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THERMAL ADAPTATIONS OF DRAGONFLIES, REVISITED

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Recent developments in understanding of the thermal ecology of adult Odonata are reviewed. Although body temperatures have been determined in the field for several species, and the mechanisms for regulation of thoracic temperature are known in broad outline, additional work, especially on temperature of other body regions and on species from extreme environments, is needed. Some preliminary new data on temperature regulation in *Anax junius* and *Arigomphus villosipes* are outlined. Knowledge of the adaptive consequences of body temperature and its regulation is still in its infancy. Suggestions are given for future research on temperature adaptations and their interaction with other biological processes and on geographic variation.

INTRODUCTION

Although the major mechanisms of response to temperature by odonates are understood in broad outline, many variations and details are incompletely explored, and their benefits and costs are only beginning to be appreciated. Beyond that, quantitative knowledge of body temperature can illuminate and help to predict many aspects of dragonfly behaviour and physiology. My aim here is to review what has transpired in this field in the last dozen years, since I attempted, at the Fourth International Symposium of Odonatology at Gainesville, to summarize and supplement current understanding of thermoregulation and behavioral reponses to the thermal environment by adult Odonata (May, 1978). I hope also to suggest how an expansion of research on thermal responses might add to the overall picture of the biology of Odonata.

MECHANISMS OF REGULATION

The distinction, first emphasized by CORBET (1963), between “fliers” and “perchers” is still useful in studies of dragonfly body temperature regulation, although not all species fit neatly into one of these categories. Generally, fliers are endotherms and control thoracic temperature (T_{th}) by modulating loss or production of internally generated heat. Perchers are ectothermic and adjust the rate of exchange with environmental heat sources and sinks, especially the sun. MAY (1976b) showed that many fliers raise the temperature of their thoracic musculature before flight by wing-whirring (endothermic warm-up) and that some of these can vary heat loss from the thorax to the environment via circulation the abdomen, as in moths and bees (HEINRICH, 1970, 1976). Subsequently, HEINRICH & CASEY (1978) explored the latter phenomenon in more detail in *Aeshna multicolor* and *Anax junius*. They showed that when the thorax of these species was heated with a focused lamp, without directly heating adjacent tagmata, T_{th} was stabilized at slightly above 40°C, accompanied by sharp increases in abdominal temperature (T_{ab}). Ligation of the dorsal vessel in the abdomen abolished the rise in abdominal temperature and the ability to stabilize thoracic temperature, whereas preventing pumping movements of the abdominal wall did neither, so stabilization of T_{th} depends on intact hemolymph circulation via the dorsal vessel. Ligation was equally effective at any point of the abdomen, indicating that hemolymph is returned to the vessel only at the posterior end. They also confirmed MAY's (1976b) observation that T_{ab} does not increase appreciably during endothermic warm-up. By contrast, in the ectothermic *Libellula saturata*, neither wing-whirring nor heat transfer between thorax and abdomen could be demonstrated. Apparently the capacity for endothermy and for active heat shunting via hemolymph circulation is characteristic mainly of fliers. This conclusion has been verified in a laboratory setting for a number of other species (MAY, 1977, and unpublished data), albeit with some exceptions noted below.

Three additional studies have reported extensive data on body temperature in the field of fliers. ROWE & WINTERBOURN (1981, and pers. comm., 1984) showed that in *Procordulia smithii* T_{th} is appreciably elevated and its slope on air temperature (T_a) is about 0.5 in patrolling males ; T_{ab} is slightly elevated and varies in parellel to T_a. MAY (1987) studied thermoregulation in *Tetragoneuria cynosura* and found that T_{th} is surprisingly high and well regulated (slope on T_a about 0.4) for a small flier, that head temperature (T_h) also is elevated substantially, and that the pattern of variation in T_{ab} suggested that excess heat may be dissipated via this route at high T_a, but not sufficiently to account for the reduction in heat retained by the thorax at high T_a. The role of other possible mechanisms of regulation, including control of heat production, is currently being explored (MAY, unpublished data). Finally, POLCYN (1988) showed that populations of *Anax junius*, *Aeshna multicolor*, and *Tramea* spp. in hot desert areas of southern California regulate T_{th} with great precision and at higher levels than expected from species or populations in more temperate areas.

Regulation of head as well as thoracic temperature occurs in a few endothermic insects, including honeybees (Heinrich, 1979), carpenter bees (Baird, 1986), and sphinx moths (Hegel & Casey, 1982). Extensive flield data on T_h in *T. cynosura* suggested active elevation of T_h but gave no clear evidence of regulation of head temperature (May, 1987). Several years ago, intrigued by the results then beginning to emerge for *T. cynosura*, I began a re-examination of body temperatures in *Anax junius*; some preliminary results appeared in May (1986). The picture of thermoregulation and heat transfer within the body of *A. junius* has proved unexpectedly complex and is still incomplete, but a brief progress report may be useful here.

Analysis of heat exchange is based on a simplified model, diagrammed in Fig. 1 and derived algebraically in Table I (see also Baird, 1986). It assumes that all heat is generated within the thorax by the flight muscle and that all three tagmata are in thermal equilibrium (heat input = heat output). Thus the model is not strictly applicable if external heat sources are present or if body temperature is changing, but it may be useful as a standard of comparison even in these cases. The main implications are that the ratio, R_h, of the temperature excess of the head ($= T_h - T_a$) to the thoracic temperature excess ($T_{th} - T_a$) depends entirely on the coefficients of heat transfer between the thorax and head (C^i_h) and the head and the environment (C_h) and thus is constant if the coefficients are constant (exactly the same argument applies to the abdomen, of course). Therefore, changes in R_h and/or R_{ab} can give information about how heat transfer between tagmata changes. If e.g., R_h is lower at high than at low T_a, decreased heat transfer from thorax to head at high T_a is implied and the possibility of regulation of T_h, perhaps to prevent oveheating of the head, is suggested. Conversely, since work already reviewed indicates that the abdomen is used as a heat exchanger to prevent overheating of the thorax at high T_a, R_{ab} should increase as T_a increases.

Collection of field data is ongoing, but Figure 2 shows preliminary regressions of *A. junius* body temperatures on T_a. The relationships apparently differ between males patrolling at rendezvous sites and both sexes in feeding swarms, with the latter having lower and less well-regulated T_{th} and lower T_h and T_{ab}. Patrolling males are generally active in sunlight while most feeding swarms occurred at dusk, so temperatures were differentially affected by solar radiation, but Anova indicates that behavior has an effect on all body temperatures independent of radiation intensity.

The magnitude of R_h is similar for patrolling and feeding individuals and is independent of T_a. Thus, there is no evidence from field data for either regulation of T_h or use of the head as a heat exchanger to regulate T_{th}, although data from a wider range of T_a are needed to settle the question. On the other

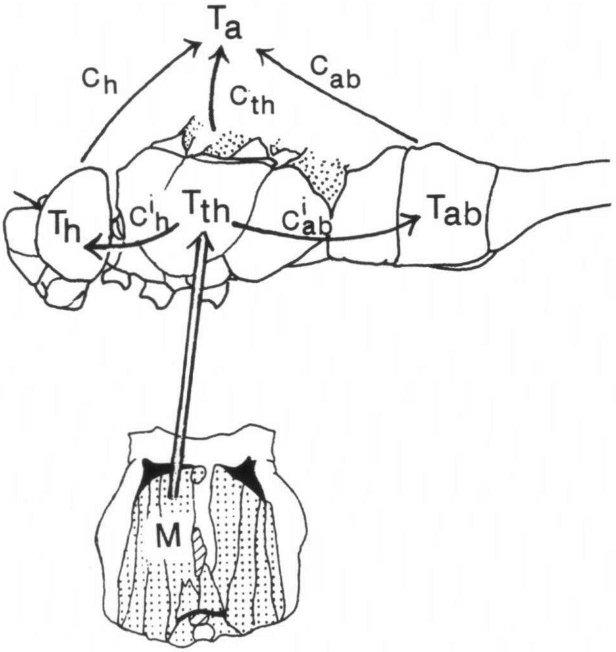

Fig. 1. Diagram of heat exchange in *Anax junius* (distal abdominal segments omitted) to illustrate quantities used in model developed in Table I. Lower diagram is transverse section of thorax to show source of heat production is metabolism (M) of flight muscles. Upper diagram is lateral view showing direction of heat flow (thin, solid arrows), temperatures, and heat conductances.

Table I

Derivation of simplified equilibrium model of heat exchange of dragonfly tagmata with the environment and among themselves.

Symbols: T — temperature; C — heat exchange coefficient with environment; C^i — heat exchange coefficient between thorax and indicated region; subscripts th, h, ab, and a indicate thorax, head, abdomen, and air, respectively

Heat gain = Heat loss

Thorax

M = loss from thorax to air + loss from thorax to head + loss from thorax to abdomen

$= C_{th} (T_{th} - T_a) + C^i_h (T_{th} - T_h) + C^i_{ab} (T_{th} - T_{ab})$

Head

$C^i_h (T_{th} - T_h) = C_h (T_h - T_a)$

$C^i [(T_{th} - T_a) - (T_h - T_a)] = C_h (T_h - T_a)$

$R_h = (T_h - T_a) / (T_{th} - T_a) = C^i_h / (C^i_h - C_h)$

Abdomen

$C^i_{ab} (T_{th} - T_{ab}) = C_{ab} (T_{ab} - T_a)$

$C^i_{ab} [(T_{th} - T_a) - (T_{ab} - T_a)] = C_{ab} (T_{ab} - T_a)$

$R_{ab} = (T_{ab} - T_a) / (T_{th} - T_a) = C^i_{ab} / (C^i_{ab} - C_{ab})$

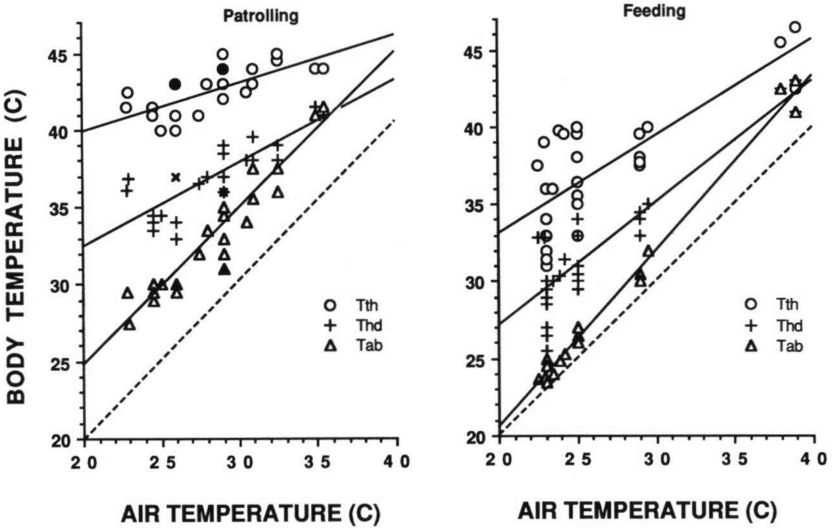

Fig. 2. Relation of body temperatures to air temperature in *Anax junius* in the field. Left panel shows data from males during sexual patrol flights (solid points are from ovipositing females and are not included in regressions that follow). Right panel shows data from both males and females during feeding flights. Solid lines are least squares regressions of body temperature on ambient temperature. The dashed line is the isothermal line. For patrolling males: $T_{th} = 0.36T_a + 32.2$, $r^2 = 0.58$; $T_h = 0.66T_a + 18.0$; $r^2 = 0.81$; $T_{ab} = 1.07T_a + 2.5$, $r^2 = 0.91$. For feeding individuals : $T_{th} = 0.57T_a + 22.8$, $r^2 = 0.47$; $T_h = 0.78T_a + 12.4$, $r^2 = 0.75$; $T_{ab} = 1.15T_a - 2.4$, $r^2 = 0.98$.

hand, R_{ab} increases significantly with T_a and is independent of solar radiation during both behaviors, so, as previously predicted, heat apparently is preferentially transferred to the abdomen at high T_a. Laboratory experiments suggest that at least 30-40% of the heat that would otherwise be retained in the thorax can be released via this route (MAY, unpublished data).

Laboratory data also support the earlier suggestion (MAY, 1987) that heat is actively transferred to the head, even though at low T_a this must make regulation of T_{th} more difficult ; T_{th}, T_h, and T_{ab} were measured in live and dead individuals as previously described (MAY, 1986), either in still air or with the specimen suspended in a wind tunnel at an air speed of about 2 m.s^{-1} (this is the average air speed of flying *Anax* during both patrol and feeding flights ; MAY, 1984, and unpublished data). The dragonflies were heated either with a focused microscope lamp or by passing current through a miniature 1K Ohm resistor implanted in the thoracic musculature. Table II summarizes the relations between T_{th} and either T_h or T_{ab} in terms of the corresponding ratios, R_h and R_{ab}. Particularly noteworthy is the striking difference between R_h in the field and in dead specimens exposed to wind in the lab ; the difference is the result of much increased transfer of heat to the head by hemolymph circulation during flight.

Data on T_h during endothermic warm-up also suggest active heat transfer to the head, despite the advantages of retaining as much heat as possible within the thorax (Heinrich & Casey, 1979). Table III summarizes data on R_h and R_{ab} during endothermic warm-up and in specimens killed with ethyl acetate and warmed internally with a resistor. During warm-up R_h is similar to that occuring in flight and is significantly higher than during passive heating. Furthermore, the extent of heat transfer may be influenced by ambient temperature. Individuals warming at $T_a = 30°C$ apparently elevated T_h less than those at lower T_a, and, in fact, in those individuals there was no difference in R_h between endothermy and passive heating.

Table II

Ratio of temperature excess of the head (R_h) and abdomen (R_{ab}) to temperature excess of thorax in living *Anax junius* in the field, dead specimens heated internally with a resistance heater, and living or dead specimens artifically heated with a microscope lamp focused on the thorax. Wind was approximately 2 m.s^{-1} in both field and lab conditions

Condition	R_h	R_{ab}
Field	0.57	0.22
External heating alive	0.38	0.19
External heating dead	0.26	0.09
Internal heating	0.14	0.12

Table III

Ratio of temperature excess of the head (R_h) and abdomen (R_{ab}) to temperature excess of thorax in *Anax junius* warming endothermically and the same specimens killed and heated internally in still air with a resistance heater

Type of Warming	T_a	R_h	R_{ab}
Endothermy	15-25	0.47	0.16
"	30	0.32	0.16
Resistor	15-25	0.30	0.19
"	30	0.27	0.25

Anax also can actively vary T_h independently of T_h and T_{ab} during endothermy. Figure 3 shows a tracing from an original record made during a prolonged bout of intermittent wing-whirring. Although T_{ab} is nearly constant initially and then increases smoothly, T_h fluctuates markedly, sometimes in parallel with T_{th} but sometimes without corresponding changes or even in opposition to changes in T_{th}. In addition, especially during warm-up at low T_a, an abrupt spike in T_h sometimes occurred at or just before

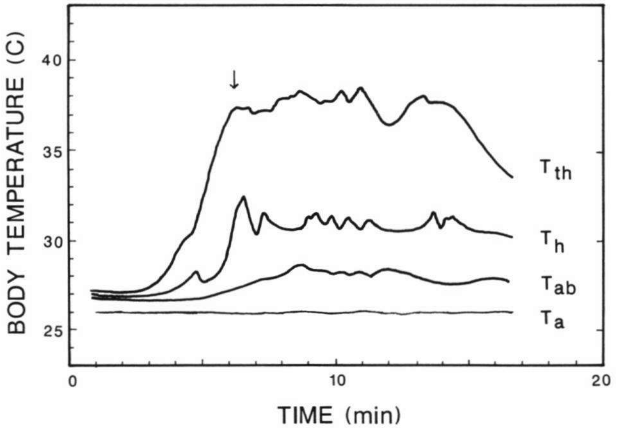

Fig. 3. Record of changes in thoracic, head and abdominal temperatures of a male *Anax junius* during endothermic warm-up followed by a period of intermittent wing-whirring; attempted takeoff after the initial warming period is indicated by the short arrow.

initiation of flight (Fig. 4); this also apparently requires active and quite rapid changes in circulation. The significance of heat transfer to the head still is uncertain, but it seems safe to conclude that it is a regular and probably important feature of the thermal responses of *A. junius.*

Control of heat production as a mechanism of thermoregulation is a real possibility in *Anax.* My earlier review (May, 1978) presented evidence that in *Tramea carolina* the proportion of gliding flight increases with increasing T_a, but later (May, 1984) I suggested that the increase might be due to slope soaring used as an energy device only incidentally associated with high T_a. Recent, careful observations of *Anax junius,* although only qualitative, have convinced me that my original conclusion probably was correct, however. On a nearly windless morning I observed feeding swarms of this species over dunes and the intervening swale at Crescent Beach, FL, from 06 : 55 until 10 : 00 EDT, while T_a increased from 24° to 31°C and solar radiation from 40 to 780 $W.m.^{-2}$. Initially flight was rapid and powered by nearly continuous wingbeats. By 10 : 00 apparent flight speed was reduced and long perriods of gliding were interspersed with occasional, shallow wingbeats. Polcyn (1988) reports similar observations in *A. junius* in hot desert areas even during territorial patrol flights. Thus the low wing loading of dragonflies compared to other large endotherms (May, 1978) may indeed permit them to exploit a thermoregulatory mechanism not generally available to the latter.

In contrast to the varied physiological alterations of heat transfer and production seen in fliers, perchers rely primarily on adjustments of posture and substrate choice in response to temperature and sunlight to control body

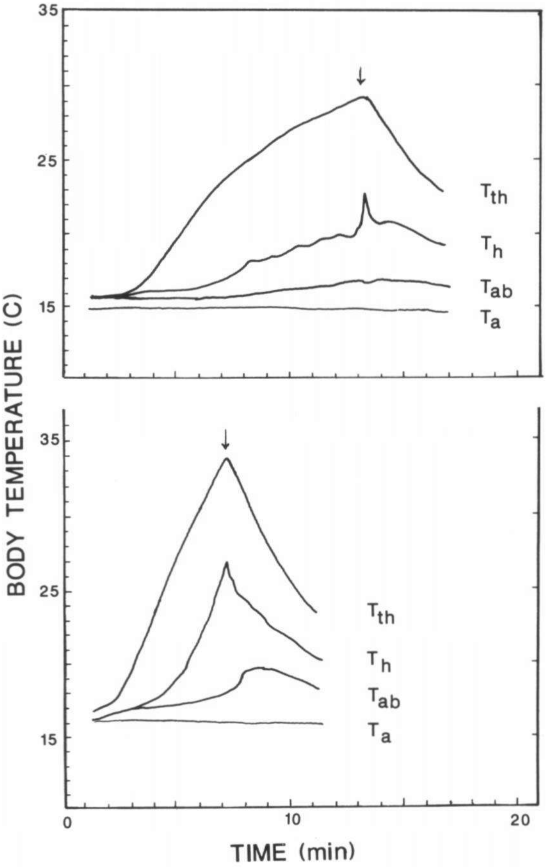

Fig. 4. Record of changes in thoracic, head and abdominal temperatures of a male *Anax junius* during endothermic warm-up ; attempted takeoff after the initial warming period is indicated by the short arrow. Note the abrupt increase in T_h at takeoff.

temperature. MAY (1976b, 1978) showed that these tactics can be effective. TRACY *et al.* (1979) elucidated in more detail the effects of some of them in the large gomphid, *Hagenius brevistylus.* By appressing its body to the ground and tilting its wings to minimize convective heat loss this insect can attain T_h equal to or greater than substrate temperature, but when perching on stems with its long axis parallel to the sun its T_{th} can approximate T_a.

Several other studies have reported on relations of T_{th} to T_a in perchers in the field. PEZALLA (1979) found that male *Libellula pulchella* in Minnesota regulated T_{th} very effectively, about as well and at about the same level as *L. auripennis* and *L. needhami* in Florida (MAY, 1976b). SINGER (1987) reported very poor ability to control T_{th} in *Sympetrum obtrusum* at rendezvous sites. By contrast, my preliminary data for *S. vicinum* indicate that this species is able to maintain T_{th} of 25-30°C at T_a down to 9°C by basking on warm, reflective substrates like large stones and concrete walls ; data at high T_a are not yet available. POLCYN (1988) found that several libellulid perchers from the Mojave Desert of California regulate T_{th} very precisely and at strikingly high levels ; he also found that they flew frequently at high T_a (in contrast to observations of HEINRICH & CASEY, 1978, for *Libellula saturata*) and suggested that convective cooling was important to maintain T_{th} within tolerable limits.

Two studies have examined thermal relations of Zygoptera. ROWE & WINTERBOURN (1981, and pers. comm., 1984) found that the small coenagrionid, *Xanthocnemis zealandica*, is a thermal conformer with no apparent behavioral adaptations to control body temperature. *Austrolestes colensonis*, however, is heliophilic, basking broadside to the sun while on territory, and exhibits a modest degree of control over T_{th}, with a maximum thoracic temperature excess of about 4°C. SHELLY (1982), showed that in the shade-seeking megapodagrionid, *Heteragrion erythrogastrum*, T_{th} is nearly equal to T_a, while in *Argia difficilis*, which selectively perches in sun flecks in tropical forest, T_{th} is about 7°C above T_a ; the range of T_a studied was too narrow to assess the ability of these species to thermoregulate.

Some exceptions to the generalization that perchers are strict heliotherms are known. MOORE (1953) reported wing-whirring in *Sympetrum striolatum* preceding early morning flight. MILLER (1964) and MAY (1976b) observed wing-whirring in large gomphids during active periods when heliothermy was not possible. I have noted the phenomenon frequently in *Arigomphus villosipes*. This species is a percher and an extremely effective heliothermic regulator of T_{th} (MAY, unpublished), with a varied repertoire of postures, including the obelisk posture (CORBET, 1963) at high T_a. Wing-whirring apparently is not used for long periods but occurs at cool or moderate T_a when, e.g., a cloud obscures the sun for a few minutes (see also MILLER, 1964). The behavior enables the dragonflies to maintain T_{th} up to 16°C above T_a under conditions of low light intensity, but in some cases they probably also are taking advantage of substrate warmth, as they typically perch on soil or broad leaves. In the laboratory, individuals warm up very readily at T_a in the range of 18-21°C, initiating flight at a mean T_{th} of 29.3°C (± 1.3 C, S.D.). At 25°C, however, they rarely initiate warm-up and usually attempt to fly immediately. The minimum temperature at which flight could be sustained after chilling and rewarming (MAY, 1976b) was 21.3 ± 1.6°C. Very little change in T_{ab} occured either during or after wing-whirring. Also, heating of the thorax with a focused microscope lamp to near lethal levels resulted in no sharp increase in T_{ab} and no evidence that T_{th} could be stabilized in the absence of behavioral responses, nor did clamping the abdomen to prevent circulatory heat exchange have a marked effect on either T_{th} or T_{ab}. Thus, although these perchers obviously can respond to cool conditions by endothermic increase in T_{th}, they show no evidence of physiological thermoregulatory responses to high T_{th}.

A final possible mechanism of ectothermic regulation has received renewed attention fairly recently. Physiological color change, controlled by temperature, was reported in Zygoptera by O'Farrell (1963), Veron (1976) and May (1976a) but among Anisoptera was known only in the basal abdominal segments of *Anax junius* (May, 1976a) and *A. imperator* (Jurzitza, 1967). Sternberg (1987) observed a similar phenomenon in male *Aeshna caerulea* and associated it with basking behaviour. It is still not entirely clear that reversible color change is primarily a mechanism for regulating body temperature in odonates, but further studies of this large species, with its very extensive blue markings, offer a good opportunity for resolution of the issue.

SIGNIFICANCE OF THERMAL RESPONSES

The importance of temperature and thermoregulation in the life of adult dragonflies is widely recognized, but their precise consequences have rarely been determined. These issues have received more attention in recent years (Heinrich, 1981 ; May, 1985), for insects in general and for Odonata in particular, but the sum total of our knowledge is still small.

In species that are routinely active at T_a below the minimum T_{th} required for flight, the ability to warm the flight muscles either endothermically or by basking is clearly important in initiating any activity. It is often reported that low T_a may delay the onset of activity (e.g., May, 1987), but few studies give specific information on the initiation of morning activity or cessation of activity in the evening. Corbet & Eda (1969) reported that *Anax junius* may feed briefly early in the morning, presumably having preceded flight by wing-whirring, but then return to sunny perches where they bask before finally abandoning their overnight roost. I observed that *Erythemis simplicicollis* and *Libellula needhami* roosted at widely scattered sites in an abandoned field and did not begin activity unless disturbed until sunlight reached their perch, at which time they evidently quickly raised T_{th} by basking and began feeding (May, 1976b). Activity at breeding sites by some *Micrathyria* species in Panama (May, 1977) and by *Tetragoneuria cynosura* in New Jersey (May, 1987) begins at T_a at or below the minimum for flight and presumably must be preceded by active warming (probably by wing-whirring in the case of *T. cynosura*), but this has not been observed.

The most extensive study of temperature at the onset of morning flight is that of Vogt & Heinrich (1983) in Maine. They found, as expected, that fliers warmed endothermically and initiated flight at T_{th} of 27°C or above (usually at least 30° C). Perchers, on the other hand, flew only when T_{th} reached about 4-12° C above the minimum for flight due to rising air temperature or warming in the sun. Interestingly, individuals placed on sunny perches flew at higher T_{th}, but still were able to take off several hours earlier on the average than those tethered in the shade. The authors concluded that "The benefit of takeoff with speed and agility at high T_{th} versus more sluggish flight at lower T_{th} apparently outweighs the energetic cost or delay in time to attain a high temperature." They went on to suggest that agile flight improves ability to capture prey and/or avoid predators. BAIRD (pers. comm., 1989) has found that foraging rate (flights per minute), although not the proportion of flights resulting in prey capture, is markedly reduced at low T_{th} in the libellulid percher, *Pachydiplax longipennis.*

Perhaps the most thorough published study to date of the effects of body temperature and thermal niche on dragonfly biology is that of SHELLY (1982) on foraging behavior of two Neotropical damselflies. *Heteragrion eythrogastrum* selects shaded perches and has low T_{th} (see above), and their foraging rate and distance is also low. *Agria difficilis*, on the other hand, behaves in more typical heliothermic fashion, choosing sunny perches and maintaining higher T_{th}; their foraging rate and distance is correspondingly greater but is dependent on T_{th}, which varies with light intensity. SHELLY pointed out the tradeoff implied by these contrasting strategies, i.e., high metabolic rate and high energy input vs. low metabolism and input. He suggested that higher T_{th} may permit *A. difficilis* to capture prey not available to *H. erythrogastrum* and perhaps to avoid predators more easily. On the other hand, during periods of low food abundance, *H. erythrogastrum* may be less affected by limited food resources.

Thermal adaptations are also closely intertwined with breeding activities, but again the relationships are complex and poorly known, most reports being anecdotal. My own studies of *Micrathyria* spp. in Panama (MAY, 1977, 1980) showed that some larger species (*M. atra, M. ocellata*) behave as fliers at cool T_a and that this enables males to establish territories and females to oviposit shortly after dawn, several hours before smaller congeners are present. I suggested that, despite the high cost of continuous flight, females may gain some advantage by reduced disturbance by males during oviposition and males by access to these early females and by reduced interspecific competition for territorial sites. The last suggestion received support from the observation that early morning activity was less frequent in the absence of congeneric species.

More recently, SINGER (1987) suggested that in *Sympetrum obtrusum*, male flight performance is strongly affected by T_{th} and that this largely determines whether contact or non-contact mate guarding is performed. He found that the probability of non-contact guarding, which he reasonably assumed to be less demanding in terms of aerodynamic power and agility, is strongly and negatively correlated with T_{th}. MARDEN (1989) demonstrated a close positive relationship between mating success and the proportion of total mass devoted to flight muscle in male *Plathemis lydia*, apparently because individuals with high flight muscle have superior flight performance ; although he did not explicitly examine temperature effects, it is clear that if temperature does affect flight performance, it may have profound and multiple effects on mating success. For example, MILLER & MILLER (1985) present evidence suggesting that flight speed may be critically important in determining mating success in *Onychogomphus forcipatus.*

A final, and perhaps the most direct, effect of temperature on reproduction is via its effect on oviposition rate. McVEY (1984) showed that the rate of egg depostion by female *Erythemis simplicicollis* increased about 2.5-fold with an increase in the temperature of the abdomen tip from 23 to 33°C ; the temperature of the basal abdominal segments had relatively little effect. This may well explain in part the restriction of reproductive activity by many Odonata to the warmest parts of the day, even though they may be capable of other activities over a wide daily time span. No evidence suggests that regulation of the temperature of the terminal abdominal segments occurs, and it is inherently unlikely given the rapid heat exchange to which this region must be subject. McVEY's experiments using models (black painted thermistor probes) suggest that the tip temperature probably varies widely and rapidly. BANKS & THOMPSON (1987) also showed a marked effect of ambient temperature on oviposition rate in *Coenagrion puella.*

GEOGRAPHIC VARIATION

In many organisms, temperature tolerance and/or sensitivity of various systems may be adapted to the thermal environment of a particular population or species. Alternatively, organisms may be confined to microhabitats that permit activity and development in the face of evolutionarily conservative temperature responses, as in odonate larvae (PRITCHARD, 1982). Earlier (MAY, 1978), I devoted considerable space to an investigation of geographic and habitat correlates of behavioral and gross physiological responses to temperature of dragonflies from Panama, Florida, and Illinois. I concluded that such correlates do occur, especially with respect to maximum voluntarily tolerated temperature, but in general they were not striking. However, VOGT & HEINRICH (1983) subsequently found that the minimum temperature at which flight is possible is 6-8°C lower in perchers from Maine than in similar species from Florida and Panama. This degree of adaptation among perchers was considerably greater than had previously been supposed. Fliers show no similar reduction in the temperature at which they normally take off after warm-up. The minimum temperature at which flight was possible was not reported for the fliers, but it is reasonable that fliers, which are independent of ambient conditions to a greater extent than perchers, should show less marked adaptation in flight temperature« At the opposite extreme of temperature, Polcyn (1988) found marked elevation in temperatures inducing heat torpor in Mojave Desert species, both fliers and perchers, and smaller, but still substantial, increases in the minimum temperature for flight.

Differing thermal adaptations of fliers and perchers might even be reflected in the composition of entire faunas. Assuming that the ability to cope with extreme or variable temperature is a significant selective force on Odonata, I surmised that in the warm and relatively equable tropics and subtropics. Zygoptera and percher Anisoptera might be at a relative advantage whereas in colder temperate and subarctic conditions, fliers would be more predominant. Table IV shows the results of a preliminary and rather superficial survey of several such areas. The distribution of some species is not well known, and in a number of cases I was uncertain whether particular species are fliers

Table IV

Comparison of faunal composition of selected temperate/subarctic vs. tropical/subtropical regions

Region	Category		
	% Zygoptera [a] (N)	% Anisoptera [a] (N)	% Fliers [b] (N)
Canada [1]	27 (51)	73 (141)	45 (63)
Central America [2]	47 (188)	53 (215)	32 (68)
"Chilean Region" [3]	31 (8)	69 (18)	56 (10)
Subtropical Argentina/Chile [3]	27 (42)	73 (111)	35 (35)
Scandinavia [4] (except Denmark)	29 (15)	71 (36)	47 (17)
Mediterranean Europe [4]	39 (37)	61 (56)	38 (21)
Southern Africa [5]	—	— (90)	28 (25)
Central Africa [5]	—	— (278)	31 (85)
Southern Australia [6]	32 (46)	68 (98)	63 (62)
Northern Australia [6]	36 (76)	64 (133)	52 (69)

[a] % of all Odonata. [b] % of Anisoptera.

[1] Walker (1953, 1958); Walker & Corbet (1975). [2] Paulson (1982). [3] Paulson (1977). [4] D'Aguilar *et al.* (1986). [5] Pinhey (1962).. [6] Houston & Watson (1988).

or perchers. Nevertheless, I think these potential errors are unlikely to obscure general patterns. With some modification, the data tend to bear out my initial hypotheses. Except in Africa, fliers do seem to be more common in regions of cooler and more variable climate. Zygoptera seem to be about as common in middle latitudes as in the tropics but are poorly represented in far northern regions. SAMWAYS (1989) found that along an altitudinal gradient in Southern Africa, Aeshnidae comprise an increasing fraction of the odonate assemblage at higher altitudes, and Libellulidae are under-represented ; this could reflect a similar effect of thermal environment on the relative advantages of fliers vs. perchers. Thus there seems to be some support for the supposition that thermal adaptations influence faunal composition over broad geographic areas.

FUTURE DIRECTIONS

Thermoregulation and adaptation to temperature among Odonata are still far from completely understood. Even behavioral and physiological mechanisms of regulation, which have been studied in some detail, are by no means fully known. Each species so far investigated shows individual peculiarities of behavior. Although currently under study in our lab, the role of intermittent endothermy in perchers, especially large gomphids, is a potentially interesting line of investigation because its effects and the circumstances of its occurrence have not been fully described and may vary among species. Perhaps even more interesting, largely uninvestigated, and of potentially wide importance, is the role of evaporative cooling, especially in fliers. MILLER (1962) initially suggested this possibility, but no quantification of water loss in the field or active control of evaporation in response to heat stress have been carried out. I estimated that in *Tetragoneuria cynosura* effective evaporative cooling would require loss of about 11% of body mass per hour and thus could at best be only an emergency measure to combat short term overheating (MAY, 1987). This assumes, however, that water supplies are not rapidly replenished. TOOLSON (1987) showed that in a cicada, which continually takes in abundant water from its food plants, evaporative cooling, with very rapid water loss, is routinely used to withstand high temperature in its desert habitat. While water is not so freely available to dragonflies, their food probably is 60-80% water, and food intake of fliers, as yet unknown, may well be substantially higher than the 10-15% of body mass seemingly characteristic of perchers (FRIED & MAY, 1983). Thus evaporative cooling may be a more practical strategy than previously thought.

Most studies of thermoregulation in insects have concentrated exclusively on T_{th}. Only since HEINRICH's (1979) work on honeybees has the possible importance of head temperature been appreciated. Although evidence for regulation of T_h independent of T_{th} is lacking for odonates, the data certainly point to the liklihood that T_h is actively elevated during flight. We are still some distance from a full appreciation of the mechanisms and even more of the adaptive advantages involved in this phenomenon.

The adaptive significance, or possibly maladaptive consequences, of temperature responses have only begun to be explored. Undoubtedly body temperature and its regulation will prove to have important effects on foraging behavior, both through effects on ability to perceive and capture prey and on energy metabolism and thus food requirements. CORBET (1963) noted that dusk feeding by some fliers is probably an adaptation allowing exploitation of food not available to perchers. The dichotomy between shade- and sun-seeking, as described by SHELLY (1982), may apply to many other tropical Zygoptera and Anisoptera, as well as to temperate zone Zygoptera, with possible shade-seekers including some *Ischnura*, *Nehalennia*, and *Xanthocnemis* that generally remain in the shelter of vegetation and are comparatively inactive.

As suggested by FRIED & MAY (1983), the influence of temperature on energy requirements is probably greatest on very sedentary species, since metabolic costs of flight are thought to be largely independent of temperature as long as normal flight is possible. Nevertheless, accurate estimation of energy requirements in the field will require knowledge of body temperature. So, in fact, will assessment of many physiological processes, including digestion and assimilation (FRIED & MAY, 1983), water loss, oogenesis, and others. Thus field and laboratory studies of temperature responses can contribute to understanding of many aspects of the life of Odonata.

The interaction of temperature and thermoregulatory behavior with mating behavior and other aspects of reproduction is clearly complex. Some suggestions for future studies have been made earlier. The potential effect of temperature through its influence of egg maturation rate, oviposition rate, and flight performance should be considered carefully in studies of reproductive behavior. SINGER (1987) correctly pointed out that physical factors such as temperature are often correlated with social factors like population density, and unless the former are considered explicitly, "behavior resulting from physiological constraints may be incorrectly attributed to social factors." There is a crying need for further work to assess the effects in the field of temperature on oviposition and male territory holding potential.

It is also possible that thermoregulatory behavior may interfere with mating or other behaviors. For example, male *Arigomphus villosipes*, when perching on shore, typically face the water during periods of moderate temperature but apparently orient primarily in response to the direction of solar radiation at low and high temperature; these latter orientations might involve some disadvantages in terms of detection or response to potential mates or rivals (MILLER & MILLER, 1985).

Biologists commonly assume that organismal characteristics are species-typical, and ethologists and physiologists rarely concern themselves with interpopulational differences. Nevertheless, differences clearly exist (cf., CAMPANELLA & WOLF, 1974 ; KOENIG & ALBANO, 1985). For that matter, association of interspecific differences with particular thermal habitats has received little attention, although the few studies to date suggest that both sorts of differences that occur may be of considerable importance. Studies of all aspects of the thermal biology of dragonflies from a variety of habitats and geographic regions would be of considerable value. Boreal species would be of particular interest in this regard, as would species from deserts and a variety of tropical habitats, especially forest.

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