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FACTORS IN THE SELECTION OF OVIPOSITION MODE IN *SYMPETRUM INFUSCATUM* (SELYS) (ANISOPTERA: LIBELLULIDAE)

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The study was conducted at rice paddies in the cool temperate area of central Japan. The oviposition time period was limited to between ca 10:00 a.m. and 14:00 p.m. with a peak around noon. At an ambient temperature (Ta) below 30°C most pairs oviposited in tandem (TO) but at a Ta above 30°C in mid-summer most pairs separated shortly after the start of TO. The ♀♀ continued to oviposit while being escorted by their partners. The regression coefficient of ♂ body temperature (Tb) in ovipositing pairs was characteristically greater than that of the ♀, and it is suggested that the ♂ is more dependent on Ta than is the ♀. Although the duration of oviposition was a little longer in pairs that separated after the start of oviposition, this difference was not significant. The reason why *S. infuscatum* starts oviposition in such a hot season of summer seems to be due to the morphological feature of its slender abdomen, which decreases abdominal light absorption at low Ta in the autumn.

INTRODUCTION

Sympetrum infuscatum (Selys) is one of the larger species in the genus in Japan, and the abdominal dorsum of adults is dark brown. It is distributed in Kyushu, Shikoku and Hokkaido as well as in the Mainland of Honshu. This dragonfly is seen even at heights of 2000 m above sea level in central Japan in the summer (ISHIDA et al., 1988; TSUBUKI, 1997, 2001); hence it has a migratory aspect like *S. frequens* (ISHIKAWA, 1985; ISHIZAWA, 1995). There are only a few fragmentary reports apart from those of WATANABE et al. (2004, 2005).

S. infuscatum is known to oviposit in tandem (ARAI, 1982; ISHIDA et al. 1989). However, Mr Usui (pers. comm.) witnessed oviposition at a bog in the north of Nagano prefecture at the end of July, where pairs appeared in tandem and, as soon as oviposition started, the pairs separated and the females oviposited alone under escort by the males. As to oviposition in other species of the genus, UEDA (1979) reported on *S. parvulum*, noting its social behaviour, with both tandem oviposition (TO) and separate oviposition under male escort (SO – also referred to as non-contact oviposition) and suggested that the mode of oviposition was related to territoriality of males. However, SINGER (1987) rejected Ueda's hypothesis, since in *S. obtrusum* selection of the oviposition mode was related to the male body temperature (Tb). If the Tb of males fell below 30°C, SO prevailed. Therefore, selection of mode had no relation to social behaviour such as territoriality.

Mr Usui's observation was made in mid-summer, and the oviposition mode of *S. infuscatum* might have been influenced by high ambient temperature. Also, WATANABE et al. (2005) referred to the oviposition of the species in Nagano prefecture in mid August, but they did not note the different oviposition modes.

I investigated the factors for selection of oviposition mode from two points of view: thermoregulation and morphology.

METHODS

STUDY SITE. – Field data on the reproductive behaviour of *S. infuscatum* were collected at rice paddies at Sano (750 m a.s.l.), the same spot where WATANABE et al. (2004, 2005) studied, Hakuba-cho, Nagano prefecture, from 29 August to 2 September 2005 for five days and from 14-19 August in 2006 for six days. Observations were conducted from 8:30 a.m. to 2:30 p.m. every day. For a comparative test of increase of body temperature, *S. infuscatum* were collected at Yokoze-machi, Chichibu-gun and Asaka city in Saitama prefecture and Noda city, Chiba prefecture and *S. frequens* were collected at Mikajima, Tokorozawa city, Saitama prefecture in early and mid October in 2006.

FIELD TECHNIQUES. – Numbers of ovipositing tandem pairs (TO) or ovipositing females under male escort (SO) were counted every fifteen minutes, and the ambient temperature (Ta) at each end of the intervals was measured using a digital thermistor thermometer (diameter: 3.0 mm, CT-410WR, made by Custom Corporation). Duration of oviposition of TO or SO was measured using a stopwatch and Ta was measured at the finish of oviposition using the above mentioned thermometer.

Body temperatures during *S. infuscatum* reproductive behaviour were measured in the following phases: perching (phase I), copulation (phase II), pre-oviposition (phase III), oviposition for more than one minute (phase IV), oviposition for more than three minutes (phase V), soon after separation of tandem oviposition (phase VI), separate oviposition under male escort (phase VII) and single oviposition (phase VIII).

Body temperatures were measured to 0.1°C as described by ISHIZAWA (1998), with a Hoskins F-V-K-002 thermocouple probe (0.05 mm diameter chromel-alumel) embedded in a hypodermic needle (external diameter 0.3 mm), which was connected to a John-Fluke 52 double channeled digital thermometer. The probe was inserted into the thorax of perching individuals or pairs in copula or individuals in oviposition through the mesh of an insect net. In pairs taken together, females were probed prior to males in rapid succession within 15 seconds. Ambient temperatures at a height of 1 m in the sun (Ta) were measured with the thermistor mentioned above after Tb was measured.

Body size was measured by the length of abdomen, thorax, hindwing and the height and the width of the slimmest part of the fifth abdominal segment using a slide caliper, and the body weight of the specimens collected in 2006 was measured to 0.001 g using an A & D FA-200 electronic balance within five hours after collection of them.

Wingloading (WL) of *S. infuscatum* was calculated as follows: specimens of six males and seven females were selected from the measured specimens at Hakuba-cho to use as a standard, and their wing areas were calculated. The wings of the specimens were photocopied. Using an image size of 200%, the wing shapes of the photocopies were cut out and weighed. The ratio of each weight of these shapes to the weight of a 100 cm^2 cut out was calculated. This gave a value of 12.6±0.8 cm^2 for the male and 13.5±0.8 cm^2 for the female. These were taken as the standard wing areas (STWA). Wing areas of other specimens were calculated as follows:

(STWA (cm^2) × the square (cm^2) of each hindwing length)/ (the square (cm^2) of the standard hindwing length). Then each WL was calculated by dividing the body weight (mg) by this value (cm^2). The wingstroke of ovipositing *S. infuscatum* was videotaped using a Panasonic NV-MX2000 3CCD digital camcorder, and the frequency (Hz) was counted from the ovipositing images in a slow mode of 60 fields/sec (one frame is composed of two fields).

INDOOR TEST. – The effect of the dorsal and lateral light absorption of the body of *S. infuscatum* and *S. frequens* on the increase of Tb was examined as follows: The specimens were lit for three minutes (starting Tb 29.5°C) by a 75 W halogen lamp from a height of 25 cm at an indoor temperature of 27°C, and their Tbs were measured with a 0.05 mm chromel-alumel thermocouple, not embedded in a hypodermic needle, connected to the thermometer mentioned above.

For two sets of data t-tests were used; for three sets ANOVA was used.

RESULTS

OVIPOSITION

S. infuscatum individuals were sighted perching in the sun on stems of low trees or bushes in the morning and, as the sun grew strong, many of them repaired to the shade of the edges of the surrounding deciduous forest. Only a few males appeared at the rice paddies.

Tandem pairs were sighted flying over rice paddies at 8:00 a.m. at the earliest and the number of pairs became more frequent after 10:00 a.m. However, more than half of them passed over the paddies without ovipositing.

Oviposition started after 10:00 a.m. Pairs oviposited in TO at low heights near the ears of rice at the paddies and, as the ambient temperature rose, the number of pairs increased. The Ta at the start of oviposition was 30°C on 15 August 2006, and 23.6°C on 30 August 2005. On the latter day only a single oviposition by a single female was observed. When the Ta rose up to 32-33°C, most of the pairs submerged into the spaces between the rows of rice. Hence, I did not count the disappeared pairs because I could not ascertain whether they oviposited or not. Oviposition reached a peak at 1:30 p.m. on 15 August, and about noon on 30 August, although, on both days, oviposition finished at 2:00 p.m. in spite of a Ta high enough for oviposition to continue (Fig. 1A-B).

Among ovipositing pairs, SO was sighted frequently on 15 August when the ambient temperature remained above 29°C (Fig. 1A). However on 30 August, when the ambient temperature never exceeded about 27°C SO was rarely sighted (Fig. 1B). SO accounted for 12 pairs (23.5%) of all the oviposited pairs (n = 51). The reason why SO was not observed at around 12:30 p.m. on 15 August was that the wind was blowing then. Even when it was hot, if the wind blew, SO was rarely seen. The average Ta from 9:00 to 14:00 on 15 August 2006 was 31.0±1.2°C. On 30 August 2005 the daylight Ta did not exceed 30°C, and the average Ta from 10:00 to 14:00 was 25.6±1.6°C.

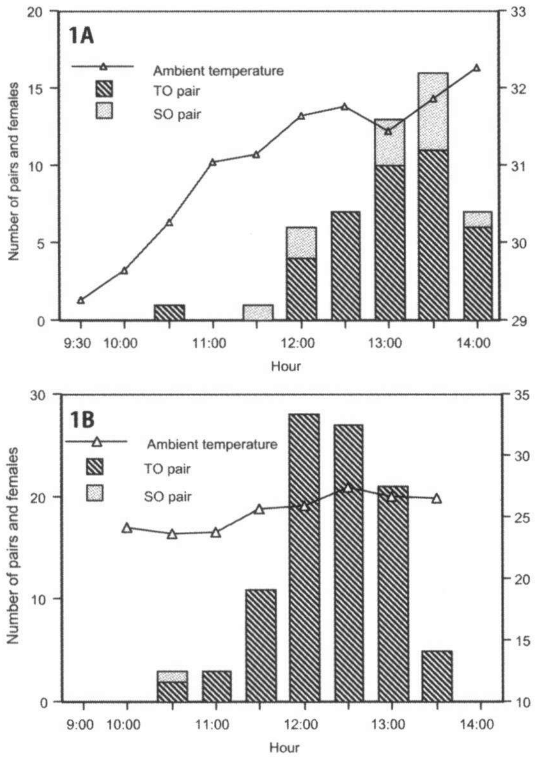

Fig. 1. Diurnal changes in the number of ovipositing *Sympetrum infuscatum* pairs in tandem (TO) and separate oviposition (SO) in relation to ambient temperature at Hakuba village, A: on August 15, 2006, B: on August 30, 2005. [Line indicates ambient temperature].

THERMOREGULATION

The difference of Tbs of perching males and females in the sun was small but significant (P = 0.03) (Fig. 2; Tab. I) In the pairs that appeared in tandem at the rice paddies, the Tb of males increased, while that of the females fell (P = 0.037). The Tb of both sexes thereafter rose from phase II to phase V (the difference of Tb among phase I-V was significant, P<0.0001 in each sex, F = 10.81 in the male and F = 15.87 in the female, ANOVA). From phase V to phase VI the Tb of both sexes fell a little, although a high level of Tb was maintained. From phase VI to phase VII there was a further increase in Tb and male Tb was no longer different from female Tb (phases III-VII P>0.05). The Tb of single oviposition from the start and those of SO were not so different among phases (phase VI-VIII, P = 0.22, F = 1.543, ANOVA). (Fig 2; Tab. I)

In phase V the regression coefficients of the relationship of Tb on Ta were larger in males than in females in the pairs that oviposited for more than 3 minutes (1.187 for males, 0.973 for females) (Fig. 3A). This was also the case in phase VI (1.281 for males and 0.842 for females) (Fig. 3B) and in phase III (Tab. I).

DURATION OF OVIPOSITION

TO was observed over a wide range of Ta from 24 to 34°C, whereas SO was

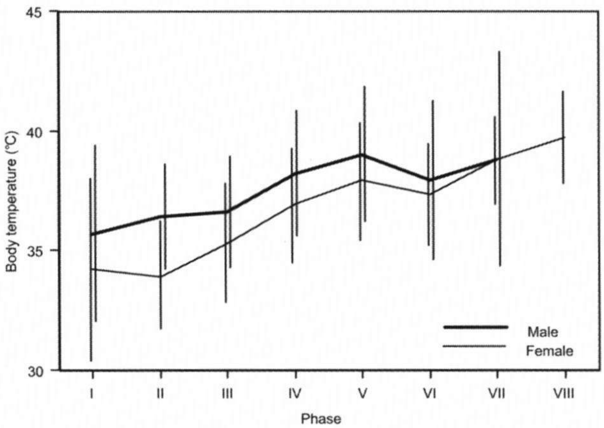

Fig. 2. Changes in the body temperature of males and females *Sympetrum infuscatum* in various phases of the reproductive sequence. Phase I: perching, – II: copulation, – III: pre-oviposition, – IV: oviposition for more than 1 min, – V: oviposition for more than 3 min, – VI: soon after separation, – VII: escorting, – VIII: single oviposition by a female alone from the start of oviposition. [Vertical bars are s.d.]

observed over a narrower range from 26 to 34°C (Fig. 4). The average duration of oviposition was 212.5±112.4 sec (n = 48) in TO and, 147.3±83.7 sec (n = 17) in SO. The average Ta was 29.4±3.0°C in TO, and 31.0±1.9°C in SO, The differences of duration and Ta between both oviposition modes were both significant (duration and Ta, $P<0.05$, Tab. III). The average duration of TO of the pairs that finished oviposition in TO was 234.3±112.3 sec (n = 36), and the part of TO of the pairs that oviposited in TO and in SO was 153.3±86.6 sec (n = 13), and the SO part was 147.5±80.4 sec (n = 13; total duration of TO and SO 300.8±111.4

Table I

Statistics calculated from least squares linear regression of body temperature (Tb) on ambient temperature (Ta) in each phase of the reproductive sequence of *Sympetrum infuscatum*. – [al = slope; r = correlation coefficient; p = probability; s.d. = standard deviation]

									Expected Tb	
	Phase	Sex	*N*	al	r	p	Tb ± s.d.	Range (°C)	27°C	30°C
I	Perching	♂	85	0.812	0.788	3.8E-19	35.7±3.7	21.5-41.2	34.8	37.2
		♀	54	0.947	0.868	2E-17	34.2±3.8	20.4-39.4	33.8	36.6
II	Copulation	♂	9	0.919	0.870	0.002	36.4±2.2	32.1-39.2	34.4	37.1
		♀	9	0.818	0.730	0.025	33.9±2.3	30.5-37.1	32.1	34.6
III	Pre-oviposition	♂	22	0.560	0.634	0.001	36.6±2.3	32.5-41.6	35.7	37.3
		♀	27	0.606	0.653	0.0002	35.3±2.5	31.3-40.4	33.9	35.7
IV	Oviposition for 1 m.	♂	26	0.903	0.663	4.2E-07	38.2±2.6	33.6-43.1	35.9	38.6
		♀	26	0.783	0.784	2.2E-06	36.9±2.4	32.5-42.0	34.8	37.2
V	Oviposition for 3 m.	♂	33	1.187	0.803	1.9 E-08	39.0±2.8	33.2-43.8	37.0	40.6
		♀	35	0.973	0.764	9.5E-08	37.9±2.5	32.1-42.5	36.2	39.1
VI	Soon after separation	♂	11	1.281	0.901	0.00016	37.9±3.3	33.3-43.7	35.9	39.7
		♀	19	0.842	0.825	1.4E-05	37.3±2.1	33.2-40.4	36.0	38.5
VII	Single oviposition	♀	6	1.171	0.751	0.0854	39.7±1.9	37.1-42.7	36.5	40.0
VIII	Escorting	♂	4	-	-	-	38.8±4.5	32.8-42.7		
		♀	2	-	-	-	38.8±1.8	37.5-40.1		

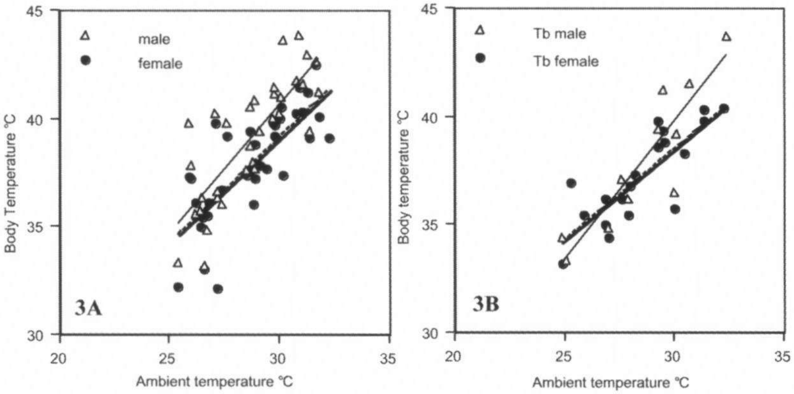

Fig. 3. Relationship between body temberature (Tb) and ambient temperature (Ta) in pairs of *Sympetrum infuscatum* that oviposited in TO of phase V, for more than three minutes (3A) and in SO of phase VI (3B). The regression equations are as follows, phase V, male: $Y = 1.187X+4.993$ $r = 0.803$, $p = 1.9E-8$; – female: $Y = 0.973X+9.934$ $r = 0.764$, $P = 9.5E-8$; – phase VI, male: $Y = 1.281X+1.315$ $r = 0.901$, $P = 0.00016$; – female: $Y = 0.842X+13.248$ $r = 0.825$, $P = 1.4E-5$

sec [Ta, 31.2±1.8°C]); there was no significant difference between the TO part and the SO part ($P = 0.862$). There was no significant difference between the total duration and the average duration of oviposition of those pairs that finished oviposition in TO at low Ta (26.9±1.9°C)($P = 0.483$).

In relation to the duration of oviposition to Ta, the correlation coefficient of TO was significantly larger ($r = 0.623$, $P<0.001$), while that of SO was lower than

Table II

Oviposition duration in tandem pairs and single female; TO: tandem oviposition, SO: separate oviposition, which includes single oviposition (*) without escort by a male; Ta: ambient temperature

	TO		SO		Total duration
Oviposition mode	Duration (sec)	Ta (°C)	Duration (sec)	Ta (°C)	Duration (sec)
Range 23-34°C	212.5±112.4 (n=48)	29.4±3.0	147.3±83.7 (*n=17)	31.0±1.9	
Only TO (23-34°C)	234.3±112.3 (n=36)	28.7±3.0			234.3±112.3 (n=36)
Only TO (lower than 30°C)	275.0±101.4 (n=23)	26.9±1.9			275.0±101.4 (n=23)
SO after TO (range 23-34°C)	153.3±86.6 (n=13)	31.2 ±1.8	147.5±80.4 (n=13)		300.8±111.4 (n=13)
SO after TO (higher than 30°C)	134.3±78.3 (n=10)	31.9±0.8	129.5±77.9 (n=10)		263.8±98.2 (n=10)

the former (r = 0.231, P = 0.755). At a Ta of 27°C some of the duration of oviposition of TO exceeded eight minutes. Estimating a peak duration from the equation for TO in Fig. 4, the duration of TO is 285 sec at Ta 27°C and 170 sec at 30°C. The duration of oviposition in TO or SO tended to be shorter at low Ta (lower than 25°C) and at high Ta at a Ta of 34°C it was less than two minutes in both modes.

Although SO was observed at high Ta, in the case of one female, which was abandoned by the escorting male after about one minute, SO continued for more than five minutes by taking several rests of more than one minutes, and besides when the wind blew, some females oviposited for more than 7 minutes of total duration of TO and SO by hovering against the wind.

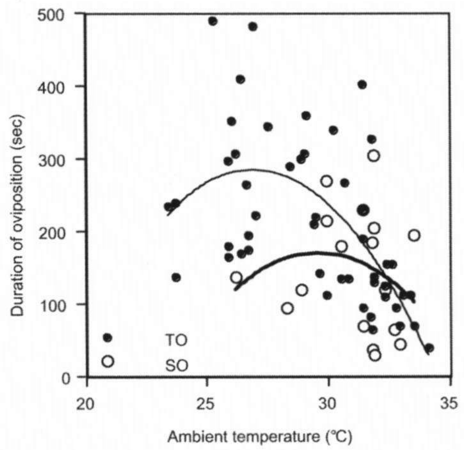

Fig. 4. Relationships between duration of oviposition and ambient temperature in *Sympetrum infuscatum* pairs. TO: oviposition in tandem, SO: separate oviposition. The regression equations are: TO: $Y = -4.971X^2+267.716X-3319.082$ r = 0.623, P<0.05, SO: $Y = -4.391X^2+259.948X-3676.551$ r = 0.231, P>0.05.

WINGLOADING AND WINGSTROKE FREQUENCY

The body size of *S. infuscatum* was significantly different between sexes in weight, thoracic and abdominal length and the height and the width of the fifth abdominal segment (Fig. 5; Tab. III) except for the hindwing (P<0.05). The thorax of *S. infuscatum* was larger than that of *S. frequens*, but the difference was not significant between each sex (male, P = 0.065, female, P = 0.196). In *S. frequens* the abdominal length was 27.7±1.0 mm (n = 40) in the male and

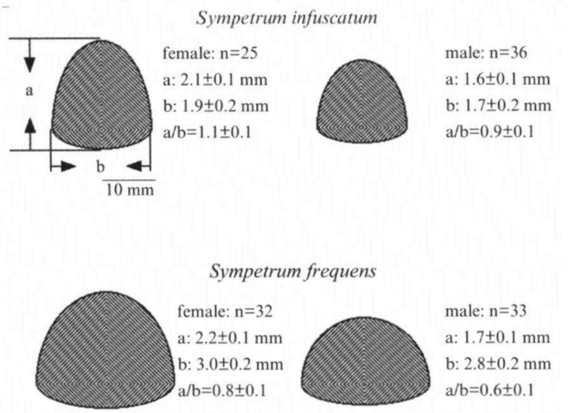

Fig. 5. Comparison of cross sections of the fifth abdominal segment of *Sympetrum infuscatum* and *S. frequens*. The ratio (a/b) of each group was significantly different (p<0.001, ANOVA).

27.7±1.1 mm (n = 33) in the female, with the hindwing length 31.3±1.1 mm (n = 40) in the male and 31.8±1.2 mm (n = 33) in the female. The corresponding values for *S. infuscatum* were significantly larger than those for *S. frequens* ($P<0.001$). The wingloading of *S. infuscatum* was larger in the female than in the male ($P<0.01$). In tandem oviposition, pairs swung their bodies slightly up and down with frequent large up and down swings of about 10 cm; hence this seemed to be a rather heavy burden for males.

The wingstroke frequency at TO was 26.5±0.6Hz (n = 4) in the male and 25.8±1.1Hz (n = 5) in the female, but it was not significantly different between the sexes. In the slow motion images of *S. frequens* flying in tandem (video-taped by a high speed Hi-vision video camcorder and televised by NHK on October 11, 2006) the wingstroke of the female of the pair was lower than that of the male, and the stroke angle of the wings was also smaller in the female. Therefore, in tandem oviposition, males swing females, and it may be necessary for females to lower the wingstroke frequency and minimize the stroke angle.

EFFECT OF LIGHT ABSORPTION ON Tb

When oviposition is conducted when it is hot, it is assumed that the sunlight on the abdominal dorsum may affect the Tb in *S. infuscatum* to a large extent. The abdomen of *S. infuscatum* is extremely slim in comparison with the congeners. For example, the differences between the height and width of the fifth abdominal segment were interspecifically and intersexually significant in *S. infuscatum* and *S. frequens* ($P<0.0001$, $F = 97.74$, ANOVA), (Fig. 5).

The increase of Tb in *S. infuscatum* and *S. frequens* was tested on the dorsal side and the lateral side of the specimens by lighting a 75 W halogen lamp for three minutes at a height of 25 cm above the specimens. Increases of Tb in *S. infuscatum* for the dorsal side (TbD) and for the lateral side (TbL) were signifi-

Table III

Body size, wing loading and wingstroke frequency of *Sympetrum infuscatum* and *S. frequens*; P: probability of the difference between the sexes

	Sympetrum infuscatum			*Sympetrum frequens*		
	♂	♀	P	♂	♀	P
Weight (mg)	252.6±29.6 (50)	272.3±42.0 (43)	0.01	257.9±29.4 (37)	285.4±26.0 (34)	0.0002
Thorax (mm)	8.6±0.4 (91)	7.9±0.4 (75)	9.17E-27	8.2±0.4 (18)	7.7±0.3 (11)	2.26E-07
Abdomen (mm)	30.9±1.1 (81)	29.7±1.4 (74)	2.55E-05	27.7±1.0 (40)	27.7±1.1 (33)	0.725
Hindwing (mm)	34.4±1.2 (91)	34.1±1.4 (75)	0.335	31.3±1.1 (40)	31.8±1.2 (33)	0.126
Wing loading (mg/cm^2)	20.8±1.6 (50)	21.9±2.6 (43)	0.008	-	-	
Wingstroke frequency (Hz)						
Tandem oviposition	26.5±0.6	25.8±1.1	0.289	-	-	
Single oviposition		25.1±2.9				

cantly different between the sexes (P<0.001, P<0.05), but the difference between TbL and TbD was not significant between sexes (P = 0.774). On the other hand, in *S. frequens*, increases of Tb for the dorsal and lateral sides and the difference between TbL and TbD were not significantly different between sexes (P = 0.721, P = 0.343, P = 0.229). The comparison of the odds of TbL and TbD among the four groups of both species and both sexes proved that the light absorption of the lateral side was significantly larger in *S. infuscatum* than *in S. frequens* (P<0.001, F = 7.119, ANOVA) (Tab. IV).

Thus the light absorption in *S. infuscatum* was smaller on the dorsal side and larger on the lateral side. In *S. infuscatum* at Noda city in the middle of October, Ta was only about 23°C and males were sighted perching low to avoid the wind and with their body axis perpendicular to the sun. Females, of which TbL was the same as in *S. frequens*, perched at higher positions (as in *S. frequens*) than the males, although their body axis was oriented perpendicularly to the sun as in intraspecific males.

DISCUSSION

Selection of oviposition mode in *S. infuscatum* varies with the ambient temperature (Fig. 1). SO seemed to occur at high Ta, exceeding 30°C and, at a Ta lower than that, TO tended to occur. Oviposition started after 10:00 a.m. and finished at 14:00. It is reported that *S. frequens* starts oviposition early in the morning before 8:00 a.m. at the hottest time of summer (ISHIZAWA, 1998) and the starting hour of oviposition varies with the season. However, in *S. infuscatum* the starting and finishing hours characteristically do not vary, although the peak time of oviposition shifts a little.

Table IV

Comparison of increase in body temperatures (Tb) in *Sympetrum infuscatum* and *S. frequens* between the cases, in which bodies were dorsally and laterally lighted as a result of dorsal and lateral lighting. Bodies were illuminated by a 75 W halogen lamp from a height of 25 cm above. Tb were those after 180 seconds from the start of lighting (Starting Tb 29.5°C). Indoor temperatures were regulated at 27±0.5°C. Specimens of *S. infuscatum* were collected at Noda city, Chiba prefecture in October and *S. frequens* were collected at Tokorozawa city, Saitama prefecture in September and October. Probability of (b-a) among 4 groups was 0.0005 (ANOVA)

Species	sex (*N*)	Dorsal Tb °C (a)	Lateral Tb °C (b)	(b-a)
Sympetrum infuscatum	♂ (9)	31.6±0.3	35.7±0.6	4.1±0.6
	♀ (8)	30.7±0.6	34.8±0.7	4.2±0.4
Sympetrum frequens	♂ (16)	31.6±0.8	34.9±0.9	3.3±0.7
	♀ (19)	31.8±0.8	34.9±0.8	3.1±0.8

From the viewpoint of thermoregulation, Tb of *S. infuscatum* perching (phase I) was higher than that of copulation (phase II) at the same Ta. Tbs of copulating pairs that appeared in tandem at the rice paddies were low, particularly in females, which have a smaller thorax than males, and this was the same as in *S. frequens*. ISHIZAWA (1998, 2006) noted that, in *S. frequens*, Tbs of pairs were lowered during the flight from their roosting sites to the oviposition sites. As the thorax of the female is smaller than that of the male (ISHIZAWA, 1998, 2006; UÉDA, 1993; MAY, 1998), the fall of Tb by Ta in flight is larger in the female than in the male.

In *S. infuscatum*, when Ta exceeded 30°C, male Tb between phases IV and VI rose to 39-40°C, and simultaneously the Tb of females increased, and the odds of Tb between sexes in each phase diminishes. Besides the metabolic heat of the flight muscle, the rise in Tb of the female may probably be due to the higher Tb during the ejection of eggs, which was reported in *S. frequens* (ISHIZAWA, 1998). The regression coefficient of Ta on Tb was larger in the male than in the female and this was the same as reported by WATANABE et al. (2005). In other *Sympetrum* species, such as *S. frequens* (ISHIZAWA, 1998, 2006) and *S. vicinum* (MAY, 1998), the coefficient is contrarily larger in the female than in the male. That is to say, in ovipositing pairs of *S. infuscatum* the influence of Ta on Tb is greater in the male than in the female and hence, when Ta is high, the Tb in the male can rise more easily than that in the female. Oviposition in *S. infuscatum* tended to be affected by Ta. At both low and high Ta duration of oviposition is shortened. The optimum Ta for oviposition is assumed to be ca 27°C, and the duration is estimated at four and a half minutes. In *S. frequens*, the duration of oviposition is not so correlated with Ta and was less than 6 minutes, i.e. longer than in *S. infuscatum* (ISHIZAWA, 1998). At high Ta tandem pairs often separated and shifted to SO. The duration of the former was short, ca 2 minutes, and the total duration of TO and SO was not as long as in the pairs that finished oviposition through TO only. However, both sexes endeavoured to engage in oviposition as long as possible and oviposition followed by SO tends to be longer than TO only so that TO followed by SO may extend the duration of oviposition and be profitable for the female.

In tandem, oviposition pairs hover in general against the wind with a slight up and down movement. Hovering against the wind brings air speed, and this decreases the induced power for hovering, which requires much energy, and the parasite power occurs for horizontal flight which decreases energy expenditure (AZUMA, 1988; ISHIZAWA, 2007) and hence suppresses increase of Tb. Then, when the wind blows and Ta is high, the pairs adopt only TO without SO.

The wingloading of the female in tandem pairs in TO was significantly greater than that of the male. The male swings the female at oviposition and hence this may be a heavy burden on the male. The limited data on the wingstroke frequency may have obscured any difference between the sexes. However, it does seem to be larger in the male than in the female. In general, in the case of living creatures that fly by wing fluttering, the required power for fluttering flight is proportional to the product of the 5th power of wing length (*l*) and the cube of wingstroke frequency (*f*), while the available power is proportional to the product of the thoracic mass (*m*) and the wingstroke frequency (*f*) (AZUMA, 1986). Thoracic mass can be substituted by the cube of thoracic length (Thl) and ignoring the coefficients of both equations:

$l^5 \times f^3 = Thl^3 \times f \qquad f = \surd(Thl^3/l^5)$

The length of the hindwing in *S. infuscatum* is the same in the two sexes; but, the thorax is longer by ca 9% in the male than in the female, so that the wingstroke frequency of the male seems to be higher than that of the female. The metabolic energy of the male thorax may be larger and, indeed, the Tb in the male is higher than in the female.

The abdomen of *S. infuscatum* is more slender than that of *S. frequens*; particularly in the male whose abdomen is slim for its length in comparison with that of *S. frequens* male. The dorsal light absorption of *S. infuscatum* was not so different from that of *S. frequens*, and in the female it was inferior to that of *S. frequens*. On the other hand, the lateral light absorption of *S. infuscatum* was larger than that of *S. frequens* and influences the perching posture. The slender abdominal dorsum in *S. infuscatum* seems to suppress the rise of Tb by the low light absorption at summer high temperatures. In autumn, when Ta is lower, *S. infuscatum* inevitably depends upon lateral light absorption, as its dorsal light absorption is small. However, the sun irradiates from aslant above and hence, the lateral light absorption is low even if the slender abdomen is oriented perpendicularly to the sun's rays. Thus, it is difficult to increase Tb, therefore *S. infuscatum* males perch low to avoid the wind, with the abdomen perpendicular to the sun.

S. infuscatum starts oviposition at the middle of the summer, though the duration of TO is short. Of course, TO at an optimal Ta may extend the duration of oviposition. That is to say, for *S. infuscatum* males selection of the oviposition mode is influenced by factors of its morphology and the ambient temperature.

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REFERENCES

ARAI, Y., 1982. *Observations on dragonflies in Saitama prefecture*. Privately published. – [Jap.]

AZUMA, A., 1986. *Creature, its wonderful motion*. Kyoritsu Shuppan, Tokyo. – [Jap.]

AZUMA, A. & T. WATANABE, 1988. Flight performance of a dragonfly. *J. exp. Biol.* 137: 221-252.

ISHIDA, S., K. ISHIDA, K. KOJIMA & M. SUGIMURA, 1988. *Illustrated guide for identification* *of the Japanese Odonata*. Tokai Univ. Press, Tokyo. – [Jap., with Engl. title]

ISHIKAWA, H., 1985. Observations of migrating Sympetrum dragonflies. *Nature & Insects* 20(9): 29. – [Jap.]

ISHIZAWA, N., 1995. Observations on migrating Sympetrum frequens Selys (Libellulidae, Odonata). *Gekkan-Mushi* 293: 22-27. – [Jap.]

ISHIZAWA, N., 1998. Thermoregulation in Sympetrum frequens (Selys), with notes on other Sympetrum species (Anisoptera: Libellulidae). *Odonatologica* 27: 317-334.

ISHIZAWA, N., 2006. Changes of body temperatures in Sympetrum frequens (Selys) reproductive pairs (Anisoptera: Libellulidae). *Odonatologica* 35: 23-29.

ISHIZAWA, N., 2007. Energy expenditure in patrolling males of Cordulia aenea amurensis Selys (Anisoptera: Libellulidae). *Odonatologica* 36: 381-397.

MAY, L. M., 1998. Body temperature regulation in a late-season dragonfly, Sympetrum vicinum (Odonata: Libellulidae). *Int. J. Odonatol.* 1: 1-13.

SINGER, F., 1987. A physiological basis of variation in postcopulatory behaviour in a dragonfly, Sympetrum obtrusum. *Anim. Behav.* 35: 1575-1577.

TSUBUKI, T., 1997. Sympetrum infuscatum sharply increased at Yunomaru Heights, Nagano. *Symnet* 6: 4. – [Jap.]

TSUBUKI, T., S. IKEDA & N. OTSUKA, 2001. Sympetrum infuscatum and Sympetrum frequens at the Yunomaru Heights in early August, 2000. *Symnet* 9: 8. – [Jap.]

UEDA, T., 1979. Plasticity of the reproductive behaviour in a dragonfly, Sympetrum parvulum Bartenef, with reference to the social relationship of males and the density of territories. *Res. Popul. Ecol.* 21: 135-152.

UEDA, T., 1993. Questions in the life history of Sympetrum frequens, Pt 2. *Insectarium* 30: 346-355. – [Jap.]

WATANABE, M., H. MATSUOKA & M. TAGUCHI, 2004. Habitat selection and population parameters of Sympetrum infuscatum (Selys) during sexually mature stages in a cool temperate zone of Japan (Anisoptera: Libellulidae). *Odonatologica* 33(2): 169-179.

WATANABE, M., H. MATSUOKA, K. SUSA & M. TAGUCHI, 2005. Thoracic temperature in Sympetrum infuscatum (Selys) in relation to habitat and activity (Anisoptera: Libellulidae). *Odonatologica* 34(3): 271-283.