



## Body temperature regulation in the dragonfly, *Arigomphus villosipes* (Odonata: Anisoptera: Gomphidae)

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Regulation of thoracic muscle temperature has been investigated in a number of dragonfly species but is poorly known in the large and diverse family, Gomphidae. Moreover, temperatures of other body regions have been recorded in very few ectothermic insects. In addition, correlations among multiple components of thermoregulatory behavior have rarely been examined quantitatively. Here I examine thermoregulation in *Arigomphus villosipes*, a medium-sized gomphid common at the shores of lakes and ponds in the northeastern USA. Measurements of the temperatures of the thorax ( $T_{th}$ ), head ( $T_h$ ) and abdomen ( $T_{ab}$ ), using standard "grab and jab" techniques, indicate that both  $T_{th}$  and  $T_h$  are relatively independent of air temperature ( $T_a$ ). It is not clear whether  $T_{th}$  and  $T_h$  are independently regulated, although some data suggest that they might be. *Arigomphus villosipes* can warm its thoracic musculature endothermically to maintain high  $T_{th}$  during cool  $T_a$  in conditions of low solar radiation intensity. However, regulation is principally behavioral, involving variation in body and wing postures and perhaps in perch substrate choice. Certain of these behaviors are closely associated to form suites of behavior that together are adapted to enhance or inhibit heating, while others are constrained by trade-offs with other functional demands. The former have a significant demonstrable effect on  $T_{th}$ . These combinations of behaviors results in a well-developed capacity for thermoregulation, allowing the insects to expand their activity periods and choice of perches, and probably improving male performance during competitive chases of females prior to mating.

**Keywords:** body temperature; ectothermy; endothermy; insect; thermoregulation

### Introduction

It is now well known that many large diurnal insects regulate the temperature of their thoracic flight muscles. Of these, dragonflies are among the most accomplished (Heinrich, 1993; May, 1976, 1985). Most dragonflies fall rather easily into one of two behavioral categories: perchers, which alight on various perches from which they sally to pursue prey or interact with other dragonflies, and fliers, which spend most of their active periods on the wing (Corbet, 1962; Corbet & May, 2008). This distinction, although not absolute, has substantial implications for the mode of temperature regulation; perchers are largely or entirely ectothermic, while fliers rely principally on endothermy (Corbet & May, 2008; Heinrich & Casey, 1978; May, 1976).

The great majority of data pertain to just two families of Anisoptera: Libellulidae, mostly perchers, and Aeshnidae, nearly all of which are fliers. Notably, the Gomphidae, the second most diverse family of Anisoptera after Libellulidae, has received very little attention to date.

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Miller (1964) and Tracy, Tracy, and Dobkin (1979) provided behavioral data for the very large species, *Ictinogomphus ferox* and *Hagenius brevistylus*, respectively, but no field data on body temperatures have been recorded for any gomphid.

*Arigomphus villosipes* is a gomphid of moderate size that is common in much of the eastern USA in late spring and early summer. Males typically perch on bare ground, stones, or floating vegetation along the shores of lakes and perennial ponds waiting for females to appear. During this time they may interact aggressively, but, like several other gomphids, they apparently do not occupy spatially fixed territories (Kaiser, 1974; McMillan, 2006; Miller & Miller, 1985; Rehfeldt, 2004). Females appear relatively briefly to oviposit, when they are rarely approached by males. When detected, however, females are rapidly chased by one or more males, as reported by Miller and Miller (1985) and McMillan (2006).

Since males occupy perches on bare ground during periods of bright sunlight at air temperature ( $T_a$ ) up to 35°C, they probably risk overheating. On the other hand, because rapid flight is required during male–male interactions and sexual chases, high thorax temperature ( $T_{th}$ ) and, perhaps, high head temperature ( $T_h$ ) are probably necessary for optimal functioning of the flight muscles and nervous system. Thus I expected effective regulation of body temperature in these insects. The present paper documents thermoregulation and critical functional temperature levels and identifies behavioral correlates of temperature that apparently are the main mechanisms of temperature regulation.

## Materials and methods

Studies were carried out along the northeast shoreline of Davidson's Mill Pond and on the upper end of Farrington Lake in East Brunswick, Middlesex County, NJ, USA (approximately 40° 24' 43.2" N, 74° 29' 56.4" E). Body temperatures of 67 males and five females were measured as described elsewhere (May, 1987, 1995) using a 0.3 mm diameter Cu–Cn hypodermic thermocouple probe. The probe was inserted in rapid succession (< 15 s) into the thorax ( $T_{th}$ ), abdomen ( $T_{ab}$ ), and head ( $T_h$ ). Behavior just before capture was noted, including, for perched individuals: posture, orientation relative to the sun, and substrate.  $T_a$  and solar radiation intensity (SR) were measured near the site of capture as described by May (1987). In addition, two dead, dried male specimens with chronically implanted thermocouples in the thorax were glued to small cardboard squares and positioned at ground level in the sun (living individuals very rarely perched in shade if sunlight was available) to approximate the effective environmental, or operative (Bakken, Santee, & Erskine, 1985) temperature,  $T_e$ , for the thorax;  $T_e$  was estimated as the mean of the two dead models. Each field-collected individual was retained in an envelope placed in a tightly closed container with moist paper or aquatic plant foliage and at the end of each field day weighed to 0.001 g using a Mettler analytical balance.

Perch substrates, angle of the long axis of the body relative to azimuth of the sun, degree of abdominal elevation, and wing position were noted both in males just before capture for temperature measurements ( $n = 64$ ) and in undisturbed males during separate surveys ( $n = 252$ ) along the shore of Davidson's Mill Pond; stance (crouching or stilting) was also recorded in the undisturbed individuals, as was direction (facing toward or facing away from the sun) in individuals oriented parallel to or at an intermediate angle to the sun. During the latter surveys, measurements of the thermal and radiation environment were taken as above at the beginning and end of each survey.

The minimum temperature for controlled flight (MF), maximum voluntarily tolerated temperature (MVT), temperature inducing heat torpor (HT), and characteristics of endothermic warm-up including temperature at attempted takeoff (TO) were measured in the laboratory ( $T_a = \sim 25^\circ\text{C}$ , except for warm-up and TO; see below) as described by May (1976), with  $T_{th}$  recorded at 15 s

intervals on a Honeywell Elektronik 112 Multipoint thermocouple recorder (Morris Plains, NJ, USA) during measurements of warm-up and of MVT. The insects perched on a flat surface and sometimes moved spontaneously without heating, so only assumption of the obelisk posture, with the abdomen almost fully erect (May, 1976) was recorded as an unambiguous indication of MVT. Individuals used in these measurements were weighed to 0.001 g, as above.

## Results

As seen in Figure 1, expected temperatures of all three body regions were relatively independent of  $T_a$ , with slopes significantly  $< 1.0$  (May, 1985). The mean mass  $\pm$  SD of males probed in the field was  $0.307 \pm 0.032$  g (mean  $\pm$  SD;  $n = 64$ ), that of females was  $0.414 \pm 0.039$  g ( $n = 5$ ). Solar radiation had a significant effect on all body temperatures (see Figure 2 for  $T_{th}$ ) although this was less than that of  $T_a$  (F values for SR were  $0.1\text{--}0.3 \times$  those for  $T_a$ ). Controlling for SR did not affect slopes of body temperatures on  $T_a$ . Likewise, the slope (0.34) of  $T_{th}$  on  $T_e$  did not differ significantly from the slope of  $T_{th}$  on  $T_a$ .

Males and females apparently maintained similar  $T_{th}$ , and probably  $T_h$ , although too few females were measured to allow a confident description of their patterns of temperature variation and so were excluded from further analyses except as noted. Females, unlike males, were generally collected while in flight, and all were captured at  $T_a \leq 26^\circ\text{C}$ .

In both the head and abdomen, expected temperature at any given  $T_a$  is less than  $T_{th}$ . The slopes of  $T_h$  and  $T_{ab}$  on  $T_a$  are both significantly higher than that of  $T_{th}$  ( $p = 0.0011$  for  $T_h$ ,  $p < 0.0001$  for  $T_{ab}$ ), although also quite significantly less than 1.0 (Figure 1). Variances of  $T_h$  and  $T_{th}$  do not differ significantly ( $F = 1.18$ ,  $p > 0.1$ , 67 and 63 df), but that of  $T_{ab}$  is significantly higher than that of  $T_{th}$  ( $F = 2.13$ ,  $p < 0.005$ , 67 and 56 df). The ratio  $R_H = (T_h - T_a)/(T_{th} - T_a)$  (May, 1995) decreases slightly with increasing  $T_a$  (slope =  $-0.0082^\circ\text{C}^{-1}$ ,  $p = 0.007$ ; identical in multiple regression with SR) but is not significantly affected by SR ( $p = 0.44$ ), while  $R_{AB} = (T_{ab} - T_a)/(T_{th} - T_a)$  is not significantly related to  $T_a$  but decreases with SR (slope =  $0.00024 \text{ W m}^{-2}$ ,  $p = 0.004$ ). Neither ratio changes significantly when regressed against  $T_e$ .

Mean values of HT, MVT, TO, and MF are indicated by arrows along the right margin of the graph (Figure 1). In the field  $T_{th}$  always exceeded MF by  $10^\circ\text{C}$  or more and mean TO by no less than about  $3^\circ\text{C}$ , and it also frequently exceeded mean MVT. In field collected individuals  $T_{th}$  never approached mean HT to within less than  $3.5^\circ\text{C}$  and was at least  $2.5^\circ\text{C}$  below the minimum recorded HT ( $46.5^\circ\text{C}$ ).

Wing-whirring (Figure 1, black symbols) was infrequent and occurred only when clouds obscured the sun or when an individual perched in partial shade, but not all individuals in those circumstances wing-whirred. Although seen on other occasions, only five wing-whirring individuals were captured. Of these,  $T_{th}$  was near the level expected for basking individuals at the same  $T_a$  in four, while the fifth, which appeared to be shivering relatively weakly, had  $T_{th}$  about  $4^\circ\text{C}$  lower than expected. Neither  $T_h$  nor  $T_{ab}$  in any of these insects was markedly different from similar measurements in basking individuals.

In the laboratory, males readily began wing-whirring at  $T_a$  of  $18.5\text{--}23.5^\circ\text{C}$  ( $n = 9$ ) when stimulated by light abdominal pinching;  $T_{th}$  at takeoff ranged from  $28.5$  to  $31.3^\circ\text{C}$  (mean  $29.3^\circ\text{C}$ ; Figure 1), with the rate of warming averaging  $3.2^\circ\text{C min}^{-1}$  ( $2.5\text{--}4.8$ ). At  $T_a = 25^\circ\text{C}$ , only one of five individuals wing-whirred, at a rate of  $6.3^\circ\text{C min}^{-1}$  and takeoff temperature of  $33.4^\circ\text{C}$ . The others either took off immediately or struggled without warming to takeoff. Obviously wing-whirring may be maintained at appreciably higher  $T_{th}$  in undisturbed individuals in the field.

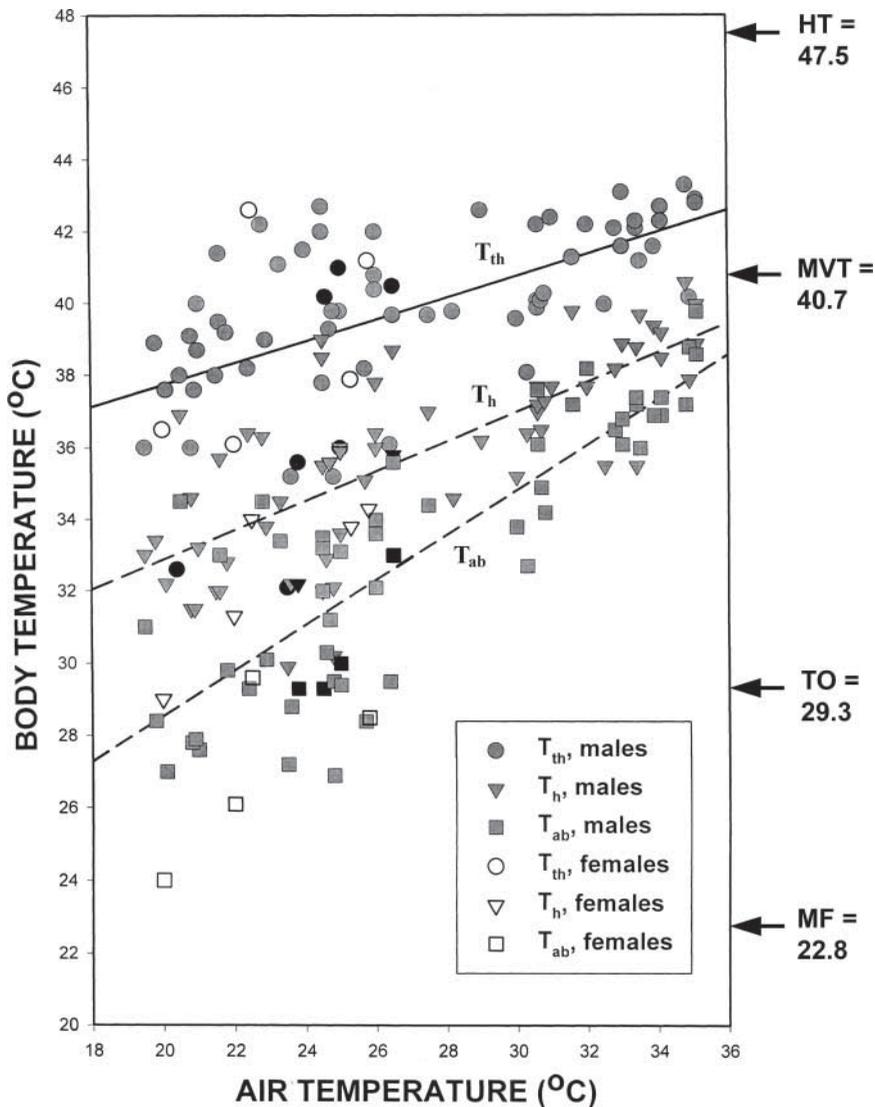


Figure 1. Body temperature as a function of air temperature in both sexes of *A. villosipes*. Black symbols represent males that were wing-whirring when captured. Lines are least squares linear regressions of the temperature of each tagma on air temperature,  $T_a$ . For thoracic temperature,  $T_{th} = 0.31T_a + 31.6$ ,  $n = 67 \sigma 5 \varphi$ ,  $r^2 = 0.34$ ,  $p < 0.0001$ ; head temperature,  $T_h = 0.44T_a + 23.8$ ,  $n = 53 \sigma 4 \varphi$ ,  $r^2 = 0.57$ ,  $p < 0.0001$ ; abdominal temperature,  $T_{ab} = 0.67T_a + 14.7$ ,  $n = 50 \sigma 4 \varphi$ ,  $r^2 = 0.34$ ,  $p < 0.0001$ . HT is the temperature acutely inducing heat torpor and MVT is the maximum voluntarily tolerated  $T_{th}$  as determined in the lab; TO is the  $T_{th}$  at takeoff after endothermic warm-up with  $T_a$  in the range 18–24°C; and MF is the minimum  $T_{th}$  for level flight.

Male behavior in the field underwent a complex sequence of changes during the course of the day, including perch choice, body angle relative to the sun, adjustments of position of the abdomen and wings, and crouching or stilted to regulate body temperature (Figure 3). In general, the proportions of behaviors expected to result in greater elevation of  $T_b$  – aligning the body perpendicular to the sun, holding the abdomen parallel to the substrate or lower, skewing the wings downward, crouching, and perching on dry soil – were high at the lowest observed air temperatures and declined as  $T_a$  increases, while those of heat avoidance postures – body axis

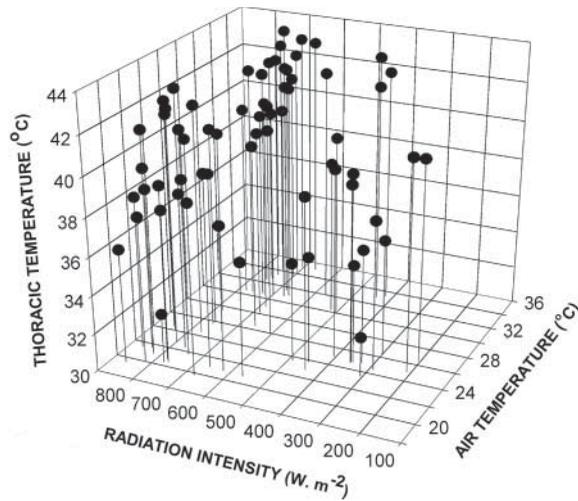


Figure 2. Thoracic temperature as a function of  $T_a$  and SR in male *A. villosipes*. The least squares plane multiple regression equation is  $T_{th} = 0.31T_a + 0.0043SR + 28.7$ ,  $r^2 = 0.44$ .

parallel to sun, abdomen elevated into the obelisk posture, wings raised, stiling, perching on elevated perches (leaves or small rocks) – increased with  $T_a$  (see also Figures 5 and 6, below).

## Discussion

### *What temperatures are regulated?*

The three tagmata of insects are necessarily in thermal contact via conduction and convection, the latter principally due to circulation of hemolymph among regions (Heinrich, 1970; May, 1995; Stavenga, Schwering, & Tinbergen, 1993), so their temperatures influence one another even in the absence of active regulation. When  $T_{th}$  and  $T_h$  are at equilibrium in insects that regulate  $T_{th}$  endothermically, using only the thoracic muscles as a heat source,  $R_H$ , as defined above, should be constant across all  $T_a$  if heat transfer to the head is passive but should decrease as  $T_a$  increases if  $T_h$  is being regulated independent of  $T_{th}$  (May, 1995). In heliotherms, the primary heat source is solar radiation and body temperatures may quite sensitive to subtle differences in behavior. Nevertheless, if the average relative rates of heat transfer among body regions and between the body and the environment are independent of  $T_a$ ,  $R_H$  should be approximately constant. In *A. villosipes*, the regression of  $R_H$  on  $T_a$  is slightly but significantly negative and the relation is unchanged if solar radiation intensity is accounted for. This raises the possibility that this ectothermic species might also regulate  $T_h$ , as in several endothermic insects, including other dragonflies (May, 1995). Alternatively, however, some uncontrolled aspect of behavior might bring about this result; e.g. it is possible that the head is shaded more than the thorax during the obelisk posture simply as a consequence of its lower position, even if only  $T_{th}$  is actively regulated. Still, given the known thermal effects on neural function of insects, the possibility of independent regulation of  $T_h$  in ectotherms is worth further investigation.

### *Effectiveness of temperature regulation*

*Arigomphus villosipes* differs not only taxonomically from other Odonata for which body temperature data exist but also in perching on or near the ground regardless of ambient temperature

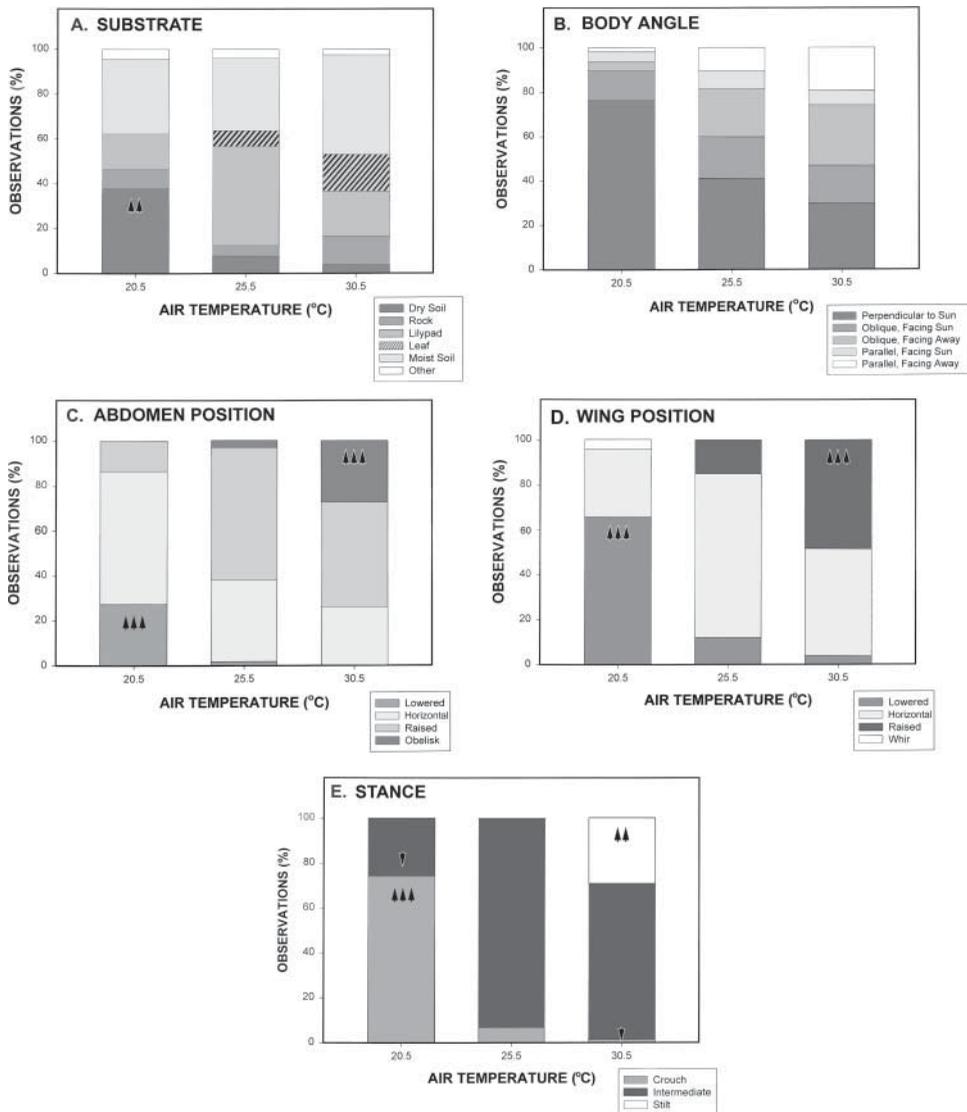


Figure 3. Changes in behavior of *A. villosipes* males as a function of air temperature; temperatures indicated in each part of the figure are the midpoints of the ranges 18–23°C, 23–28°C, and 28–33°C. Data are from surveys during which body temperature was not measured. In every case, frequencies of various behavioral alternatives was very highly significantly ( $p < 0.0001$ ) affected by  $T_a$ , as indicated by  $\chi^2$  value: (A) perch substrate selected –  $df = 10$ ,  $\chi^2 = 61.0$ ; (B) body angle relative to the sun –  $df = 8$ ,  $\chi^2 = 32.2$ ; (C) wing position relative to substrate –  $df = 4$ ,  $\chi^2 = 123.0$ ; (D) position of abdomen relative to substrate –  $df = 6$ ,  $\chi^2 = 100.2$ ; (E) stance (body elevation relative to substrate) –  $df = 4$ ,  $\chi^2 = 117.6$ . Upward pointing arrowheads indicate behavioral states occurring significantly more frequently than expected within the indicated temperature range, downward pointing arrowheads those occurring significantly less frequently than expected; one arrowhead –  $p < 0.05$ , two arrowheads –  $p < 0.01$ , three arrowheads –  $p < 0.001$ . A very stringent criterion was used, namely that cell  $\chi^2 > =$  critical value for significance of  $\chi^2$  for the table of behavior versus temperature for an entire category of behavior [e.g. wing position], in an effort to avoid type I error even at the risk of increasing type II error.

and thus experiencing a relatively warm and variable microhabitat. As noted before (May, 1976), the effectiveness of regulation of  $T_{th}$ , as measured by the slope of  $T_{th}$  on  $T_a$ , generally increases with body mass (that is, slopes decline with increasing mass; Figure 4). The capacity of *A. villosipes* to thermoregulate is slightly, but not strikingly, better than that predicted for libellulid

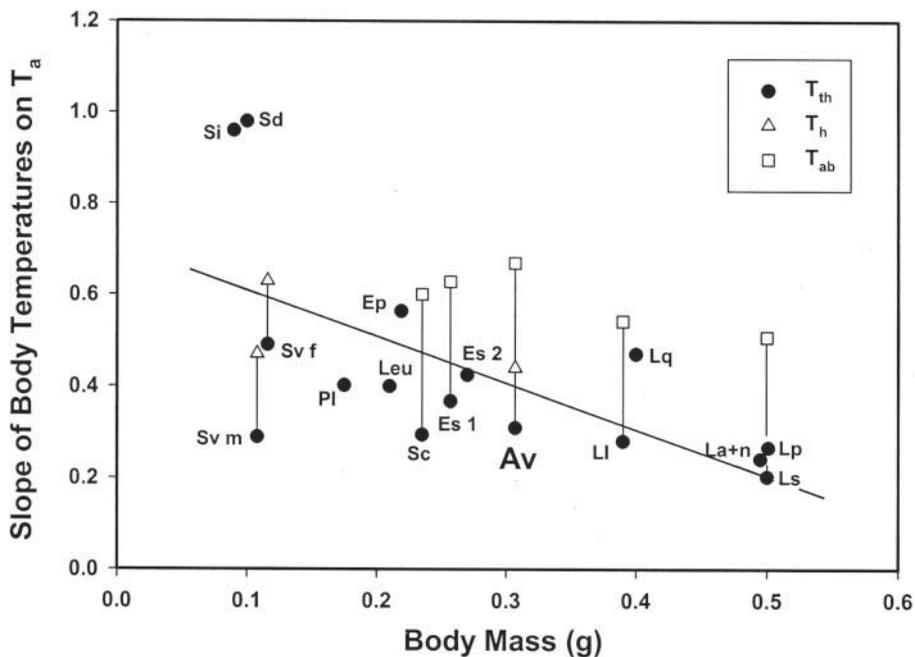


Figure 4. The slopes of plots of  $T_{th}$  and other body temperatures of percher dragonflies as a function of mean fresh body mass; for *A. villosipes* the value of mass is the mean mass of males from which field data were obtained. The heavy line shows the regression of the slope of  $T_{th}$  versus mass; vertical lines connect slopes for  $T_{th}$ ,  $T_h$ , and  $T_{ab}$  for a given species. Species codes are: Av, *Arigomphus villosipes* (this study); Es1, *Erythemis simplicicollis*; Li, *Libellula luctuosa*; Ls, *L. saturata*; Sc, *Sympetrum corruptum* (Polcyn, 1994); Es2, *Erythemis simplicicollis*; Ep, *E. plebeja*; La + n, *Libellula auripennis* and *needhami*; Pl, *Pachydiplax longipennis* (May, 1976); Leu, *Leucorrhinia* spp.; Lq, *Libellula quadrimaculata*; Sd, *Sympetrum danae*; Si, *S. internum* (Sforno & Doak, 2006); Lp, *Libellula pulchella* (Pezalla, 1979); Sv f, Sv m, *Sympetrum vicinum*, females and males (May, 1998).

perchers of similar size and is, for example, similar to the smaller *Sympetrum vicinum* (males) and *S. corruptum*. The libellulid datasets include individuals selected in a variety of ways (e.g. as in this study, only those at mating sites; Pezalla, 1979; Polcyn, 1994; Sforno & Doak, 2006; but cf. May, 1976, 1998, in which feeding individuals and even those basking prior to diel activity were included). No obvious differences in slope are attributable to such differences, however.

### Behavior and body temperatures

Postural adjustments to thermal conditions (Figure 3) were likewise mostly similar to those reported for libellulids (May, 1976), although stilting was usually less well developed in the latter. Undoubtedly stilting is favored when perching on hot soil or stones. Its efficacy is probably enhanced by the longer metathoracic legs characteristic of many gomphids; Tracy et al. (1979) also reported well-developed crouching and stilting in *Hagenius brevistylus*.

Some of these different behavioral responses are strongly associated and form rather clearly defined suites of behavior (Figure 5, Table S1). Thus, having the abdomen raised into the full obelisk posture is almost always accompanied by raised wings and stilting, although both the latter, especially elevated wings, may also occur in conjunction with a partly raised abdomen. These movements normally occur together to produce coordinated expression of the full obelisk, and all are necessary for maximally effective avoidance of excessive heating in sunlight.

Perch angle is clearly correlated with temperature (Figure 3) in a way that is consonant with increasing body temperature under cool environmental conditions (e.g. perching perpendicular to

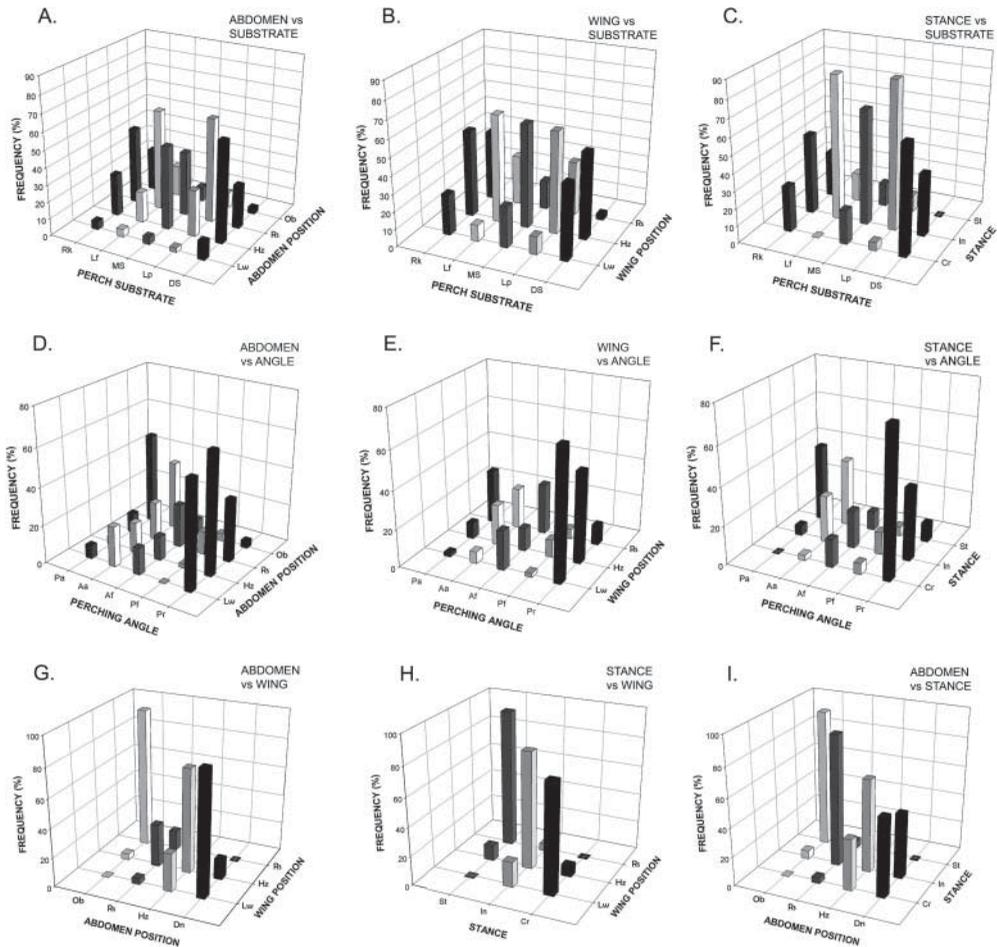


Figure 5. Frequency of simultaneous combinations of different states of the various categories of behavior thought to be adapted, at least in part, for regulation of body temperature in *A. villosipes* males. Within behavior categories, the possible behavior states are as follows: perch substrate – DS, dry soil; LP, lily pad; MS, moist soil; Lf, leaf (elevated above water surface); Rk, small rock. Body angle – Pr, perpendicular to sun; Pf, parallel to and facing sun; Af, intermediate angle facing sun; Aa, intermediate angle facing away from sun; Pa, parallel to and facing away from sun. Abdomen position – Lw, lowered below horizontal; Hz, horizontal; Rs, raised somewhat above horizontal; Ob, fully elevated into obelisk posture. Wing position – Lw, lowered below horizontal; Hz, horizontal; Rs, raised. Stance – Cr, crouching; In, intermediate; St, stilting. In some graphs the angle of view has been adjusted slightly to make all bars visible.

the sun or, less clearly, facing the sun and raising the abdomen; see May, 1976) or at reducing it at high temperature (e.g. perching parallel and facing away from the sun). This aspect of behavior, however, is less closely correlated with either temperature or other behaviors such as stance or abdomen position (Figure 5). In part this may reflect the greater difficulty of scoring perch angle, especially at high solar declination. Perch direction may also be influenced by other conditions. For example, males generally perch facing the water, presumably to maximize their chances of detecting a female; Miller and Miller (1985) found that male *Onychogomphus forcipatus* perched facing the water, with no correlation of perch angle with  $T_a$  or sunlight. Hence, even if a male *A. villosipes* stilted and assumed an obelisk posture, it might be less ready to adjust its body angle if that also entailed facing away from the water. The ability to adjust stance and wing and abdomen position allows some flexibility to vary perching angle independent of thermal conditions.

Substrate choice was even less tightly tied to temperature than was perch angle, although some choices appear to be influenced by temperature (Figure 3) and related to postural adjustments (Figure 5). Thus, perching on leaves, which would raise perched individuals out of the warm boundary layer near the ground and expose them to increased convective heat loss, is associated with high air temperature and, with the exception of stones, was the substrate on which individuals in an obelisk were found most frequently (although the association was not shown to be significant for either substrate; Figure 3, Table S1). Nonetheless, perching on elevated leaves was infrequent even at high temperatures, possibly because this substrate either afforded a poor vantage point or an unstable perch. Dry soil, on the other hand, probably provides the warmest microenvironment of the possible substrates and was rather strongly associated with low  $T_a$  and crouching, and suggestively, if not significantly, with lowered wings and abdomen (Figures 3, 5, 6).

### Operative temperature and thermal thresholds

Physical thermal models of organisms have the potential inform studies of thermal biology by defining an envelope of temperatures that the modeled organism could encounter within a given environment (Bakken et al., 1985). My two “model” *Arigomphus* did not reflect the full range available, as  $T_{th}$  of live individuals often fell above or below both models. Nonetheless, their

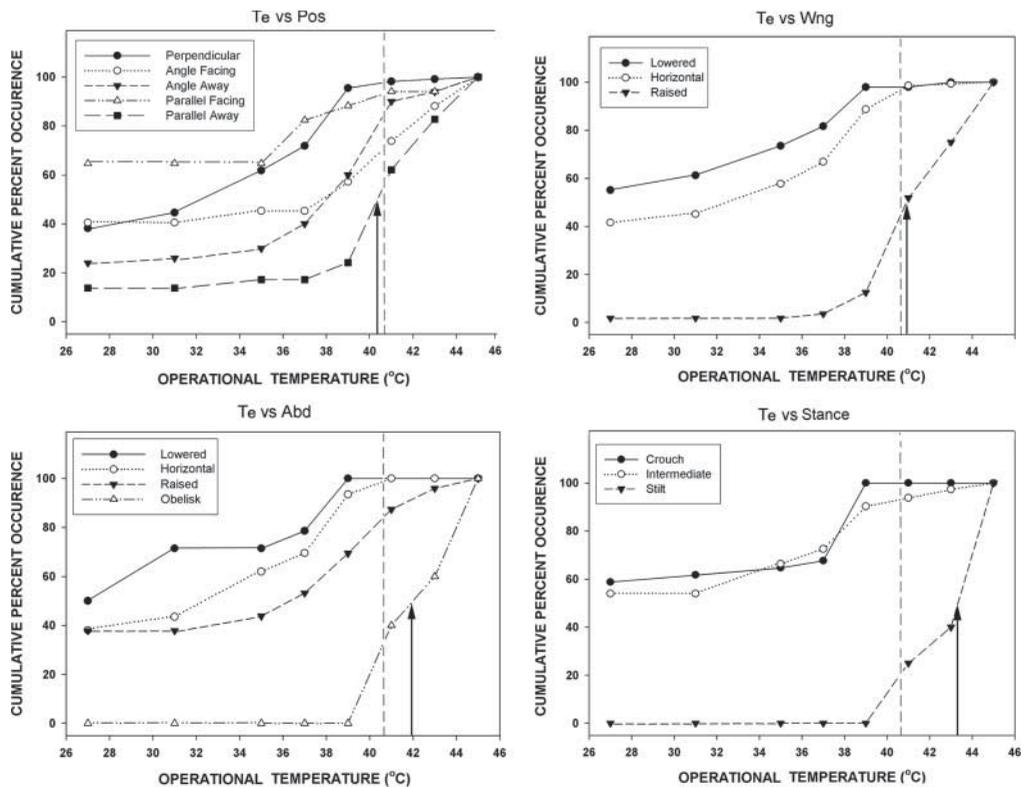


Figure 6. Cumulative percentage of different behavioral states within categories of behavior thought to be adapted, at least in part, for regulation of body temperature in male *A. villosipes*, as a function of operative environmental temperature ( $T_e$ ); arrow indicate the  $T_e$  at which half of the individuals had assumed the maximal heat avoidance state for each behavioral category. Vertical dashed lines intercept the percentage curves at mean MVT (see Figure 2). See text for description of behaviors. Data are from surveys on days when body temperature was not measured.

temperatures probably approximated the combined effects of air temperature and radiant heat flux on *Arigomphus* perched on the ground during sunlit periods. They thus give at least a rough idea of the upper bound of the thermal environment of *A. villosipes*, and, at high  $T_a$  in bright sunlight,  $T_e$  exceeded MVT by up to  $5^\circ\text{C}$ . At the opposite end of the temperature range,  $T_a$  was effectively the lower limit in the absence of substantial evaporative cooling.

Consequently, if: (1) the behaviors associated with maximum heat avoidance are correctly identified, and (2) MVT as measured in the lab is applicable in the field, then mean MVT should correspond approximately to the median of the frequency distribution of the avoidance behavior on  $T_e$ , i.e., the 50% level of the cumulative distribution. This is the case within  $< 0.5^\circ\text{C}$  for body angle and wing elevation (Figure 6). Raising the abdomen into the obelisk, however, was brought into play at median  $T_e$  of ca.  $1.2^\circ\text{C}$  higher than MVT from the lab, while stiling (stance) reached the 50% criterion only at ca.  $2.7^\circ\text{C}$  above the lab value of MVT. Lab measurements of MVT were based almost entirely on observations of obelisk behavior and might thus be expected to be closely similar to field measurements of the same behavior. In part, this discrepancy exists because the sun's elevation in the field at approximately  $40^\circ \leq N$  latitude is maximally only about  $73^\circ$ ; thus to minimize solar radiation on the thorax (or head), the abdomen will not need to be held exactly erect and may not have been scored as representing an obelisk even when optimally positioned to minimize heating. It also appears likely that these heat avoidance behaviors typically are employed in a rather regular sequence from ca.  $38$  to  $43^\circ\text{C}$ . Since substrate choice appears to be only modestly affected by temperature, the lack of coincidence with MVT of the behavior most closely related to high  $T_e$  (not shown), perching on rocks, is perhaps not surprising. Overall, these observations support the conclusion that MVT, although not always reflecting the full range of heat avoidance responses, is relevant to the field situation and that the inferred associations of specific behaviors with avoidance of excessive heating is correct.

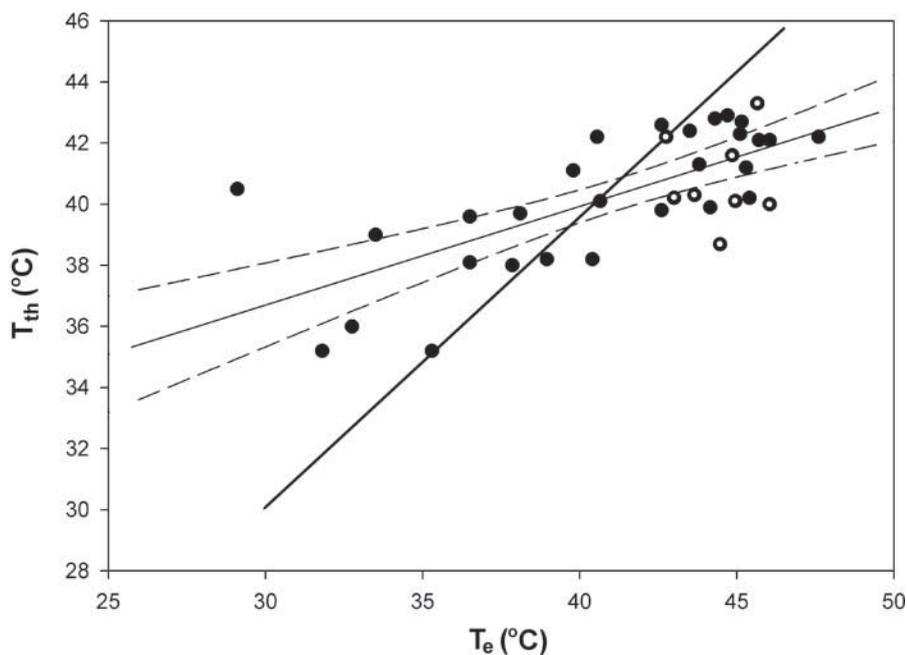


Figure 7. Thoracic temperature plotted against operative temperature (see text) in *A. villosipes* males;  $T_{th} = 0.33T_e + 27.0$ ,  $n = 36$ ,  $r^2 = 0.50$ ,  $p < 0.001$ . Thin solid line is regression of  $T_{th}$  on  $T_e$ , dashed lines show confidence intervals of the regression, heavy solid line is line along which  $T_{th} = T_e$ ; points with white centers represent individuals in the obelisk posture.

The association of MVT with strong heat-avoidance behavior in the field is reinforced by noting the effectiveness of the latter. Figure 7, based on data from male specimens in which  $T_b$  was measured, and on environmental conditions at the same time, shows that expected  $T_{th} > T_e$  up to about the level of MVT (39.8–41.7°C), after which  $T_e > T_{th}$ . That is, above MVT, the insects regulated  $T_{th}$  so as to remain within the acceptable range of body temperature. Individuals in the obelisk posture always had  $T_{th} < = T_e$ ; despite being in full sun, the live insects kept  $T_{th}$  at or below the level it would have reached passively with the abdomen horizontal.

### *Selection for body temperature regulation*

It is clear from the previous discussion that ectothermic regulation of body temperature allows *Arigomphus* males to maintain  $T_{th}$  within functional limits – well above MF and below HT. Since  $T_e$  sometimes exceeded HT, regulating  $T_b$  may have been necessary to avoid fatal overheating, at least occasionally. Some evidence (May, 1978) suggests that MVT is adapted fairly closely to climate and habitat in libellulid dragonflies. The same is suggested for gomphids, based on the only two species tested. Although *A. villosipes* is confined to temperate northeastern North America, its mating habitat and season is near the upper thermal extreme for that region, and its MVT and HT are comparable to those of open country, ground perching libellulids in the Neotropics and southern USA. On the other hand, the tropical forest gomphid, *Epigomphus quadracies*, is rarely exposed to  $T_a > 30^\circ\text{C}$  along mostly shaded streams with dappled sun, and displays mean MVT of only 34.9°C and HT of 41.5°C (May, 1978).

The question remains, however, what is the advantage of continuing activity at the risk of exposure to lethal temperature. In the present case, nearly all activity is directly related to reproduction: for males, mating, for females, mating and oviposition. I made only casual, qualitative observations of mating behavior during this study. Nevertheless, aggressive interactions among males were obvious and frequent, as also reported for *A. villosipes* by McMillan, (2006) and for *Onychogomphus forcipatus* by Kaiser (1974) and Miller and Miller (1985) and *O. uncatius* by Rehfeldt (2004). Most gomphids apparently are not territorial (but see Miller, 1964; Moore & Machado, 1992), but Kaiser (1974) and McMillan (2006) concluded that aggressive interactions resulted in more even spacing in the species they studied. This was not obviously the case in the dense population I observed. At times males were displaced from their perching site (most often on a horizontal surface near ground level) and took up another site some distance away, but on other occasions they might return to the original site. Most aggression seemed to be directed at males that were already in flight.

Females appeared infrequently at the water. McMillan (2006) reported that all females attempted to oviposit and that most of these were not disturbed by males. My impression was that ovipositing females mostly hovered while tapping the water surface to release eggs and that females I saw doing this (less than half a dozen) were ignored by males. On the other hand, as described by Miller and Miller (1985), other females flew rapidly past the perching sites of a number of males, and these were usually pursued by one or more males, also flying very rapidly. The timing of female activity during the day was not recorded systematically, but, although they seemed more frequent before mid-morning and in late afternoon, a few occurred during the hotter parts of the day.

The positive effects of temperature, within limits, on flight metabolism, muscle power output, and wing kinematics are well known (e.g. Esch, 1976; Neville & Weis-Fogh, 1963; Stevenson & Josephson, 1990). It is very likely that, as in many other insects, *A. villosipes* can produce more power and fly faster at  $T_{th}$  near the upper limit of the range they tolerate. They may also enjoy enhanced visual function when their  $T_h$  is high (May, 1995). It appears that, for a male, being the first to perceive a female, and the fastest in the ensuing pursuit, is likely to lead directly to

mating success. Hence, maintaining high  $T_{th}$  and  $T_h$ , without exceeding harmful limits, may be essential to be successful obtaining a mate. Neither the mating nor the thermoregulatory strategy of females is as clear, but if, as Miller and Miller (1985) suggest, the rapid pre-mating flight of females acts as a mechanism of sexual selection on males, possibly indicating a “good genes” advantage of the successful male, then rapid flight and high  $T_{th}$ , might also be of particular advantage to females in this context.

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