

**THERMOREGULATION IN *SYMPETRUM FREQUENS* (SELYS),
WITH NOTES ON OTHER *SYMPETRUM* SPECIES
(ANISOPTERA: LIBELLULIDAE)**

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Thermoregulation in *S. frequens* was investigated throughout its adult life, from emergence to reproduction. Data were analyzed by the least squares method. Body temperature was highly correlated to ambient temperature in the sun in the teneral stage and as the life stage advanced the correlation of body temperature to ambient temperature was lowered. Sexual differences were confirmed on thermoregulation; in the male the correlation decreased, whereas, in the female it decreased less. Males have lower body temperatures at high ambient temperatures than the females, and when ambient temperatures were low at the reproductive period in autumn, they maintained high body temperatures. The sexual difference of T_b ranged 2.5-3.4°C. This seem to be due to the sexual difference in body size. Females have smaller thorax and are likely to be influenced by ambient temperature. Because of the small thorax, females seem to be tolerant of high ambient temperature. High body temperature in ovipositing males were not caused by metabolic heat production at the tandem flight, but by the elevation of it during copulation. At low ambient temperatures males were seen warming up at the last stage of copulation. Body temperature in non-contact ovipositing females approximated to that of ovipositing males in tandem and the duration of the former was shorter than that of the latter. *S. frequens*, in spite of small size and disadvantage for warm-up, is a periodic endotherm.

INTRODUCTION

Thermoregulation in dragonflies had been remarked in general by CORBET (1962). MAY (1976a) was the first to report quantitative data on body temperature and thermoregulatory behaviour. With regards to thermoregulation in the genus *Sympetrum*, general remarks on several species (ISHIZAWA, 1994, 1996; VOGT & HEINRICH, 1983) or on specific species at the reproductive period (SINGER, 1987; TAGUCHI et al., 1995) have been made. But, no reports have followed on thermoregulation throughout the adult life of a specific species. *Sympetrum frequens*

Selys is one of the most common and familiar dragonflies in Japan. This dragonfly is medium in size (abdominal length: around 28 mm, mass: 240 mg in the male and 280 mg in the female, thus not so large as aeshnids) and belongs to 'perchers' defined by CORBET (1962). This dragonfly, emerging in lowlands in early summer, migrates to highlands and summers there throughout the hot season. When it matures in autumn, it descends from the highlands and begins to reproduce in the lowlands. Some of the dragonflies, however, stay in deciduous forests or at small parks in lowlands and summer there (MIYAKAWA, 1989, 1990, 1992, 1994; ISHIZAWA, 1994a, 1995a; UÉDA, 1988, 1993a, 1993b; ARAI, 1995; ASAHINA, 1990, 1991, 1992). Such a dragonfly that emerges in early summer and reproduces in autumn UÉDA (1990) defined as 'autumnal species'. In this report I will show how *S. frequens* thermoregulates in response to these environmental changes, especially emphasizing its thermoregulation at the reproductive period.

METHODS

STUDY SITES. – Field data were collected; in lowlands: in teneral adults at rice paddies at Asaka (20 m a.s.l.), in matured adults at the reproductive period, at rice paddies at Tokorozawa (80 m a.s.l.), Yokoze (260 m a.s.l.) and Motokaji (80 m a.s.l.), Hanno at a large rain puddle that had been made by a typhoon and in immature adults at the margin of the deciduous forests in the Sayama Hills (150 m a.s.l.) at Iruma and the Okumusashi Hills (240 m a.s.l.) at Nishi-Agano at Hanno, Saitama Pref.; in highlands: in mature adults at Mt Mitsumine (1150 m a.s.l.) in Saitama Pref., Mt Nyugasa (1955 m a.s.l.), Nyugasa marsh (1650 m a.s.l.) and the Yunomaru Heights (1780 m a.s.l.) in Nagano Pref. during the period of July 1987 to November 1996. These sites are located on the latitude from around 35°50'N to 36°20'N.

FIELD TECHNIQUES. – Age of *S. frequens* was estimated as follows: emerged adults (tenerals, varying in adult age from a few hours to perhaps 2-3 days) were distinguished by their relatively weak fluttering flight, glossy wings and their softer exoskeleton, and in migrating tenerals the age was estimated by adding 4 days for migration so far to Tokorozawa (20 km per day from rice paddies in Chiba) to 2-3 days of resting at emergence sites. Adults at Nishi-Agano were regarded populations which had migrated at the same time when the one at Tokorozawa had been seen. In the population at the Yunomaru Heights, it was regarded about two weeks old, emerged in late July at the foot of the heights. The foot is around 700 m above sea level, and in such a high altitude *S. frequens* emerges late, about in late July.

Body temperatures (T_b) were measured to 0.1°C with a Hoskins F-V-K-002 thermocouple (chromel-alumel, diameter, 0.05 mm, the same with other probes) set in a hypodermic needle, which was insulated with paper covering, connected to a John-Fluke 55 double channeled digital thermometer. The measurements were made within about 10 seconds after netting the dragonflies, by inserting the probe through the mesh of the net to the center of the thorax, 1 mm up the mesothoracic spiracle, because body temperatures were different between mesothorax and metathorax.

Both mesothoracic and metathoracic temperatures were measured as follows: the location of the probe was not varied and the same specimen was probed twice, first in the center of the metathorax and next of the mesothorax. The former was higher than the latter by 0.6°C in the male and 1.2°C in the female ($p < 0.01$, respectively). Ambient temperatures at the height of 1 m in the sun (T_a) were measured with an Omron HC-100 thermo-clock soon after T_b were measured. The thermistor probe is 3 mm in diameter and the responses of it to T_a are rather slow, so T_a were assumed to be those when T_b were measured.

Body temperatures of the dragonflies adopting obelisk postures were measured on the individuals soon after adopting the posture and those that continued the posture for one minute.

Body temperatures of pairs during copulation were measured after the lapse of one minute from the start of copulation and those of ovipositing pairs were measured after one minute's, three minutes' and five minutes' lapse from the beginning of oviposition, respectively.

In these pairs measurements were made on females prior to males. As body temperatures of pairs less than 1 min. after start of oviposition ranged widely, these data were omitted because I could not easily distinguish those pairs coming to oviposition sites to oviposit after copulation from those soon after arrival there from their roosting sites. Duration of copulation and oviposition were measured at rice paddies at Tokorozawa, Iruma, Hanno and Yokoze. Ovipositing pairs and females were recorded with a SONY CCV 90 8 mm video camera. Oviposition rhythm was determined by calculating frequencies and durations of oviposition on a TV display.

INDOOR EXPERIMENTS. – Minimum flight temperature at which level flight can be sustained was determined by tossing cooled *S. frequens* in the air by the same method of MAY (1976).

Body temperatures of dragonflies warming up endothermically were investigated as follows: a thermocouple was implanted in the center of the thorax of specimens which were not restrained. I used the video camera to record continuously the output of the thermocouple thermometer.

Thermoregulation by haemolymph circulation were investigated as follows: specimens were restrained on a wooden plate with their wings put together by a clothespin which was hung down from an arm of a support, with one probe implanted in the abdomen and another in the center of the thorax through a pinhole to the depth of 2 mm; the thorax was heated 1 cm away from the side with a heater (National BG-112-P, 2.88 W; its internal diameter: 7.9 mm) that was connected to 3 V AC/DC converter. The abdominal temperature and Tb of the specimens were measured at 30 seconds intervals. These experiments were made indoors at the temperature of 19–20°C.

Rapid rising of Tb in females ejecting eggs were observed at an experiment as follows: specimens were fixed at the prothorax with insect-pins on a styrofoam plate, with a probe implanted in the center of the thorax; wings and thorax were covered with a slip of Kent paper, upper side of which was pasted with aluminum foil; specimens were lighted 20 cm away from above with a 75 W halogen lamp and Tb were measured at 30 seconds intervals.

RESULTS AND DISCUSSION

MINIMUM FLIGHT TEMPERATURE

A female *S. frequens* made a level flight at Tb of 15°C. Some of the specimens could fly below 15°C. Dr. M.L. May (pers. comm., 1993) estimated the minimum flight temperature (MFT) of *S. vicinum* at 15.4°C. VOGT & HEINRICH (1983), however, reported that MFT of the same species is 12.5°C, lower than May's estimation. In the field, Tb of a male *S. parvulum* that made a level flight was 15.9°C at Ta 14.5°C. These suggest MFT of the species in genus *Sympetrum* is near at 15°C.

WARMING-UP AND VOLUNTARY ACTIVE TEMPERATURE

Dragonflies can take level flight at MFT, but they need higher Tb for their voluntary activities in the daytime. *S. frequens* sometimes warm up with their wings shivering at low Ta. In my experiments, they continued to do it until Tb rose up

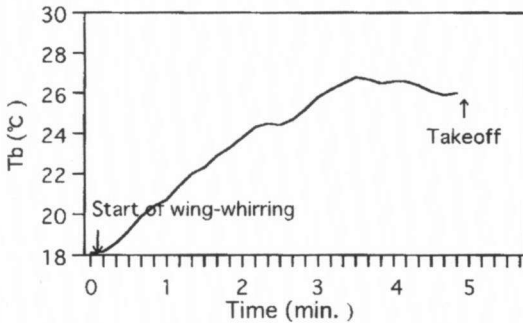


Fig. 1. Thoracic temperature during wing-whirring in a ♂ *S. frequens*. $T_a = 19^\circ\text{C}$.

there still for a while and flew away. The surface temperature on the sunny side was 27°C . MAY (1976b) reported that heat loss increases more rapidly with decreasing body size, and that loss is so rapid that metabolism cannot fully compensate. As warm-up costs much energy, it may be disadvantageous for *S. frequens* that has a rather small thorax (around 140 mg). *S. frequens* seems, however, to do it for maintaining the necessary T_b (voluntary active temperature) for activities in the daytime. Then, T_b at which it stops warm-up is presumed to be the lower limit of voluntary active range. On the other hand, the upper limit of the range is T_b where the dragonfly begins to thermoregulate not to rise so far in spite of rising T_a . In *S. frequens*, it may be estimated near $36\text{--}37^\circ\text{C}$ (shown in Fig. 2). These suggest that the voluntary active range in *S. frequens* may be estimated $25\text{--}37^\circ\text{C}$.

TENERALS

S. frequens emerge at rice paddies in lowlands on lulls in the rainy season in late June. Teneral soon after emergence were sighted perching low in the grass at irrigated fallow paddies at Asaka (ISHIZAWA, 1994b, 1995a). When I drove some of them, they flew around for a while and again landed on the grasses at the same area. TAKETO (1992) also reported on this behaviour. At non-irrigated fallow paddies

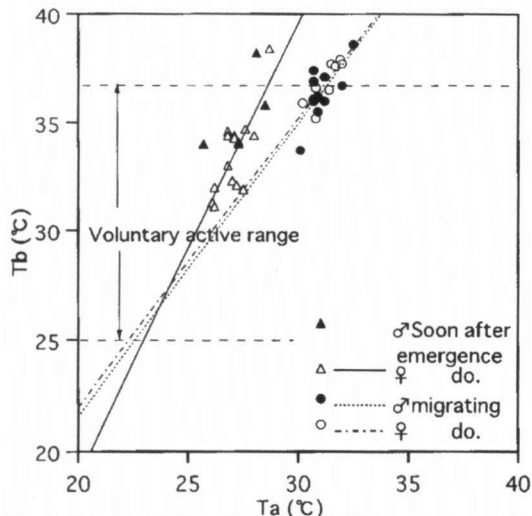


Fig. 2. Relation of T_b to T_a in teneral *S. frequens* soon after emergence and in migrating teneral resting in the lowlands.

near to 25°C (Fig. 1). At Amaike pond (2060 m a.s.l.) at Mt Yatsugatake, I observed *S. frequens* that were kept in the cool shade ($T_a: 14^\circ\text{C}$) and were put on the shaded side of a boulder, a half of which was shaded by me. All of them put in the shade warmed up for a while and flew away. On the other hand, *S. frequens* put on the sunny side never warmed up and they stayed

ambient temperatures at the same height were higher, and none of *S. frequens* was seen. They seemed to stay there for a few days (TAKETO, 1992). The mean body temperature of males was $35.5 \pm 1.7^\circ\text{C}$, and that of females was $33.5 \pm 1.8^\circ\text{C}$ ($n=15$). Male Tb was higher than Ta by 8.1°C , and female Tb was 6.4°C higher, and as MARDEN et al. (1996) noted, these Tb's were relatively lower than those of mature adults (except matures in the lowlands in mid-summer). The regression coefficient of female teneral soon after emergence was the largest (2.08, $r=0.77$, $p<0.001$) among the stages in *S. frequens* in lowlands (Tab. I). That for male teneral *S. frequens* was not available because of the scarcity of data ($n=4$), but the scattering of male data in Fig. 2 suggests that male correlation coefficient may be about the same as that of the teneral female. MAY (1976a) reported that teneral *Pachydiplax* had been found in deeply shaded areas and thermoregulated poorly and tended to have lower Tb than adults and this was due to the incompletely hardened cuticle.

Table I

Statistics calculated from least squares linear regression of Tb on Ta in each stage of free-ranging *S. frequens*; - [a] = slope; r = correlation coefficient; p = probability; S.D. = standard deviation]

Stage	Sex	N	a]	r	p	Average		Expected Tb at:		
						Tb	S.D.	20°C	25°C	30°C
Soon after emergence in the lowlands	♂	4	-	-	-	35.5	1.7	-	-	-
	♀	15	2.08	0.77	<0.001	33.5	1.8	-	25.0	39.6
During migration in the lowlands	♂	11	1.34	0.72	<0.1	36.4	1.2	-	28.2	35.0
	♀	10	1.32	0.85	<0.005	36.8	0.9	-	28.6	35.2
In the daytime in the lowlands	♂	8	-0.17	0.10	-	33.0	1.8	-	33.9	33.1
	♀	9	1.69	0.84	<0.005	33.8	1.6	-	25.0	33.4
Soon after adopting obelisk posture	♂	7	0.19	0.20	<0.8	38.9	0.7	-	37.2	38.1
	♀	8	-0.00	0.00	-	39.3	1.0	-	39.3	39.3
1 min. after adopting obelisk posture	♂	7	2.58	0.82	<0.05	38.7	1.1	-	-	30.4
	♀	5	0.66	0.83	<0.1	38.3	0.8	-	-	35.9
Early morning in the highlands	♂	12	2.88	0.90	<0.001	26.5	3.7	27.3	-	-
	♀	10	1.87	0.83	<0.005	25.0	1.9	26.5	-	-
In the daytime in the highlands	♂	55	1.08	0.59	<0.001	32.1	3.6	27.7	33.1	38.5
	♀	55	1.08	0.58	<0.001	31.8	3.9	27.5	32.9	38.3
Perching at repro- ductive period	♂	21	0.11	0.16	<0.5	34.7	1.7	34.6	35.2	35.7
	♀	6	0.35	0.59	<0.5	33.8	0.9	33.6	35.4	37.1
1 min. after the start of copulation	♂	20	0.43	0.49	<0.05	34.4	1.7	34.1	36.2	38.4
	♀	20	0.84	0.53	<0.02	31.0	2.8	30.3	34.1	38.0
Tandem oviposition 1 min. after	♂	21	0.70	0.84	<0.001	36.3	1.4	35.4	38.9	42.3
	♀	21	0.70	0.59	<0.01	33.8	2.0	32.9	36.4	39.9
3 min. after	♂	22	0.57	0.61	<0.005	36.0	1.5	35.8	38.7	41.5
	♀	22	0.87	0.65	<0.001	32.9	2.1	32.6	36.9	41.2
5 min. after	♂	21	0.36	0.56	<0.01	36.3	1.4	36.1	37.9	39.6
	♀	21	0.85	0.77	<0.001	32.9	2.5	32.5	36.7	40.9
Non-contact oviposition	♀	10	0.54	0.92	<0.001	35.8	2.7	34.4	37.1	39.8

UÉDA (1988, 1993a, 1993b) also noted the thin cuticle of teneral *S. frequens*, which is relatively thinner than that of *Lestes sponsa*, a species that does not migrate to highlands and undergoes prereproductive diapause in summer. The propensity of teneral *S. frequens* to stay at irrigated areas and maintain relatively lower Tb is probably related to the thin and incompletely hardened cuticle and the consequent danger of excessive water loss.

MIGRATING *S. FREQUENS*

S. frequens were found resting at deciduous forest in the Sayama Hills during their migration to highlands on July 2, 1994. They seemed about one week old. It was very sultry and Ta often exceeded 33°C. The mean Tb of males was $36.4 \pm 1.2^\circ\text{C}$ ($n=11$) and of females was $36.8 \pm 0.9^\circ\text{C}$ ($n=10$), higher than Ta by 5.3°C and 5.6°C in the males and females, respectively. The regression coefficients of the equations on both sexes in migrating dragonflies were rather smaller than those of teneral (Tab. I, Fig. 2).

In migrating *S. frequens*, Tb was not so high as would be predicted in teneral at similarly high Ta, and was apparently less variable than in newly emerged specimens. Most of Tb was controlled below 37°C at Ta 31°C. Probably with the lapse of time the cuticle of teneral *S. frequens* was hardened enough for migration and so the insects could tolerate high Ta. Most of migratory swarms were observed on fine or hot days (MATSUMURA, 1984; HASEGAWA, 1991; ARAI, 1992; ISHIZAWA, 1995c). High Ta seems to release the migration.

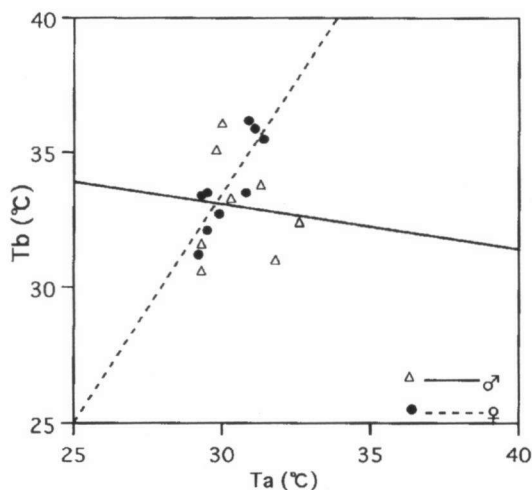


Fig. 3. Relation of Tb to Ta in immature *S. frequens* in the lowlands in mid-summer.

ADULTS IN LOWLAND IN THE HOT DAYTIME

Most teneral *S. frequens* migrate to highlands, but some seem to stay in lowlands and summer there in the hot season. MIYAKAWA (1989, 1991, 1992, 1994) was the first to have made precise reports on *S. frequens* summering in the lowland of the Sayama Hills. These *S. frequens*, most of which were female, were seen perching in the canopies of trees in the deciduous forests, and they were inactive during the hot daytime. Their body tem-

perature was maintained near the ambient temperature in the sun flecks (ISHIZAWA, 1994a).

At Nishi-Agano, Hanno, in lowlands, *S. frequens*, seemingly more than two month old, were perching at the margin of a deciduous forest. The mean Tb of males was $33.0 \pm 1.8^\circ\text{C}$ ($n=8$), that of females was $33.8 \pm 1.6^\circ\text{C}$ ($n=9$), higher than Ta by 2.4°C in the male and 3.6°C in the female, respectively. In the male, especially, the regression coefficient was less than zero and the correlation coefficient was 0.10 (Tab. I, Fig. 3). It suggested that the relation of Tb to Ta was not significantly correlated, and as Ta increased, their Tb was rather lowered. On the other hand, in the female the correlation was highly significant and Tb was a little higher than that in the male. Both correlation and regression coefficients in the female were far larger than those in the male. They did not seem to regulate Tb, but probably this is due to the scarce data. According to the data in the Sayama Hills (ISHIZAWA, 1994a) correlation coefficient in adults was smaller: 0.45, and regression coefficient was 0.26. According to MAY (1976a), dragonflies in tropical zone do not thermoregulate well. In lowlands Ta is high enough for *S. frequens* to be active, and they only need to take care not to overheat themselves. So, they stay at the edge of forests or at the open spaces there for them to take refuge easily from the high Ta at any time.

ADULTS ADOPTING OBELISK POSTURES

At the same place where the data above were collected, the Tb of individuals adopting obelisk postures were measured during late July and early August 1996. These *S. frequens* also seemed more than one month old. The mean Tb of individuals soon after adoption of obelisk postures was $38.9 \pm 0.7^\circ\text{C}$ ($n=7$), $39.3 \pm 1.0^\circ\text{C}$ ($n=8$), in the male and in the female, respectively. The correlation coefficients soon after adoption of obelisk postures were strikingly small (Tab. I, Fig. 4.). But the mean Tb of individuals that continued the postures for one minute was $38.7 \pm 1.1^\circ\text{C}$ ($n=7$), $38.3 \pm 0.8^\circ\text{C}$ ($n=5$) in the male and

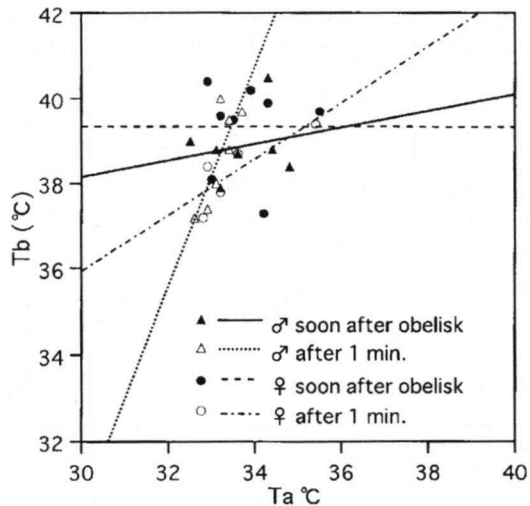


Fig. 4. Relation of Tb to Ta in *S. frequens* adopting obelisk postures.

the female, respectively. In the male the effect of the posture to decrease Tb seemed small, and in the female it seemed a little larger (the difference was 1.0°C) than in the male (0.4°C).

CORBET (1962) described that perchers tend to point the abdomen towards the sun at higher temperatures. This posture is said to minimize exposure of the body surface to the direct rays of the sun. MAY (1976a) reported that the strict association of the obelisk with high Tb demonstrated a thermoregulatory function of the posture, and which were effective in preventing or slowing further rise in Tb. According to his data, in *Pachydiplax* obelisk postures were adopted at Tb higher than 36°C. In *S. frequens* adopting this posture in the field, the mean Tb was higher than 36°C, and this coincides with MAY's data. Tb at which *S. frequens* begins to adopt obelisk posture varies according to the degree of maturity (ISHIZAWA, 1996) and also varies with sexes. Teneral in highlands often adopted the posture at Tb lower than those in lowlands, and males tend to adopt the posture at lower Tb than females.

IMMATURE ADULTS IN HIGHLANDS

S. frequens at the Yunomaru Heights seemed more than two weeks old, and most of them spent time perching on the grasses in the meadow in the highland. Early in the morning they were seen perching on the grasses or on the twigs of larches at the margin of the meadow with their bodies perpendicular to the sunlight.

As shown in Fig. 5 & 6, Tb of *S. frequens* in highlands seemed to be highly correlated with Ta, and particularly early in the morning between 6:00 and 7:00 a.m. the body temperatures of *S. frequens* seemed to rise faster, and regression coefficients were far larger. This may be due to the probability that *S. frequens*

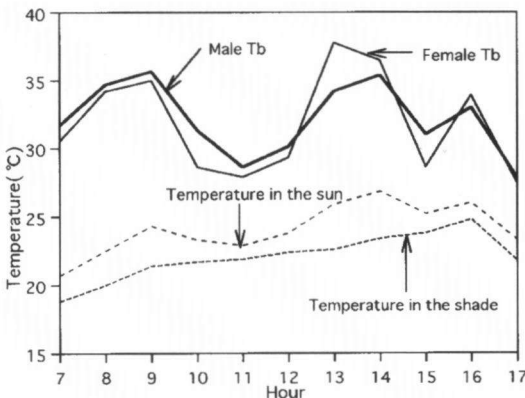


Fig. 5. Changes of temperatures of immature *S. frequens* at the Yunomaru Heights in the daytime. Five specimens were collected of each sex, at intervals of one hour.

were eager to attain quickly high Tb for them to be active. No differences of correlation and regression coefficients in the daytime were observed between both sexes (Tab. I). Their Tb in the daytime was maintained at the range from 25 to 38°C at Ta from 22 to 26°C; the mean Tb: 32.1±3.6°C (n=55) in the male, 31.8±3.9°C (n=55) in the female, respectively, relatively high compared with those in lowlands at higher Ta. As Ta in highlands is not so higher

than in lowlands, once their T_b is elevated up to the preferable range, they seem to be able to keep their T_b within the free range of the voluntary active temperature.

TSUBUKI (1987) studied the flight activity of *S. frequens* in relation to the environment factors at Yunomaru Heights, the same area where my observation was done, and reported the dragonfly was most active in the air at the ambient temperature, 18-24°C in the shade.

UÉDA (1988, 1993a) estimated the upper limit of the most suitable ambient temperature in the shade for the dragonfly at 23°C, judging from the vertical distribution of *S. frequens* in summer. As the ambient temperature in the shade is usually by 2-3°C lower than T_a , T_a of 25°C, where *S. frequens* begins to thermoregulate T_b at 36°C, is consistent with their conclusions.

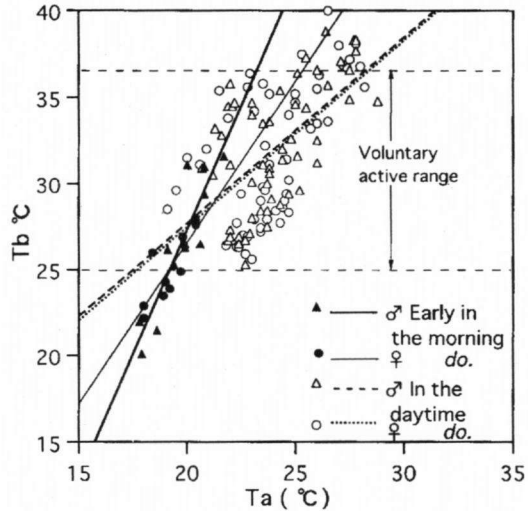


Fig. 6. Relation of T_b to T_a in immature *S. frequens* at the Yunomaru Heights in mid-summer.

MATURE ADULTS AT THE REPRODUCTIVE PERIOD

PERCHING ADULTS.—During the reproductive period in autumn, most *S. frequens* came to oviposit in tandem to harvested rice paddies, but some males came there about 9:00 a.m., before pairs arrived, and perched here and there at ridges between rice paddies. They occasionally flew over the rice paddies, dipping their abdomens in the puddles, in the same way as females oviposited. These males rarely succeeded in copulating, because fewer unmated females appeared there.

Figure 7 shows the relation of T_b of perching and copulating *S. frequens* to T_a . The mean body temperature of perching males ($34.7 \pm 1.7^\circ\text{C}$, $n=21$) was not so higher than that of females ($33.8 \pm 0.9^\circ\text{C}$, $n=6$); the sexual difference of T_b (0.9°C) was insignificant. Regression and correlation coefficients were smaller in both sexes perching in reproductive period than in the previous stages except in adopting obelisk posture; in the male the decrease was larger than in the female (Tab. I). This suggests that in reproductive period males maintain high T_b independent from T_a and this may be useful for males to copulate with females and to oviposit in tandem. According to the report by TAGUCHI & WATANABE (1995), T_b of *S. darwinianum* searching for females was as high as that of ovipositing males. Probably this propensity of males for high T_b is not limited to males of these species

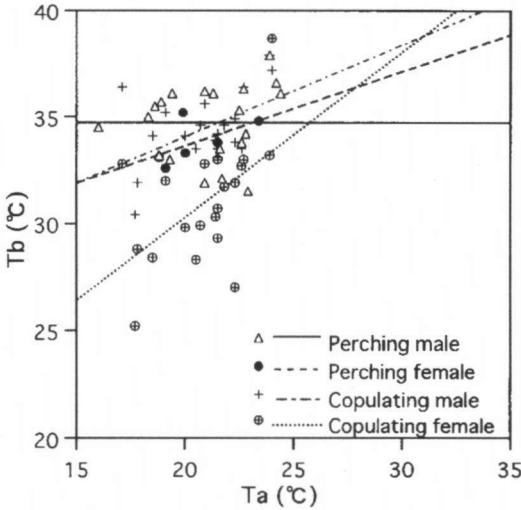


Fig. 7. Relation of Tb to Ta in perching and copulating *S. frequens*.

roosting sites, they flew over the paddies to and fro unskillfully. This flight, unlike the rhythmical oviposition, seemed as if the males of the pairs were checking whether the oviposition sites were preferable for their partners to lay eggs. This behaviour can be termed “trial oviposition”. Consequently, when pairs were first observed at oviposition sites I could not easily distinguish the trial oviposition from the real oviposition. This trial oviposition continued for about one minute, and then males in pairs translocated sperm in the air and soon landed on the ground near the oviposition sites or flew away from there to copulate. They landed in depressions in dead grasses or on seemingly warmer spots, such as sunlit fences, logs or ridges between paddies. These pairs might have selected the spots to avoid predators, because they were very sensitive to disturbance, and often changed the perching spots. Some of them changed the spots for warmer places.

Figure 8 shows the relation of duration of copulation to ambient temperature. The mean duration was 882.9 ± 401.9 sec at $T_a 24.0 \pm 1.4^\circ\text{C}$ ($n=18$). The correlation coefficient of the duration to T_a is only marginally significant ($r=0.44$, $p<0.1$), but this seems to suggest that as T_a rises higher, the duration is shortened. According to MICHIELS (1992), in *S. danae* copulation shortened with increasing temperature: early morning copulations lasted longer than midday copulations. Considering that T_a in the morning is usually lower than in midday, it seems natural that copulations lasted longer in the early morning. However, he attributed this to social factors.

Figure 7 shows the relation of Tb to Ta of pairs copulating for one minute. The mean Tb of the pairs was $34.4 \pm 0.4^\circ\text{C}$ (males $n=20$) and $31.0 \pm 0.6^\circ\text{C}$ (females $n=20$) at $T_a 20.9 \pm 1.9^\circ\text{C}$, in the male and in the female, respectively. The sexual differ-

and may be general in Odonata that oviposit in tandem.

COPULATION. – The hour of appearance of tandem pairs varied with the day. In late summer they appeared early in the morning, about 7:00 a.m. When ambient temperature was low in mid autumn, the first appearance was rather late, about 9:30 a.m. and late autumn they appeared about 10:00 a.m. Ambient temperatures seem to affect their appearance. As soon as *S. frequens* came over in tandem to the rice paddies from their

ences of Tb in copulating pairs were significant ($p < 0.01$) by Wilcoxon signed rank test. These Tb's were lower than those of perching individuals and particularly low at low ambient temperatures. The reduction of Tb might have been due to cooling throughout the coming flight from their roosting sites. One minute or more might not have been enough for them to attain preferable body temperatures. I could not measure Tb after longer copulation durations because of the sensitiveness of pairs. I often missed catching pairs after long copulations. In two examples I observed warm-up at low Ta for a few minutes at the end of copulation prior to oviposition. One of them warmed up after around 30 minutes copulation, and started oviposition.

OVIPOSITION. - Oviposition was observed mostly before noon. The number of pairs ovipositing decreased rapidly at about noon. The oviposition hour changed with the day and the weather. During hot periods tandem pairs began oviposition early in the morning. When it was cloudy, pairs did not appear at the rice paddies,

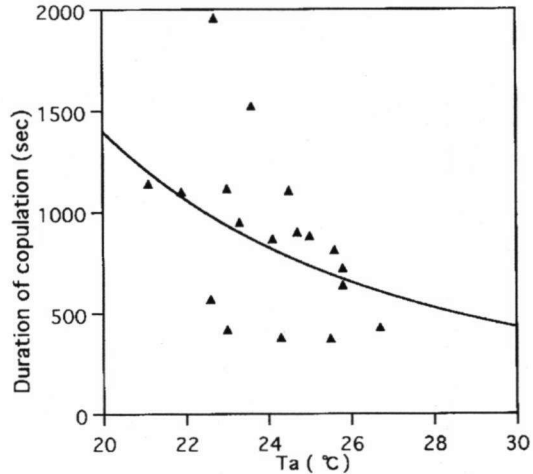


Fig. 8. Relation of copulation duration in *S. frequens* to Ta. - [$y = 8261182.593 \times x^{-2.898}$ $r = 0.412$, $p < 0.1$].

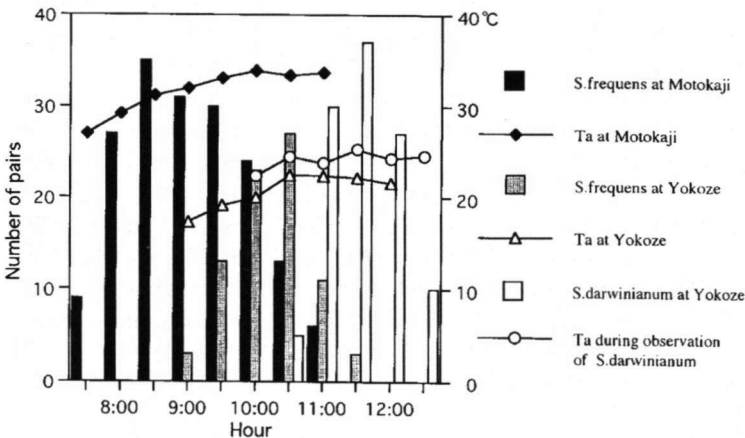


Fig. 9. Number of pairs of *S. frequens* and *S. darwinianum* appearing at oviposition sites. Data were collected at Motokaji on 28 August 1993, at Yokoze on 15 October 1995 in *S. frequens*, and in *S. darwinianum* at Yokoze on 11 October 1993.

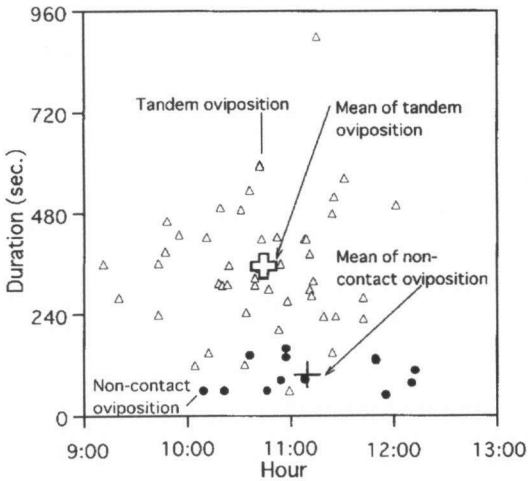


Fig. 10. Duration of tandem oviposition and non-contact oviposition.

was not significantly affected by the hour (Fig. 10) or by ambient temperature. The mean duration of tandem oviposition was 353.4 ± 144.9 s ($n=47$), while that of non-contact oviposition by females was shorter, 86.8 ± 38.2 s ($n=8$), (Fig. 10). The ovipositing rhythm (duration of oviposition / frequency) of pairs and females in non-contact oviposition was 0.83 ± 0.13 s ($n=25$, total measured duration: 1422 s) and 1.07 ± 0.23 s ($n=10$, 373 s), respectively. The rhythm in tandem oviposition was significantly faster than that in non-contact oviposition ($p < 0.01$).

Figure 11 shows the relation of T_b of ovipositing pairs in *S. frequens*, *S. darwinianum* and non-contact ovipositing female *S. frequens* to T_a . For the convenience of comparison, data on ovipositing pairs in *S. frequens* are shown on three minutes' lapse from the start at Yokoze and Tokorozawa in late autumn and at high T_a at Motokaji in late summer. The mean temperature of ovipositing pairs (Tab. I), T_b of one minute's lapse from the start of oviposition, three minutes', and five minutes', was in the male; $36.3 \pm 1.4^\circ\text{C}$ ($n=21$), $36.0 \pm 1.5^\circ\text{C}$ ($n=22$), $36.3 \pm 1.4^\circ\text{C}$ ($n=21$); in the female, $33.8 \pm 2.0^\circ\text{C}$, $32.9 \pm 2.1^\circ\text{C}$, $32.9 \pm 2.5^\circ\text{C}$, respectively, higher than T_a around 15°C in the male and 12°C in the female. Dr M.L. May (pers. comm., 1991) referred to tandem male *S. vicinum* maintaining T_b around 10°C above T_a . T_b of the male was significantly higher than those of the female by from 2.5 to 3.4°C ($p < 0.01$). In *S. darwinianum*, T_b was in the male $35.5 \pm 2.7^\circ\text{C}$ ($n=44$); in the female, $34.3 \pm 2.8^\circ\text{C}$, higher than T_a by 9.9°C in the male and 8.8°C in the female, respectively. Each equation of the linear regression of T_b to T_a was highly significant (Tab. I, $p < 0.01$). The sexual differences of T_b in ovipositing pairs were reduced as T_a rose.

The slopes of the linear regression were smaller in *S. frequens* than in *S. darwini-*

but when it began to clear they appeared and oviposited. Figure 9 shows numbers of ovipositing pairs in relation to time of day and T_a . The peak time of oviposition also varied with the season and the species. In *S. frequens* that oviposited late in summer, the peak of activity occurred between 8:30 and 9:00 a.m., earlier than usual oviposition in mid-autumn (10:00 to 10:30 a.m.) In *S. darwinianum*, the peak time occurred about 11:00 a.m., later than in *S. frequens*.

The duration of oviposition

anum. Moreover, the slope in non-contact ovipositing female *S. frequens* is smaller than in tandem ovi-positing females. This suggest that male and non-contact ovipositing female *S. frequens* maintain higher Tb rather independent from Ta during oviposition. Also, during conditions of high Ta in late summer, the slope in *S. frequens* became small (0.38, 0.22, in the male and in the female, respectively) and Tb was controlled well to avoid overheating.

NON-CONTACT OVIPOSITION. – Early in the reproductive pe-

riod, when the rice was not harvested yet, I have seen females alone continued non-contact oviposition at the narrow space among the rice grass, while males, disengaging from tandem, flew up and perched on the grasses (ISHIZAWA, 1994b). At the harvested rice paddies, however, only females that came alone to the oviposition sites engaged in non-contact oviposition. The regression coefficient of non-contact ovipositing female approximated to those of males in ovipositing pairs (Tab. I). Tb of the non-contact ovipositing female in *S. frequens* was $35.8 \pm 2.7^\circ\text{C}$ ($n=9$), higher than that of the tandem ovipositing female. I haven't seen females alone warming up prior to oviposition. However, they may elevate Tb at warm spots or by endothermic warm-up. Also I found in the experiment of heating abdomen that females ejecting eggs accelerated warming. Their Tb rose faster by 0.7°C per 3 min. ($n=3$) than that of the same specimens after ceasing ejection of eggs. As the body weight reduced by the weight of ejected eggs, their Tb's should have risen physically faster than the previous, but as a matter of fact it was reverse. These may compositely raise female Tb as high as male Tb. I saw a female of *S. parvulum* warming up before starting her non-contact oviposition (ISHIZAWA, 1986). This high Tb of non-contact ovipositing female is common with other females of genus *Sympetrum*; in *Sympetrum eroticum eroticum*, Tb of the female was as high as that

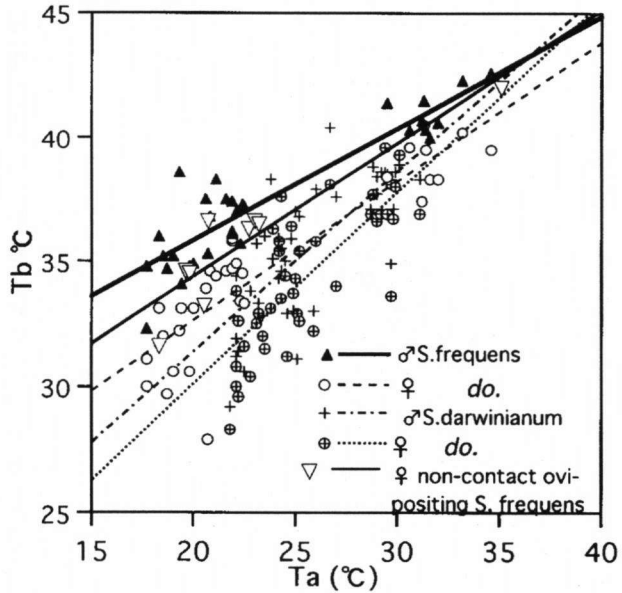


Fig. 11. Relation of Tb to Ta in three minutes ovipositing *S. frequens* and *S. darwinianum*. Data in *S. frequens* at high Ta were collected at Motokaji on 28 August, 1995 and data at Ta below 25°C were collected at Yokoze and Tokorozawa in late autumn 1995. Data in *S. darwinianum* were collected at Yokoze in early autumn 1993 and 1995.

of the male (ISHIZAWA, 1994c). Also, the duration is usually short. I saw a female *S. parvulum* oviposit five times for one minute every time, spending 26 minutes from the start to finish (1995d). Non-tandem oviposition occurs when Ta is high, and in *S. frequens* usually it occurred about 11:00 a.m. In other species of the genus it seems to occur later.

CHANGES OF CORRELATION COEFFICIENT AND REGRESSION COEFFICIENT

Correlation and regression coefficients varied with changes of life stage of *S. frequens* (Tab. I & Fig. 12). In the teneral stage both coefficients were larger and as the stages advanced they were reduced especially the regression coefficient. In early autumn *S. frequens*, which passed the hot summer in highlands, migrate to lowlands and most of them are seen perching on the electric wires or on the wood canopies. As the season advances they lower the perching height. This shift of perching height suggests postural adjustment for thermoregulation. MIYAKAWA (1994) termed this 'downward modification'.

Changes in correlation coefficients followed a similar pattern in both sexes from emergence to summering in highlands. The correlation coefficient in the perching male at the reproductive period was the smallest, successively increasing through copulation to oviposition. With the lapse of time during oviposition it decreased, while in the female it increased.

Regression coefficient soon after emergence was the largest except the special cases of individuals during adopting obelisk postures or perching in highlands in the early morning, and the smallest at the reproductive period. Sexual differences in regression seem small in teneral stages and somewhat greater during the reproductive period.

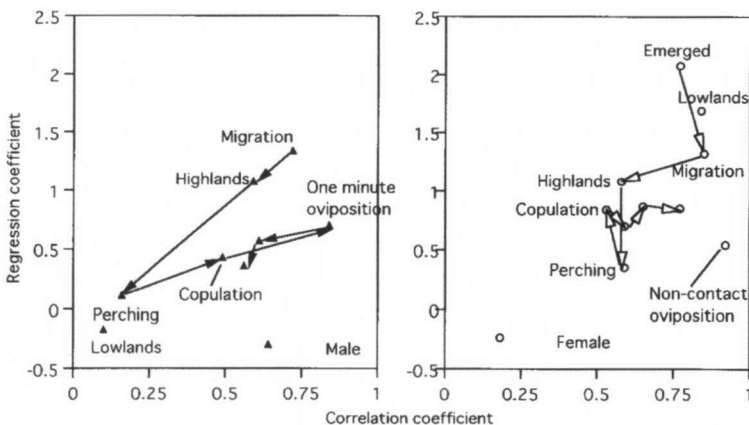


Fig. 12. Shifts of the correlation coefficient and regression coefficient with changes in maturity and behaviour.

SEXUAL DIFFERENCE IN THERMOREGULATION

Thus sexual differences in thermoregulation in various life stages were observed in *S. frequens*. MAY (1976a) suggested; there are significant sexual differences in MVT (maximum voluntary tolerance) in summer and fall in *Pachydiplax*. The differences may be due to sexual difference in body size. MAY (1977) indicated that body size is very important in determining rates of heat exchange and is a major influence on thermoregulation. In *S. frequens* the male has a larger thorax than the female. UEDA (1993b) reported thorax of *S. frequens* at the reproductive period is twice as heavy as that of teneral, and his data showed that a male thorax is heavier than a female's by around 20%. Also, my data (ISHIZAWA, 1988) collected at Mt Nyugasa suggest that the length of male thorax was longer than a female's by 4.1%; equivalent to 17.3% of the estimated mass, and coincides with UEDA's data. Therefore males may have higher T_b than females that have smaller thorax, and thermoregulatory ability may also be enhanced in the male by postural adjustments or shade seeking. Males tend to have higher T_b at low T_a , and as T_a rises, most of them take refuge to the shade of bushes. This behaviour was observed in highlands as well as in lowlands. At the top of Mt Nyugasa, when I collected *S. frequens* in the early time of a day, about 9:00 a.m., male specimens were collected more than females, and at high noon the collected number of males in the sun decreased, and they were seen perching at the stems of trees in the shade. TSUBUKI (1991) indicated that the sex ratio of this dragonfly in the morning was skewed toward males, and this may be related to the sexual difference of activities. TAGUCHI & WATANABE (1985) reported that in *S. pedemontanum elatum* males were more active early in the morning and late in the afternoon.

Females, having a smaller thorax and thus likely to be more strongly influenced by T_a , actively perch in the sun to maintain higher T_b . Particularly at lower temperature, females seem to frequent warm stones or to similar substrates. After rain in a paved road at Mt Nyugasa females hit and run over by cars outnumbered males. Low T_a might have caused females to be inactive and thus unable to avoid cars.

As shown in Figure 13, the sexual difference of T_b in perching *S. frequens* during the reproductive period was small, but from copulation onward it was enlarged, particularly at lower T_a . T_b in both sexes increased rapidly in pairs ovipositing for one minute from the start. This rapid elevation of T_b is not considered caused by the only one minute oviposition from the start. SINGER (1987) described that 20 seconds of tandem flight did not significantly elevate male T_b . It would be rather naturally considered that the high T_b of the male was caused by the long duration of copulation; of course T_b in the female also was elevated. Actually, at low T_a males were seen warming up at the last stage of copulation. Also, it is naturally presumed that during oviposition metabolic heat was produced in the thoraces of both males and females, and this seemed to elevate T_b to some extent. Moreover

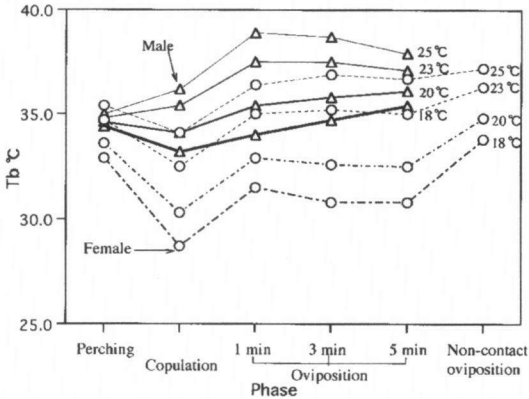


Fig. 13. Changes of Tb in *S. frequens* in various phases at the indicated Ta during the reproductive period; — [males: triangles and solid lines; — females: circles and broken lines].

they should start oviposition even on cloudy days or early in the morning. Since they hardly ever do so, the presumption that oviposition activity is limited by Tb seems reasonable.

The sexual difference during oviposition, however, varies with species. In *S. frequens*, *S. e. eroticum* (4.2°C, n=11, p<0.01) and *S. parvulum* (1.6°C, n=16, p<0.01), which lay eggs dipping in the water or in the mud, it is large, but, in *S. darwinianum* and *S. infuscatum* (0.7°C, n=9, p<0.1), which scatter eggs over the grass, it is small.

THERMOREGULATION BY HAEMOLYMPH CIRCULATION

I investigated thermoregulation by haemolymph circulation in *S. frequens*. But, as HEINRICH & CASEY (1978) noted, abdominal temperature was not elevated in spite of the increase of Tb at Ta 20°C. But I stated above, there is a fact that Tb of the metathorax was lower than that of the mesothorax and this was also observed in a flier, *Anotogaster sieboldii* (1.2°C, n=18). I could not confirm the reason of it, but it may be related to haemolymph circulation from abdomen.

Thus, *S. frequens* thermoregulates rather well throughout its life stages. Some of *S. frequens* reproduce in the hot season of late summer, but most of the species reproduce at low Ta in autumn. For the oviposition of this time of the year higher Tb is required for *S. frequens*. MAY (1976b) described that dragonflies are insulated mostly by subcuticular air sacs, and other insects are insulated by hairs or scales. In *S. frequens*, however, I suspect the ability of maintaining high Tb at low Ta may depend upon insulation partially by the hair of thorax. In Japan, *S. danae* is very hairy, and so is *S. frequens*, especially individuals in Hokkaido, which lies to the north of the Main Island, is extremely hairy. *S. infuscatum*, large in size

males mostly take initiative in tandem oviposition, metabolic heat may be produced more in the male than in the female, and this might have enlarged the sexual difference of Tb. Other species of genus *Sympetrum* as well as *S. frequens*, however, do not oviposit on cloudy days. This may be because on cloudy days they can not elevate Tb enough for oviposition during copulation. If metabolic heat production during oviposition fully compensates heat loss,

among genus *Sympetrum*, is thin even in Hokkaido, and *S. darwinianum* is not so hairy. *S. frequens* has thinner cuticle than any other species of genus *Sympetrum*. With the lapse of stages, however, the cuticle becomes thick. This may enhance the ability of input of the radiant heat and with the insulation by the thick hair may enable *S. frequens* to maintain high Tb. It can be said that in Japan seasonal variations in climate are very marked, and the propensity of *S. frequens* for relatively higher Tb at low Ta enables this dragonfly to adapt to it. Also, because of the propensity most of this dragonfly migrate to highlands in hot summer.

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