THERMAL ADAPTATIONS OF DRAGONFLIES

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Most Odonata probably exert some control over their body temperature. Such behaviour is favored by the high, variable temperature of their terrestrial habitat and by the fact that dragonflies are relatively large insects and thus exchange heat with the environment comparatively slowly. Different species may thermoregulate behaviorally by controlling the external heat load or physiologically by altering the amount of heat generated by or dissipated from the thoracic muscles. The former method is characteristic of perchers, which are usually in a situation that permits considerable modulation of intercepted solar radiation, mostly by postural adjustments. There is also evidence that some species may perch more frequently in the shade when ambient temperature is high. Fliers, by contrast, have little opportunity to control intercepted solar radiation but continually generate large amounts of heat during flight. They may alter their rate of heat loss by controlling haemolymph flow from the thorax or their rate of heat gain by changing the proportion of gliding vs. flapping flight. Some species combine behavioral and physiological modes of regulation. Adaptive geographic, seasonal, and inter-habitat variation occurs in the responses of dragonflies to temperature. Voluntary avoidance of high temperature seems most closely adapted to the thermal environment. Temperature responses and thermoregulatory ability also vary with age and sex. The effects of temperature on the activity patterns of Odonata and the adaptive significance of thermoregulation have yet to be rigorously demonstrated in most cases.

INTRODUCTION

Some years ago CORBET (1963) discussed adaptations to temperature of adult dragonflies and mechanisms by which they control their thoracic temperature (T_b). At that time, no data existed on the temperatures that dragonflies experience in the field or on the limits of thermal tolerance. Since then,

Corbet's suppositions have been largely confirmed. Considerable information has accumulated showing that Anisoptera thermoregulate, some quite effectively, and that they are adapted to function at rather high T_b (MAY, 1976b, 1977). In the present paper I will attempt to identify some of the selective forces that influenced the evolution of thermoregulation in Odonata, the principal mechanisms by which dragonflies have met the thermal challenges of their environment, and the ways in which adaptations to temperature are related to specific features of the biology of various species, as well as point out some gaps in our knowledge of their thermal biology.

Thermoregulation is the maintenance by an animal of body temperature relatively independent of ambient temperature, by means of specially-adapted behavioral or physiological responses. Body temperature need not be held constant or be uninfluenced by environmental temperature. In fact, T_b is never absolutely independent of environmental conditions, even in very specialized thermoregulators like man. Thermoregulation does require an active response by the animal. HEATH (1964) showed that even inanimate objects in a heterogeneous environment can have a temperature distribution that could be interpreted as indicating thermoregulation. Thus it is necessary to determine the mechanisms by which T_b is controlled or at least to show that the distribution of T_b could not occur passively.

Thermoregulation is indicated if a linear regression of T_b on environmental temperature is significantly less than 1.0. As a matter of convenience I will use air temperature in the shade (T_a) in the general vicinity of the insects as a measure of effective environmental temperature (T_e; BAKKEN & GATES, 1975). In many cases T_a and T_e are not equal, since T_e is also influenced by radiant and evaporative heat exchange. Generally T_a is a conservative estimate of T_e, since the latter is usually more variable. By substituting T_a for T_e thermoregulation that actually occurs may be obscured, but it is unlikely that an insect would appear to thermoregulate when it does not.

All thermoregulatory mechanisms require a source of energy plus some means of controlling rates of heat gain and/or loss. Heat is exchanged with the environment via (1) evaporation of water from the respiratory or body surfaces, (2) exchange of radiant energy with other objects, (3) conduction to or from other objects, and (4) convection to the surrounding air. In all but the first case, the rate of exchange depends on the instantaneous difference between the body and its surroundings. Thermoregulating animals in general, and dragonflies in particular, may be classified as ectotherms or endotherms depending on the source of heat used in thermoregulation. Ectotherms require an external heat source, such as the sun; the latter special case is known as heliothermy. Endotherms depend primarily on heat-producing metabolic processes. Dragonflies may use both sources simultaneously or they may switch between endothermy and ectothermy from time to time.

The size of an animal greatly influences its ability to thermoregulate and its thermoregulatory strategy. In small objects the ratio of surface area to mass is greater than in large objects of the same shape. As a result, heat exchange with the environment is more rapid in small animals and their T_b is more closely coupled to T_a. In addition, convection becomes more important relative to other modes of heat exchange (PORTER & GATES, 1969). Some of the consequences for dragonfly thermoregulation will be explored below.

METHODS

Techniques for measuring T_b in the field, maximum voluntarily tolerated temperature (MVT) and heat torpor (HT), endothermic warm up rates, effects of circulation on heat transfer, and cooling constants (K) have been described (MAY, 1976b). Maximum voluntarily tolerated temperature is the temperature at which dragonflies heated with a lamp in the laboratory act to avoid further increase in T_b. Heat torpor is the point at which paralysis occurs as a result of overheating. All new experiments on MVT and HT were performed the same day that the animals were captured. The last parameter, K, is a constant defined by Newton's law of cooling, $dT_b/dt = K(T_b - T_a)$, where t is time in minutes. This relationship accurately describes passive cooling in dragonflies under most circumstances (MAY, 1976b, 1976c). The cooling constant can be converted to thermal conductance, a measure of the ease of heat transfer, by multiplying by the specific heat of insect tissue [0.8 cal $(g \cdot °C)^{-1}$; KROGH & ZEUTHEN, 1941].

Data on variation of the thermal environment were obtained with a BAT-4 portable thermocouple thermometer and copper-constantan thermocouples. One thermocouple junction was implanted in the thorax of a freshly killed male *Erythemis simplicicollis*. The dragonfly was mounted in a lifelike posture on a chip of bark and a second thermocouple was taped to the bark so the junction was about 2 cm from the dragonfly and 1 cm above the substrate. The assembly was placed on an exposed log at the shore of a lake. Other ambient temperatures were taken with a thermocouple mounted in a hypodermic needle. All thermo-couples were calibrated against an accurate mercury thermometer before use.

The effects of postural adjustments on the area of body surface exposed to sun was determined in *Pachydiplax longipennis*. I tethered individuals, with a short length of wire implanted in the thorax, on a piece of tracing paper taped to the top of a Plexiglass box. The entire apparatus was placed outside on a hot, sunny day. A mirror was placed at an angle of approximately 45° beneath the insect and the reflection of the dragonfly's shadow was photographed. As they warmed to levels exceeding the MVT, some individuals assumed the obelisk posture (CORBET, 1963; MAY, 1976b) that is a characteristic heat avoidance posture in this species. The difference in the area of the shadows of individuals oriented horizontally and the same individuals in the obelisk represents the

proportional reduction in effective area exposed to solar radiation. The approximate maximum and minimum cross-sectional areas of the tagmata of *Pachydiplax* were calculated from external measurements made with an ocular micrometer.

Wing areas of various species were determined by making pencil rubbings of excised wings in paper of known weight per unit area. The outlines obtained were cut out and weighed. Wing loading was calculated by dividing the body mass of each specimen by its wing area.

The effect of temperature on the tendency to glide rather than continuously flap the wings was examined in *Tramea carolina*. On several sunny days near Gainesville, Florida, I observed flying individuals far from breeding sites. I followed each individual as closely as possible with binoculars. Every 5 or 10 seconds I noted whether the wings were moving at the instant of observation.

RESULTS AND DISCUSSION

SELECTION PRESSURES

Three major aspects of dragonfly biology seem critical in the evolution of thermoregulation. Adult dragonflies are terrestrial and diurnal, they are powerful fliers and depend on their aerial ability during most activities, and they are comparatively large insects. These are all characteristics that favor thermoregulation.

The terrestrial and diurnal habitat presents both the necessity and the opportunity for thermoregulation. Because of the high density and specific heat of water, the aquatic environment from which the ancestors of insects arose was thermally more stable than the environment into which they spread. At the same time, heat exchange between the animal and the surrounding medium is much reduced in air as compared to water. Thus terrestrial organisms can maintain a sizable difference between T_b and T_a, provided they are exposed to some heat source such as sunlight or metabolic heat, much more easily than aquatic organisms. The variation and average level of environmental temperature experienced by dragonflies is probably greater than is faced by most insects since dragonflies usually occupy habitats exposed to direct sunlight, and they are frequently active during the warmest portion of the day when radiation intensity is high. Their reliance on vision may influence this tendency, but the result is that dragonflies must be adapted to cope with high temperature. Table I shows temperature variation in various habitats near a small lake at Urbana, Illinois, between 1300 and 1530 h on several afternoons in July. Also shown is the variation in body temperature of a dead specimen of *Erythemis simplicicollis* exposed to direct sunlight. The latter provides an approximate model of the thermal environment (T_e) to which a living dragonfly in a similar situation is

Table I

Variation in environmental temperatures and of the body temperature of a dead male
Erythemis simplicicollis exposed to the sun. Data were obtained at Crystal Lake,
Urbana, Illinois, between 1300 and 1530 h on 22-24 July 1977

Site	Temperature mean and range [$^{\circ}$C]
Dragonfly	39.7 (35.0 - 48.0)
1 cm above substrate, beside dragonfly	32.6 (30.5 - 37.0)
0.5 m above ground in open, shaded area	27.9 (27.0 - 29.5)
0.5 m above ground in open, sunny area	29.5 (28.0 - 30.5)
0.5 m above ground in thicket	28.0 (27.0 - 29.5)
Beneath litter in thicket	26.1 (24.5 - 28.0)
In sunny and shaded patches of grass	28.4 (25.0 - 32.5)

exposed, including effects of radiation and, to some extent, evaporation. Clearly, a dragonfly would risk exposure to lethal high temperatures even on relatively mild days unless it somehow maintained T_b within narrower limits. It is likewise clear that insects in more sheltered habitats would encounter less thermal stress. Some dragonfly species may also become active even before sunrise (MAY, 1977) or remain active at dusk and so must maintain activity in the face of relatively cool temperature. On the other hand, adult dragonflies avoid low temperature extremes by passing the temperate zone winter as aquatic nymphs, usually in diapause (CORBET, 1963).

The ability to fly is property of the utmost importance in the evolution of thermoregulation in insects. Flight requires the expenditure of large amounts of energy and thus the production of considerable heat. In large insects thoracic temperature is inevitably elevated above T_a during sustained flight, and if the thorax has structures that retard heat flow quite large temperature differentials may result. Maintenance of an elevated T_b does not in itself constitute thermoregulation. The insect must also possess a means of controlling the amount of heat generated or lost. Nevertheless, the high heat production concomitant to flight affords the possibility of endothermic temperature regulation. There is probably strong selection pressure toward regulation, especially in insects like dragonflies that depend on flight for all activities. Since flight automatically results in high T_b under warm ambient conditions, the flight muscles must be adapted to operate at high temperature, and the insects must evolve a means of unloading excess heat from the thorax or else cease flying (CHURCH, 1960a; HEATH & WILKIN, 1970). Since biological systems usually can adapt only to a restricted range of temperature, those insects that adapt to high T_b generally must raise the temperature of their flight muscles well above T_a under cool conditions. This is often accomplished by rapid, synchronous contractions of the flight muscles, accompanied by low amplitude wing vibration or wing-
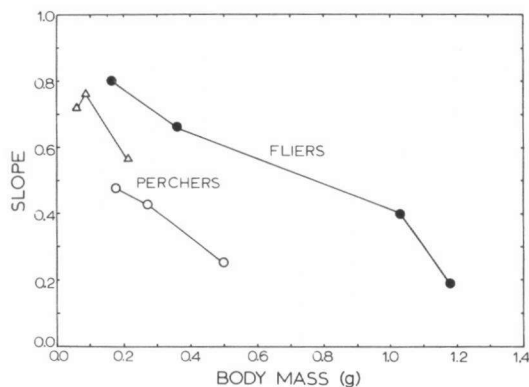
Fig. 1. Dependence of T_b on T_a as a function of mean body mass in dragonflies in the field. The ordinate is the slope of a linear regression of T_b on T_a. Closed circles are fliers studied near Gainesville, Florida, open circles are perchers from near Gainesville, open triangles are perchers from the Panama Canal Zone. A slope of 0 indicates perfect thermoregulation, a slope of 1.0 maximum dependence of T_b on T_a. Data are from MAY (1976b, 1977).

whirring (KROGH & ZEU-THEN, 1941; HEATH & ADAMS, 1967; MAY, 1976b). Among Odonata, fliers (sensu CORBET, 1963) are much more likely than perchers to be endotherms because of their continuous heat production.

Rapid heat production is a consequence of flight, but so is rapid heat loss. Even in still air, a flying dragonfly is subject to forced convection. Heat loss increases approximately in proportion to the 1/4 power of wind velocity (MAY, in prep.). The result is indicated in part in Figure 1. At a given body size, the T_b of fliers is more dependent on T_a than is that of perchers, although very large fliers thermoregulate quite well.

As indicated already, body size is very important in determining rates of heat exchange and thus is a major influence on thermoregulation. Figure 2 shows the relation of cooling constant to thoracic mass in dragonflies and several other groups of insects, plus one of the smallest mammals. Even the largest sphinx moths lose heat about twice as readily as the shrew, and in the largest dragonflies K is about three times the shrew value. Thus insects are at a substantial disadvantage, compared to vertebrates, in their ability to thermoregulate. Small damselflies (thoracic mass about 5-10 mg) must have greater difficulty maintaining a difference between T_b and T_a than does the average sized anisopteran. No data are available for Zygoptera, but Figure 1 clearly shows the increasing dependence of T_b on T_a with decreasing size in a variety of Anisoptera. At the upper end of the size range dragonflies can, under favorable conditions, achieve a degree of thermal independence comparable to many small vertebrates (MAY, 1976b), but at the lower end their T_b is tightly coupled to T_a.

Large size facilitates both heliothermic and endothermic thermoregulation, but it particularly favors endothermy. Wing loading, the ratio of body mass to wing surface area, increases in proportion to approximately the 0.4 power of mass (Fig. 3). Considerable theoretical and empirical evidence indicates that
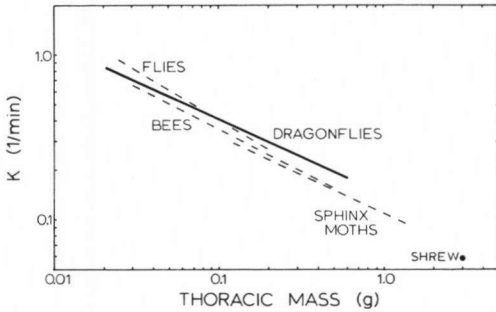
Fig. 2. Cooling constant (K) as a function of thoracic mass in various insects and of whole body mass in a shrew, *Sorex cinereus* (MORRISON et al., 1959). Data on insects from MAY (1976b, 1976c).
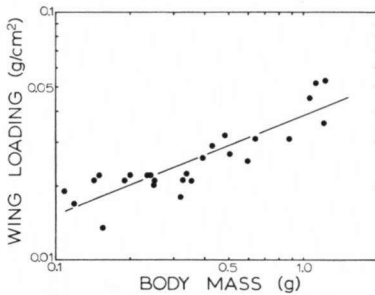

Fig. 3. Wing loading (W_L) as a function of body mass (m) in Anisoptera. Each point represents the mean for one species. The regression is log W_L = 0.40 log m − 1.42.

the power required to stay aloft during flapping flight increases with wing loading (BARTHOLOMEW & HEINRICH, 1973; CASEY, 1976; PENNYCUICK, 1969). Thus increased mass specific heat production, as well as decreased heat loss, may be a consequence of large size. The relatively high wing loading of large species also means that they are less likely than small species to be able to fly effectively if they cannot translate power produced by the muscles into aerodynamic power with maximum efficiency. Since low temperature may reduce the efficiency of the flight system (NEVILLE & WEIS-FOGH, 1963; MACHIN et al., 1962), large dragonflies are more likely to evolve endothermic warm-up as a prelude to flight.

Size also affects thermoregulation in another way, such that small size can be an advantage. For small insects the thermal environment is very patchy. They can take advantage of small regions of exceptionally warm or cool air, such as boundary layers along the ground, tree branches, or other substrates (HEATH & WILKIN, 1970). HOCKING & SHARPLIN (1965) have suggested that Arctic mosquitoes bask at the focus of flowers like parabolic reflectors. Ground perching Anisoptera, such as *Erythemis* (see below), and especially Zygoptera, probably use similar strategies. Odonata are mostly relatively large, however, and are so frequently on the move that selective utilization of thermally favorable microhabitats is probably less important to them during active periods than it is to many other insects.

The characteristics of the terrestrial environment, body size, and flight are

important determinants of thermoregulatory strategy in all insects. One charac-
teristic of dragonflies in particular that has influenced thermoregulatory be-
havior, especially in heliothermic species, is their elongate body form. The shape
is probably primarily a result of selection for streamlining and control of pitch
and yaw in flight (PRINGLE, 1967), but an additional consequence is that a
dragonfly perched in the sun can greatly vary the effective surface area exposed
to solar radiation. Measurements on 5 male *Pachydiplax longipennis* show that
the maximal cross sectional area of the thorax, in the mid-sagittal plane, is about
1.6 times the minimum transverse section at the base of the forewing (34 vs. 21
mm^2). For the abdomen, the maximum (mid-sagittal) is roughly 6 times the
minimum transverse section at the second abdominal segment (41 vs 6.5 mm^2).
As judged by the areas of the resulting shadows, *Pachydiplax* can reduce their
effective area by 13-59% (mean 39%) by switching from a horizontal posture
into an obelisk posture. These data undoubtedly underestimate the reduction
usually obtained under natural conditions since the experimental insects were
on a substrate very unlike their usual perches, and the tether interfered with
normal posturing. The three individuals that managed what appeared to be a
normal obelisk all reduced their shadow area by more than 50%.

THERMOREGULATORY MECHANISMS

Effective thermoregulators usually have some adaptation to increase thermal
insulation. In the case of dragonflies, portions of the tracheal system form air
sacs that virtually surround the thoracic musculature except at the ventral in-
sertions. Figure 4 gives an idea of their extent in *Anax junius*. CHURCH
(1960b) showed that these sacs provide effective insulation. Assuming that
his large dragonflies were similar to *A. junius* in size and thickness of air
sacs (about 1.0 mm), Church's data indicate an average conductivity of
approximately 1.2 x 10^{-4} cal (sec-cm·°C)$^{-1}$, compared to 0.7 x 10^{-4} cal
(sec·cm·°C)$^{-1}$ for mammalian fur (BIRKEBAK, 1966). A much more thorough,
quantitative, morphological description of the dragonfly thorax is required be-
fore this figure can be considered accurate, however.

This insulation will tend to stabilize T_b somewhat, and it undoubtedly per-
mits dragonflies in flight to generate much larger excesses of T_b over T_a than
would otherwise be possible (CHURCH, 1960b). Nevertheless, dragonflies must
continually modify heat input and/or outflow to maintain a regulated T_b. Un-
doubtedly the principal mechanisms for regulating T_b in perchers are changes in
posture or choice of perches. Postural adjustments are most important in the
cases that have been carefully studied, probably because of the great capability
for modifying solar heat input merely by changing the exposed surface. Changes
in perch choice are less well documented. LIEFTINCK (1953) described a shift
in activity in *Diplacina paula* from high in trees in early morning to perches near

streamside near midday. Presumably the insects were able to warm themselves by basking at treetop level earlier than this was possible lower down. I have noted an apparently similar phenomenon among the fliers, *Tauriphila argo* and
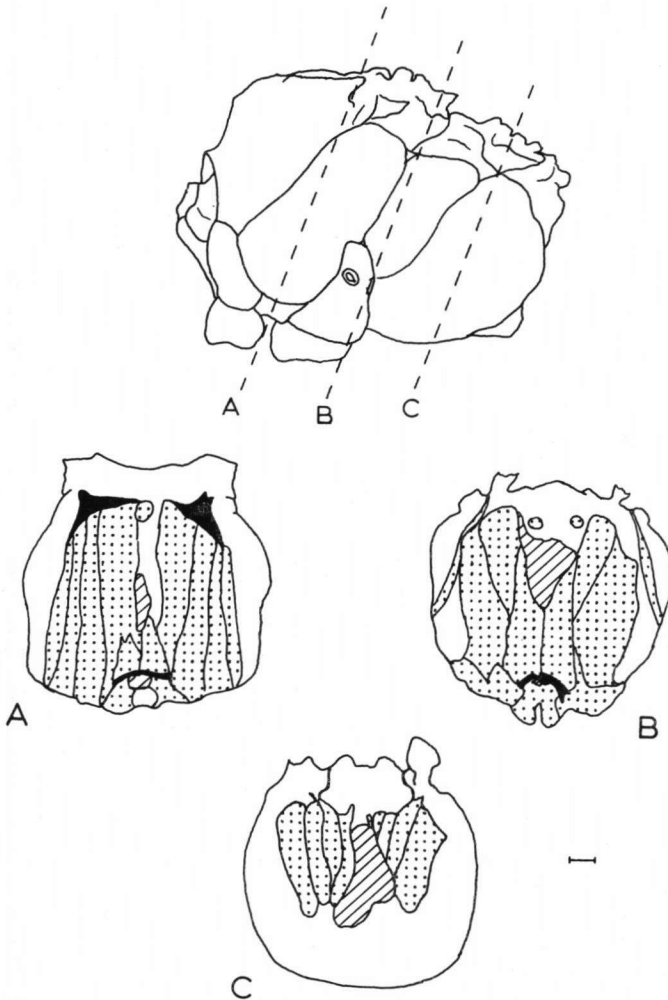

Fig. 4. Camera lucida drawings of the thorax of a male *Anax junius* (thoracic mass — 0.415g), showing the insulating subcuticular air sacs. The horizontal bar indicates 1 mm. The three lower drawings are cross-sections in the planes indicated in the lateral view at top. Sclerotized areas are black, muscles stippled, and other tissues hatched; white spaces are air sacs.

Tramea spp. on Barro Colorado Island in Panama. A small scale movement of similar nature may occur in *Micrathyria hageni* and *M. schumanni*. At a pond at Hacienda Taboga, Prov. Guanacaste, Costa Rica, I determined the relative positions of individuals of these species in vertical sticks that I set out as perches. The proportion perched at the tops of sticks, compared to those perched low along the sides, was negatively correlated with T_a ($r = -0.505, t = 2.48, p < 0.05$; May, unpublished data). This may reflect a tendency of these species to select more exposed perches early in the morning in an effort to maintain high T_b. On the other hand, perch height is positively correlated with T_a in *Erythemis simplicicollis* (MAY, 1976b), largely as a result of their tendency to perch on the ground or other broad substrates at low T_a, thereby taking advantage of the warm boundary layer associated with such surfaces. CORBET (1963) cites a number of instances in which other species may utilize the same strategy.

Horizontal movements between sunny and shaded areas are common among vertebrate ectotherms (HEATH, 1965; TEMPLETON, 1970) but have not been demonstrated in dragonflies. I attribute this in part to the fact that many Odonata apparently remain on 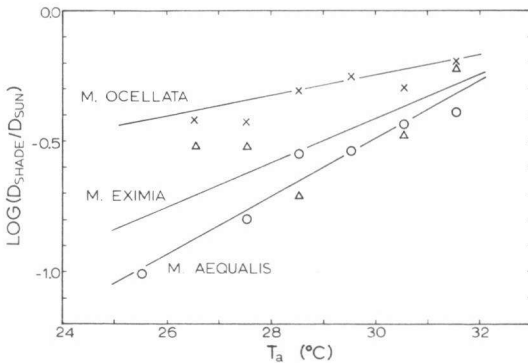and defend specific perches within a breeding territory. Abandonment of their position might result in loss of an opportunity to mate. For the most part dragonflies perch preferentially in the sun regardless of T_a (although at very high temperature they may be forced to abandon normal activities and seek shelter), but there is some evidence that the tendency declines with increasing T_a in some species. During a study of three species of *Micrathyria* in the Panama Canal Zone I mapped the extent of sunny and shaded areas and the position of dragonflies (MAY, 1977). Thus I could determine the relative density of dragonflies in the sun and shade (Fig. 5). Each species always preferred sunny areas, but

Fig. 5. Relative tendency to perch in the sun or shade in three species of *Micrathyria* in Panama. The ordinate is the log of the ratio of density, in individuals/m², of dragonflies perched in the shade (D_{shade}) to density of dragonflies perched in the sun (D_{sun}). The abscissa is T_a. The regression equations are: *M. aequalis* (circles), $\log (D_{sun}/D_{shade}) = 0.11 T_a - 3.78, r = 0.521; - M. eximia$ (triangles), $\log (D_{sun}/D_{shade}) = 0.085 T_a - 2,96, r = 0.455; -M. ocellata$ (crosses), $\log (D_{sun}/D_{shade}) = 0.035 T_a - 1.30, r = 0.217$. For clarity, only the mean $\log (D_{shade}/D_{sun})$ is shown within each 1°C interval, but the regressions are based on all individual observations.

the preference decreased with increasing T_a (the trend is not significant for *M. ocellata*). At a second, forest bordered pond in the Canal Zone, *M. atra* clearly preferred shaded perches at high T_a (MAY, 1977), but I could not quantify the tendency in this case. At a similar forest pond near Rincon, Peninsula de Osa, Costa Rica, I observed libellulid dragonflies of several species, mostly *M. atra* and *Orthemis ferruginea*, perching on vertical sticks that I set around the margin, extending about 0.5 m above the surrounding emergent vegetation. Again there was a preference for sun that decreased with increasing temperature. In this case untransformed values of D_{shade}/D_{sun} were positively correlated with the temperature of a mercury thermometer with the bulb blackened and exposed to the sun ($r = 0.704$, $p < 0.001$, $n = 13$). These results were probably consequences of increased avoidance of shaded perches at low T_a. Overall density of dragonflies at the ponds increased with increasing temperature, however, so some individuals may have been forced to less favorable, shaded perches by increased territorial pressure rather than as a direct response to temperature. A completely satisfactory demonstration of shade-seeking awaits more observation and experimentation. The phenomenon is most likely at sites where T_a is usually high and where shaded perches are available that do not subject their occupants to a great disadvantage in procuring a mate.

A final thermoregulatory adaptation of ectothermic Odonata is the ability to change color reversibly in response to ambient temperature (O'FARRELL, 1963, 1964, 1968; VERON, 1973, 1974, 1976; MAY, 1976a). The capability is probably widespread among Zygoptera and may occur in a few Anisoptera (VERON, 1974; MAY, 1976a). I have recently found that blue areas of *Lestes rectangularis* and *Enallagma civile* darken reversibly at $T_a = 15°C$, but those of *E. exsulans* apparently do not even at $10°C$ (one specimen tested). The precise role of the color change in thermoregulation is not clear, but it probably amplifies the sensitivity of cuticular heat sensors, thus facilitating optimal orientation to the sun (VERON, 1974).

Three broad categories of endothermic regulatory mechanisms are identifiable. The first is wing-whirring that raises or maintains high T_b before or between flights, as described above. This phenomenon has recently been reviewed (HEINRICH, 1974; MAY, 1976b, 1976c). The second category includes the means by which rates of heat loss are controlled during flight. The principal one in dragonflies appears to be control of circulation. *Anax junius* modifies the rate of heat loss from its thorax by altering the flow of haemolymph to the abdomen where heat can be dissipated more rapidly (MAY, 1976b). Under conditions of high heat load, circulation is increased and T_b stabilized. This may be the primary means of controlling T_b in fliers, as it apparently is in some other large insects (HEINRICH, 1971b). Perchers may also benefit from such a mechanism, particularly since many thermoregulatory postures probably reduce the heat load on the abdomen more than on the thorax.

A third strategy that could be used in endothermy is control of heat production during flight. Changes in heat production are very important in vertebrate endotherms, and HEATH & ADAMS (1967) suggested that sphinx moths deliberately alter the efficiency of their aerodynamic power output and produce more heat at low T_a. The best evidence now indicates that this is not the case and that these moths depend entirely on control of heat loss (HEINRICH, 1971a; CASEY, 1976). Sphinx moths, however, have relatively high wing loading (BARTHOLOMEW & HEINRICH, 1973) and must flap their wings continuously to remain aloft. Dragonflies, even large ones, have much lower wing loading and can glide for relatively long intervals, thus greatly reducing their average rate of heat production. HANKIN (1921) and CORBET (1963) noted that many species seem to glide more at high T_a. Figure 6 shows that in *Tramea carolina* there is indeed a significant positive correlation of the amount of gliding with T_a, suggesting that dragonflies may vary heat production as a means of thermoregulation. HANKIN (1921) suggested that the insects glide to take advantage of thermal updrafts and that the prevalence of such drafts at high temperature explains the prevalence of gliding at high T_a. The data of Figure 6 are all from bright, sunny days when the thermal gradient between ground and air was probably high, favoring updrafts even at lower T_a. Also, the insects did not circle upward or show other behavior suggesting that they utilized updrafts. Even if they did, the result must be lower heat production at high T_a, thus stabilizing T_b.
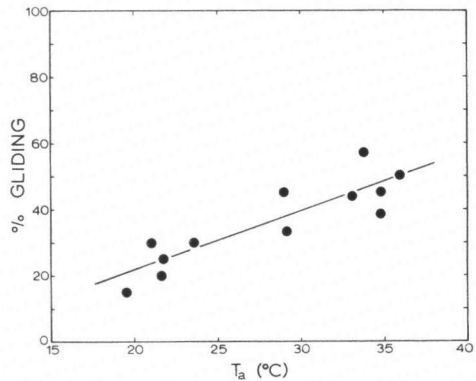

Fig. 6. Pattern of flight in *Tramea carolina* as a function of T_a. The percentage of sightings at which the wings were not moving is % Gliding. The regression equation is % Gliding = 1.76 T_a − 13.6, r = 0.879, n = 12.

Finally, dragonfly species may combine endothermy and ectothermy. Some large Gomphidae perch without wing-whirring in bright sunshine, but during cloudy periods or in the shade they vibrate their wings vigorously (MILLER, 1964; MAY, 1976b). *Micrathyria ocellata* and *M. atra* in Panama employ a quite different strategy (MAY, 1977). Early in the morning, if T_a is below a certain threshold, they fly continuously, maintaining T_b 10 − 15°C above T_a. At warmer T_a they drastically reduce their period of flight and behave like ordinary perchers, preventing overheating by postural changes. The transition from flight to perching occurs at T_b levels well below the maximum tolerated, so I infer that

these species fly continuously in order to maintain high T_b rather than perching to prevent overheating. *Brachythemis leucosticta* apparently behaves similarly (CORBET, 1963) but may terminate flight only to avoid excessive T_b. Wing-whirring while perched and flying specifically to elevate T_b are energetically expensive, but they may confer a degree of thermal independence not available to pure ectotherms or endotherms. Species employing such strategies can take advantage of the sun's heat much more readily than fliers but are still capable of maintaining elevated T_b in the absence of sun and thus may be able to extend their periods of activity. Therefore, such behavior should be strictly distinguished from cases in which species fly continuously early or late in the day but then terminate activity altogether during the hottest periods (CORBET, 1963).

ADAPTATION OF THERMAL RESPONSES

One aspect of the thermal biology of dragonflies that has perhaps excited more interest and speculation than any other is the effect of temperature on daily or seasonal periods of activity. It is commonly assumed that activity in general is restricted by excessively low or high environmental temperature and that certain specific behaviors, like territorial defense or mating, can occur only within still narrower ranges of temperature (CORBET, 1963; LUTZ & PITTMAN, 1970; CAMPANELLA & WOLF, 1974). There is considerable evidence, cited above, that thermoregulation permits some species to extend their activity through periods that might otherwise be too cool. Certainly there is a lower limit of T_b below which flight is impossible (MAY, 1976b) but a dragonfly may be active at lower T_a if it can bask or wing-whirr. On the other hand, many species are not active, or at least are not usually observed, until T_a is well above the minimum for flight. Low temperature may still prevent activity in these species, but other factors cannot be dismissed.

There is no entirely convincing evidence that activity of dragonflies is prevented by high temperature. *Tramea carolina* and *Macromia taeniolata* may stop flying and perhaps seek shelter at $T_a > 35°C$ (MAY, 1976b), as may *Aeshna multicolor* (PAULSON, pers. comm.). CORBET (1963) cited several other possible examples of fliers that seem to be restricted to cooler parts of the day. LUTZ & PITTMAN (1970) noted a sharp decrease in activity of several species at $T_a > 39°C$. This evidence is largely anecdotal, however, and in no case have all other explanations been eliminated. It is particularly difficult to separate the effects of light and temperature, since the T_b of many dragonflies is strongly dependent on absorption of solar radiation. Other factors besides light that might limit activity in odonates include humidity, activity patterns of prey, and interspecific competition for space (MAY, 1977). All of these could result in activity patterns that are correlated with but not caused by variation in temperature. While temperature is probably the limiting factor in some cases, a thorough

knowledge of the biology of a species must precede unequivocal demonstration
of the influence of temperature on its activity.

Table II

Geographic and seasonal variation in maximum voluntarily tolerated temperature (MVT)
and heat-torpor (HT) in two libellulid dragonflies. Bracketed pairs are significantly (s)
or not significantly (ns) different at the p = 0.05 level

Species	Locality	Months (Temp.)[a]	Sex	MVT ± s.d. [°C]	HT ± s.d. [°C]
Erythemis simplicicollis	Gainesville[b], Florida	Apr. - May (16.0 - 29.0)	♂, ♀	38.4 ± 2.25 (n = 8)	45.1 ± 2.39 (n = 8)
		June - Sept. (21.2 - 32.3)	♂, ♀	41.1 ± 1.19 (n = 16)	47.2 ± 1.30 (n = 14)
		June - Sept. (21.2 - 32.3)	♂	40.6 ± 1.46 (n = 10)	47.5 ± 1.57 (n = 9)
	Urbana, Illinois	July (18.1 - 30.3)	♂	39.0 ± 1.67 (n = 9)	48.1 ± 0.77 (n = 9)
Pachydiplax longipennis	Gainesville, Florida	May (17.6 - 30.7)	♂, ♀	36.9 ± 2.00 (n = 28)	44.9 ± 1.64 (n = 25)
		July - Oct. (20.2 - 31.2)	♂, ♀	38.2 ± 2.10 (n = 23)	46.1 ± 1.80 (n = 22)
		July - Aug. (21.8 - 32.6)	♂	38.0 ± 2.19 (n = 14)	46.1 ± 1.27 (n = 13)
	Urbana, Illinois	July (18.1 - 30.3)	♂	36.0 ± 1.86 (n = 14)	46.3 ± 1.29 (n = 14)

The bracketed significance indicators: for *Erythemis simplicicollis* Apr.-May vs June-Sept.(♂,♀) pair = s (both columns); June-Sept.(♂) vs Urbana July pair = s for MVT, ns for HT. For *Pachydiplax longipennis* May vs July-Oct. pair = s (both); July-Aug.(♂) vs Urbana July pair = s for MVT, ns for HT.

[a] Mean low – mean high temperature (°C) for period indicated.
[b] Data on Gainesville individuals are in part from MAY (1976b).

Behavioral responses of dragonflies to high temperature seem to be closely
attuned to their environment. Table II shows that in *Pachydiplax longipennis*
and *Erythemis simplicicollis*, specimens from Illinois, avoided further heating at
lower temperature than specimens from Florida tested at the same time of year.
This corresponds to differences in average summer temperatures between the
two areas. By contrast, HT, was nearly identical in both areas. There were
significant seasonal changes in HT as well as MVT among Florida dragonflies,
however, suggesting that acclimatization of thermal responses occurs. Re-
sponses to high temperature are also adapted to differences in habitat, as shown
in Figure 7. I subjectively placed several species of perchers from Florida and
Panama into one of three habitat categories depending on where they usually

perch. *Epigomphus quadracies* and two species of *Micrathyria* frequent shaded areas like forested streams or ponds. Two other *Micrathyria, Pachydiplax* and *Libellula auripennis* and *L. needhami* choose unshaded perches well above the ground. Three *Erythemis* species characteristically perch in exposed areas on or near the ground and are thus probably subjected to the highest environmental temperatures. There is a clear increase in MVT from the coolest to the warmest habitat. A similar but much less marked trend occurs in HT. Analysis of variance shows that both MVT and HT are different among dragonflies from each habitat (p < 0.01 for all comparisons). Nevertheless, it appears that MVT is more adaptable than HT. It is likely that dragonflies from cooler situations readily maintain T_b well below HT and thus enjoy a large margin of safety between their usual T_b and deleteriously high temperatures. Dragonflies from hot regions, on the other hand, would have to devote much more time and effort to thermoregulation in order to maintain such a large safety factor. Their behavioral responses thus permit higher body temperatures. This forces them to live nearer their HT but has the advantage of avoiding excessive costs of thermoregulation, whatever these may be.

Table III shows variation within species and genera from Florida and Panama in the minimum T_b at which flight is possible (MF). In most taxa the mean MF was higher in Florida, but in no case was the difference statistically significant. During the summer mean low temperature in Florida is barely lower than in Panama (WALKER, pers. comm.; RUBINOFF, 1974), but the Gainesville *Gynacantha, Triacanthagyna,* and *Orthemis* were tested in October when the mean low temperature in Gainesville is much lower. Thus, the present evidence suggests that MF is subject to only slight modification in response to climatic variation although data on species from cool climates are needed. The general pattern, with MVT closely adapted to environmental temperature and HT and MF relatively constant, agrees well with the findings of HEATH et al. (1971) who showed that in a number of species of cicadas in Arizona, MVT declined sharply with increasing altitude, but HT and MF dropped only slightly.

Variation in temperature tolerance or thermoregulatory ability with sex and stage of development is another largely unexplored area. GARTEN & GENTRY (1976) determined the critical thermal maximum (corresponding approximately to HT) and lethal temperature in nymphs of several species of libelluloids in South Carolina. They found both parameters adapted to the thermal conditions to which the nymphs were subject. In nymphs of *Pachydiplax longipennis* and *Libellula auripennis* the critical thermal maximum was markedly lower than the HT of adults (MAY, 1976b), and even the lethal temperature was slightly lower than adult HT. It would be interesting to know if there is any influence of nymphal temperature adaptations on those of adults or vice versa.

Critical temperatures are unknown in teneral adults, but my impression is that tenerals are much less thermophilic than mature specimens since tenerals

often congregate in shaded areas. In Figure 8 T_b as a function of T_a in tenerals is compared to the T_b expected in mature individuals. In all cases tenerals tend to have lower and probably less well-regulated T_b. These data were collected inci-
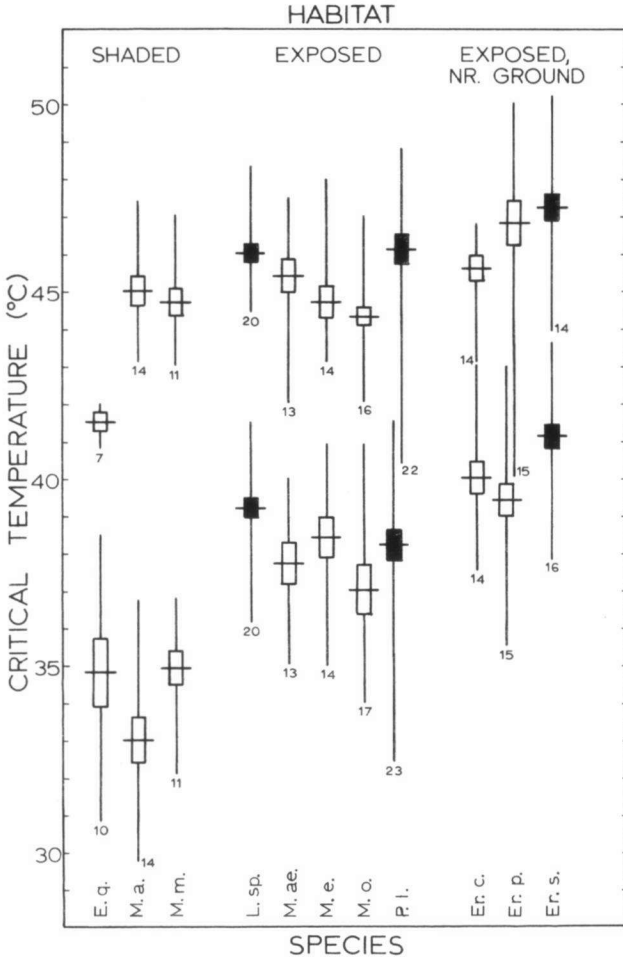

Fig. 7. Maximum voluntarily tolerated temperature (lower symbols) and temperature at onset of heat torpor (upper symbols) in dragonflies from different habitats. Horizontal lines indicate the mean, vertical lines the range, and vertical bars ± 1 S.E. The open bars are species from Panama, filled bars are species from Florida. Numerals indicate the number in each sample. The species are, from left to right: E. q.: *Epigomphus quadracies*; – M. a.: *Micrathyria atra*; – M. m.: *M. mengeri* (or an undescribed species); – L. sp.: *Libellula auripennis* and *L. needhami* (lumped data); – M. ae.: *Micrathyria aequalis*; – M. e.: *M. eximia*; – M. o.: *M. ocellata*; P. l.: *Pachydiplax longipennis*; – Er. c.: *Erythemis credula*; – Er. p.: *E. plebeja*; – Er. s.: *E. simplicicollis*.

Table III

Minimum flight temperature (MF) in conspecific or congeneric dragonflies from
Gainesville, Florida, and the Panama Canal Zone

Species	Locality	Months (Temp.)[a]	MF ± s.d. [°C]
Gynacantha nervosa	Florida	Oct. (16.3 - 28.1)	20.8 ± 1.99 (n = 16)
	Panama	Jan. - May (22.9 - 32.4)	21.7 ± 1.15 (n = 3)
Miathyria marcella	Florida	July - Sept. (21.4 - 32.3)	19.1 ± 1.21 (n = 20)
	Panama	Jan. - May (22.9 - 32.4)	20.1 ± 1.41 (n = 11)
Orthemis ferruginea	Florida	Oct. (16.3 - 28.1)	21.3 ± 1.47 (n = 9)
	Panama	Jan. - May (22.9 - 32.4)	22.3 ± 1.82 (n = 10)
Tramea carolina	Florida	July - Sept. (21.4 - 32.3)	20.7 ± 1.99 (n = 20)
Tramea spp.[b]	Panama	Jan. - May (22.9 - 32.4)	20.2 ± 2.38 (n = 22)
Triacanthagyna trifida	Florida	Oct. (16.3 - 28.1)	19.9 ± 1.35 (n = 12)
Triacanthagyna spp.[c]	Panama	Jan. - May (22.9 - 32.4)	20.3 ± 0.96 (n = 10)

[a] Mean low — mean high temperature (°C) for period indicated.
[b] Lumped data for *T. cophysa* and *T. walkeri*.
[c] Lumped data for *T. caribbea*, *T. ditzleri*, and *T. satyrus*.

dentally to the data on matures and are biased toward specimens collected in
exposed areas. A random sampling of teneral individuals would probably show
even lower T_b. The apparent avoidance of hot situations may be an adaptation
to reduce water loss through the relatively permeable teneral cuticle.

Male *Pachydiplax* have higher MVT than females in the summer, and HT, but
not MVT, is higher in male than female *Erythemis simplicicollis* (MAY, 1976b).
It is not clear how these differences are related to the biology of the species, as I

found no corresponding differences in the expected T_b of males and females in the field. The last panel of Figure 8 suggests that mature females of *E. plebeja* tend to have lower T_b than males. This is in accord with my observation that females most often perch at the shaded forest edge, while males generally choose
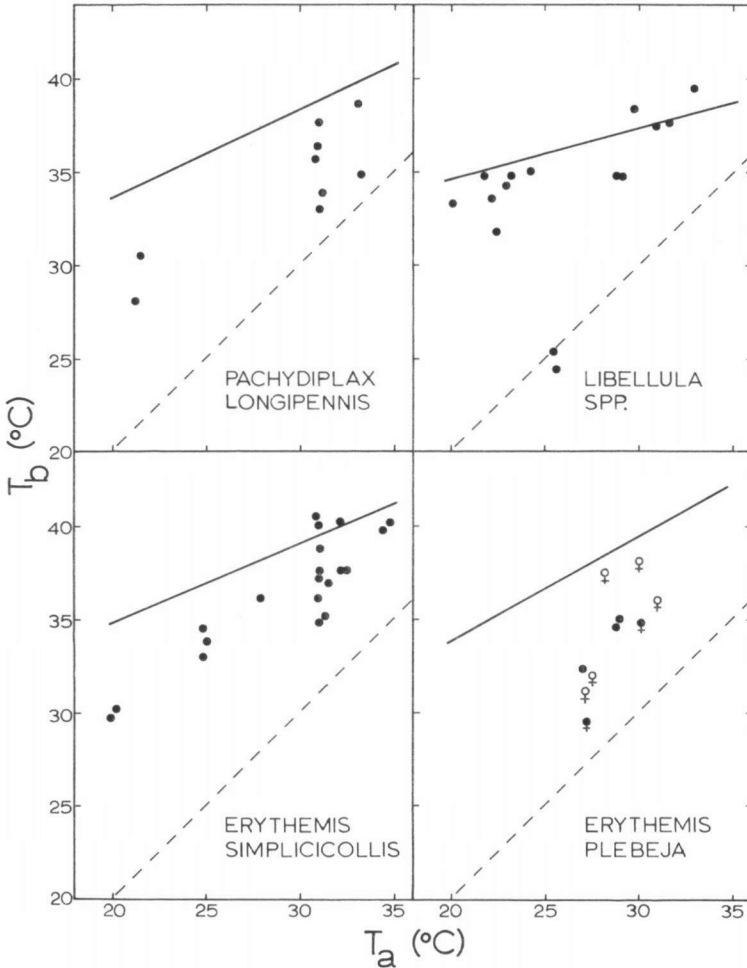

Fig. 8. Body temperature as a function of air temperature in teneral specimens of four species of libellulid perchers. The dashed line is the isothermal line, the solid line is the expected relation to T_b to T_a in mature specimens (MAY, 1976b). Each point is an individual determination. In the graph for *E. plebeja* closed circles represent teneral males, closed female symbols represent teneral females, and open female symbols represent mature females. In the other graphs sexes are not distinguished and all points are for tenerals.

perches fully exposed to the sun.

The preceding discussion should serve to illustrate a glaring weakness in our knowledge of odonate thermal biology. In very few instances has the adaptive significance of thermoregulation been determined. Thermoregulation must often be a costly process in terms of energy expenditure, time, or inattention to predators, mates, etc. What, then, are its advantages? This raises questions on two levels, physiological and ecological. Physiologically, the effect of temperature on the flight mechanism may be very important (NEVILLE & WEIS-FOGH, 1963; MACHIN, et al., 1962) and there are extremes of temperature outside which flight is impossible. However, temperature might also markedly affect water loss, digestion, maturation, and functioning of the nervous system, to name only a few of the possibilities. Ecologically, the questions are, why are dragonflies active at times when thermoregulation is necessary or, if they reduce or stop activity in response to temperature, how does this restriction affect their behavior and ecological relationships?

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REFERENCES

BAKKEN, G.S., & D.M. GATES, 1975. Heat transfer analysis of animals: some implications for field ecology, physiology, and evolution. *In*: D.M. Gates & R.B. Schmerl [Eds.], Perspectives of biophysical ecology. Springer, Berlin.

BARTHOLOMEW, G.A., & B. HEINRICH, 1973. A field study of flight temperatures in moths in relation to body weight and wing loading. *J. exp. Biol.* 58: 123-135.

BIRKEBAK, R.C., 1966. Heat transfer in biological systems. *Int. Rev. gen. exp. Zool.* 21: 269-344.

CAMPANELLA, P.J., & L.L. WOLF, 1974. Temporal leks as a mating system in a temperate zone dragonfly (Odonata: Anisoptera). I. Plathemis lydia (Drury). *Behaviour* 51: 49-86.

CASEY, T.M., 1976. Flight energetics of sphinx moths: power input during hovering flight. *J. exp. Biol.* 64: 529-543.

CHURCH, N.S., 1960a. Heat loss and the body temperature of flying insects. I. Heat loss by evaporation of water from the body. *J. exp. Biol.* 37: 171-185.

CHURCH, N.S., 1960b. Heat loss and the temperature of flying insects. II. Heat conduction within the body and its loss by radiation and convection. *J. exp. Biol.* 37: 186-212.

CORBET, P.S., 1963. *A biology of dragonflies.* Quadrangle Books, Chicago.

GARTEN, C.T., & J.B. GENTRY, 1976. Thermal tolerances of dragonfly nymphs. II. Comparison of nymphs from control and thermally altered environments. *Physiol. Zool.* 49: 206-213.

HANKIN, E.H., 1921. The soaring flight of dragonflies. *Proc. Camb. phil. Soc. biol. Sci.* 20:

460-465.

HEATH, J.E., 1964. Reptilian thermoregulation: evaluation of field studies. *Science* 146: 784-785.

HEATH, J.E., 1965. Temperature regulation and diurnal activity in horned lizards. *Univ. Calif. Publs Zool.* 64: 97-128.

HEATH, J.E., & P.A. ADAMS, 1967. Regulation of heat production by large moths. *J. exp. Biol.* 47: 21-33.

HEATH, J.E., J.L. HANEGAN, P.J. WILKIN, & M.S. HEATH, 1971. Adaptation of the thermal responses of insects. *Am. Zool.* 11: 147-158.

HEATH, J.E., & P.J. WILKIN, 1970. Temperature responses of the desert cicada, Diceroprocta apache (Homoptera, Cicadidae). *Physiol. Zool.* 43: 145-154.

HEINRICH, B., 1971a. Temperature regulation of the sphinx moth, Manduca sexta. I. Flight energetics and body temperature during free and tethered flight. *J. exp. Biol.* 54: 141-152.

HEINRICH, B., 1971b. Temperature regulation of the sphinx moth, Manduca sexta. II. Regulation of heat loss by control of blood circulation. *J. exp. Biol.* 54: 153-166.

HEINRICH, B., 1974. Thermoregulation in endothermic insects. *Science* 185: 747-756.

HOCKING, B., & C.D. SHARPLIN, 1965. Flower basking by arctic insects. *Nature* 206: 215.

KROGH, A., & E. ZEUTHEN, 1941. The mechanism of flight preparation in some insects. *J. exp. Biol.* 18: 1-10.

LIEFTINCK, M.A., 1953. Revisional notes on the genera Diplacina Brauer and Huonia Förster (Odon.). *Treubia* 22: 135-216.

LUTZ, P.E., & A.R. PITTMAN, 1970. Some ecological factors influencing a community of adult Odonata. *Ecology* 51: 279-284.

MACHIN, K.E., J.W.S. PRINGLE, & M. TAMISAGE, 1962. The physiology of insect fibrillar muscle. IV. The effect of temperature on a beetle flight muscle. *Proc. R. Soc. Lond.* (A) 155: 493-499.

MAY, M.L., 1976a. Physiological color change in New World damselflies (Zygoptera). *Odonatologica* 5: 165-171.

MAY, M.L., 1976b. Thermoregulation and adaptation to temperature in dragonflies (Odonata, Anisoptera). *Ecol. Monogr.* 46: 1-32.

MAY, M.L., 1976c. Warming rates as a function of body size in periodic endotherms. *J. comp. Physiol.* 111: 55-70.

MAY, M.L., 1977. Thermoregulation and reproductive activity in tropical dragonflies in the genus Micrathyria. *Ecology* 58: 787-798.

MILLER, P.L., 1964. Notes on Ictinogomphus ferox Rambur (Odonata, Gomphidae). *Entomologist* 97: 52-66.

MORRISON, P.R., F.A. RYSER, & A.R. DAWE, 1959. Studies on the physiology of the masked shrew Sorex cinereus. *Physiol. Zool.* 32: 256-271.

NEVILLE, A.C., & T. WEIS-FOGH, 1963. The effect of temperature on locust flight muscle. *J. exp. Biol.* 40: 111-121.

O'FARRELL, A.F., 1963. Temperature-controlled physiological colour change in some Australian damselflies (Odonata: Zygoptera). *Austr. J. Sci.* 25: 437-438.

O'FARRELL, A.F., 1964. On physiological colour change in some Australian Odonata. *J. ent. Soc. Austr. (N.S.W.)* 1: 1-8.

O'FARRELL, A.F., 1968. Physiological colour change and its significance in the biology of some Australian Odonata. *Proc. 13th int. Congr. Ent.* 1: 534.

PENNYCUICK, C.J., 1969. The mechanics of bird migration. *Ibis* 111: 525-556.

PORTER, W.P., & D.M. GATES, 1969. Thermodynamic equilibria of animals with environ-

ment. *Ecol. Monogr.* 39: 245-270.

PRINGLE, J.W.S., 1967. Comparative physiology of the flight motor. *Adv. Ins. Physiol.* 5: 163-227.

RUBINOFF, R.W., [Ed.], 1974. *1973 environmental monitoring and baseline data.* Unpublished report of Smithsonian Environmental Sciences Program, Smithsonian Institution, Washington.

TEMPLETON, J.R., 1970. Reptiles. *In*: G.C. Whittow, [Ed.], Comparative physiology of thermoregulation. Vol. I. Invertebrates and nonmammalian vertebrates. Academic Press, New York.

VERON, J.E.N., 1973. Physiological control of chromatophores of Austrolestes annulosus (Odonata). *J. Ins. Physiol.* 19: 1689-1703.

VERON, J.E.N., 1974. The role of physiological colour change in thermoregulation of Austrolestes annulosus (Selys) (Odonata). *Austr. J. Zool.* 22: 457-469.

VERON, J.E.N., 1976. Responses of Odonata chromatophores to environmental stimuli. *J. Ins. Physiol.* 22: 19-30.