact" here means contact with solid substrate, not male–female contact; Eda, 1975). Sometimes, however, the female shifts its oviposition mode from TO to SO, and thereafter the up and down movement is not observed. The authors thus concluded that males control flight movements during TO. The leading role of the male in TO is also obvious in *S. sanguineum* (Rüppell, 1984) and in *S. striolatum*, of which it is reported that a male made aerial in-tandem dipping movements with a dead female previously killed by a spider (Wildermuth,

1984). The fact that body temperatures in males of *S. frequens* and *S. darwinianum* are higher than in TO females reinforces the conclusion that the male largely controls TO and expends more energy than the female. WSF and the body temperature are closely related (May, 1995), and, since TO apparently requires more effort from males, the latter must maintain high body temperature (Ishizawa, 1998, 2006). Therefore, at low Ta they are likely to elevate WSF to thermoregulation; consequently WSF is negatively correlated to Ta. Females in TO are partly supported by males, so they do not need to maintain high WSF, whereas females in SO must support their entire weight and complete manoeuvres without assistance, and they consequently must sustain high WSF and body temperature. Thus, for females TO is energetically advantageous compared to SO, in addition to the advantage in egg deposition rate due to the higher dip frequency. For males, TO is also profitable, because contact-guarding warrants paternity to a high degree (Corbet, 1999, 528 ff).

Acknowledgements

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