Odonatologica 35(1): 23-29 *March 1, 2006*

CHANGES OF BODY TEMPERATURES IN *SYMPETRUM FREQUENS* (SELYS) REPRODUCTIVE PAIRS (ANISOPTERA: LIBELLULIDAE)

N. ISHIZAWA
1644-15 Yamaguchi, Tokorozawa City, Saitama pref., 359-1145, Japan
isizawa7@rivo.mediatti.net

Received April 5, 2005 / Revised and Accepted Augsut 27, 2005

The reproductive behaviour was divided into four phases: perching (phase I), less than 1 min from the start of copulation (phase II), more than 3 min from the start of copulation (Phase III) and more than 1 min from the start of oviposition (phase IV). The body temperature (Tb) of the ♂ was highest in phase III, while in the ♀ Tb was not significantly different among phases. The changes of Tb are different between the sexes, however, they are both influenced largely by the wind as well as by the air temperature, and particularly in the ♀ the effect seems to be larger than in the ♂, possibly because of its smaller body size.

INTRODUCTION

There have been so far several reports made on thermoregulation in dragonflies (DE MARCO & RESENDE, 2002; ISHIZAWA, 1998; MAY, 1977, 1998; SINGER, 1987; TAGUCHI & WATANABE, 1995). ISHIZAWA (1998) investigated thermoregulation in *Sympetrum frequens* from the teneral stage to the reproductive period and noted that the body temperatures of reproductive pairs was particularly high. At that time he did not examine the body temperatures of pairs at the last half of copulation, and he only suggested the probability of the highest peak of body temperature at that stage.

This dragonfly, indigenous to Japan, is most abundant and inhabits dominantly rice paddies. This species was defined as "autumnal species" by UÉDA (1990) due to its prolonged reproductive period in late autumn (late September to November). The aim of this study is to clarify why *S. frequens* maintain high body temperatures during reproductive behaviour, particularly in the course of copulation.

METHODS

STUDY SITES. – Field data were collected at rice paddies (80 m a.s.l., located at 35°46'N, 139°26'E) in the Sayama Hills at Yamaguchi, Tokorozawa City, Saitama prefecture from late October to middle November 2002 and late October 2003. As the reproductive activity is mostly limited in the morning, collection of data was conducted from 9:00 h to 12:00 h.

FIELD TECHNIQUES. – Body temperatures (Tb) of individuals were measured in the following four phases; perching (phase I), less than 1 min from the start of copulation (phase II), more than 3 min from the start of copulation (phase III) and more than 1 min from the start of oviposition (phase IV). Individuals of males and females in phase I were perching on leaves of weeds in the sun around the oviposition site, and particularly in the female data were scanty, because most of them flew away from the site after oviposition. In phase III most of data were collected on pairs copulating for 4 or 5 min and included those for more than 5 min.

The reason why data of phase IV were collected only on pairs ovipositing for more than 1 min. is to distinguish pairs in genuine oviposition from those soon after the arrival at the oviposition site, which always adopted dipping movement similar to genuine oviposition for scores of seconds before copulation. This ambiguous behaviour was noted by MILLER et al. (1984) and the author (ISHIZAWA, 1998) called it trial oviposition.

Body temperatures were measured as described in the previous report (ISHIZAWA, 1998), using a 0.05 mm diameter chromel-alumel thermocouple embedded in a 0.3 mm hypodermic needle. The probe was inserted into the thorax of perching individuals or pairs in copula or in oviposition. In pairs taken together, females were probed prior to males in rapid succession within 10 s. Ambient temperatures at the height of 1 m in the sun (Ta) were measured with an Omron HC-100 thermister (3 mm diameter) after Tb was measured.

INDOOR EXPERIMENTS. – The effect by the wind on the body temperature of specimens was examined as follows: Tb of specimens was raised up to 33°C (near the mean Tb in nature) by a 75 W halogen lamp at indoor temperature of 20°C, and they were exposed to varying velocities of wind (windless, 1 m/s, 2m/s and 3 m/s), at the same time as switching off the lamp. The lowering of the Tb was recorded at intervals of 30 s for 3 min using 0.05 mm chromel-alumel thermocouple, not embedded in a hypodermic needle. The wind was generated using a mini desk-fan (Senju 100, diameter, 14 cm) powered by alkaline batteries. Wind speed was measured by a thermo-anemometer (CUSTOM, CW-10) of which resolution was 0.1m/s.

RESULTS

BODY TEMPERATURE BY PHASE

Figure 1-A and Table I show the changes in the mean Tb of *Sympetrum frequens* in phases I, II, III and IV. Tb in the male stayed the same in phases I (32.9 ± 2.7°C, n = 30) and II (32.9 ± 1.8°C n = 28), increased to reach the highest peak in phase III (34.2 ± 2.0°C, n = 27, z = 2.9559, $p < 0.01$Mann-Witney U-test), then fell in phase IV (32.4 ± 2.9°C, n = 29, z = 2.7806, $p < 0.01$). Similarly, in the female, Tb was not significantly different between phases I (29.4 ± 5.2°C, n = 5) and II (27.9 ± 2.5°C, n = 29, z = 0.8272, $p > 0.05$), (although the mean was higher in the former), increased in phase III (28.9 ± 3.1°C, n = 27, z = 2.3293, $p < 0.02$) and fell in phase IV (28.1 ± 3.2°C, n = 26, z = 2.0915, $p < 0.02$).

Body temperature is influenced by ambient temperature and at low Ta Tb tends

Table I
Statistics calculated from least squares linear regression of Tb on Ta in each phase of free-ranging *S. frequens* – [al = slope; r = correlation coefficient; p = probability; s.d. = standard deviation]

Phase	Sex	N	al	r	p	Mean Tb±s.d.	Range (°C)
(I) Perching	♂	30	0.185	0.191	$p > 0.1$	32.9±2.7	25.4-38.3
	♀	5	1.394	0.951	$p < 0.005$	29.4±5.2	21.5-35.9
(II) Less than 1 min from the start of copulation	♂	28	0.367	0.595	$p < 0.005$	32.9±1.8	29.1-38.3
	♀	29	0.477	0.572	$p < 0.005$	27.9±2.5	23.4-34.0
(III) More than 3 min from the start of copulation	♂	27	0.192	0.273	$p > 0.1$	34.2±2.0	31.7-39.5
	♀	27	0.659	0.602	$p < 0.001$	28.9±3.1	24.5-35.3
(IV) More than 1 min from the start of oviposition	♂	29	0.682	0.726	$p < 0.001$	32.4±2.9	25.4-37.0
	♀	26	0.851	0.759	$p < 0.001$	28.1±3.2	22.0-35.0

to be low. Figure 1-B shows the changes of the mean difference T(b-a) between Tb and Ta. In the male T(b-a) lowered significantly from phase I (16.8 ± 3.5°C) to phase II (14.6 ± 2.4°C, $z = 2.5445$, $p < 0.02$ Mann-Whitney U-test), then in phase III T(b-a) raised to the highest (17.5 ± 3.0°C, $z = 2.7535$, $p < 0.01$) and lowered in phase IV (14.3 ± 2.2°C, $z = 3.239$, $p < 0.01$). While in the female, T(b-a) traced the same process as in the male from phase I to phase III; phase I (11.6 ± 2.1°C), phase II (9.4 ± 2.6°C, $z = 1.8243$, $p > 0.05$), phase III (11.2 ± 3.9°C, $z = 3.4934$, $p < 0.001$). However, T(b-a) raised to the highest in phase IV (11.9 ± 4.3°C, $z = 0.3515$, $p > 0.05$), though the difference of T(b-a) between phase III and phase IV was not significant.

During observations tandem pairs came over the rice paddies and conducted

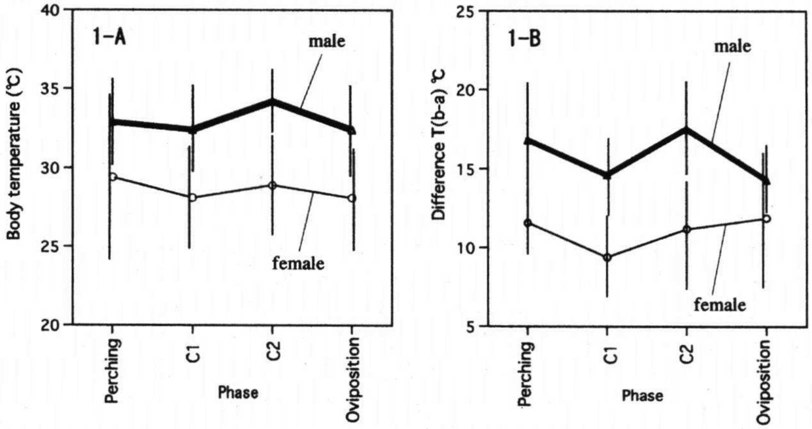

Fig. 1. *Sympetrum frequens*: A, changes of mean Tb by the phase in the reproductive behaviour; means are indicated by horizontal solid lines, and s.d. by vertical lines. C1: within 1 min from the start of copulation, C2: within 3 min from the start of copulation; – B, the changes of the mean difference T(b-a) between Tb and Ta.

trial oviposition for less than 1 min, then moved in copula to sunlit depressions adjacent to the rice paddies and continued copulation for several minutes.

DIFFERENCE OF BODY TEMPERATURE BETWEEN BOTH SEXES

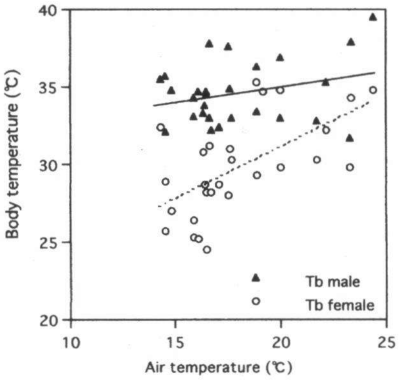

Fig. 2. The relationship of Tb to Ta in pairs in phase III for more than three min from the start of copulation. Data include Tb of pairs and individuals where the partner escaped before Tb was measured. Solid line and dotted line are least squares regressions of Tb on Ta; in males ($Tb = 0.192Ta + 31.152$, $r = 0.273$, $n = 27$) and females ($Tb = 0.659Ta + 17.964$, $r = 0.602$, $n = 27$).

Difference of the mean Tb between both sexes was significantly higher in the male than in the female from phase II to phase IV (comparison between both sexes in tandem pairs except phase I). The data of the pairs, in which either sex escaped were not included, $p < 0.0001$, Wilcoxon Rank sum-test (see Tab. I & Fig. 2). The difference was enlarged from phase II (5.1 ± 1.4°C, $n = 26$) to phase III (5.7 ± 2.6°C, $n = 26$). However, in phase IV it fell to 4.6 ± 1.9°C ($n = 23$). But the difference among phases was not significant.

Figure 2 shows the relation of Tb to Ta in pairs copulating for more than 3 min. Males in pairs maintained their Tb higher than females. The regression coefficient was generally smaller in the male than in the female, especially in phase I that of perching males was the smallest (Tab. I).

EFFECT OF WIND SPEED ON BODY TEMPERATURES OF BOTH SEXES

Figure 3 shows the decrease of Tb in 3 min in the specimens cooled by the wind. The difference of decreasing of Tb in the condition of windless was not significant between both sexes (7.6 ± 0.4°C, $n = 10$ in the male; 7.9 ± 0.4°C, $n = 9$, in the female, respectively, $z = 1.4801$, $p > 0.05$, Wilcoxon Rank sum-test). However, the difference was significant in the condition of the wind speed of 1m/s (9.8 ± 0.3°C, $n = 10$, in the male, 10.3 ± 0.4°C, $n = 9$, in the female, respectively, $z = 2.4581$, $p < 0.02$), 2m/s (10.5 ± 0.3°C, $n = 10$; 10.9 ± 0.3°C, $n = 9$, $z = 2.7027$, $p < 0.01$). But in the condition of faster than 3m/s, the difference was not significant (11.1 ± 0.5°C, $n = 8$, in the male, 11.5 ± 0.3°C, $n = 6$, in the female, respectively, $z = 1.1109$, $p > 0.05$).

The maximum wind speed at the oviposition site often exceeded 2.5 m/s and the ovipositing pairs oriented to the wind direction usually at more than 0.5 m/s.

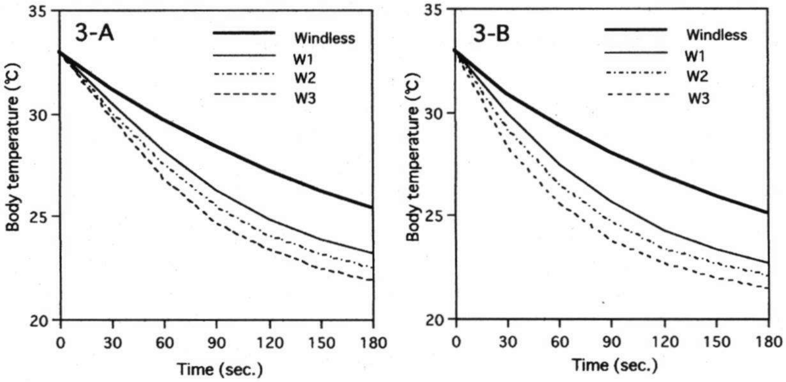

Fig. 3. Body temperatures recorded in specimens of *S. frequens* cooled by the wind for 3 min. A: in the male, B: in the female. Tb of specimens was raised up to 33°C by a 75 W halogen lamp at indoor temperature of 20°C, and they were then exposed to various wind speeds (windless, 1 m/s, 2m/s and 3 m/s) at the same time as switching off the lamp. The decrease in Tb were recorded at intervals of 30 s for 3 min.

DISCUSSION

According to MILLER et al. (1984), pairs of *Sympetrum depressiusculum* that is the vicariant of *S. frequens* move from their roosting sites to rice paddies in tandem early in the morning and wait there until the ambient temperature becomes warm. This waiting of pairs in tandem is regarded as guarding females by males from rival males. On the other hand, in *S. frequens* searching females by males at the roosting sites starts around at 7:00 h (though the time prolongs as the season advances), and taking tandem formation with females there they move to the oviposition sites of rice paddies. As soon as arrived there they conduct trial oviposition for scores of seconds and move in copula to sunlit depressions adjacent to rice paddies, where they copulate. A small number of pairs remained in tandem without copulation for several minutes. However, in most cases, as in *S. depressiusculum*, there was no waiting time.

The fact that the Tb of both sexes in *S. frequens* in phase II of the start of copulation after arriving at the oviposition site was the lowest suggests that the pairs lost Tb on the flight from the roosting sites to the oviposition sites. As pairs in tandem fly mostly towards the wind, the airspeed may be faster than the apparent speed. The flight speed of pairs in tandem was not measured, however, it is assumed to be around 2.5-3m/s faster than the normal flight speed in single of 2 m/s (ISHIZAWA, 1995; MIYAKAWA, 1994). As suggested by the experiments, the effect of the wind on Tb is large, and as the wind force increases the lowering of Tb becomes great. Consequently, the metabolic heat in thorax may not compensate the loss of heat during the flight to the oviposition sites. It is known that body size influences thermoregulatory ability in dragonflies (MAY, 1978), and especially in the female the thoracic mass is smaller by 20% than in the male (ISHIZAWA, 1998; UÉDA, 1993; MAY, 1998). In *S. vicinum* the dry weight of thoracic mass in the female is 50% of that of the male (MAY, 1998). Thus, the effect of the wind may be larger on the female than on the male. This is shown by the fact that the regression coefficient is larger in the female than in the male (ISHIZAWA, 1998; MAY, 1998).

The difference of Tb between the sexes tends to be diminished in phase IV, and this is due to the elevation of Tb of the female that is ejecting eggs (ISHIZAWA, 1998). Tb of the female in single oviposition is as high as that of the male in tandem (ISHIZAWA, 1998), and this may be because when the Tb of the female is very high it may be difficult for the male to form a tandem with the female. SINGER (1987) noted that in *S. obtrusum* tandem formation was rarely adopted when Tb of the male was less than 30°C. The reason why *S. frequens* and *S. vicinum* (MAY, 1998) oviposit in tandem even if their Tb was as low as 23°C, may be that the Tb of the females are lower than those of males.

Some of the pairs could not copulate soon after arriving at the oviposition sites; therefore Tb of pairs may be necessary to be raised at some extent before they copulate. The reason why the Tb of the male in phase III reaches a peak is assumed to be the preparation for the maintenance of Tb as high as possible because decreasing of Tb by the wind is expected at oviposition, in which the male takes the initiative. *S. frequens* prolongs copulation duration at low Ta, and this suggests that pairs wait until their Tb becomes high enough. In *S. danae* pairs that copulate early in the morning prolong copulation duration (MICHIELS, 1992). MAY (1998) noted that males of tandem pairs in *S. vicinum* (that reproduces late in autumn) maintain Tb higher up to 20°C than Ta (MAY, 1998), and also in *S. frequens* males similarly maintain a high Tb.

Thus, as *S. frequens* reproduces late in autumn, they are likely to be affected by the wind and the ambient temperature, and for that they may maintain a high Tb, particularly at the end of copulation.

ACKNOWLEDGEMENT

I wish to thank an anonymous referee for correction of my manuscript and his useful comments.

REFERENCES

DE MARCO, P. & D.C. RESENDE, 2002. Activity patterns and thermoregulation in a tropical dragonfly assemblage. *Odonatologica* 31(2): 129-138.

ISHIZAWA, N., 1995. On the 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(3): 317-334.

MAY, L.M., 1977. Thermoregulation and reproductive activity in tropical dragonflies of the genus Micrathyria. *Ecology* 58: 787-798.

MAY, L.M., 1978. Thermal adaptations of dragonflies. *Odonatologica* 7: 27-47.

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

MICHIELS, N.K., 1992. Consequences and adaptive significance of variation in copulation duration in the dragonfly Sympetrum danae. *Behav. Ecol. Sociobiol.* 29: 429-435.

MILLER, A.K., P.L. MILLER & M.T. SIVA-JOTHY, 1984. Pre-copulatory guarding and other aspects of reproductive behaviour in Sympetrum depressiusculum (Selys) at rice fields in southern France (Anisoptera: Libellulidae). *Odonatologica* 13: 407-414.

MIYAKAWA, K., 1994. Autumnal migration of mature Sympetrum frequens (Selys) in western Kanto Plain, Japan (Anisoptera: Libellulidae). *Odonatologica* 23(2): 125-132.

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

TAGUCHI, M. & M. WATANABE, 1995. Ecological studies of dragonflies in paddy fields surrounded by hills, 6. "Non-contact flying-oviposition by tandem" and thoracic temperatures of Sympetrum darwinianum Selys. *Bull. Fac. Educ. Mie Univ.* (Nat. Sci.) 46: 25-32. – [Jap.]

UEDA, T., 1990. Life history of “autumn species” of Odonata, its characteristic and variation. *Bull. Soc. Pop. Ecol.* 46: 62-67.