

THORACIC TEMPERATURES OF *LESTES SPONSA* (HANSE-MANN) PERCHING IN SUNFLECKS IN DECIDUOUS FORESTS OF THE COOL TEMPERATE ZONE OF JAPAN (ZYGOPTERA: LESTIDAE)

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Thoracic temperatures (T_{th}) were monitored while the insects were perching. Mean T_{th} was about 28°C in both sexes perching in sunflecks. T_{th} was positively correlated with ambient temperature (T_A) in both sexes. The radiant heat load, which was termed the radiation temperature (T_R), in sunflecks ranged from 27°C to 50°C. T_{th} was regulated against T_R . After capture 1 live and 1 dead ♂ were taped with spread wings onto brown paper. The pair was put in a sunlit point of a sunfleck to measure T_{th} . T_{th} of perpendicular males, to direct sunlight, was kept lower than T_R under a high radiation temperature of more than 35°C. T_{th} of live males was usually kept higher than that of dead ones. The role of perching in sunflecks is discussed with regard to thermoregulation in this sp.

INTRODUCTION

The Emerald damselfly, *Lestes sponsa*, exhibits characteristic postures while perching mainly on stems of *Sasa* spp. in deciduous forests in the cool temperate zone of Japan. Damselflies tend to stay in the understory of deciduous forests throughout their adult lives (WATANABE et al., 1986). They perch on the stems all day long with a few intermittent periods of flight. Most of the perching points are sunlit areas, i.e. sunflecks, so that they are exposed to direct sunlight. Radiant heat load might effectively contribute to an increase of the body temperature of damselflies perching in direct sunlight (WATANABE, 1991).

The ability of dragonflies to maintain a relatively constant body temperature is related functionally to their body size and behaviour (CORBET, 1980). Al-

though thermoregulation in some Odonata species inhabiting temperate zones has been investigated (HEINRICH & CASEY, 1978; VOGT & HEINRICH, 1983), data on the body temperature in *L. sponsa*, with a lek-like mating system (WATANABE & MATSUNAMI, 1990) have so far been lacking. The following observations on thermoregulation were obtained in the Japanese deciduous forests, and the thermal behaviour of *L. sponsa* in such habitats is discussed.

MATERIAL AND METHODS

Field data were collected in late August 1988 in Urabandai, Fukushima Pref., NE Japan. The study area has already been described in detail (OHSAWA et al., 1985; WATANABE & MATSUNAMI, 1990). The experimental plot was a secondary forest where the dominant tree species is the larch, *Larix leptolepis*, beside a pond (about 200 m long).

The measurements relating to thoracic temperature (T_{th}) and heating rates were made between 08:00 and 16:00 h on 4 windless sunny days. On each sampling day, we patrolled the forest floor to capture damselflies perching in sunflecks. All the Emerald damselflies sampled were mature.

The thoracic temperatures of live damselflies were measured with a copper-constantan thermocouple probe of 0.5 mm diameter, and read from a digital thermometer (accuracy 0.1°C). The thermocouple was inserted approximately near the centre of the thorax, and only one measurement was taken from a given damselfly. Damselflies which were perching for more than 1 min were captured by net and T_{th} was measured within about 10 sec. The detailed procedure is described elsewhere (WATANABE, 1991).

The heating rates in sunshine were measured on a couple of live and a recently killed (by decapitation) damselfly taped with spread wings onto brown paper. The effects of convective heat loss and reflective heat gain were eliminated by the positioning of the thick brown paper block with the damselfly. The damselfly was placed perpendicular to the direct rays of the sun in the sunfleck 0.5 m above the ground. The heating rates were then measured with a thermocouple inserted into the ventral thorax. Temperatures of both damselflies were read every 15 s. The measurements lasted over a period of 10 min.

We examined 14 pairs of mature males. Each male was captured and measured within 4 min.

Ambient air temperatures (T_A) were taken from an Assmann's aspiration psychrometer at ca 1.5 m above the ground in the deciduous forests. A digital thermometer, with the sensor covered by black dye, was exposed to the direct sunlight, and the temperatures measured were termed the radiation temperature (T_R). They were recorded near the taped insects.

RESULTS

BEHAVIOUR AND BODY TEMPERATURES

Every *L. sponsa* was capable of immediate and rapid flight without prior warm-up after a long duration of perching, even in the morning with relatively low ambient temperature (T_A). Basking and shivering were not observed at cool temperatures, particularly early in the morning or at dusk when the sun is visible but solar radiation is low. Wing beating and consequently heat production was not found, except when they shifted perching points, fought against conspecifics or showed mating behaviour. All such flight behaviour lasted less than 2 s after

which they perched again. At rest, the wings were always held distinctly away from the body.

Mean T_{th} of both sexes was not significantly different: $27.9 \pm 0.2^\circ\text{C}$ (SE, $n=49$) in males and $28.0 \pm 0.7^\circ\text{C}$ (SE, $n=9$) in females. Mean T_A during the experiment was about 24°C each day (max. 25.0°C and min 21.9°C). Consequently, mean T_{th} was usually about 4°C higher than T_A . However, the rate of increase for T_{th} apparently accorded with that of T_A . Regression coefficients of T_{th} on T_A were 0.83 ($r^2=0.12$, $n=56$), 1.07 ($r^2=0.27$, $n=35$) and 0.83 ($r^2=0.00$, $n=7$) respectively for males perching in sunflecks, for males in semi-shade points, and for females in sunflecks.

HEATING RATES IN SUNSHINE

The radiation temperature (T_R) varies from morning to evening. The mean radiation temperature in the sunfleck was about 34°C , ranging from 26.9°C to 50.0°C each day, most of which values were higher than T_{th} . Radiant heat load is expected effectively to contribute to increasing the body temperature of *L. sponsa*. Figure 1 shows that the difference between T_{th} and T_R increased linearly with T_R . The regression coefficients were -0.85 ($r^2=0.71$) and -0.90 ($r^2=0.86$) in males and females respectively. The regression also showed that a T_R of about 27°C was equal to T_{th} . Thus, there must be a specific mechanism for thermoregulation against radiant energy.

In order to assess the mechanism for thermoregulation, changes in T_{th} for males perpendicular to direct sunlight were measured. The pairs were divided into 3 groups according to the degree of radiation temperature: 3 pairs below ca 30°C , 5 pairs between ca 35 and 40°C , and 6 pairs above ca 40°C . Figure 2 shows no significant

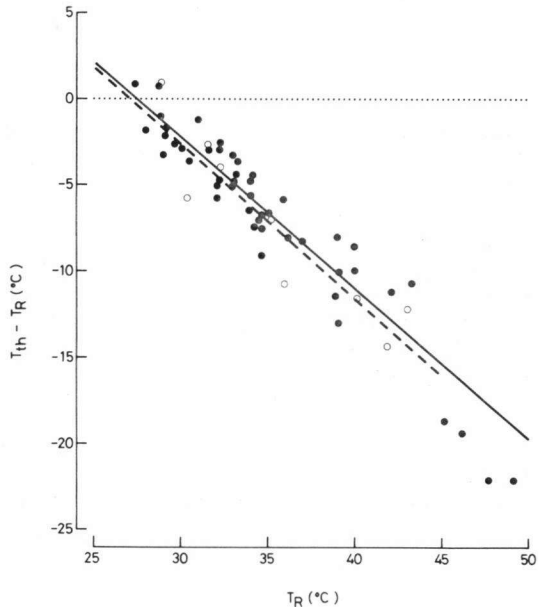


Fig. 1. The relationship between the radiation temperature (T_R) and the differences between the thoracic temperature and the radiation temperature in *L. sponsa*. — [A solid circle and an open circle represent a male and a female, respectively].

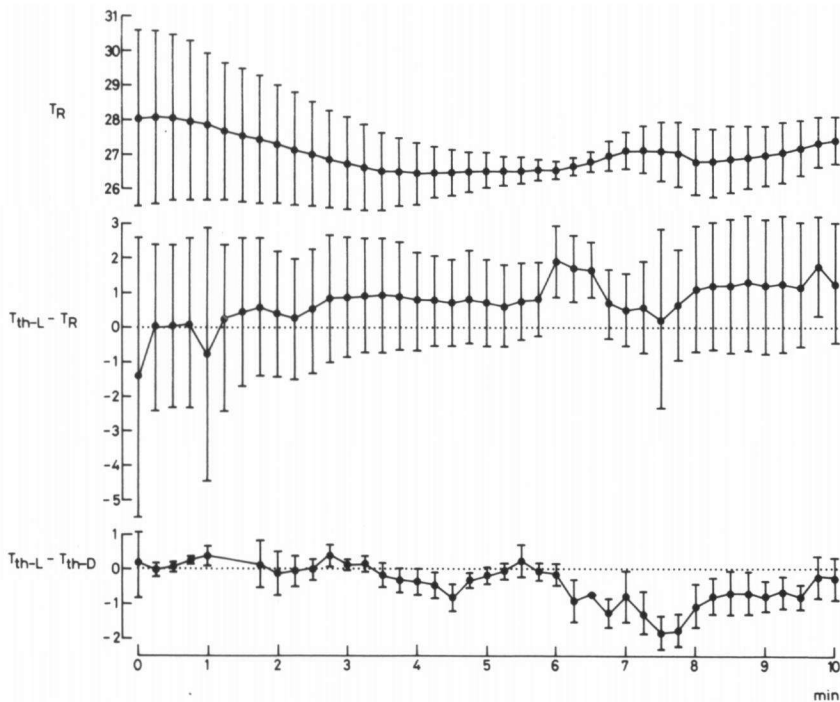


Fig. 2. Changes in radiation temperature (upper), the difference between thoracic temperature of live males and radiation temperature (middle) and the difference between thoracic temperature of live and dead males taped in full sunshine (bottom) under low radiation temperature.

difference between T_{th} and T_R under low radiation temperatures. During the 10 min experiment, 1 out of 3 live males died, but we did not know when. The changing pattern of the T_{th} was the same between live and dead males.

Under the median radiation temperature, T_{th} compensatingly changed with T_R (Fig. 3). The differences sometimes increased by more than 10°C. In this condition, 1 out of 5 live males died within 10 min. Most T_{th} of live males at the respective measuring times did not significantly differ from dead ones. However, it was kept slightly higher than that of dead ones.

T_{th} of live males inversely changes with T_R under high radiation temperatures (Fig. 4). The differences were then maintained around 10°C. During the 10 min, 2 out of 6 live males died. T_{th} of live males was usually kept higher than that of dead ones. The change in T_{th} was more inversely correlated with T_R as T_R increased.

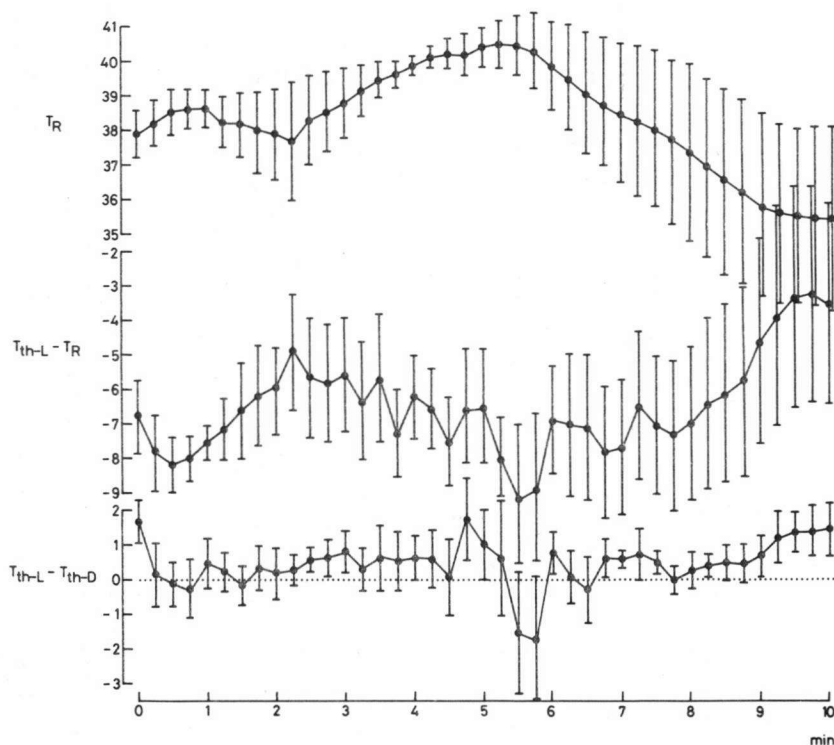


Fig. 3. Changes in radiation temperature (u p p e r), the difference between thoracic temperature of live males and radiation temperature (m i d d l e) and the difference between thoracic temperature of live and dead males taped in full sunshine (b o t t o m) under median radiation temperature.

DISCUSSION

L. sponsa was termed a "percher" by CORBET (1962). Perchers display a wide range of behaviour possibly related to thermoregulation (HEINRICH & CASEY, 1978), because they perch in sunshine. They thermoregulate primarily by making postural adjustments which involve the body and wings (CORBET, 1980). Small perchers such as *Leucorrhinia hudsonica*, *Sympetrum obtrusum* and *S. vicinum* require a T_{th} more than 16°C above T_A for flight (VOGT & HEINRICH, 1983). In some species, such temperatures are achieved either by basking (MAY, 1976) or by both metabolic heat production (shivering) and basking (MAY, 1977, 1979). During the experiment, however, no *L. sponsa* showed basking or shivering behaviour. Shivering thermogenesis is an expensive process from the viewpoint of energy expenditure, but solar radiation is a relatively "free" source of energy (HEINRICH, 1972). Since *L. sponsa* is a relatively small damselfly, therefore,

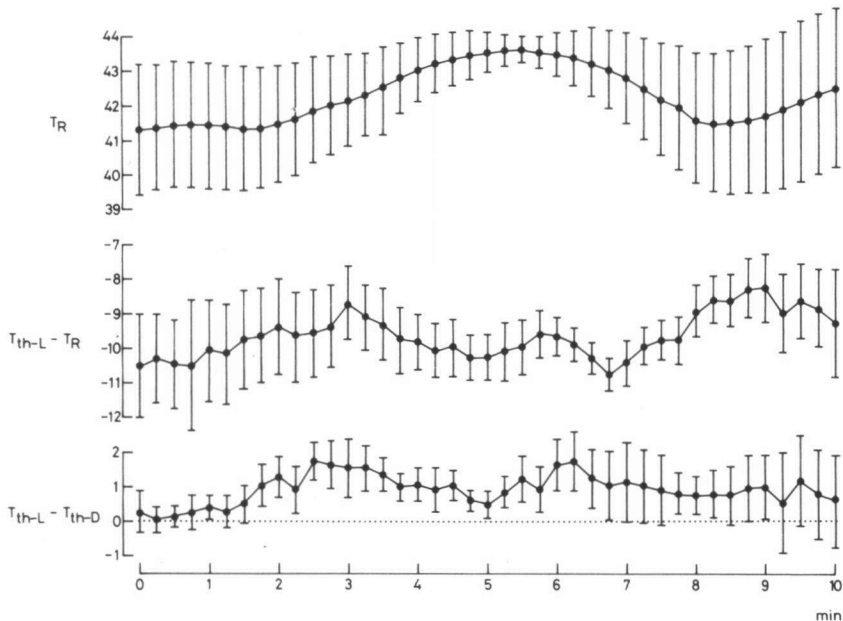


Fig. 4. Changes in radiation temperature (u p p e r), the difference between thoracic temperature of live males and radiation temperature (m i d d l e) and the difference between thoracic temperature of live and dead males taped in full sunshine (b o t t o m) under high radiation temperature.

it did not adopt metabolic heat production for thermoregulation. Since T_{th} was usually higher than T_A , it has probably evolved to use solar radiation.

Insects, which retain much heat in their thorax during flight, require the highest muscle temperatures in order to maintain sufficient power output to continue flight (HEINRICH, 1974). Essentially everything that an active adult damselfly does depend on being able to fly instantly and quickly: it catches prey in flight, takes mates on the wing and so on (WATANABE & MATSUNAMI, 1990). Physiologically, the advantage of maintaining a high T_{th} probably lies in permitting active flight (MAY, 1977). Although there is no direct evidence in Odonata, flight efficiency probably continues to increase with body temperatures (GIBO, 1981). However, the length of time on the wing in *L. sponsa* is too short to increase body temperature. Alternatively, wing-beating produces so much heat that *L. sponsa* may be unable to continue on the wing for a long time.

L. sponsa perched by holding their wings distinctly away from their bodies, and exposing the whole body to direct sunlight in sunflecks. Solar radiation can then go directly into the body. However, no *L. sponsa* showed obelisk behaviour either at high T_A or at high T_R . Few adults shifted their perching points into shaded areas in high T_A , while some moved into shade on high T_R . Although

such behaviour should accelerate heat loss by radiation, most individuals stayed perching without any particular postural adjustments.

Changes in T_{th} of taped live males showed that they have a mechanism to aid in heat loss by radiation. Although structural modifications, as well as shade-seeking behaviour are apparently sufficient to achieve thermal balance, males seemed not to adopt such traits against T_R . They stayed in sunshine but kept their body temperature at about 33°C. Rapid rates of cooling, due to their small size, may preclude appreciable endothermy.

Changes in the differences between T_{th} of live and dead males showed that *L. sponsa* loses heat by forced convection. Control of convection may be important in some butterflies (HEINRICH, 1972). It might include a mechanism as altered haemolymph circulation. WATANABE (1991) showed that the quantity of haemolymph contributed to thermoregulation in male *Mnais* perching in open streams. The metabolic rate, and therefore the rate of heat production may, in part, account for the positive differences between T_{th} of live and dead males. Studies on the complete quantitative connection of absorption and heating rate awaits determination of the parameters such as the efficiency of energy transfer from the damselfly surface to its interior.

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