OBSERVATIONS ON THE BODY TEMPERATURE AND TEMPERATURE ASSOCIATED BEHAVIOUR OF THREE NEW ZEALAND DRAGONFLIES (ODONATA)

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ABSTRACT

Temperatures and thermoregulatory behaviour of three species of Odonata were investigated at a pond at Cass in the central South Island. Thoracic temperatures recorded for two zygopterans, Xanthocnemis zealandica and Austrolestes colensonis and an anisopteran, Procordulia smithii ranged between 18 and 24°C, 19 and 28°C, and 23 and 32.5°C respectively, at ambient air temperatures between 14.5 and 26°C. No thermoregulatory behaviour was observed in X. zealandica, heliothermy was exhibited by A. colensonis, while P. smithii which is an active flier exhibited bouts of wing whirring when perched. Some P. smithii were voluntarily active at an air temperature of 14°C whereas the two zygopterans were not voluntarily on the wing until ambient temperatures reached at least 18 or 19°C.

INTRODUCTION

Many dragonflies are noted for their ability to maintain body temperatures well above and less variable than that of the surrounding air (May 1978). Mechanisms involved in such thermo-regulation include posturing and orienting to the sun (helio-thermy), controlling heat production during flight (e.g. by alternating flapping flight and gliding), metabolic heat production by wing-whirring and circulatory adaptations which enable heat to be transferred within or dispatched from the body (May 1976, 1977, Tracy et al. 1979).
Corbet (1962) recognised two general types of dragonfly on the basis of their behaviour: fliers which spend much of their active period on the wing, and perchers which spend most of their time on a perch from which they make short flights. Members of the two groups thermoregulate in different ways, perchers mainly through postural adjustments and fliers principally via circulatory shunts (Tracy et al. 1979). Perchers and fliers may also utilize different metabolic pathways (Kallapur 1975). Despite such an apparent dichotomy, it seems that some dragonflies, e.g. large Gomphidae, may combine endothermic and ectothermic methods (May 1977) the mode of behaviour depending on environmental factors in some species (Corbet 1980).

The temperature relations of New Zealand Odonata have not previously been investigated although observations over many years by one of us (R.J.R.) indicate that among the species the complete spectrum of behaviours from perchers to fliers is found. Thus, our only resident libellulid, Diplacodes bipunctata (Brauer) behaves as a typical percher. Males and females settle on clay banks, roads and other exposed surfaces where they orient themselves towards the sun. On cool, clear days, especially in autumn, individuals can be seen facing the sun with abdomens raised to increase the body surface directed at the sun. On cool, clear days, especially in autumn, individuals can be seen facing the sun with abdomens raised to increase the body surface directed at the sun. Several other anisopterans also include perching and basking in their behavioural repertoires. The petalurid, Uropetala chiltoni Till-yard\(^1\) basks on rock outcrops during the morning until air temperatures reach about 16°C when it will take wing. Males frequently settle and bask for several minutes at a time on rocks and clay banks at other times of day. U. carovei (White) has been seen basking on tree trunks and tar-sealed roads in the early morning and later afternoon but in the middle of the day, at least in the northern North Island, many individuals act more or less as fliers. All four New Zealand corduliid species are good examples of fliers as is Aeshna brevistyla Rambur, although males of this species have been observed basking for periods of up to half an hour. Finally the New Zealand zygopterans (damsel-flies) are typical perchers whose flights are of only short duration.

The aim of the work reported here was to investigate the relationship between body temperature, environmental temperature and behaviour in three common species of Odonata.

1. For a discussion of the status of Uropetala species see Rowe (this issue).
METHODS

Observations were made on 21-22 March 1981 at a small pond alongside Grasmere Stream, about 100m south-west of the Cass biological station (43° 02' S; 171° 45' E). The pond lies in a steep-sided depression open to the south and is surrounded on three sides by tussock grassland and matagouri (Discaria toumatu), and on the fourth by a bed of raupo (Typha orientalis). Hummocks of niggerhead (Carex secta) emerge above the water surface and provide resting sites for adult dragonflies. Larvae of three odonatans, Xanthocnemis zealandica, Austrolestes colensonis and Procordulia smithii inhabit the pond and adults of all three species are commonly seen above the water or nearby.

Air temperatures were recorded with shaded laboratory thermometers hung from stakes at four sites around the pond. One was situated at the northern pond margin, and the others were in a line east of the pond, one at the water's edge, one 5m back and one 10m further back on the ridge overlooking the pond. They were read at approximately 30 min intervals during observation periods.

Dragonflies were captured with an insect net and held on a shaded, dry board alongside the pond. Body temperature ($T_b$) was measured to $0.5^\circ C$ by inserting the 3.5 x 0.7 mm tip of a silicon diode thermometer (constructed by Mr T.J. Carryer, Zoology Department, University of Canterbury) into the thorax (and the abdomen of P. smithii). This was done within 10s of capture during which period changes in body temperature can be expected to be less than $1^\circ C$ (May 1976). Ambient air temperature ($T_a$) at a recording site was taken immediately before each insect temperature was measured. All thermometers used in the study were calibrated against a Parr bomb calorimeter thermometer of known accuracy.

RESULTS

Observations of dragonfly behaviour and recordings of insect and environmental temperatures were made between 0915h and 1545h N.Z.S.T. on 21 March, and between 0925h and 1300h the following day (1233h N.Z.S.T. = solar noon).

Air temperature during these periods ranged from $14.5^\circ C$ to $26^\circ C$ (Fig.1) with the mean on the ridge ($22.5\pm SD 2.0^\circ C$) slightly exceeding that around the pond ($20.9\pm SD 1.5^\circ C$).
Body temperatures of 93 dragonflies were taken and are summarized in Table 1. Ambient shade temperatures ($T_a$) shown differ for each species since dragonflies were captured at different times (and air temperatures), but were within $1^\circ$C for all three species, and within $1^\circ$C of the mean calculated from pondside thermometer readings over the 5.5h period.

Mean thoracic temperature of *X. zealandica*, the smallest species (body weight about 0.03g), was only $1^\circ$C above ambient with a maximum of $24^\circ$C (Fig.2a). All individuals tested were males taken from emergent vegetation within 2cm of the water surface. They remained stationary for long periods, exhibited no heliothermic orientation, wing whirring or other thermo-regulatory behaviour, but did react to passing conspecifics with wing warning (Corbet 1962). In the late morning of 21 March when air temperatures fell below $18^\circ$C *X. zealandica* males quickly left the pond.

*A. colensonis* is a larger damselfly than *X. zealandica* (body weight about 0.09g) and over the air temperature range considered (17-24°C) most individuals had body temperatures 0.5 - 2.0°C greater than ambient (Fig.2b). All were in the
TABLE 1. BODY TEMPERATURES (°C) OF ODONATA AND AMBIENT AIR TEMPERATURES AT CASS, 21-22 MARCH 1981.
MEAN ±SD ABOVE, RANGE BELOW. NM = NOT MEASURED.

<table>
<thead>
<tr>
<th>Sample size</th>
<th>Xanthocnemis zealandica</th>
<th>Austrolestes colensonis</th>
<th>Procordulia smithii</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>11</td>
<td>56</td>
<td>26</td>
</tr>
<tr>
<td>Thoracic temperature (T_b)</td>
<td>21.1±1.7 (18 - 24)</td>
<td>22.2±1.9 (19 - 28)</td>
<td>26.5±2.5 (23 - 32.5)</td>
</tr>
<tr>
<td>Abdominal temperature</td>
<td>NM</td>
<td>NM</td>
<td>24.0±1.9 (20 - 27.5)</td>
</tr>
<tr>
<td>Ambient temperature (T_a)</td>
<td>20.1±1.1 (18.5 - 23)</td>
<td>20.9±1.8 (17 - 24)</td>
<td>21.1±2.2 (14.5 - 24)</td>
</tr>
<tr>
<td>Mean temperature elevation above ambient (T_b - T_a)</td>
<td>1.0</td>
<td>1.3</td>
<td>5.4</td>
</tr>
</tbody>
</table>

bright blue colour phase and most were taken from vegetation 0.5-1.2m above the pond where they occupied territorial perches with their bodies oriented broadside on to the sun to maximise heat uptake by heliothermy. When sunning themselves in this way the wings are held together on the side of the abdomen away from the sun where they do not shade it and they may even act as heat reflectors. No wing whirring or other physiological thermoregulatory behaviour was seen. A few animals were observed flying in tandem (with the male clasping the female) between 1100h and 1300h on 22 March, including one vigorously flying pair, both with thoracic temperatures of 28°C.

*P. smithii* was the largest species examined (about 0.5g body weight) and possessed the most elevated body temperatures. All animals tested were males taken on patrol flights during which they may fly continuously for long periods (possibly hours). This activity occurred throughout the observation periods except in the late morning of 21 March when heavy cloud appeared and the air temperature fell to 18°C whereupon males left the pond. Thoracic temperatures ranged up to 32.5°C (Fig.2c) with a mean of 26.5°C, whereas abdominal temperatures (Fig.2d) were lower (mean 24°C) but still about 3°C above ambient. The first males localised at water between 0830 and 0900h when the air temperature was about 14°C. One of these early arrivals was captured and had
Fig. 2. Body temperature ($T_b$) plotted against ambient air temperature ($T_a$) in 3 species of Odonata. a) Xanthocnemis zealandica, b) Austrolestes colensonis, c) Procordulia smithii (thorax), d) $P$. smithii (abdomen). ◊ single records, ▲ multiple records. The oblique line shows where $T_b = T_a$. 
a thoracic temperature of 24°C. P. smithii is known to raise its body temperature by active bouts of wing whirring which is frequently seen in males and females perched on vegetation during the last minute or so of copulation.

DISCUSSION

Xanthocnemis zealandica, Austrolestes colensonis and Procordulia smithii occurred together at a pond at Cass but differed in body temperature and their ability to thermoregulate. The smallest species X. zealandica showed no thermoregulatory behaviour over the range of environmental temperatures considered and body temperatures of individuals were the same as or only slightly above that of the surrounding air. For purely physical reasons (small size, large area: volume ratio) thermoregulation may be impracticable in X. zealandica, at least at relatively low environmental temperatures. The larger A. colensonis, on the other hand, exhibited heliothermic behaviour and its body temperatures were consistently higher than those of X. zealandica. P. smithii contrasted with the damselflies in its even larger size, stronger and more continuous flight activity, wing whirring behaviour and more elevated body temperatures. As in species examined elsewhere (Corbet 1980), abdominal temperatures were lower than thoracic ones. Heat can be lost from the abdomen of some dragonflies by altering circulation between it and the thorax, and it is possible that this occurs in P. smithii, at least at high temperatures. The thoracic air sacs may also serve as sites for heat loss and we found that their temperature was normally lower than that in the adjacent musculature.

Both damselfly species were seen at the pond when air temperatures reached 17-18°C whereas P. smithii was observed flying at 14°C. This is presumably a reflection of P. smithii's ability to raise the temperature of its flight muscles at lower ambient temperatures by wing whirring, in contrast to the more passive environmental warming upon which the damselflies depend. It is interesting to note that Crumpton (1975) observed active (presumably flying) X. zealandica and A. colensonis at air temperatures as low as 14°C at unidentified South Island localities, but she provided no information on body temperatures or times of day of her observations. The mean minimum body temperatures at which flight of several tropical and temperate zone Odonata is possible range from about 19-26°C (May 1976, 1978). This range encompasses those recorded early in the morning ($T_a$, 14-19°C) from all three species we examined. The maximum voluntary tolerance temperatures and the thresholds of heat torpor given by May (1976) for various American species (33.2 - 42.5°C and 41.1 - 48.5°C respectively) are higher than
any body temperatures recorded in our study, but as environmental temperatures were only moderate this is not surprising. An obvious extension of our work would be to investigate body temperature regulation over a wider range of environmental temperatures (air temperatures as high as 37°C can occur at the Cass Biological Station; Greenland 1977), at different times of year and under varying conditions of cloud cover, in order to determine the full thermo-behavioural repertoires of both sexes of all three species. An examination of changes in colour phase in *A. colensonis* would also be of interest as work on the Australian *A. annulus* (Selys) indicates it is likely to have a thermoregulatory function (O'Farrell 1964, Veron 1974).

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LITERATURE CITED