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# BODY TEMPERATURE REGULATION AND RESPONSES TO TEMPERATURE BY MALE *TETRAGONEURIA CYNOSURA* (ANISOPTERA : CORDULIIDAE)

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Measurements of body temperatures of male *T. cynosura* in the field indicate that temperatures of all three tagmata are elevated above air temperature and that thoracic temperature is unusually high and well-regulated ; head temperature may be regulated weakly. Hemolymph circulation between thorax and abdomen probably is augmented at high temperature to enhance heat loss, but the effect is apparently insufficient to account for the decline in heat retained by the thorax. The proportion of time spent hovering is reduced at high temperature, perhaps contributing to reduction of metabolism in these circumstances. The insects are also more likely to patrol in shaded areas at high temperature, but the ability to thermoregulate is evidently independent of solar radiation ; in the laboratory, however, body temperature is strongly dependent on radiant load. The capacity for endothermic warm-up is well-developed ; the head is warmed as well as the thorax, but to a much smaller extent. Despite excellent thermoregulation, territorial activity is restricted by low ambient temperature.

## INTRODUCTION

That temperature and sunlight affect the activity of adult dragonflies is readily apparent. CORBET (1963) first analyzed in detail the effects of temperature on adult behavior and recognized that these insects probably regulate their body temperature. Several subsequent studies have clarified the mechanisms by which thoracic temperature ($T_{th}$) is regulated (HEINRICH & CASEY, 1978 ; MAY, 1976, 1977, 1978 ; PEZALLA, 1979). Temperatures of the head ($T_h$) and abdomen ($T_{ab}$) have rarely been studied, however, although

it is clear they may differ markedly from $T_{th}$ (HEINRICH & CASEY, 1978 ; MAY, 1984 ; MAY & CASEY, 1983) and that some species regulate $T_h$ (HEGEL & CASEY, 1982 ; HEINRICH, 1979).

CORBET (1963) also made the important (although not absolute) distinction between the "percher" and "flier" modes of adult behavior. With respect to thermoregulation, perchers are in general ectothermic, using sunlight as their principal heat source and behavioral responses to regulate $T_{th}$, while fliers are more commonly endotherms, relying on heat produced by the flight muscles and on physiological modulation of heat generation and dissipation (MAY, 1976). Small species usually regulate $T_{th}$ less precisely than large species, primarily owing to the larger surface : mass ratio of the former, and, for a given size, perchers usually regulate more precisely than fliers as a result of lower rates of convective heat loss and greater opportunity for behavioral modulation of heat input (MAY, 1976, 1978).

Nonetheless, it is possible for a small flier to thermoregulate precisely if its rate of internal heat generation is unusually high or its rate of heat loss very low (thus making the maximum attainable difference between $T_{th}$ and air temperature, $T_a$, large) and it can control heat loss and/or gain well. This paper will present evidence that the small corduliid flier, *Tetragoneuria cynosura*, has just these characteristics and, as a result, regulates $T_{th}$ with remarkable precision. I will also present data on $T_h$ and $T_{ab}$ and their relation to environmental parameters and thermoregulation.

## METHODS

Except as noted below, all data pertain to male *T. cynosura* observed or collected near the west end of Farrington Lake, Middlesex County, NJ, U.S.A. (40°25'N, 74°27'W), during mid-May to early July, 1981-1985. This moderately eutrophic reservoir, formed in approximately 1920, has a stable water level. The primary study area for census and behavioral observations (Fig. 1) was located where the main inlet stream merges gradually into the lake ; it was partially overhung by trees and contained abundant submerged, floating, and emergent vegetation (largely *Cabomba ; Brasenia, Nuphar* and *Nymphea* ; and *Sagittaria* and *Docedon*, respectively) ; current was barely perceptible. An adjacent area, with more open water and much less shading by terrestrial vegetation, immediately downstream from the bridge of Fig. 1, was the site of most measurements of body temperature and a few behavior and census observations.

Body temperatures in the field were measured as described by MAY (1976) but using a 0.002-inch diameter copper-constantan thermocouple embedded in a 0.4 mm diameter hypodermic needle and read on a Bailey BAT-4 portable thermocouple thermometer. The probe was inserted in rapid succession into the thorax, head, and abdomen (2nd-4th segment). Measurements not completed within 10-15 s were discarded. Air temperature in the shade was read immediately afterwards with the same probe, and solar radiation intensity (SR) near the point of capture was recorded from the output of a Science Associates Dome Solarimeter. Other weather conditions and behavior were noted as appropriate.

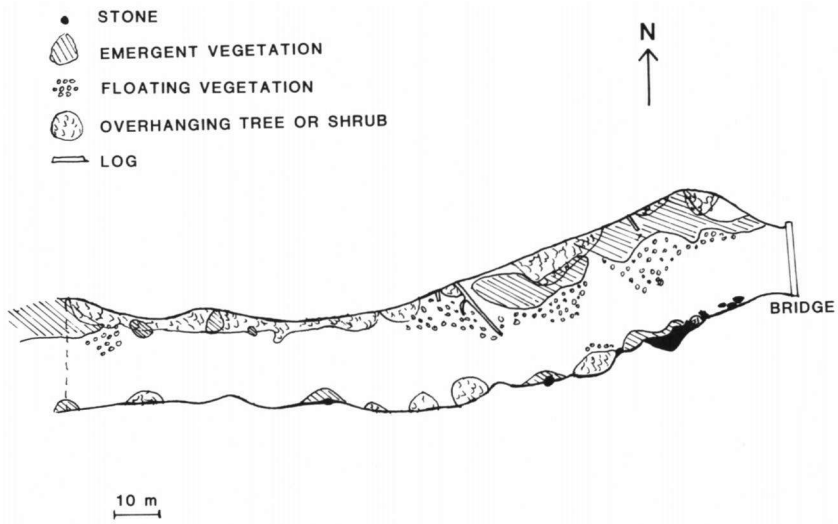


Fig. 1. Map of the primary study site at Farrington Lake.

Visual censuses of defined areas were conducted from a canoe at 0.5 or 1 h intervals on several days. The great majority of individuals were males that were clearly localized in a restricted area, flew about 50 cm above the water surface, and were apparently territorial; females and the few males that were obviously transient or were feeding several meters above the water surface are not included in the data. During each census, $T_a$ and SR were measured. The extent of sunlight and shade and the locations of each individual were also mapped on most days. Thus the relative density of individuals in shade vs sun could be calculated as [(% of individuals in shade) / (% of surface in shade)] / [(% of individuals in sun) / (% of surface in sun)]. A linearized index, hereafter called the shade-seeking index, was in turn calculated as log (relative density + 1). Thus if, e.g., the pond surface were 50% shaded but 75% of dragonflies were in sun, relative density = (25/50)/(75/50) = 0.167, and the index = log (0.167 + 1) = 0.067 ; if dragonflies were distributed with equal density in sun and shade, the index = log (2) = 0.301.

The proportion of hovering flight in selected individuals was measured by timing with a stopwatch the cumulative time hovering within 2-5 min intervals of continuous observation. Movements were irregular and sudden, and the insects rarely held absolutely constant position, so "hovering" included appreciable periods of very slow ($<0.25$ m $s^{-1}$) forward flight, and the distinction between hovering and forward flight was to some extent subjective. Measurements were not made during strong wind.

Flight speed was determined in a single male whose territory was adjacent to a bridge on Farrington Lake some distance from the main study areas. Its movements were filmed with an 8 mm cine camera held about 3 m above the water. Since the dragonfly remained within a distance of about 30-60 cm of the water, vertical movements were nearly negligible relative to lateral movements, and velocity could be measured from the frame-to-frame displacement of the insect's image. A rod of known length was suspended in the plane of flight and filmed to provide a distance reference.

Endothermic warm-up was measured in the laboratory at ambient temperatures from 15-30°C, either in a walk-in controlled temperature chamber or a room in which $T_a$ was controlled within ± 1°C with air conditioning and a heater. Copper-constantan thermocouples (0.002-inch) were implanted as described by MAY (1976) and the output recorded at approximately 15 s intervals with a Honeywell Electronik 112 Multipoint thermocouple recorder. Each individual was measured at only one $T_a$. In two additional individuals, $T_h$ and $T_{ab}$ were recorded simultaneously with $T_{th}$. Thermocouples were positioned near the center of the head capsule and in the second abdominal segment. I also determined the minimum $T_{th}$ for controlled flight ($MFT_{th}$) as described by MAY (1976).

Cooling curves were determined in the laboratory for each tagma. Thermocouples were implanted as described above in freshly killed specimens, which were then heated about 15°C above $T_a$, placed in a wind tunnel, and allowed to cool in still air or an airstream of 0.25, 0.5, 1.0, 2.0, or 3.5 m $s^{-1}$. The tunnel consisted of a 120 cm length of PVC pipe, 7.5 cm i.d., with a centrifugal blower at one end. Specimens were glued to a small wooden mount positioned about 5 cm within the tube, so that the body was at the center of the tunnel and oriented parallel to the airstream. Turbulence was reduced by stretching several layers of cheesecloth within the tube, slightly downstream from the blower. Airspeed was controlled by occluding the intake of the blower and measured with a Thermonetics HWA-103 hot wire anemometer. Cooling constants (K) were calculated from these data by the method of HEATH & ADAMS (1969).

Simultaneous effects of wind and radiation on body temperatures of freshly killed specimens were also measured. I inserted thermocouples as above and positioned the insects a few cm outside the mouth of the wind tunnel, under a Harwood XR1 650-W lamp ; the spectral output of this lamp is very similar to solar radiation. Airspeed was measured as above, while radiant intensity was measured with a YSI-Kettering Model 65A radiometer ; for both measurements, the sensor was placed at exactly the position that the thorax of the dragonfly would later occupy. Radiation intensity was controlled by varying the distance from lamp to insect and was considered to be effectively zero with the lamp off. Combinations of wind speed of 0, 0.5, 1.0, and 3.5 m $s^{-1}$ and radiation of 0, 200, and 800 W $m^{-2}$ were used. Each specimen was tested in sequence under each set of conditions, each time remaining in position until the temperature of all tagmata equilibrated (± 0.2°C). The temperature excess of each tagma (i.e., its elevation above $T_a$) was recorded.

Morphometric data for 10 specimens were obtained as described by MAY (1981a). In an additional 4 specimens I determined thoracic muscle mass by initially isolating the pterothorax and splitting it mid-sagittally with a scalpel, then as quickly as possible removing all the muscles with microdissection forceps and scissors. The muscles were placed in a pre-weighed gelatin capsule as they were removed, to reduce water loss, and weighed within the capsule as soon as dissection was complete.

In all statistical comparisons an alpha level of 0.05 was the criterion for significance.

## RESULTS

Figure 2 shows the relation of $T_{th}$, $T_h$, and $T_{ab}$ to $T_a$ in the field. Temperatures of all tagmata were elevated well above $T_a$, with $T_{th}$ the highest by a wide margin, $T_h$ intermediate, and $T_{ab}$ lowest. In every individual measured $T_{th}$ exceeded both $T_h$ and $T_{ab}$, and in nearly all $T_h > T_{ab}$. Although all three temperatures were significantly affected by $T_a$, slopes of both $T_{th}$ and $T_h$ are also significantly different from 1.0. The slope of $T_{th}$ on $T_a$ is much

lower than for previously investigated fliers of similar mass and even slightly lower than perchers of comparable size (MAY, 1978). Multiple regression analysis indicates that $T_{th}$ was independent of SR and body mass of the insect. In fact, the relation of $T_{th}$ to $T_a$ is indistinguishable from that of Fig. 2 if individuals captured when light levels exceeded 200 W $m^{-2}$ are excluded ($T_{th} = 0.370T_a + 30.23$, $r^2 = 0.750$). The open circles of Fig. 2 indicate data for $T_{th}$ only, taken in Florida in 1971-73. The constancy of $T_{th}$ appears similar to that of the New Jersey data, while its magnitude seems slightly less. The Florida data were too few for meaningful statistical analysis, however. Both $T_h$ and $T_{ab}$ were slightly dependent on SR, and $T_{ab}$ was also dependent on mass. In both cases, however, the influence of $T_a$ was much greater than other factors (partial $r^2 = 0.88$ for $T_h$ and 0.91 for $T_{ab}$).

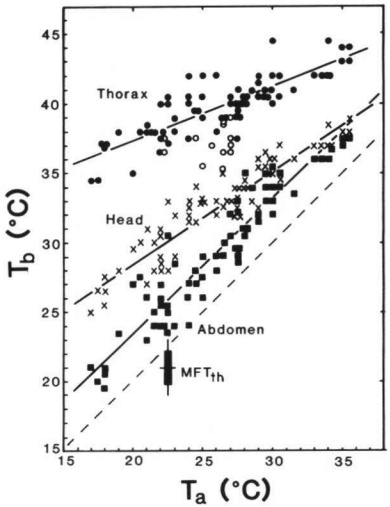


Fig. 2. Relation of body temperature to $T_a$ in male *T. cynosura*: $T_b$ refers to body temperature without specifying a particular tagma. Circles represent $T_{th}$ (open circles are data from Florida, not included in the regressions), x's represent $T_h$, and squares represent $T_{ab}$. Solid, oblique lines indicate regressions of $T_b$ on $T_a$, as follows: $T_{th} = 0.390T_a + 29.61$, $r = 0.710$, $n = 68$; $T_h = 0.673T_a + 14.99$, $r^2 = 0.886$, $n = 68$; $T_{ab} = 0.975T_a + 3.91$, $r^2 = 0.906$, $n = 67$. The dashed line is the isothermal line. The short, horizontal line labeled MFT$_{th}$ indicates the mean minimum thoracic temperature at which level flight was possible; thick and thin vertical bars indicate the standard deviation and range, respectively.

Also shown in Fig. 2 is MFT$_{th}$. The value is similar to that of other dragonflies of comparable size (MAY, 1978) and is far below $T_{th}$ of field-collected individuals. This parameter is probably independent of $T_a$, although it is shown at the laboratory $T_a$ at which it was measured, 22.5°C.

Hovering flight entails relatively high heat production (PENNYCUICK, 1969) and low heat loss, owing to reduced convective cooling. The proportion of time spent hovering by *T. cynosura* is not correlated with $T_a$ if all data are considered, but among individuals patrolling mostly in sun, a loose but significant negative correlation exists (Fig. 3); multiple regression indicates no effects of SR or time of day when effects of $T_a$ are accounted for. The point indicated by the arrow in the figure is from the first male observed on 22 May 1985. It had very recently arrived at the site and, although clearly localized, patrolled a larger than normal area with very erratic flight.

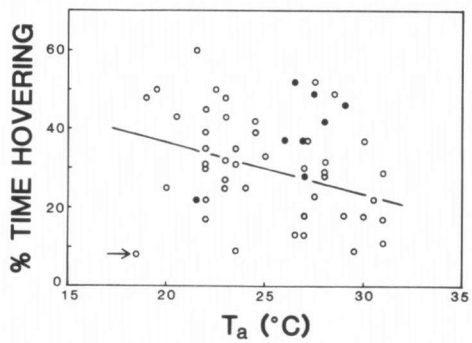


Fig. 3. Percentage of time spent hovering during continuous observations in male *T. cynosura*. Open circles represent individuals active primarily in the sun, closed circles those primarily in the shade. The arrow indicates an individual with an unusual flight pattern (see text). The regression equation (solid line), which appies only to individuals in sun is: % hovering = $-1.34T_a + 65.15$, $r^2 = 0.131$, $n = 45$.

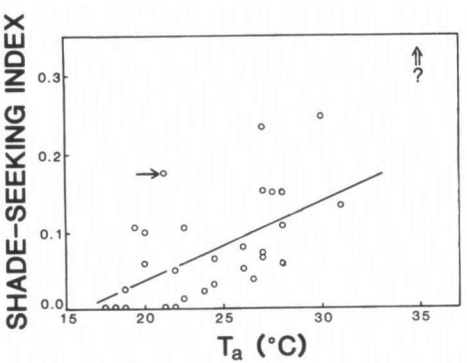


Fig. 4. Shade-seeking index (see text for definition) as a function of $T_a$ for male *T. cynosura*. Horizontal arrow indicates a point obtained during overcast that made determination of sun and shade difficult; ? and vertical arrow indicate a point estimated from qualitative observations (see text). Regression equation (solid line) is: index = $0.0121T_a - 0.215$, $r^2 = 0.350$, $n = 29$).

Mean flight speed (± S.F.), from the film analysis, was $0.40 \pm 0.44$ m s$^{-1}$, with a range of 0-2.73 m s$^{-1}$. There was no measurable displacement in 19% of interframe intervals and an apparent speed of $<0.25$ m s$^{-1}$ in 53%. Only 1.7% of the time was speed $>2$ m s$^{-1}$. Very rapid acceleration sometimes occurred, e.g. 0.36 to 1.5 m s$^{-1}$ in 0.042 s and 0.09 to 2.5 m s$^{-1}$ in 0.25 s. Flight direction (course) often departed markedly from body orientation (heading), especially during slow flight, probably largely the result of the light ambient breeze. Nine separate flights that came within the camera field of view were analyzed, encompassing 604 interframe intervals.

Shade-seeking index is significantly positively correlated with $T_a$. That is, individuals had a significantly greater tendency to occupy shaded areas, relative to the amount of shade available, under warm than under cool conditions (Fig. 4). One somewhat aberrant point (horizontal arrow) is from a period so overcast that it was difficult to determine the extent of shade or whether individuals were in sun or shade. At all temperatures within the range observed, however, there was a preference for sunny areas (i.e., the index was $<$ log2). The index was also significantly correlated with SR and time (measured as hours before or after 1400 h EDT) but not with number of conspecifics present. All these variables were themselves significantly correlated, however, so it is difficult to separate the influence of one from another.

The ? in figure 4 refers to a qualitative observation (not included in the correlation) at a pond about 10 km from the main study site, at about 35°C. It was clear that, although most of the pond surface was in sun, most of the patrolling *T. cynosura* were in shade and often seemed to restrict their movements to the boundaries of shaded areas. I made the conservative assumption that dragonflies were evenly distributed in sun and shade, so the estimated index value is shown as 0.3. As suggested by the vertical arrow, the actual value would probably have been much higher.

Figure 5 shows the number of localized males present at the Farrington Lake study sites over the course of several mostly sunny days, along with corresponding $T_a$. Activity either was bimodal or was restricted to mid-late afternoon. The latter pattern predominated after early June regardless of $T_a$. Earlier in the season, when morning activity occurred, its onset clearly was delayed by cool $T_a$ (cf. 20 and 22 May 1985, 27 and 30 May 1985 ; Fig. 5). The threshold for activity apparently was near 19°C. The data also weakly suggest reduction of midday activity at high $T_a$ (cf. 16 and 27 June 1984 ; Fig. 5), but further study of this phenomenon is required.

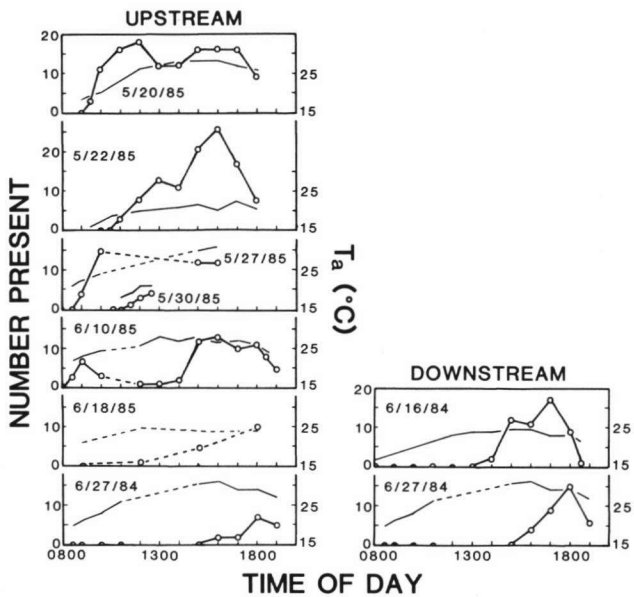


Fig. 5. Number of localized male *T. cynosura* present over the course of several days (dates indicated on each graph as month/day/year) at Farrington Lake ; data labeled "upstream" were obtained at the site shown in Fig. 1, those labled "downstream" at an immediately adjacent area. Each point represents a single census. Thin, broken lines show the change in $T_a$ (righthand axis) over the course of each day. Solid lines connect observations taken at 1 h intervals or less, dashed lines those taken at longer intervals.

Warming rates and $T_{th}$ at which takeoff was attempted were similar at $T_a$ = 25°C to values reported by MAY (1979). Both parameters were significantly correlated with $T_a$ (Fig. 6), but the relation is non-linear, with marked changes from 15-18°C and virtually none above 25°C. At takeoff, $T_{th}$ varied much less than $T_a$, suggesting regulation of $T_{th}$, but the average values were below those normally encountered in the field at all $T_a$ (cf. Fig. 2). All specimens warmed readily at $T_a$ from 17.5-25°C, but at 15°C wing-shivering was difficult to elicit and often sporadic. Only 2 of 6 individuals warmed to takeoff. At 30°C, also, the insects were reluctant to warm up and often struggled without wing-shivering or took off immediately upon stimulation. Once initiated, however, warning was rapid and sustained to takeoff at elevated $T_{th}$.

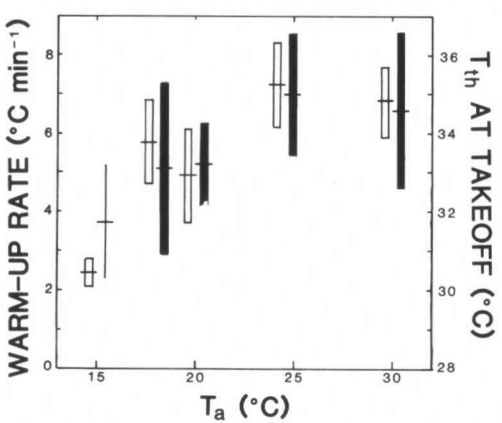


Fig. 6. Endothermic warming rates (open bars) and $T_{th}$ at attempted takeoff (filled bars) as a function of $T_a$ in male *T. cynosura*. Horizontal lines represent the mean, vertical bars ± 1 S. D. (except that the thin bar for $T_{th}$ at 15°C is the range); bars are slightly offset from true $T_a$ to permit plotting on the same graph. Sample size was 5 in each case except at 15°C, where sample size was 3 for rate and 2 for $T_{th}$.

In two specimens in which $T_h$ and $T_{ab}$ were measured simultaneously with $T_{th}$, $T_h$ rose and fell in parallel with $T_{th}$, but head temperature excess was only 1/4 to 1/3 that of $T_{th}$. Abdominal temperature hardly rose during warming, but sometimes increased abruptly by 1-2°C immediately after wing shivering ceased (Fig. 7).

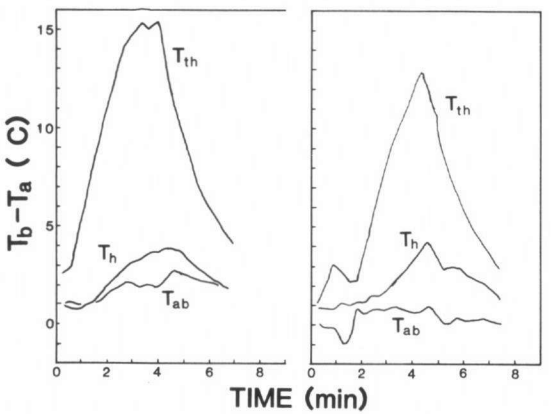


Fig. 7. Variation in $T_b$-$T_a$ for all tagmata during endothermic warm-up in two male *T. cynosura*. In both cases, $T_a$ was about 23 ± 1°C.

Cooling constants are shown in relation to wind speed in Fig. 8. Since heat is lost primarily by free convection and radiation in still air and by forced convection in moving air (CHURCH, 1960), still air values are not included in the regressions and are plotted at an arbitrary abscissa. Thoracic cooling constants ($K_{th}$) also were significantly correlated with total mass and thoracic mass, but the effects of mass were not significant for cooling constants of the head ($K_h$) or abdomen ($K_{ab}$); effects of mass are not considered further. Values of $K_{th}$ are close to those of other dragonflies of similar mass (MAY, 1984). The slope on wind speed appears lower than expected but is not significantly so. No comparable data exist for $K_h$ or $K_{ab}$ of dragonflies, but, as expected in view of the their smaller mass and much less extensive insulating air sacs, both are much higher than $K_{th}$. At 0.25 m $s^{-1}$ $K_{ab}$ increased much less from its value at 0 m $s^{-1}$ than did $K_{th}$ or $K_h$. The slope of $K_{ab}$ on wind speed is also appreciably greater than those of $K_{th}$ of $K_{ab}$. These observations may be the result of shielding of the abdomen by the more anterior tagmata, so that a region of relatively stagnant air is maintained until free-stream wind speed reaches relatively high levels.

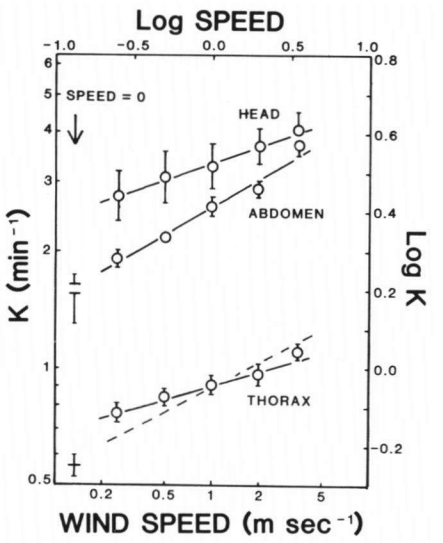


Fig. 8. Cooling constants as a function of wind speed for all tagmata of male *T. cynosura*. Circles represent means, error bars ± 1 S. E. Regressions of the log transformed variables (solid lines) are as follows: $\log K_{th} = 0.1281 \log T_a - 0.0405$, $r^2 = 0.426$, n = 35 (7 individuals at each of 5 speeds); $\log K_h = 0.1471 \log T_a + 0.526$, $r^2 = 0.153$, n = 35; $\log K_{ab} = 0.2461 \log T_{th} + 0.417$, $r^2 = 0.755$, n = 35. Cooling constants in still air are placed at an arbitrary point on the abcissa; means are represented by horizontal lines; n = 7 in each case.

Temperature excess resulting from radiant heating in the laboratory is shown for four wind speeds in Fig. 9. Even at radiant intensity as low as 200 W $m^{-2}$, temperatures of all tagmata were raised by several degrees under all wind conditions. Data were not obtained at a radiant intensity of 0 and wind speeds of 0.5 or 1.0 m $s^{-1}$, but in all cases these lines extrapolate to nearly the same zero point as at 0 or 3.5 m $s^{-1}$ (this point was consistently a few tenths of a degree above true 0, probably due to low levels of ambient radiation when the heating lamp was off). Thus the relation of temperature

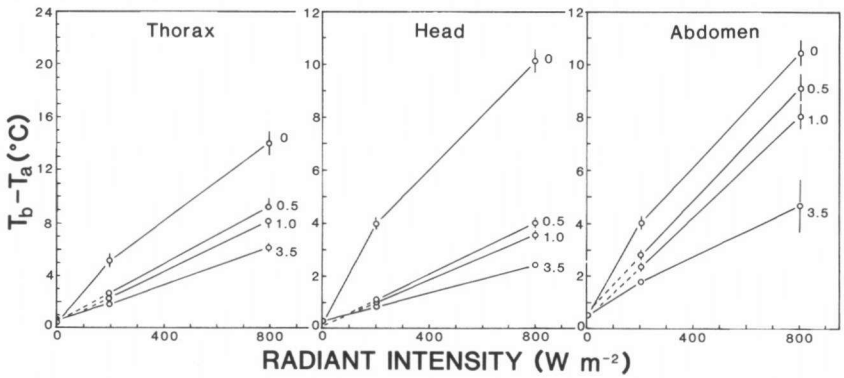


Fig. 9. Temperature excess of all tagmata of male *T. cynosura* as a function of radiant intensity and wind speed in the laboratory. Note that the vertical scale is compressed for thoracic data (left panel) relative to other plots. Circles represent means, error bars ± 1 S. E. ; n = 8 for each point. Dashed lines indicate that 0 radiation values were estimated by extrapolation. Figures to the right of each line indicate the corresponding wind velocity.

excess to radiant intensity is linear at wind speeds $> 0.5$ m s$^{-1}$. It departs markedly from linearity at 0 m s$^{-1}$, presumably owing to non-linear effects of external heating on free convection. Consistent with the effects of wind speed on K, slow speeds have much less effect on abdominal temperature excess than on that of the thorax or abdomen, but the additional decrease with increasing wind speed is greater for the abdomen.

Table I summarizes morphometric data for *T. cynosura*. Individuals in this sample were slightly smaller in average mass than those captured for field determinations of body temperature (mean = 0.176 g) and slightly larger than those used in determination of K (mean = 0.138 g). Male *T. cynosura* are similar in most dimensions, relative to total mass, to other fliers (MAY, 1981a). Two exceptions are their slightly higher wing loading and slightly lower wing moment of inertia. Both characteristics suggest that wingbeat frequency in flight may be higher than in other fliers of comparable size (MAY, 1981b). Also, muscle mass averages about 35% of body mass, higher than estimated for two much larger fliers, but somewhat lower than in two perchers (MAY, 1981a).

## DISCUSSION

HEATH (1964) correctly argued that plots of body vs. ambient temperature cannot conclusively demonstrate thermoregulation in the absence of information on other aspects of the thermal environment and of the recent

Table I

Morphometric analysis of male *T. cynosura*

| | Mass (*g*) | Mass thorax (*g*) | Diameter thorax (*mm*) | FW[a] length (*mm*) | HW[a] length (*mm*) | Wing area ($cm^2$) | Wing[b] load ($g\ cm^{-2}$) | Wing[c] disc load ($g\ cm^{-2}$) | FW[a] mass (*mg*) | HW[a] mass (*mg*) | Iw[d] ($g\ cm^2$) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Mean | 0.158 | 0.078 | 4.82 | 28.6 | 27.4 | 7.52 | 0.0210 | 0.00640 | 2.75 | 3.39 | 0.0130 |
| S.D. | 0.015 | 0.0078 | 0.210 | 0.98 | 1.10 | 0.323 | 0.00170 | 0.00042 | 0.205 | 0.350 | – |
| Range | 0.133-0.178 | 0.066-0.087 | 4.6-5.2 | 27.0-30.0 | 25.5-29.0 | 7.0-8.0 | 0.0180-0.0224 | 0.00560-0.00692 | 2.35-3.08 | 2.87-4.00 | – |
| *N* | *10* | *10* | *10* | *10* | *10* | *10* | *10* | *10* | *10* | *10* | *1*[e] |

| | Mass (*g*) | Mass thorax (*g*) | Mass thorax muscle (*g*) |
|---|---|---|---|
| Mean | 0.158 | 0.085 | 0.056 = 32.5% of body mass |
| S.D. | 0.0061 | 0.0025 | 0.0061 |
| Range | 0.152-0.166 | 0.082-0.087 | 0.050-0.064 |
| *N* | *4* | *4* | *4* |

[a] Fore wing (FW) and hind wing (HW) length or mass
[b] Wing loading = mass ÷ wing area
[c] Wing disc loading = mass ÷ {Π[(FW Length + HW Length)/2]²}
[d] Moment of inertia of wings
[e] Mass = 0.176 g ; HW Length = 27.0 mm

thermal history of the animal. Nonetheless, in the present case the strikingly low slope of $T_{th}$ on $T_a$ is evidence *prima facie* for regulation of $T_{th}$. Many individuals were observed in continuous flight for several minutes before capture, and they remained in a relatively homogeneous thermal environment. The major potential source of variation in $T_{th}$, other than $T_a$ or metabolism, was SR, and this parameter was measured and accounted for. Wind and humidity were not measured and could affect heat balance, but neither apparently varied regularly with $T_a$ ; in any case, several studies have shown that these parameters typically have much less effect than $T_a$ and SR on $T_{th}$ of insects, especially, in flight (BAIRD, 1986 ; MAY, 1982). Thus temperature regulation almost certainly occurred, but the mechanisms are not immediately clear.

One possible means of regulating $T_{th}$ is to alter heat loss, via control of hemolymph circulation from the pterothorax to other body regions in response to variations in $T_{th}$. This phenomenon is well-documented in moths (HEINRICH, 1970, 1971), bees (HEINRICH, 1976) and aeshnid dragonflies (HEINRICH & CASEY, 1978 ; MAY, 1976). Indirect evidence suggests that *T. cynosura* also has this capacity but that it cannot entirely account for regulation of $T_{th}$. If $T_{ab}$ is determined entirely by heat exchange between the abdomen and either the thorax or the air, and if exchange between the abdomen and thorax is due only to passive conduction or to a constant rate of circulation, then $T_{ab}$-$T_a$ should be a constant fraction of $T_{th}$-$T_a$. On the other hand, if resistance to heat flow from the thorax to the abdomen is reduced under conditions of heat stress, the the ratio ($R_{ab}$) of $T_{ab}$-$T_a$ to $T_{th}$-$T_a$ should increase with increasing $T_a$, since a smaller difference between $T_{th}$ and $T_{ab}$ is needed to maintain a given rate of heat transfer. In fact, regression of $R_{ab}$ on $T_a$ has a significant ($p = 0.0003$), positive slope, even when the effects of SR (also significant, $p = 0.0006$) are accounted for ($R_{ab} = 0.010T_a + 0.0016SR - 0.086$, $r^2 = 0.448$, $n = 50$). The actual magnitude of $T_{ab}$-$T_a$ is independent of $T_a$, however, while $T_{th}$-$T_a$ decreases (Fig. 2), so the total calculated heat loss, assuming a simple Newtonian mosel, decreases by nearly 50% as $T_a$ increases (MAY, 1984). In other words, although resistance to heat flow between thorax and abdomen apparently decreases, the decrease is insufficient by a large margin to compensate for the greatly reduced rate of heat loss from the thorax directly to the air as a result of the smaller temperature gradient from thorax to air. On the face of it, this suggests that heat production must be reduced. Alternatively, a simple model of heat exchange, using K determined in dead specimens, may be inadequate to describe heat loss, especially from the abdomen under conditions of rapid

heat gain from the thorax (MAY, 1984). Also, the possible errors inherent in field determination of $T_{ab}$ are probably greater than for other tagmata, owing to rapid post-capture changes and the difficulty of rapidly and accurately positioning the thermocouple probe. Nevertheless, it is clearly premature to conclude that augmented circulation to the abdomen adequately accounts for regulation of $T_{th}$.

In principle, heat loss to the head might also be augmented to regulate $T_{th}$ (HEINRICH, 1979). Regression of $R_h$ (defined analogously to $R_{ab}$) on $T_a$ reveals, however, that the slope is only marginally significant ($p = 0.09$) and negative ($R_h = -0.0040T_a + 0.00012\ SR + 0.53$, $r^2 = 0.194$, $n = 51$). This is inconsistent with use of the head as a heat sink at high $T_a$ and suggests that, if anything, $T_h$ itself might be regulated weakly by augmenting heat transfer from the thorax at low $T_a$. Again, definite conclusions are not yet warranted. It is possible, in fact, that heating of the head is the result merely of physical conduction through the tissues. Transfer of heat via circulation seems more probable, however, in view of the narrow physical connection between head and thorax and in light of data from *Anax junius* showing that heat is transferred from the thorax to the head at least in part by an active process that is also partly independent of transfer to the abdomen (MAY, 1986).

If $T_h$ is elevated by an active process, then a strong adaptive advantage may be inferred, because the costs must be considerable. Elevation of $T_h$ represents an appreciable drain of heat from the thorax and must increase the difficulty of regulating $T_{th}$ in flight at low $T_a$ and of elevating $T_{th}$ during warm-up. The relative magnitude of heat loss from the head may be crudely estimated by noting that during warm-up (when radiation was negligible) $T_h$-$T_a$ was about 0.25 ($T_{th}$-$T_a$), $K_h$ about $3K_{th}$ (Fig. 8), and head mass about 0.25 times thoracic mass ; since heat loss is proportional to mass x $K(T_b$-$T_a)$, heat loss via the head may be as much as 25% of heat loss direct from the thorax. Possibly nutrient requirements of the head preclude interruption of circulation, but this seems unlikely since during flight at low $T_a$ the thorax, with its much higher metabolism, is presumably maintained with minimal circulatory exchange with the abdominal fat body. Alternatively, high $T_h$ may itself be adaptive, as it seems to be in male carpenter bees (BAIRD, 1986). The nature of the benefits is unknown, but improved visual or brain function are possible.

To return to the question of regulation of $T_{th}$, the possibility that flight metabolism is lower at high $T_a$ remains open and receives support from two sources. First, since the metabolic cost of hovering probably exceeds that of most forward flight, the negative correlation between time hovering and $T_a$

(Fig. 3) suggests that average flight metabolism is less at high than low $T_a$. This is still insufficient to account entirely for regulation of $T_{th}$, however. MAY (1984) calculated that heat production is about 1.8 times as high at $T_a < 20°C$ than at $T_a > 30°C$. From Fig. 3, the predicted % hovering varies roughly from 40 to 20 over this range. Even if hovering were on the average twice as costly as forward flight, this percentage difference would make heat production only about 1.2 times higher at the lower $T_a$ range. In addition, the correlation of hovering with $T_a$, although significant, is so poor that I question whether hovering could be a regulatory response. Hovering must, in any event, affect or be affected by not only $T_{th}$ but also territorial patrol patterns and chases with intruding conspecifics; the unusual individual indicated on the figure may exemplify the effect of such non-thermal factors. Finally, $T_{th}$ is regulated equally well at high or low SR, but the correlation of hovering with $T_a$ applies only at fairly high SR. Hovering time probably is limited by $T_a$ extremes (especially high $T_a$) and may as a by-product affect $T_{th}$, but hovering behavior most likely does not serve as a thermoregulatory mechanism *per se*.

A second way in which insects might control flight metabolism to regulate $T_{th}$ is suggested by the observation (UNWIN & CORBET, 1984) that in some large bees, despite severe aerodynamic restraints on flight power output, a negative correlation exists between wingbeat frequency and $T_a$ during forward flight. These authors propose that such insects may reduce heat production as $T_a$ increases by reducing wingbeat frequency (at the cost of reducing flight speed). Efforts to test this possibility in *T. cynosura* have so far been unsuccessful. Insects with low wing loading, like dragonflies, might also glide more at high $T_a$ (MAY, 1978), but I observed no gliding in territorial *T. cynosura*.

Whether or not it is used to regulate $T_{th}$, flight metabolism in *T. cynosura* must be quite high. Since $K_{th}$ is not lower than in other dragonflies (Fig. 8), heat production must be higher than in other small species studied, to account for the unusual elevation of $T_{th}$ at low $T_a$ and SR ($T_{th}$-$T_a$ is 40-130% higher than in species of similar size; MAY, 1976, 1977). This may be a consequence of the high wing loading and low wing moment of inertia noted above, and of the fact that laboratory measurements of wingbeat frequency (45-49 Hz) were slightly higher than predicted for other dragonflies of similar mass (42-44 Hz; MAY, 1981 b). MAY (1984) calculated maximum flight metabolism as about 0.76 $W g^{-1}$, a value which exceeds estimates based on $O_2$ consumption measurements for other very high energy fliers such as euglossine bees (CASEY, MAY & MORGAN, 1985) and sphinx moths (BAR-

THOLOMEW & CASEY, 1978). The high rate is explained in part by the greater thoracic muscle mass of *T. cynosura* (Table I). Thoracic muscles are only about 15% of total mass in bees (GREENEWALT, 1962) and probably < 25% in sphingids (BARTHOLOMEW & CASEY, 1978 ; GREENEWALT, 1962). From these values, metabolism per gram of muscle is about 2.2 W $g^{-1}$ for *T. cynosura* vs. about 4.4 w $g^{-1}$ for euglossines and 2.2 w $g^{-1}$ for sphingids.

A third general mechanism of regulating $T_{th}$ is behavioral modulation of external heat loads or sinks. The increasing tendency to fly in shade at high $T_a$ (Fig. 4) indicates that the insects do vary external heat load in response to temperature. This was especially striking during the observation at 35°C, described above, in which most patrolling individuals clearly avoided flying into direct sunlight, and during several early-morning observations, when individuals likewise appeared to avoid shade. Nevertheless, this mechanism, too, fails to account fully for the observed ability to regulate, since $T_{th}$ was independent of SR measured at the site of capture (i.e., not necessarily in sunlight) and was regulated as well at very low SR as over the full range of SR. Also, the index describes the distribution of the dragonflies as a group, but individuals did not shuttle between sun and shade over short periods of time. Thus, while choice of patrol areas in response to sunlight may be part of the suite of thermoregulatory tactics, it is probably of major importance only at extremes of the activity range of $T_a$.

Based on the evidence in hand, then, changes of abdominal circulation to facilitate heat loss, of heat production, and of behavior all probably play some role in thoracic thermoregulation. No single mechanism is adequate to account entirely for the constancy of $T_{th}$, but together they may be sufficient. A final possibility, controlled evaporative cooling, also deserves mention, although its role can only be the subject of speculation for the moment. MILLER (1962) noted that the physiology of spiracle control in some Anisoptera suggests the possibility that they use evaporative cooling to regulate body temperature. A reasonable estimate of maximum evaporative heat loss at high $T_{th}$ may be calculated based on WEIS-FOGH's (1964) estimate that ventilatory volume in dragonflies is about 1200 ml $g^{-1}$ $h^{-1}$ and on the assumptions that air is inspired at 35°C and 30% RH and expired at 45°C and 100% RH. This would entail loss of about 0.115 g of water per g body mass per h, i.e., 11% of body mass per h, obviously not a sustainable rate but possible for emergency cooling. Heat of vaporization for water is about 2400 J $g^{-1}$, so this amounts to a heat loss of about 0.076 W $g^{-1}$, or 10% of the maximum calculated heat production. On purely physical grounds, then, evaporation cannot account for more than 25% of the calculated difference

in heat production (MAY, 1984) between high and low $T_a$ (i.e., 0.76-0.41 = 0.35 W $g^{-1}$) even on a short term basis, but it could contribute, along with other mechanisms, to reduction of $T_{th}$ at high $T_a$.

Despite their well-developed ability to regulate $T_{th}$, morning territorial activity by *T. cynosura* males was apparently restricted to $T_a > 18$-19°C. I believe that temperature was at least indirectly a cause as well as a correlate of the activity restriction, because during the mornings of sunny days other physical conditions were relatively favorable: wind was seldom strong, saturation deficits were probably low, and SR was generally high and not well-correlated with $T_a$ or onset of activity. The reason for the restriction by temperature is not altogether clear, but I offer several more or less plausible suggestions and point out questions raised by these data.

Air temperature may have acted through its effect on another biotic factor, e.g. by restricting availability of food or females. Neither possibility can be evaluated at present, but studies of the effects of $T_a$ on prey and female behavior would be of interest. A simpler explanation is that $T_a$ restricted activity by its direct effect on male body temperature. Since males maintained $T_{th}$ at least 14°C above $MFT_{th}$, it seems unlikely that inability to maintain elevated $T_{th}$ in flight sharply limited activity at low $T_a$. The possibility that activity might be limited by low $T_h$ is intriguing, but without knowing the real significance of $T_h$, it is again impossible to evaluate. The most likely possibility is that at $T_a$ much below 18-19°C, *T. cynosura* are unable to warm-up rapidly or effectively by wing-shivering. This is consistent with the laboratory observations of warm-up at 15°C and can be explained theoretically if maximal metabolic output of the thoracic muscles during warming is sufficiently temperature-sensitive (R. D. STEVENSON, pers. comm., 1985).

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