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THORACIC TEMPERATURE IN *SYMPETRUM INFUSCATUM* (SELYS) IN RELATION TO HABITAT AND ACTIVITY (ANISOPTERA: LIBELLULIDAE)

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The thoracic temperature of adults in a forest-paddy field complex in the cool temperate zone of Japan was measured. After emergence, individuals moved into the forest gaps, where all sexually immature adults remained on perches. Both ♂♂ and ♀♀ controlled their thoracic temperatures against a radiant heat load in a similar manner. After maturation, some of the individuals were seen to fly in tandem over the rice paddy fields under direct sunlight for oviposition. This study evaluated the impact of the thermal environment on the perching behaviour in the forest gaps and flying behaviour in tandem in the rice paddy fields. Mean thoracic temperatures of adults were consistently higher than ambient temperatures. The difference between the high thoracic and low ambient temperature was lower among flying individuals in the rice paddy fields than in perching individuals living in the forest gaps. The control of thoracic temperature in response to ambient and radiant temperature in perching mature adults was similar to that in immature adults. In the rice paddy fields, the flying in tandem resulted in a smaller difference between thoracic over radiation temperature in females than in males in tandem. The high degree of thermoregulation clearly allowed mature adults to be active under direct sunlight. The role of perching in the forest gaps is discussed with regard to thermoregulation.

INTRODUCTION

Thermoregulation is an important behavioural activity in adult dragonflies, particularly for species inhabiting open habitats. These dragonflies, such as *Sympetrum* species in rice paddy fields, spend much of their time in direct sunlight above the rice plants (MILLER et al., 1984; TAGUCHI & WATANABE, 1985;

MIYAKAWA, 1989; REHFELDT, 1993). Therefore, any behaviour that helps them to avoid overheating would be more advantageous in these dragonflies than in other species inhabiting woodlands and forest understories. Many types of behaviour have evolved in dragonflies for the regulation of thoracic temperature (MICHIELS & DHONDT, 1987). For example, CORBET (1999) found that in order to minimize solar radiation exposure to the abdomen, some libellulid species point their abdomen towards the sun, in an "obelisk position". Such behaviour helps individuals to regulate two major components of heat budgeting, i.e., radiation and convection. In particular, however, this is a problem for males and females in rice paddy fields that fly for long periods in tandem during the late summer hot season. Because flight requires a high power output of the thoracic flight muscles, resulting in an increase in the heat load, individuals that engage in contact guarding before or after mating with flying in open areas must make every effort to maintain body temperature within a certain range.

For many *Sympetrum* species in Japan, rice paddy fields are the main habitat for the larval stages. After emergence, tenerals generally embark on a maiden flight, leaving the rice paddy fields, and entering into forests or woods, where they stay throughout their sexually immature stages (WATANABE & TAGUCHI, 1988). After sexual maturation, many *Sympetrum* species return to the rice paddy fields for reproduction, while *S. infuscatum* remains mainly in forest gaps, where a few trees have been cut down (WATANABE et al., 2004).

S. infuscatum is referred to as a "flyer" (CORBET, 1999), i.e., the mature adults of this species fly over the rice paddy fields at relatively high velocity and lay eggs in tandem on the wing. They have been observed in full sunshine during the late summer season in the cool temperate zone of Japan. Consequently, both sexes are exposed to solar radiation, i.e., a free heat source, and the radiant heat load might effectively contribute to an increase in the body temperature of the flying dragonflies, for which overheating must be accounted. Therefore, field observations were carried out to clarify the effects of radiation temperature on dragonfly thoracic temperature.

WATANABE et al. (2004) found that many immature and mature males and females of *S. infuscatum* spent the whole day perching in forest gaps: these individuals are known as "perchers". Thus, this species can vary in its ability or propensity to move over different types of habitat. Both habits, i.e., perching and flying, were expected to be associated with contrasting thermal biologies. In the present study, we studied the thermal consequences of *S. infuscatum* perching in the shady forest gaps and flying in hot rice paddy fields. This study will consider adjustments in *S. infuscatum*, such as changes in site selection, that are related to changing thermal environmental conditions over the course of one day.

STUDY AREA AND METHODS

The thermoregulation of *S. infuscatum* was studied in an isolated plain of the Kamishiro region in Shirouma, Nagano prefecture, Japan in 1998-2003. The plain lies in a cool temperate zone at an elevation of 750 m (WATANABE et al., 2004). This plain is mainly composed of rice paddy fields (ca. 2 km^2) and villages surrounded by hills or mountains with coniferous cedar forests. Rice reaping in the paddy fields is carried out annually in early October.

Sexually immature adults of *S. infuscatum* were found in forest gaps near the paddy fields in late July. After maturation, some of these individuals appeared on the plain in the mornings from late August to mid-September. Pairs flew over the rice paddy fields in tandem and laid eggs on the wing above the rice plants (i.e., "non-contact flying-oviposition in tandem").

The measurement of thoracic temperature in relation to ambient and radiation temperature was carried out between 0800 and 1600 h on windless sunny days, as most activity occurred between 0900 and 1300 h in late July in the case of sexually immature adults, and in late August in the case of sexually mature adults. On sampling days, we patrolled both the forest gaps and the rice paddy fields, and captured dragonflies perching and flying, respectively. The age of the dragonflies sampled was identified by examining the degree of wing wear (WATANABE et al., 2004). In late August, the majority of adults were in the early mature stages and there were no old mature adults.

Only adults of *S. infuscatum* that were continuously perching or flying in tandem for more than 30 s were followed. Individuals were then collected using a standard aerial net and the thoracic temperature was measured by quickly inserting a copper-constantan thermocouple probe, 0.2 mm in diameter, into the thorax in rapid succession (elapsed time <10 s). Only one measurement was taken for each dragonfly. The thoracic temperature of feeding dragonflies was not recorded. The detailed procedure used to measure thoracic temperature is described in WATANABE (1991) and WATANABE & TAGUCHI (1993).

Within approximately 30 s of measuring the thoracic temperature, the ambient and radiation temperatures were measured at a level of 0.5 m above the vegetation. An Assmann's aspiration psychrometer was used for measuring the ambient temperature and the relative humidity. A digital thermometer with the sensor covered with black vinyl tape was used for measuring the radiation temperature.

Plants in the forest gaps were occasionally trimmed by local residents and farmers. Consequently, vegetation was less than 30 cm tall, and the approximate perching height of *S. infuscatum* in the forest gaps was usually less than 2 m. In the paddy fields, on the other hand, the height of the ovipositional flight in tandem was approximately 1.5 m, or 10-20 cm above the top of the rice plants, and the height of longer flights in tandem exceeded 3 m. The number of tandem pairs flying in a rice paddy field (23 m×23 m) was counted every 5 min around noon in late August.

RESULTS

In late July, both sexually immature males and females were found perching on the tips of twigs or tops of grass blades in understories of forest gaps, and made intermittent feeding flights, after which they usually returned to the same perch. There were few interactions among them. For example, there was no courtship behaviour, no mating behaviour, and no territorial behaviour. Forest gaps appeared to provide good sources of food for the immature adults.

In late August, there were few immature adults anywhere in the survey field. Most of them had matured, and were also found perching solitarily in the understories of forest gaps, and their behaviour did not differ from that of the immature adults. On the other hand, a considerable number of mature adults flew continuously in tandem above the rice paddy fields without landing, where they laid eggs in tandem on the wing. The level of activity during tandem flight appeared to be dependent in part on solar radiation intensity in the rice paddy fields, since most indi-

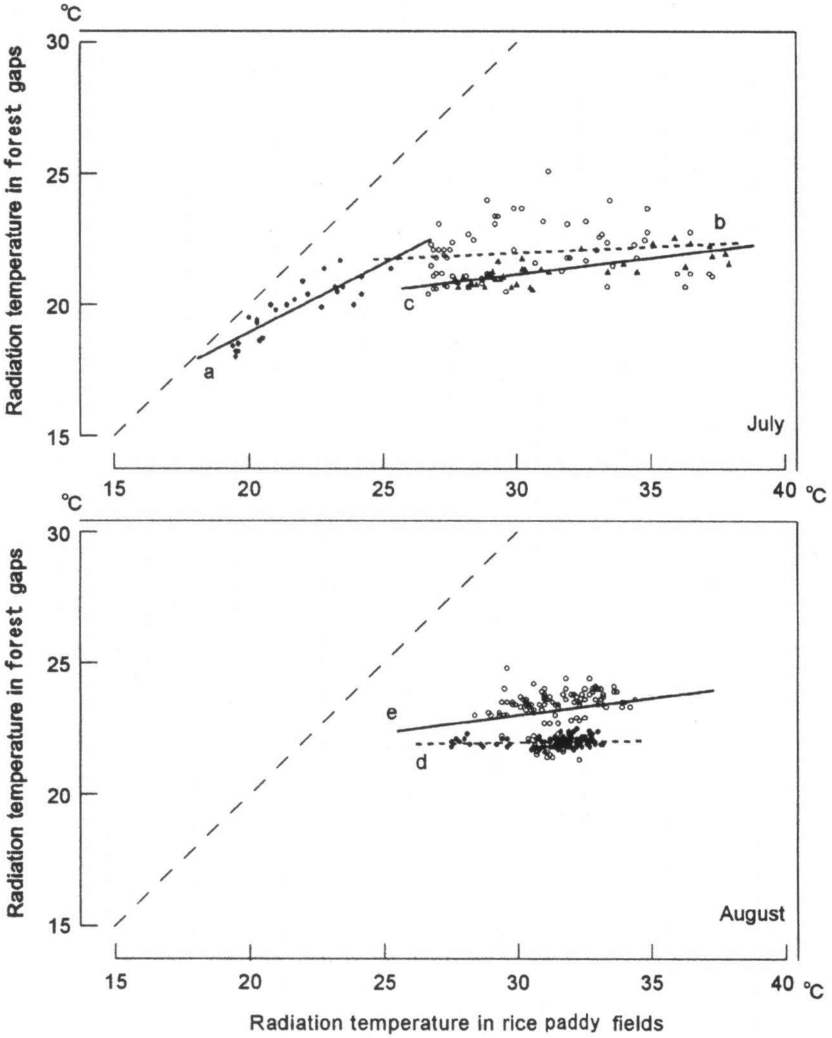

Fig. 1. The relationship in radiation temperature of forest gaps (G) and rice paddy fields (P) in late July and late August, 2003. The broken line indicates the diagonal line. Each regression line indicates a different day, when the mean ambient temperatures in the forest gaps and in the rice paddy fields were as follows: 19.3°C and 21.5°C for (a), 21.4°C and 26.3°C for (b), 21.4°C and 24.9°C for (c), 23.1°C and 28.4°C for (d), and 23.3°C and 27.4°C for (e), respectively. – a: $G = 8.30+0.53\ P$ ($r^2 = 0.75$, $p < 0.01$); – b: $G = 20.60+0.05\ P$ ($r^2 = 0.02$, n.s.); – c: $G = 17.38+0.13\ P$ ($r^2 = 0.60$, $p < 0.01$); – d: $G = 21.37+0.02\ P$ ($r^2 = 0.02$, n.s.); – e: $G = 19.00+0.13\ P$ ($r^2 = 0.05$, $0.05 > p > 0.01$).

viduals disappeared during any extended cloudy periods during the morning, the reproductive period.

The number of forest gaps examined was 27, and the mean extent of the gaps was approximately 15 m × 15 m, which was surrounded by cedars of 20 m in height. Both the size of forest gaps and the cedar size surrounding the gaps affected the light intensity at the understories of the gaps. There was some direct sunlight on the understories of the forest gaps in the middle of the day during which ambient temperatures peaked. This sunlit area was occupied by *S. infuscatum* adults in both months. Figure 1 shows the relationship between radiation temperature of forest gaps and that of rice paddy fields during the daytime, reflecting the typical summer thermal conditions in Shirouma. The mean ambient temperature corresponding to the measurements of thoracic temperatures in late July was 22.4°C (Tab. I), and the radiation temperature was always higher than the ambient temperature, and varied from 20.9°C to 30.8°C. In late August in the forest gaps, the mean ambient temperature was 22.0°C and the radiation temperature varied from 21.0°C to 28.0°C. On the other hand, the ambient and radiation temperatures in the rice paddy fields were about 10°C higher than those in the forest gaps. The relationship in the relative humidity between forest gaps and rice paddy fields around noon showed that the forest gaps had more humid air than the rice paddy fields in both months (Fig. 2). Therefore, the climatic environment of the forest gaps was shady, with a more cool and humid atmosphere than that of the rice paddy fields.

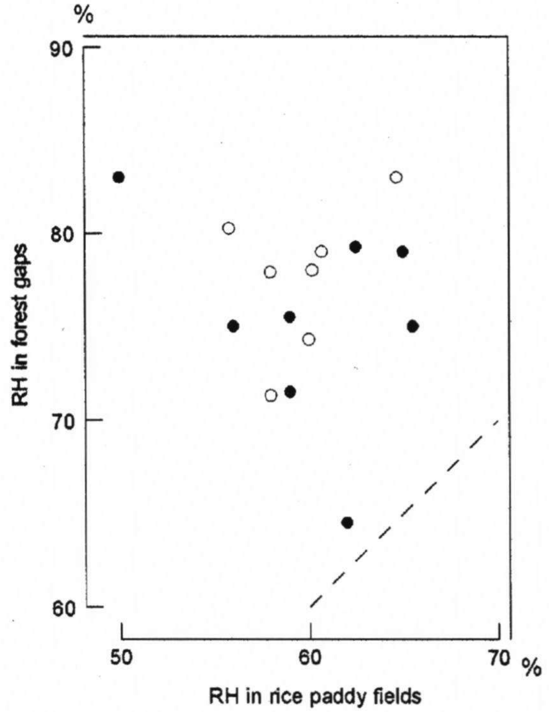

Fig. 2. The relationship in the relative humidity (RH) between the forest gaps and the rice paddy fields around noon of both late July (open circle) and late August (solid circle). The broken line indicates the diagonal line.

Late July is the hottest season in Japan; the temperature is high and the light intensity is strong. Thus, the radiation temperature of the understories of forest gaps increased, most likely affecting the body temperature of perching *S. infus-*

Table I
Thoracic temperatures of *S. infuscatum* at immature and mature stages
and their thermal environment (°C±SD)

	Ambient temperature	Males	Females		
Forest gaps					
- late July[a]	22.4±1.8 (26)	31.8±4.2 (16)	29.3±5.4 (10)	U=54.5	P>0.05
- late August[b]	22.0±0.6 (105)	25.4±2.6 (34)	26.1±2.5 (71)	U=959	P>0.05
Rice paddy fields					
- late August[c]	28.7±2.3 (21)	40.8±1.7 (20)	38.3±2.5 (13)	U=56.5	P<0.01

( ): number of samplings; – a: immature adults perching; – b: mature adults perching; – c: adults ovipositing in tandem

catum. In fact, every immature adult was capable of immediate and rapid flight without prior warm-up after a long duration of perching. Basking and shivering were not observed; moreover, wing beating, and consequently heat production, were not observed. All such flight behaviour lasted less than a few seconds, after which the insects perched again. The thoracic temperature of the perching adults in late July was thus around 30°C, which was higher than the radiation temperature as well as the ambient temperature (Tab. I). In late August, the ambient temperature decreased a little and the radiation temperature also decreased in the forest gaps. The thoracic temperature of the perching mature adults decreased at this time. However, both sexes flying in tandem in the rice paddy fields had high thoracic temperatures (around 40°C), exceeding the ambient temperature by more than 10°C. Furthermore, the thoracic temperature of males was significantly higher than that of females.

As shown in Figure 3, excess thoracic temperatures (thoracic temperature minus ambient temperature) increased as differences between the radiation and ambient temperatures increased. The regression coefficient (= slope) of the excess temperature against the difference between the radiation and ambient temperatures was 1.36 and 1.51 for immature males and females, respectively, indicating that both sexes share a similar thermoregulation mechanism.

In the forest gaps during late August, the excess thoracic temperature in mature adults also increased as differences between the radiation and ambient temperatures increased. The regression coefficients for males (1.34) and females (1.66) were roughly similar to those for immature males and females, respectively (Fig. 3). The endothermal heating mechanism cannot change during maturation among perching individuals.

In the rice paddy fields of late August, the mean radiation temperature was 33.7°C, which was much higher than the ambient temperature. The regression coefficients for males and females flying in tandem were lower than those in the forest gaps (0.68 for males and 0.43 for females). Therefore, flying dragonflies may have an additional thermoregulation mechanism, and mature females were particularly apt at thermoregulation in comparison with mature males, although they flew together in tandem.

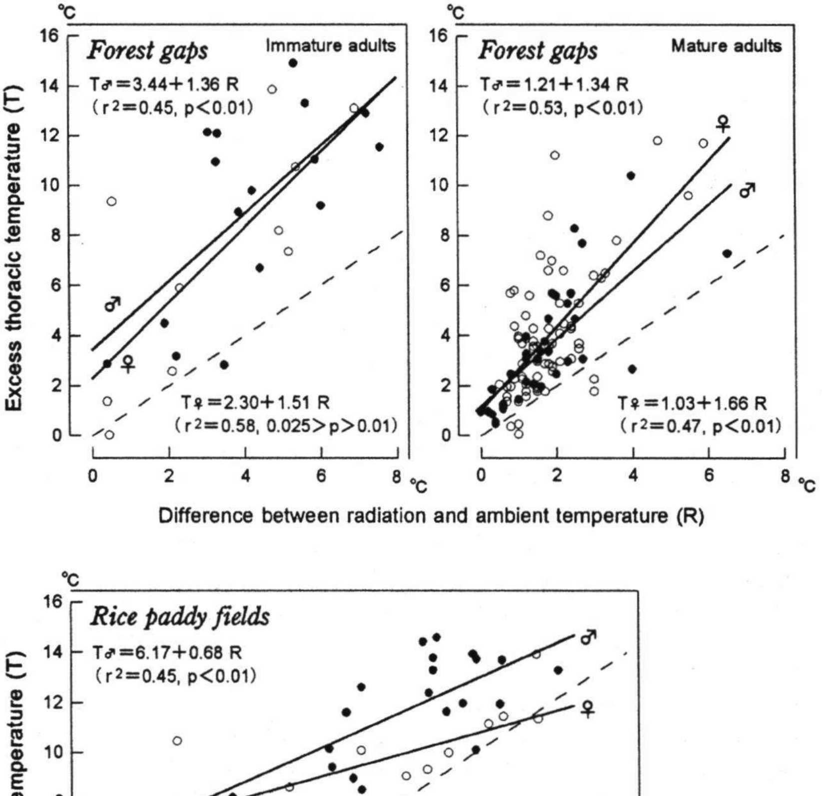

Fig. 3. The correlation between excess thoracic temperature and ambient temperature and the difference between radiation and ambient temperature for immature adults in the forest gaps in late July and mature adults in both the forest gaps and the rice paddy fields in late August. A solid and an open circle show a male and a female, respectively. In the rice paddy fields, each data was taken from a single pair in tandem flying for oviposition. The broken line indicates the diagonal line.

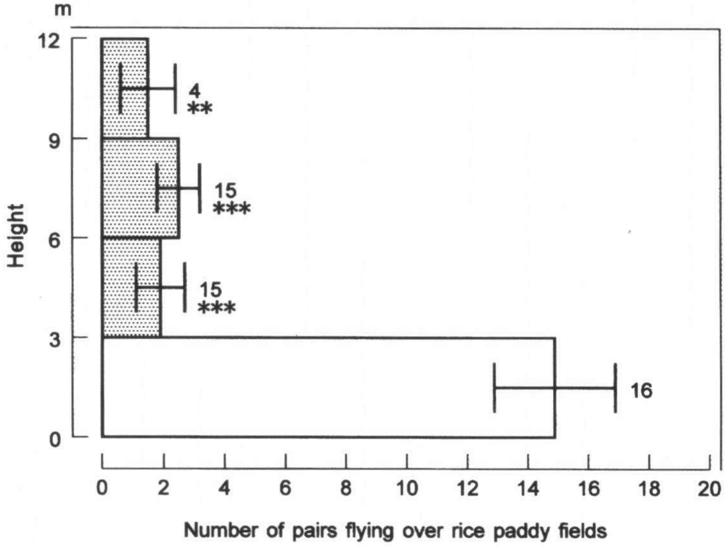

Fig. 4. Number of pairs flying above rice paddy fields (23 m×23 m) and respective heights. Each bar represents the S.E. The numbers indicate the number of measurements taken during the 2-h peak activity period in the rice paddy fields in late August, 2003. ** and *** represent the significantly difference from the number of pairs flying in 0-3 m for the probability less than 0.05 and 0.01, respectively.

Pairs in which the thoracic temperature was measured were laying eggs, which required several minutes when a pair moved to two or three different sites, as sometimes happened even in the absence of any apparent disturbance. Figure 4 shows that the mean number of pairs flying at heights of approximately 3 m in the rice paddy fields was ca 15 in each rice paddy field (23 m×23 m). Some of the pairs flying in tandem flew more than 3 m above the rice paddy fields; at such heights, insects were not captured. The pairs seemed to move across the rice paddy fields. Although in general, the ambient temperature decreased with height above the ground, the radiation temperature remained relatively constant with height. Therefore, the insects must have been exposed to similar radiation temperatures.

DISCUSSION

Although dragonflies are poikilotherms, their body temperature is thought to be regulated with respect to ambient and radiation temperatures. Several studies of thermoregulation have thus far focused on the radiant heat load obtained from thermistors with the probe painted black (MAY, 1976). The behavioural posture required for thermoregulation in response to radiation has been analyzed in many odonate species (CORBET, 1999). Perchers display a wide range of behaviours that are possibly related to thermoregulation (HEINRICH & CASEY, 1978), as most of these individuals perch in sun-exposed areas and thermoregulate primarily by making postural adjustments which involve the body and wings (CORBET, 1980). Other elaborate physiological adaptations, as well as perching behaviour, also help odonate species to regulate body temperature (MILLER, 1987).

Immature adults of *S. infuscatum* stays in cooler areas with moist air, i.e., forest gaps, than rice paddy fields. The habitat preference was not altered when they matured. MAY (1976) pointed out that the cuticle of the immature adults was generally vulnerable to hot dry air. It seems that thoracic temperature is regulated in the same way by immature and mature adults.

In some species, thoracic temperatures are achieved either by basking (MAY, 1976) or by both metabolic heat production (shivering) and basking (MAY, 1977, 1979). Small perchers such as *Leucorrhinia hudsonica*, *S. obtrusum*, and *S. vicinum* require a thoracic temperature of more than 16°C above ambient temperature for flight (VOGT & HEINRICH, 1983). ISHIZAWA (1998) reported that *S. frequens* female made a level flight with a thoracic temperature of 15°C. Small animals have a rapid rate of heat exchange between their bodies and the ambient thermal environment because they have a large surface area-to-mass ratio (MAY, 1979). Rapid rates of cooling may preclude appreciable endothermy in the cool temperate zone of Japan. During the present experiment, none of *S. infuscatum* observed showed basking or shivering behaviours. Since *S. infuscatum* is a medium-sized dragonfly, it may adopt metabolic heat production for thermoregulation. In fact, the thoracic temperature of the individuals was always higher than the radiation temperature, which was also higher than the ambient temperature in the summer season, when the air temperature was higher than 20°C enough for *S. infuscatum* to be active.

Both males and females of *S. infuscatum* that remained in the forest gaps generally used a sit-and-wait foraging tactic in order to catch prey throughout the entire day. HIGASHI (1973) observed the feeding behaviour of *S. frequens* in coniferous forests, where there was an excess of females. An active *S. infuscatum* perching in the forest gaps depends on being able to fly instantly and quickly as it catches prey in flight and escapes from predators such as birds in the same way. UEDA (1988) estimated the upper limit of the most suitable ambient temperature in the shade for *S. frequens* at 23°C. On the other hand, dragonflies, which retain much heat in their thorax, require high muscle temperatures in order to maintain sufficient power output to continue flight (HEINRICH, 1974). Physiologically, the advantage of maintaining a high thoracic temperature probably lies in permitting active flight (MAY, 1977). The thoracic temperature of 25-30°C for both immature and mature adults of *S. infuscatum* perching in gaps seemed to ensure the possibility of taking off quickly without any particular behaviour required for ectothermic thermoregulation.

Many dragonflies are known to regulate the temperature of their thoracic flight muscles, by endothermically altering heat production and by heat loss from the flight muscles themselves (CORBET, 1999). The "fliers" appear to thermoregulate exclusively through controlling blood circulation (HEINRICH & CASEY, 1978). In general, most flying insects have higher rates of metabolism, and hence heat production, than other animals (HEINRICH, 1974), because flight metabolism is inefficient, with approximately 80% - 90% of the energy converted to heat (SRYGLEY & CHAI, 1990). For dragonflies, their internal source of heat is a result of flight muscle metabolism. Thus, flying (and consequently heat production) must contribute to increases in body temperature (MAY, 1976). Since most flights of *S. infuscatum* were in tandem, some heat, which was probably derived from the flying muscles, must have been added to the thoracic temperature as well as to the radiation temperature. Controlling the radiant heat load may thus be a more important factor for regulating body temperature during flight over rice paddy fields, as these individuals were constantly exposed to direct sunlight, and therefore, received solar input.

Flight in tandem for *S. infuscatum* is essential in looking for oviposition sites, laying eggs, and moving to new habitats. Pairs may have come from a great distance (WATANABE et al., 2004), as occurs in some other *Sympetrum* species (MICHIELS & DHONDT, 1989; MIYAKAWA, 1994; McMILLAN, 1996) that lay eggs during flight above the rice paddy fields. Although there is no direct evidence in Odonata, flight efficiency probably continues to increase with body temperature (GIBO, 1981). The length of time of flight among *S. infuscatum* in the rice paddy fields is associated with increases in body temperature. However, SINGER (1987) recorded that 20 s of tandem flight did not significantly elevate body temperature. Although wing-beating produces so much heat that mature males may be unable to continue to fly with females for a long time over rice paddy fields, they still have to complete oviposition in a single day. After oviposition, every female retained few mature eggs in her ovaries.

High frequency of wing beating in *S. infuscatum* always occurred, seemingly particularly in males. We did not observe differences in the frequencies of wing beating between sexes during tandem flight. In addition, males did not soar or glide, but they were observed to hover in order to maintain the mates' egg laying process. Since the energy cost of hovering is larger than that for normal flight (MAY, 1991), the wing beat frequency of males hovering in tandem must be higher than that of females flying in tandem, suggesting a higher production of heat from the flight muscles of males than from those of females. The thoracic temperature of males in tandem was 2°C higher than that of females. The same oviposition behaviour was observed in *S. frequens* (ISHIZAWA, 1998) and *S. darwinianum* (TAGUCHI & WATANABE, 1995), which also have little site preference as regards oviposition within paddy fields. In the latter species, the duration of a single oviposition bout was about 461 seconds, during which the males withstood a 1°C higher thoracic temperature in tandem flight than females.

We found that *S. infuscatum* flying above the rice paddy fields underwent a decrease in the excess of thoracic temperature typically associated with increased radiation temperatures. Much of the heat provided by solar irradiance and the heat produced by flight muscles is expected to be lost from the body under these conditions. Rice paddy fields are open areas with little shade, and flying dragonflies cannot escape intense solar radiation. They also do not adopt any postures to reduce solar heating during flying, although the regression coefficient of the excess of thoracic temperature on the difference between radiation and ambient temperature for flying adults was observed to be lower here than that of perching adults in the forest gaps. These individuals might cool their body using the ambient air of a low temperature. Forward air speed contributes to the convectional cooling of the thorax of flying insects, as was previously shown by WATANABE & IMOTO (2003). Because flying dragonflies are exposed to air movements, flight itself is expected to contribute to decreases in body temperature. Thus, heat loss occurring by means of behavioural thermoregulation during flight may be an important adaptation for *S. infuscatum* inhabiting the open habitats a cool temperate zone.

WATANABE et al. (2004) stated that *S. infuscatum* fly extensively over a wide area of the cool temperate zone. Some of our results concur with the fragmentary information reported by UEDA (1997), i.e., this species has been shown to always fly over rice paddy fields in warm temperate zones of Japan in autumn, when the ambient temperature has decreased. Diurnal activity patterns of mature adults of the *Sympetrum* species have been well documented, particularly with respect to the relationship with the thermal environment of rice paddy fields (ISHIDA, 1969; UEDA, 1979; ARAI, 1983; TAGUCHI & WATANABE, 1987; TSUBUKI, 1987). For *S. infuscatum*, behaviours such as changing location over forest-rice paddy field complexes may extend the range of individual thermal environments in which they are able to function. This extension might allow more time for breeding, resulting in more offspring. Since behavioural adjustments are generally less expensive in terms of energy than physiological regulation, it is adaptively advantageous for *S. infuscatum* to utilize behavioural mechanisms to cope with changes in the thermal environment.

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