POST-COPULATORY BEHAVIOUR IN THE DRAGONFLY
SYMPETRUM PARVULUM BARTENEF
(ANISOPTERA: LIBELLULIDAE)

H. NARAOKA

36-71 Motoizumi, Fukunoda, Itayanagi-machi, Kita-gun, Aomori prefecture, 038-3661, Japan

According to their social status, the ♂♂ are divided into 2 categories: territory holders (territorial ♂♂) and non-territory holders (wandering ♂♂). The duration of copulation was longer in wandering (461.5±347.8 s, n = 46) than in territorial pairs (201.3±149.8 s, n = 85). Oviposition modes are 3-fold: viz. (1) single, with non-contact guarding (territorial pairs: 115.1±75.5 s, n = 27; wandering pairs: 133.9±45.5 s, n = 14); — (2) tandem oviposition (territorial pairs: 214.6±76.6 s, n = 5; wandering pairs: 141.0±76.2 s, n = 7); — and (3) tandem oviposition + non-contact guarding (NCGO) (territorial pairs: 131.6±93.8 s, n = 5; wandering pairs: 157.5±72.8 s, n = 2). The first type was most common in territorial (75%) and in wandering pairs (62.1%). The second type was in wandering pairs (24.1%) twice as frequent as in territorial pairs (10.4%). The third mode was infrequent (territorial pairs: 14.6%, wandering pairs: 13.8%). The relationships between ♂ social status and the interference of territorial ♂♂ on one hand, and the duration of copulation and the oviposition mode on the other, are discussed. The effects of vegetation and air temperature on the oviposition mode are briefly outlined.

INTRODUCTION

Sympetrum parvulum Bartenef is a small dragonfly (body length: 22-26mm), living in marshes with rich vegetation and at the forest edges in their vicinity.

UÉDA (1979) reported that males established territories in a marsh, and copulated with the females that came to the site. After copulation, the pairs separated and the males engaged in non-contact guarding of the ovipositing females. Almost all of non-territorial males (the wandering males) entered the tandem position outside the oviposition site and came to the marsh in the wheel position. Their copulation and oviposition were conducted in the sites occupied by the territorial males. Almost all of the wandering pairs oviposited in tandem. But NCGO of wandering pairs was observed when the density of the territorial males was lower than 4 individuals in total. UÉDA considered that two oviposition methods were selected by the balance

of 'take-over' and mate expectancy, as maximizing the fertilization rate of the male (poly mating hypothesis). This theory was recognized also in ALCOCK (1979), McMILLAN (1983) and WAAGE (1984).

On the other hand, SHERMAN (1983) and WAAGE (1984) thought that the function of non-contact guarding was to maintain the territory site (territory maintenance hypothesis). Moreover, SINGER (1987) argued that, in *S. obtrusum*, oviposition methods were not related to male density, because this dragonfly adopted tandem oviposition when the male thoracic temperature (Tth) was higher (> 33°C), and NCGO was selected when Tth was lower than 30°C.

CONVEY (1989) considered that *S. sanguineum* switched oviposition methods by balancing the risk of 'take-over' and survival costs associated with tandem flight.

The present study was conducted at two sites. At Yayoi Hills, *S. parvulum* was abundant and about 100 territorial males were sighted at the marshes there. At Nagadai Hills, where the marshes are narrower, there were 20-30 territorial males.

At these sites, I observed a few tandem ovipositions by both wandering pairs and territorial pairs, though most of both pairs of the territorial males and the wandering males conducted NCGO. As suggested by UÉDA (1979), this might have been caused by the high density of territorial males and the possibility of takeovers.

In the present paper, I discuss the influence of the territorial males, vegetation cover and temperature at the oviposition site on postcopulatory behaviour in males of *S. parvulum*.

METHODS

The field survey was carried out at the following two sites at the foot of Mt Iwakisan (1625 m a.s.l.).

(A) Yayoi Hills, Hirosaki, Aomori prefecture, Japan (40°40' N, 140°22' E, 200 m a.s.l.).

This site is composed by three marshes, terraced on the gentle slope of Mt Iwakisan, covering an area of 600 m^2. The site was occupied by about 100 territorial males. The observations were carried out at one of the marshes, triangularly shaped, over 13 days (about 71 h in total) from August 27 to October 14, 1996. The area of the observation site was about 82m^2, most of which was densely covered with sedges 20-30 cm tall, and there were some bare wet parts with scattered sundews and mosses. A steep slope of coppice extended upward on the southern and the eastern side of the marsh. On the opposite side of the marsh, grassland extended downward to the North and the West.

The territorial males reached a maximum of 30-32 in September, but thereafter, reduced to 15-24 in early October, and finally to 10 at the end of the study. At the peak of the reproductive season, the males occupied their territories at intervals of 0.5-3 m all over the marsh.

(B) Nagadai Hills, Ajigasawa-machi, Nishi-gun, Aomori prefecture, Japan (40°41' N, 140°16' E, 300 m a.s.l). This site was also composed of three small marshes, terraced on the slope of Mt Iwakisan. The total area was about 220 m^2, where 20-30 males occupied their territories. Observations were made at a small rectangular marsh with an area of 13.8 m^2. On the eastern side of the marsh there was a small pond (diameter of ca 10 m). The marsh was nearly bare and covered with a few low willows (under 50 cm in height), sedges, sundews and mosses. On the northern side of the marsh grew a shrub of willow, 1-1.5 m tall, under which sedges and grasses grew thickly. On the southern side, bare dry land extended 3-4 m wide toward a steep mountain slope.

There were 5-7 territorial males on average (max. 10), perching on the peripheries and at a small patch of land in the marsh. Observations were made over 10 days (about 43 h), between September 12 and October 8, 1996.

Before the field survey, male dragonflies (Yayoi: 55 ♂, Nagadai: 30 ♂) were marked individually by writing numbers with a white fib-tipped pen on the right forewing, so that they could be identified individually without catching. Some marked dragonflies, however, moved and dispersed from the marsh, or the marks faded with time, so that the survey was conducted without regard to whether the males were marked or not. Tandem pairs formed by territorial males at oviposition sites were regarded as the territorial pairs and their behaviour was recorded. On the other hand, pairs that came to the oviposition sites in wheel position were regarded as the wandering pairs. Only the data in which the social status of the male (the wandering male or the territorial male) was identified were accepted for this study.

The air temperature (Ta) was measured by an alcohol thermometer set at 1 m above the ground, in a sunny spot at each site. The readings were taken within 30 s after each observation of the oviposition behaviour, and several measurements were taken at intervals during the observations. Mean air temperature during an observation was calculated from the two readings just before and immediately after the observation.

RESULTS

REPRODUCTIVE BEHAVIOUR OF TERRITORIAL MALES AND THEIR MATES

A flow chart displaying the fate of 85 copulations by territorial males is shown in Figure 1. The number in cases is as follows; territorial males seized females while ovipositing alone (25); females resting on sedge (14); females flying away after oviposition (6); females coming to the oviposition site (3); and females separated after copulation (2). The rest (35) was unrecognized. The mean duration of copulation was 201.3±149.8 s (S.D., n = 85).

After copulation, 73 pairs separated (86%), and the females of 36 pairs oviposited while guarded by the male then mated with her. 27 females of the pairs completed oviposition (mean duration: 115.1±75.5 s, n = 27) and flew away from the breeding site. One female oviposited without being guarded (total duration: 92 s), because the male flew away while his mate was ovipositing. Five females were seized by other males ('take-over'), three of which after the male had flown away and the other two females were taken over during guarding. The remaining 3 pairs were not recorded completely.

After copulation, 12 pairs (14%) continued tandem position, and thereafter they soon oviposited in tandem (mean duration: 147.1±92.3 s, n = 12). Five pairs completed oviposition (mean duration 214.6±76.6 s, n = 5) and separated, and the females flew up in the sky. In the other 7 pairs, both sexes perched on grasses, following oviposition. However, the females soon oviposited singly whilst being guarded by the male that obtained the mating (mean duration: 35.6±29.2 s, n = 5) and two of them completed NCGO. In the other two pairs, the ovipositing females were seized by other males ('take-over'). One female was seized by another male during guarding by her mate and the other one was unrecognized. The rest of three pairs were not recorded completely. The mean total duration of the oviposition of the pairs that conducted tandem oviposition and NCGO was 131.6±93.8 s (n = 5).

Thus, the oviposition in the territorial pairs was classified into three types (Fig. 1): (1) single oviposition with non-contact guarding by the mate (75% of 48 pairs); − (2) tandem oviposition (10.4%); − and (3) tandem oviposition + NCGO (14.6%).

REPRODUCTIVE BEHAVIOUR OF WANDERING MALES AND THEIR MATES

The data on 46 wandering pairs is shown in Figure 2. Among them, 44 pairs came to the oviposition site in the wheel position from outside of the marshes. The other two pairs formed tandem position on the grass at the circumference of the marsh prior to coming to the site.

The mean duration (461.5 ± 347.8 s, n = 46) of copulation of the wandering pairs was much longer (F = 35.59, p <0.01) than that of the territorial pairs (201.3 ± 149.8 s, n = 85). After copulation, 29 pairs (63%) separated from one another. In 18 pairs, females conducted NCGO. 14 females out of the pairs that conducted NCGO, completed oviposition and they flew up in the sky. Mean duration of oviposition
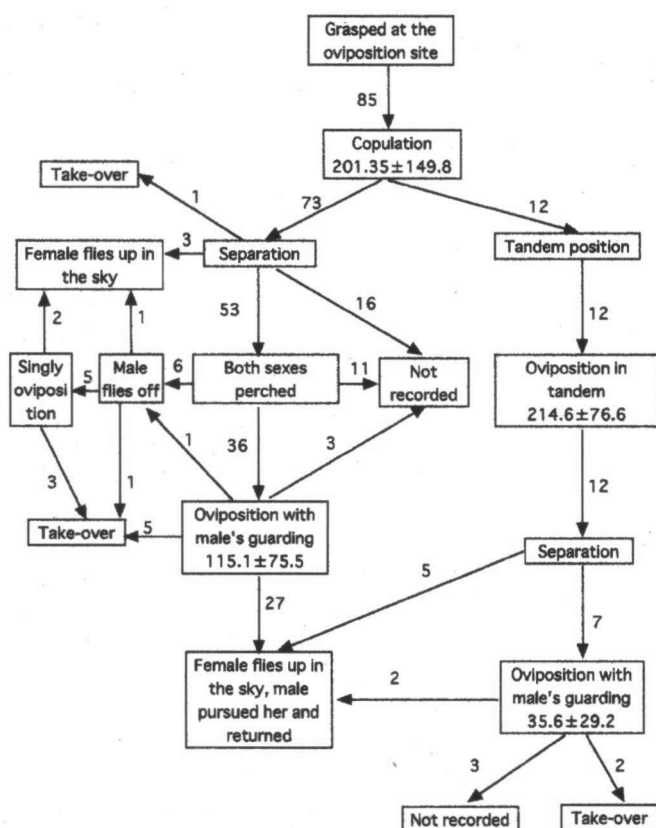

Fig. 1. Flow chart for the reproductive behaviour of territorial males and their mates. The numbers near arrows indicate the number of encounters following a particular event. The values within squares indicate the duration of the behaviour completed (mean duration in seconds ± standard deviation). — ["Not recorded": observation is ceased after previous event, "Take-over": another male seizes the female and copulates with her]

was 133.9±45.5 s (n = 14). There was one take-over of a mated female. Three pairs were not recorded completely. Two females, after separation, flew away from the site without oviposition. In one pair, the female was taken over by another male. The other 8 pairs were not recorded.

After copulation 17 pairs remained in tandem. Five pairs soon separated. The other 12 pairs began to oviposit in tandem (26%). Seven pairs completed oviposition (mean duration 141.0±76.2 s, n = 7) and the females flew away after separation. In the other 4 pairs, females oviposited singly with non-contact guarding by their respective mates, and two females completed NCGO (mean duration 51.5±60.1 s, n = 2). The other two pairs were not recorded completely. The mean total duration of oviposition of the pairs that conducted tandem oviposition and NCGO was 157.5±72.8 s (n = 2). The remaining pair was not recorded.

Thus, also in wandering pairs, three types of oviposition were recognized (Fig.2): (1) single oviposition with non-contact guarding by the mate (62.1% of 29 pairs); − (2) tandem oviposition (24.1%); − and (3) tandem oviposition + NCGO (13.8%).
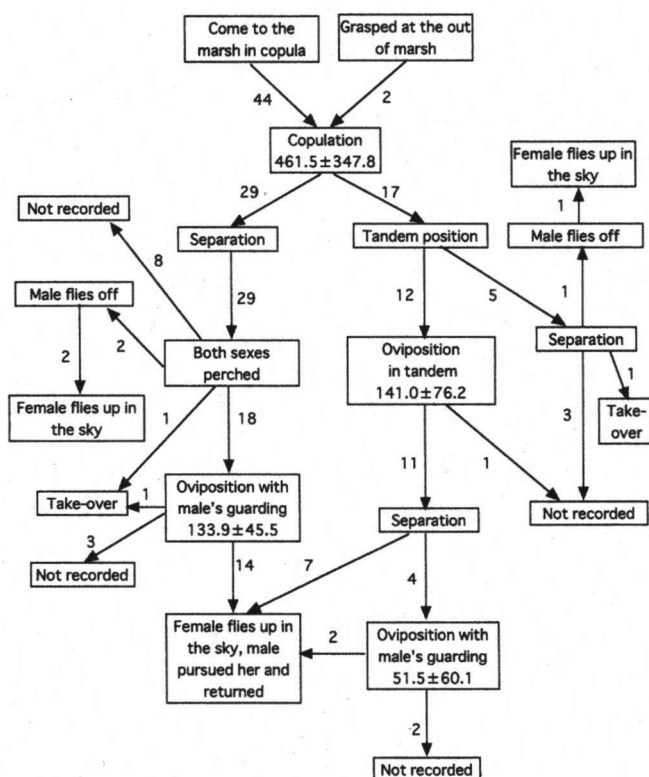

Fig. 2. Flow chart for the reproductive behaviour of wandering males and their mates. − [See Fig. 1 for explanation]

DURATION OF COPULATION AND DENSITY OF TERRITORIAL MALES

As UÉDA (1979) mentioned, the duration of copulation of the wandering pairs (mean duration: 461.5±347.8 s, range: 126-1950 s) was usually longer and much variable than that of the territorial pairs (mean duration: 201.3±149.8 s, range: 45-868 s) (F = 35.59, d.f. = 129, P <0.01). The wandering pairs were more frequently driven away and/or chased out compared with the territorial pairs (Tab. II) Also, he stated that as the density of the territorial male increased, the duration of copulation in the wandering pair became longer. From my data, there was no evidence for this phenomenon (Fig. 3).
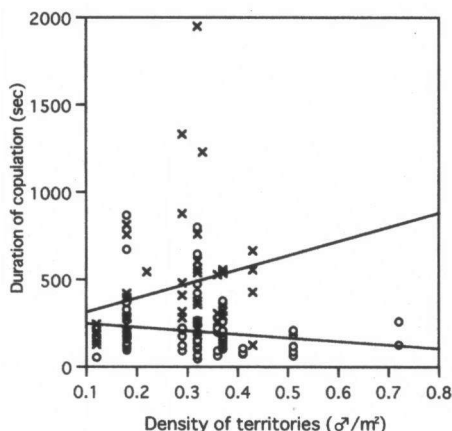

Fig. 3. Relationship between the duration of copulation and the density of territories. Solid lines are least squares regressions of the duration of copulation on the density of territories. − [O: territorial pairs, Y = -202.193X + 267.304, r = 0.152; − x: wandering pairs, Y = 812.500X + 232.400, r = 0.218]

DURATION OF COPULATION AND INTERFERENCE BY RIVAL MALES

Copulation took place mostly on grass or on the ground. The interference of rival males was violent (Tab. II, Fig. 4). In the case when pairs in copula flew up, this was usually caused by frogs, other insects (in most cases by other males) and wind, though sometimes they flew up without an apparent interference. In the wandering pairs, all of them in copula were interfered with by other males. On the other hand, seven territorial pairs (8.4% of 85 available territorial pairs) were not interfered with by other males (Tab. II). The mean number of interference events was 6.15±4.32 (n = 46) in the wandering pairs and 3.00±2.18 (n = 83) in the territorial pairs. This difference was significant (F = 32.84, P <0.01). The difference between the number of interference events between the single oviposition pairs and the tandem ovi-

Table I

Comparison of interference suffered during copulation and ratio of the tandem oviposition between territorial and wandering pairs in relation to the degree of interference suffered

Number of interference events	Number of pairs		Ratio of tandem	
	Territorial	Wandering	Territorial	Wandering
0	7	0	0.00	0.00
1 - 2	36 (5)	6 (1)	0.14	0.17
3 - 6	34 (5)	24 (7)	0.15	0.29
7 <	6 (2)	16 (4)	0.33	0.25

[The numerals in parentheses show the number of tandem oviposition.]

Table II

Comparison of the duration of copulation in relation to the degree of interference suffered by territorial males. Duration (X) is represented by seconds

Number of interference events	Territorial pairs			Wandering pairs		
	N	X	S.D.	N	X	S.D.
0	7	128.1	34.99	0		
1-2	36	149.7	21.88	6	219.7	43.1
3-6	34	232.1	22.24	24	331.5	30.8
7<	6	438.5	74.44	16	747.1	108.1

position pairs was significant (territorial pair: $F = 22.90$, $P < 0.01$; wandering pair: $F = 4.71$, $P < 0.05$). The mean number of interference events was significantly larger in the tandem oviposition pairs (territorial pairs: 3.83 ± 2.48, $n = 12$; wandering pairs: 6.92 ± 4.25, $n = 12$) than in the single oviposition pairs (territoriall pairs: 2.82 ± 2.13, $n = 72$; wandering pairs: 5.88 ± 4.38, $n = 34$), ($F = 3.96$, $P < 0.05$). In both the territorial pairs and the wandering pairs, as the interference increased, the duration of copulation became longer (a phenomenon that was more pronounced in wandering than in territorial pairs) (Tab. II). This resulted from the mean duration being much longer in the wandering pairs than in the territorial pairs (wandering pairs: 18.2 ± 18.1 s, $n = 279$; territorial pairs: 13.5 ± 15.6 s, $n = 217$), because at the oviposition site, the wandering pairs were chased often by territorial males. Thus, the duration of copulation was highly correlated with the number of interference events (territorial pairs: $r = 0.53$, $P < 0.01$; wandering pairs: $r = 0.80$, $P < 0.01$, Fig. 6).

CHANGE OF ESCORT BEHAVIOUR AND DENSITY OF THE TERRITORIAL MALE

Only one tandem oviposition was observed at Nagadai, where area of the observation marsh was small. On the other hand, in Yayoi, where the marsh was broad and sedges grew, a large number of tandem oviposition were observed. In tandem oviposition, wandering pairs were observed more often than territorial pairs, but the relationship between oviposition method and the density of territorial males was not clear (Fig.5). Table III shows that the choice of NCGO or tandem behaviour by males is not determined individually, and this coincided with the results of UÉDA (1979) and ARAI (1985). Moreover, it is not depended on the social status of the male whether it was the territo-
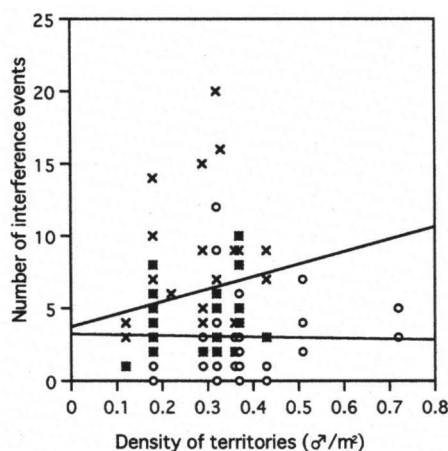

Fig. 4. The relationship between the number of interference events (to copulating pairs of territory holders) and density of territories. Solid lines are least squares regressions. — [See Fig. 3 for symbols; — territorial pair: $Y = -0.449X + 3.220$, $r = -0.021$; — wandering pair: $Y = 8.668X + 3.724$, $r = 0.204$]
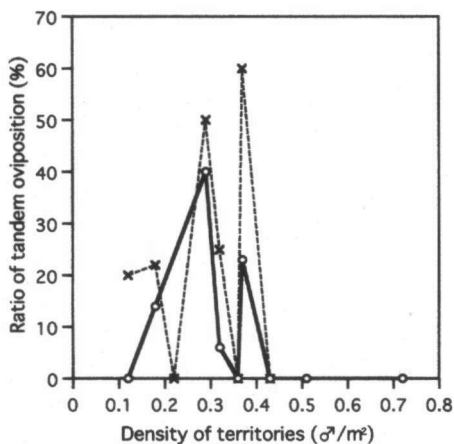
Fig. 5. Percentage composition of the tandem oviposition at various densities of territories. – [See Fig. 3 for symbols]

rial male or the wandering male (Figs 1, 2, Tab. III). This differs from the observations of UÉDA (1979) that all territorial pairs conducted NCGO.

AIR TEMPERATURE AND OVIPOSITION METHOD

Reproductive behaviour was observed at temperatures between 15 and 30°C (Fig. 7). NCGO was recorded at the mean temperature of 22.7°C, ranging from 15 to 29°C. On the other hand, tandem oviposition was recorded at the mean temperature of 23.5°C, ranging from 20 to 30°C, rather higher than in NCGO, but the difference of the mean temperatures between the oviposition methods was not significant (F = 2.07, P >0.05).
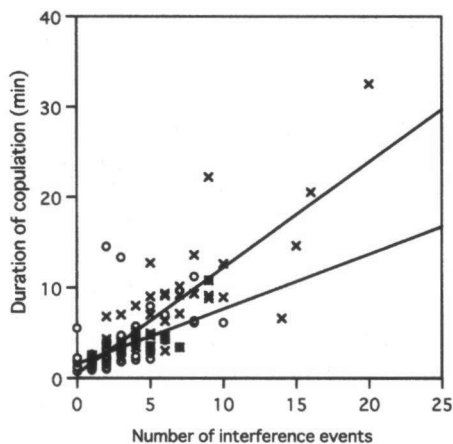
OVIPOSITION METHOD AND THE RATE OF TAPPING MOVEMENT OF THE ABDOMEN

Females deposited eggs on the wetland, tapping the tips of their abdomens. The rate of tapping was about 72 beats/min (n = 67) in tandem oviposition and 60 beats/min (n = 86) in NCGO. This result is similar to that of UÉDA (1979; tandem oviposition: 80/min, NCGO: 60/min) and ISHIZAWA (1998, tandem oviposition: 72/min, NCGO: 56/min) on *Sympetrum frequens*.

DISCUSSION

UÉDA (1979) showed that the oviposition method depends on the social status of the males, whether they are territorial or wandering, and on the density of territories. In his case, all of the territorial pairs conducted NCGO,

Fig. 6. Relationship between the duration of copulation and the number of interference events suffered by territorials males. Solid lines are least squares regressions. – [See Fig. 3 for symbols; – territorial pair: Y = 0.605X + 1.586, r = 0.526; – wandering pair: Y = 1.168X + 0.513, r = 0.802]

while the wandering pairs did both NCGO and tandem oviposition at low density of territories (below 4 ♂ in total), and all wandering pairs selected tandem oviposition at high density (above 5 ♂ in total).

In this study, tandem oviposition was observed in a small number of territorial pairs (14%, 12/85; Fig. 5). And almost all of wandering pairs (62.1%, 18/29) conducted NCGO under various male densities (0.12-$0.72/m^2$). Tandem oviposition occurred in 26% (12/46) of all the available wandering pairs and this value was about half of UÉDA's (1979) record (48%, 12/25).

UÉDA (1979) considered that interference by males led to tandem oviposition. In my observations, both territorial and wandering pairs were interfered with by other males during copulation. There was a high interrelation between the duration of copulation and the number of interference events (Tab. II, Fig. 6). UÉDA (1979) found that the duration of copulation of wandering pairs became longer as the density of territorial males increased. In my observations, however, the relationship between the duration of copulation and the density of territorial males was not so clear (Fig. 3). This suggests that the interference may be maintained to a certain degree by a large number of territorial males.

The interference by other males towards wandering pairs during copulation was more severe than towards territorial pairs (Tab. I, Fig. 4). Therefore, the mean duration of flight caused by interference by other males was significantly longer in wandering pairs (18.2±18.1 s, n = 279) than in territorial pairs (13.5±15.6 s, n =

Table III

Change in the escort behaviour of some males in relation with their social status

Males	September									October			
	4	10	11	13	21	24	25	28	29	1	2	3	11
A	SS												
B								SS					
K7				(S)				(SSSS)					
49		(S)										*T*	
C													SS
36		T	S								(T)		
K1				S	S								
15							S	S					
24						(S)				*S*		(SS)	
12									S		S(T)		
22										S			
S													
16											S		
17		S(S)					S						

S: single oviposition; — T: tandem oviposition. — Behaviour of territorial males is shown in parentheses and that of wandering males is shown by italic type. The others are males of unknown social status.
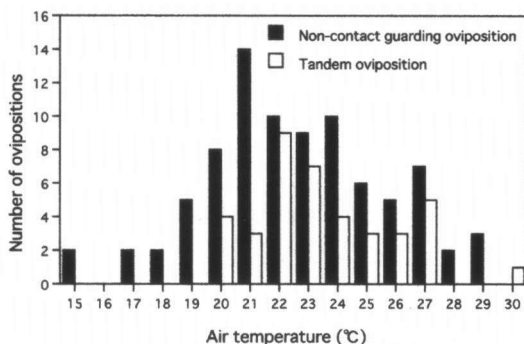
Fig. 7. Frequency of each type of mate guarding in relation to air temperature.

217) (F=9.47, P <0.01). As UÉDA (1979) described, wandering pairs were driven away one after another by the territorial males as soon as the pairs perched. This might have caused wandering pairs to oviposit in tandem more than territorial pairs.

The area of UÉDA's (1979) observation site was narrow (ca 13 m²), and the maximum number of territorial males was only 7 (male density: 0.54/m²). On the other hand, the observation site at Yayoi was broader (ca 82 m²) and the number of territorial males was 32 males at the maximum (male density: 0.39/m²). Consequently, male density in Yayoi population was lower than that in UÉDA's (1979) study. The mean number of flight times of territorial pairs in copula at Yayoi (3.0±4.8, n = 83) was almost 3 times that of UÉDA's (1979) observation (0.9±1.6, n = 20). This suggests that when the total number of territorial males at the oviposition site is large, the interference by males is intense, even if the density of the territorial males is low. It is assumed that, because of the intense interference by males, some territorial pairs in Yayoi population were obliged to select tandem oviposition.

It is said that NCGO is more advantageous for the territorial male to defend his territory than tandem oviposition (SHERMAN, 1983; WAAGE, 1984). Nevertheless, the fact that some territorial pairs selected tandem oviposition suggests that at the site where the number of territorial males is large, even for the male of the territorial pair the risk of 'take-over' of his mate by other males may become high. The territorial male must avoid such risks. Thus, in S. parvulum, the type of escort behaviour of the male in oviposition is decided essentially on the basis of the balance of the risk of 'take-over' and the mating expectancy (UÉDA, 1979, 1987; McMILLAN, 1983; WAAGE, 1984; CONVEY, 1989).

But the fact that in the wandering pairs about one third of them adopted NCGO under violent interference by other males contradicts the above mentioned hypothesis of the relation between male interference and the method of oviposition. Why is this?

Female S. parvulum often oviposit in the narrow space among the clusters of grasses (ROKUYAMA, 1963). UÉDA (1987) and co-workers noted the state of vegetation. They trampled down grasses at an oviposition site and made open spaces here and there, so they found that tandem oviposition increased more than in the previous state. Also ARAI (1983, 1985) observed that S. r. risi mostly adopted

tandem oviposition at the site where low grasses grew and adopted NCGO among the clusters of tall grasses. UÉDA (1987) thought that, at a closed site, pairs are less likely to be detected by other males and the risk of 'take-over' may be decreased. Consequently, they adopt NCGO. At an open space, pairs are likely to be detected by other males and are obliged to adopt tandem oviposition.

Most of the Yayoi marsh was covered with grasses that were 20-30 cm tall, where the rate of 'take-over' of the mate in wandering pairs was 10.0% (3/30). In territorial pairs the rate was 23.1% (12/52), i.e. higher than the former (Figs 1, 2). Most territorial males established their territories on the ground or on stones at the spots with sparse vegetation, for these sites might have been suitable for watching their territories. Most territorial pairs copulated and oviposited at such spots and this made them more easily detectable by rival males, increasing the interference of other males in proportion to male density. It is suggested, therefore, that some territorial pairs reduce the rate of 'take-over' of the mated female by adopting tandem oviposition against the intense interference by other males.

But at Nagadai, where the site was open and of the same area as that of UÉDA (1979), a single tandem oviposition (1.9%, 1/53 oviposition pairs at Nagadai) was observed. This might have been due to the low density (5-10 $\male$) of territorial males. But this was higher than that (5 $\male$ in total) of UÉDA (1979), in which all the wandering pairs adopted tandem oviposition. This suggests that, aside of the interference by males and the state of vegetation, some other factors may also be involved in determination of the oviposition method in *S. parvulum*.

SINGER (1987) noted that in male *S. obtrusum*, when body temperature was below 30°C, NCGO was used almost exclusively, and when temperature was above 33°C, tandem guarding prevailed, while there was no relationship between local or total male or female population density and variation in postcopulatory behaviour.

At my study sites, reproductive behaviour was observed at air temperatures between 15-30°C (Fig. 7), while at temperatures below 19°C no tandem oviposition was sighted. Using NCGO at low temperature may be a characteristic common to both *S. obtrusum* and *S. parvulum*. When temperature was below 19°C, *S. parvulum* was inactive and there were few males holding their territories. Even if some pairs were reproducing, interference by males was lowered, and the pairs used NCGO at low temperature.

SINGER (1987) described that there was a significant positive correlation between time in tandem and temperature, because tandem guarding was energetically more expensive than non-contact guarding. Consequently, at low temperature non-contact guarding is likely to be used. In *S. parvulum*, however, they commonly used NCGO at temperatures between 20-29°C (Fig. 7), and this is not consistent with the hypothesis of SINGER (1987).

As mentioned above, none of the factors, male density, vegetation and temperature, was sufficient on its own to determine the oviposition method in *S. parvulum*. Various ecological factors (population density, temperature, radiant energy, wind force etc.)

may be related to the reproductive behaviour of the dragonfly, as UÉDA (1987) stated. Therefore, as SINGER (1987) concluded, unless these factors are measured and analyzed in a way that separates out these potentially confounding effects, differences in behaviour resulting from physiological constraints may be incorrectly attributed to social factors. The significance of the postcopulatory behaviour will be understood when these factors will have been incorporated into a future analysis.

ACKNOWLEDGEMENTS

REFERENCES

ALCOCK, J., 1979. Multiple matings in Calopteryx maculata (Odonata: Calopterygidae) and advantage of noncontact guarding by males. *J. nat. Hist.* 13: 439-446.

ARAI, Y., 1983. Mating behaviour of Sympetrum risi risi. *Insectarium* 320(6): 10-14. [Jap.]

ARAI, Y., 1985. Ecological observations on a dragonfly, Sympetrum risi risi Bartenef with special reference to the guarding behaviour. *Gekkan-Mushi* 170: 21-24. [Jap.]

CONVEY, P., 1989. Post-copulatory strategies in the non-territorial dragonfly Sympetrum sanguineum (Müller) (Odonata: Libellulidae). *Anim. Behav.* 37: 56-63.

ISHIZAWA, N., 1998. Thermoregulation in Sympetrum frequens (Selys), with notes on other Sympetrum species (Anisoptera: Libellulidae). *Odonatologica* 27(3): 317-334.

McMILLAN, V.E., 1983. *Postcopulatory mate guarding in the dragonfly Plathemis lydia (Anisoptera: Libellulidae)*. Ph.D. thesis, Syracuse Univ.

ROKUYAMA, M., 1963. Oviposition of Sympetrum parvulum Bartenef. *Tombo* 4: 27. [Jap., with Engl. s.]

SHERMAN, K.J., 1983. The adaptive significance of post-copulatory mate guarding in a dragonfly, Pachydiplax longipennis (Odonata: Libellulidae). *Anim. Behav.* 31: 1107-1115.

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

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

UÉDA, T., 1987. The post-copulatory behaviour of males of Sympetrum parvulum Barteneff. *Nature & Insects* 22(10): 13-17. [Jap.]

WAAGE, J.K., 1984. Sperm competition and the evolution of odonate mating system. In: R.L. Smith, [Ed.], *Sperm competition and the evolution of animal mating systems*, pp. 251-290. Academic Press, New York.