

**A PRELIMINARY INVESTIGATION OF VARIATION IN TEMPERATURE
AMONG BODY REGIONS OF *ANAX JUNIUS* (DRURY)
(ANISOPTERA: AESHNIDAE)**

M. MAY

Department of Entomology & Economic Zoology, New Jersey
Agricultural Experiment Station, Cook College, Rutgers
University, New Brunswick, NJ 08903, U.S.A.

Received and Accepted August 20, 1985

Temperatures of the thorax (T_{th}), head (T_h), and abdomen (T_{ab}) of *A. junius* were investigated in free-flying individuals in the field, during endothermic warming, and during heating of the thorax with an external heat source. Field data show that T_{th} is well-regulated and T_h is strongly elevated and closely coupled to T_{th} ; variation in T_{ab} is consistent with previous suggestions that heat is pumped via hemolymph circulation from thorax to abdomen during periods of heat stress. During wingshivering in the laboratory, T_h rises in parallel with T_{th} while T_{ab} does not rise during warming of T_{th} but often increases by several degrees after peak T_{th} is reached. External heating experiments suggested that T_h is coupled to T_{th} by an active process that requires an intact circuit for hemolymph circulation but can be controlled in part independently of circulation between the thorax and abdomen.

DEDICATION

It is hardly original, yet still true, to observe that apparently trivial incidents may prove to be turning points in life. One such moment that remains vivid in my mind occurred on a spring morning in 1969 as I stood ankle deep in warm water at the edge of a lake in the sandhills of Putnam County, Florida. One of my companions netted two small insects and handed one to me, along with his ever-present hand lens. "Here, you can see the difference in color pattern". I had collected insects for years and was already seriously interested in their biology, but I seemed to see this insect with new eyes, so striking did its exquisite form seem. I had to see and know more.

*The insect was *Ischnura ramburii*, which I later came to know as a very common damselfly. The companion was MINTER WESTFALL, whom I came to know as an uncommon man, teacher, and friend. It is with pleasure and affection that I dedicate this paper to him on the occasion of his 70th birthday.*

INTRODUCTION

Not until the 1960's was the ability of large insects to elevate and regulate body temperature widely appreciated (DORSETT, 1962; HEATH, 1967; HEATH & ADAMS, 1965). Subsequent studies demonstrated this ability and revealed the mechanisms that support it in many insects, both endotherms and ectotherms (HEINRICH, 1974, 1981; MAY, 1979, 1985). Odonata, also, were found to be excellent thermoregulators (CORBET, 1963; HEINRICH & CASEY, 1978; MAY, 1976, 1977).

Initial studies concentrated on T_{th} , since the thorax is the site of the flight mechanism and hence of heat generation. HEINRICH (1970, 1971) found that sphinx moths use their abdomen at high temperature as a sink for heat produced in the thorax, but only recently has T_h been studied in some insects. In honeybees (HEINRICH, 1979), sphinx moths (HEGEL & CASEY, 1982), and carpenter bees (BAIRD, 1985) there is evidence for regulation of T_h ; in other insects, T_h is at least elevated (MAY, 1986; MAY & CASEY, 1983). Certainly T_h is of potential importance, since the head is the major center of sensory input and higher neural processing, but surprisingly little is known of the effects of temperature on these phenomena. DURUZ & BAUMANN (1968) showed that receptor potentials in the eyes of *Apis* are temperature sensitive, but no published work on dragonfly vision or other head functions takes temperature into account. A major aim of the present paper is to demonstrate that T_h normally is elevated in dragonflies and is potentially controllable. As a result, it could have important effects on the major neural centers.

METHODS

Body temperatures were measured as described by MAY (1976) but using a 0.002-inch diameter copper-constantan thermocouple embedded in a 0.4 mm diameter hypodermic needle and read on a Bailey BAT-4 portable thermocouple thermometer. The probe was inserted in rapid succession into the thorax, head, and 2nd abdominal segment. Measurements were completed within 10-15 s. Air temperature (T_a) in the shade was read immediately afterwards with the same probe, and solar radiation intensity (SR) near the point of capture was usually recorded from the output of a Science Associates Dome Solarimeter. Other weather conditions and behavior were noted as appropriate.

Endothermic warm-up was measured at room temperature (about 23°C) in the laboratory. Copper-constantan thermocouples were implanted in the thorax as described by MAY (1976) and also in the base of the third abdominal segment and in the head about 3 mm beneath the antero-medial margin of the left eye; leads were held in place with contact cement. The thermocouple output was recorded at 5-15 s intervals on a Honeywell Elektronik 112 Multipoint thermocouple recorder.

Effects of T_{th} on the temperatures of the other tagmata were also studied by restraining live dragonflies on an insect spreading board while heating the thorax with a microscope lamp focused onto the thoracic dorsum. No light from the lamp appeared to fall directly on the head or abdomen, but reflected or diffuse light may have done so. Thermocouples implanted as described above were used to monitor T_{th} , T_h , and T_{ab} . After heating and cooling, each insect was killed by injection of

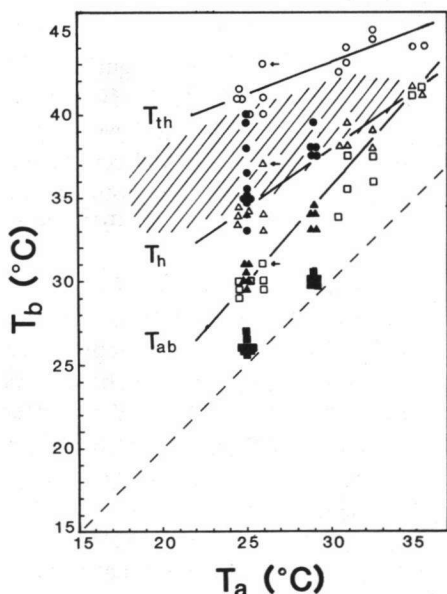


Fig. 1. Relationship of T_{th} (circles), T_h (triangles), and T_{ab} (squares) to T_a in *Anax junius* collected in the field; T_b refers to body temperature without specifying a particular tagma. Filled points are data from 2 males and 12 females collected while feeding in Florida at $SR < 40 \text{ W m}^{-2}$ (these data are from MAY, 1984); open points are from specimens captured in sunlight (SR between about 350 and 800 W m^{-2}). Arrows indicate data from a female ovipositing alone with the tip of her abdomen submerged; all other open points are from males. Hatched area describes an envelope surrounding data on T_{th} from MAY (1976). Solid oblique lines are regressions on T_a for the individuals in sunlight only: $T_{th} = 0.35T_a + 32.2$, $r^2 = 0.724$; $T_h = 0.66T_a + 17.7$, $r^2 = 0.879$; $T_{ab} = 1.08T_a + 2.5$, $r^2 = 0.956$. Dashed line is the isothermal line.

ethyl acetate, then, with the dragonfly and lamp still in exactly their original position, retested after death. In a few experiments the head was heated directly.

RESULTS

Body temperature data for *Anax junius* in the field fall into two groups, those from individuals collected while feeding at dusk (negligible SR) over beach dunes in Florida and those from individuals patrolling or ovipositing in sunlight in New Jersey. In the first group, T_{th} was mostly in the lower range of reported values for *A. junius* (MAY, 1976), while the second group had higher T_{th} ; in both cases, the effect of T_a on T_{th} was similar to previous findings (Fig. 1).

In all individuals studied, T_h was markedly elevated while T_{ab} was slightly or moderately elevated. Head temperature excess ($T_h - T_a$) was closely related to thoracic temperature excess ($T_{th} - T_a$) regardless of variations in SR exposure or site of capture. Elevation of T_{ab} was distinctly greater in the individuals exposed to strong SR (Tab. I).

Figure 2 shows variation in T_{th} , T_h , and T_{ab} during a typical bout of endothermic warming. Thoracic temperature rose rapidly and almost linearly from the onset of

wing-shivering until attempted takeoff. This individual then became quiescent and cooled passively. Changes in T_h mostly paralleled those of T_{th} , but head temperature excess was never more than half the thoracic temperature excess. The rise in T_h was more sigmoid, and a few irregularities (No. 3 of Fig. 2) in the pattern of T_h change did not correspond to simultaneous changes in T_{th} . The time course of change in T_{ab} was very different in that this temperature

Table I

Correlation of the effect of the presence or absence of solar radiation with elevation of body temperature above air temperature in *Anax junius* in the field. Values are given as mean \pm S.D.; means within a column having different letter superscripts are significantly different ($p < 0.05$)

Exposure	$T_{th}-T_a$	$T_{th}-T_a$	$T_{ab}-T_a$	1R_h	2r_h	${}^1R_{ab}$	${}^2r_{ab}$
Sun	^a 13.57 ± 2.78	^a 7.93 ± 1.71	^a 4.75 ± 1.00	^a 0.588 ± 0.073	0.254	^a 0.373 ± 0.151	0.766
Shade	^b 10.57 ± 2.20	^b 5.96 ± 1.77	^b 1.14 ± 0.31	^a 0.561 ± 0.097	0.302	^b 0.110 ± 0.025	0.386

${}^1R_h = (T_h - T_a) / (T_{th} - T_a)$; $R_{ab} = (T_{ab} - T_a) / (T_{th} - T_a)$.

2r_h = correlation coefficient of R_h with T_a ; r_{ab} = correlation coefficient of R_{ab} with T_a ; boldface type indicates that the correlation is significant at $p < 0.05$.

was constant or even declined slightly during wing-shivering, then increased rather abruptly when shivering ceased and T_{th} and T_h began to decline. Elevation of T_{ab} was always less than of T_{th} or T_h .

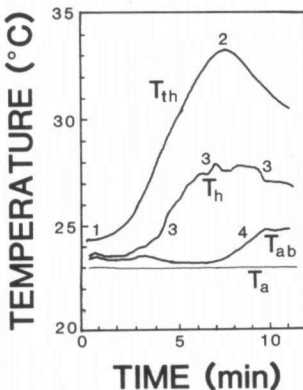


Fig. 2. Simultaneous variation in T_{th} , T_h , and T_{ab} during endothermic warm-up and subsequent cooling in a male *Anax junius*. Numbers indicate times of events discussed in text.

A record from another individual (Fig. 3) contrasts with Figure 2 in that this insect did not attempt takeoff, but after attaining a T_{th} of 35–38°C, it maintained T_{th} by continuous wing-shivering for periods of several minutes, interspersed with periods of passive cooling and rewarming. During the first prolonged bout of shivering, T_{th} reached a peak (No. 1), then declined a few degrees (No. 2), even though visible shivering continued. Again, T_h generally changed in parallel with T_{th} except that it remained nearly constant (No. 3) during the initial decline of T_{th} . Abdominal temperature was constant or dropped slightly (No. 4) during rapid increase in T_{th} and sometimes during the initial parts of sustained shivering and T_{th} maintenance, but T_{ab} rose (No. 5) during the latter parts of sustained shivering bouts, before the onset of passive cooling.

Data in Table II summarize warm-up characteristics of *A. junius*; in each case only the initial warming bout is included if more than one occurred. These confirm that the rate of T_h increase and maximum T_h excess were about half the corresponding values for T_{th} . Abdominal temperature changed little during warming, and elevation of T_{ab} at the time of the initial maximum of T_{th} was slight and not correlated with T_{th} excess ($r = 0.16$). Peak T_{ab} was delayed by 15–40 s and its magnitude was correlated with T_{th} excess ($r = 0.66$).

With one exception, T_{th} was lower and T_h and T_{ab} higher during external heating of insects heated while alive than while dead (Tab. III). The single exception was a female that behaved abnormally after thermocouple implantation. Owing to small sample size and high variability of data, the significant differences cannot be demonstrated except for the higher T_h of living individuals ($p < 0.01$).

Figure 4 records body temperatures during external heating in the individual with the most dramatic difference between heating while alive vs. dead. Besides the marked difference in magnitudes of T_{th} vs. T_h and T_{ab} , the pattern of temperature variation in life is noteworthy. Both T_{th} and T_{ab} changed relatively smoothly, although a slight drop in T_{th} (No. 1) occurred more or less simultaneously with a distinct peak in T_{ab} , and a plateau (No. 2) following a rise in T_{th}

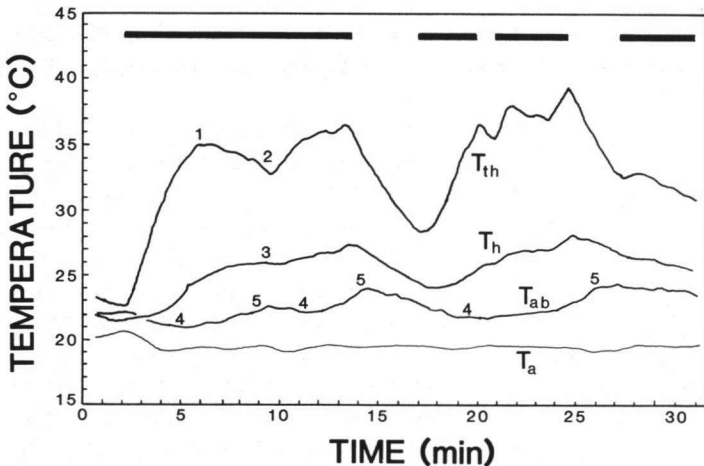


Fig. 3. Simultaneous variation in T_{th} , T_h , and T_{ab} during an extended period of alternate endothermic warm-up, maintenance of high T_{th} , and passive cooling in male *Anax junius*. Numbers indicate times of events discussed in text. Dark bars indicate periods of wing-shivering.

Table II

Temperature characteristics of the thorax, head and abdomen of *Anax junius* during endothermic warm-up. Values are mean \pm S.D. for seven male individuals; $T_a = 21.5\text{--}23.5^\circ\text{C}$

Tagma	Warm-up rate $^\circ\text{C min}^{-1}$	Temperature at maximum T_{th} $^\circ\text{C}$	¹ Maximum temperature (time delay) $^\circ\text{C}; (\text{min})$
Thorax	4.7 ± 0.9	12.2 ± 3.9	— —
Head	2.8 ± 1.2	5.3 ± 1.8	$5.9 \pm 2.1 (0.07)$
Abdomen	0.2 ± 0.5	1.9 ± 1.0	$2.6 \pm 0.9 (0.40)$

¹ Maximum temperature ($^\circ\text{C}$) attained by the head or abdomen during a warming bout; this usually occurred after peak T_{th} , and the mean time delay (min) is shown in parentheses.

Table III

Maximum elevation of T_{th} , T_h , and T_{ab} during external heating of living or dead *Anax junius*. Values are mean \pm S.D., $n = 6$. Means within a column having different letter superscripts are significantly different ($p < 0.05$)

Condition	$T_{th}-T_a$	T_h-T_a	$T_{ab}-T_a$
Alive	^a 16.63 \pm 3.28	^a 11.40 \pm 2.32	^a 9.03 \pm 2.77
Dead	^a 18.67 \pm 1.83	^b 7.45 \pm 1.86	^a 6.37 \pm 1.27

corresponded to a rise in T_{ab} following a fall. Two major, abrupt drops in T_h (No. 3) were much more marked than changes in other temperatures. Both began at about the time of much smaller rises in T_{ab} and continued after T_{ab} had peaked and declined. Numerous minor fluctuations followed the two major dips. Comparable large changes were not observed on other specimens, but T_h was consistently more variable on a short time scale than other body temperatures.

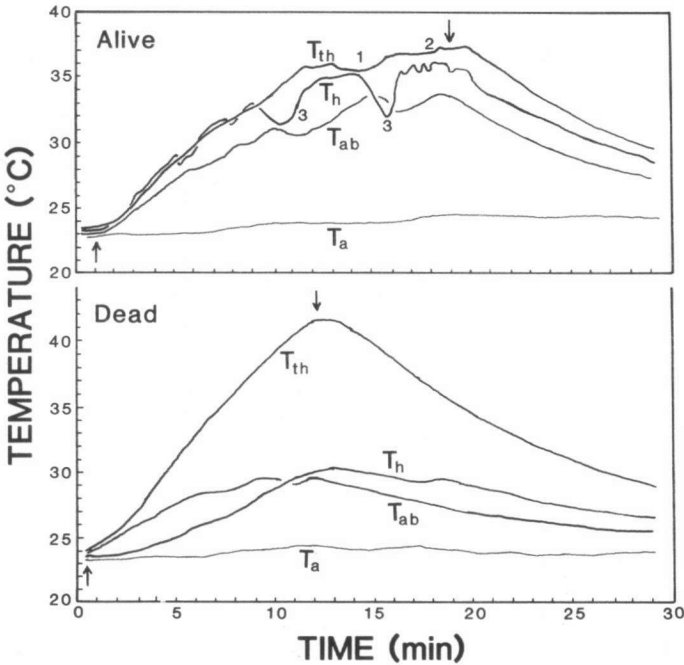


Fig. 4. Simultaneous variation in T_{th} , T_h , and T_{ab} during external heating with a lamp focused on the thorax in a live male *Anax junius* (upper panel) and in the same individual after being killed without altering its position (lower panel). Upward pointing arrows indicate when the lamp was turned on, downward pointing arrow when it was turned off. Numbers indicate times of events discussed in the text.

Figure 5 shows the results of interrupting circulation during external heating in another individual. After T_{th} stabilized at about 42°C , a small metal clamp was applied across the 6th abdominal segment. Abdominal pumping, associated with elevated tracheal ventilation at high temperature, continued after clamping. As soon as the clamp was applied, T_{th} rose and T_h fell sharply; T_{ab} initially rose slightly, then dropped. When the clamp was released, T_h remained high, but T_h quickly rose about halfway to its former level, while T_{ab} also approached its original, higher level, after an initial further drop. The preliminary rise in T_{ab} after clamping and fall after release were probably due to the fact that positioning the clamp raised the abdomen somewhat, exposing it more directly to the heating lamp, while removing the clamp lowered the abdomen.

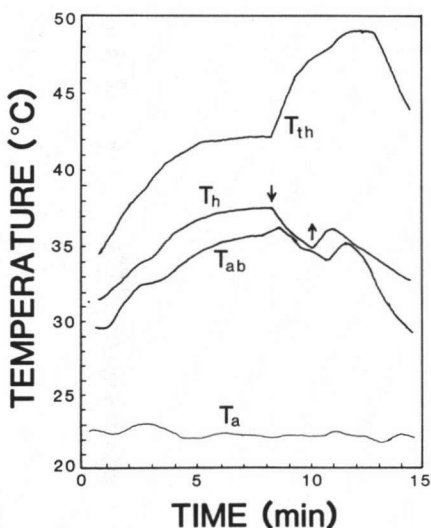


Fig. 5. Simultaneous variation in T_{th} , T_h , and T_{ab} in a live male *Anax junius* during external heating of the thorax. At the time indicated by the downward pointing arrow, a clamp was applied to the 6th abdominal segment to occlude hemolymph circulation; the clamp was removed at the time indicated by the upward pointing arrow.

temperature characteristics between New Jersey and Florida populations, behaviour-related differences in flight metabolism, and differences in SR. I earlier argued (MAY, 1984) that the many low values from the low SR group may have been associated with slope soaring and reduced flight metabolism. On the other hand, SR intensity can in principle have a strong effect on body temperatures of flying dragonflies (MAY, 1986) and may account for the elevation of T_{th} in the individuals flying in sunlight.

In any case, T_h was strongly elevated even at low SR. The ratio of $T_h - T_a$ to $T_{th} - T_a$ is independent of T_a or SR (Tab. I); considering that the coefficient of heat transfer of the head is probably about 3 times that of the thorax (MAY, 1986, and unpublished), this observation suggests strong thermal coupling between these

DISCUSSION

The low slope of the regression of T_{th} on T_a indicates that T_{th} is well-regulated, as found previously (MAY, 1976). The reasons for the differences in level of T_{th} among the various sets of field data are not clear. They may include differences in technique between the 1976 and later data (thermistor thermometers were used earlier), differences in tempera-

tagmata. There is no indication, however, that T_h is independently regulated over this range of T_a .

In individuals in sunlight the slope of T_{ab} on T_a is slightly, although not significantly, greater than 1.0. The true relationship may be non-linear, as the elevation of T_{ab} relative to T_{th} is especially marked at $T_a = 35^\circ \text{C}$. The increase, if real, is not due to effects of SR since the latter was 590-780 W/m^2 during measurements at $T_a < 26^\circ \text{C}$ but, owing to haze, only about 450 W/m^2 when $T_a > 30^\circ \text{C}$. This pattern is consistent with previous evidence that heat loss from the thorax is augmented by increased circulation to the abdomen at high T_{th} (HEINRICH & CASEY, 1978; MAY, 1976). Elevation of T_{ab} was slight under low SR conditions. This might be due either to a direct effect of SR on T_{ab} or to relatively low T_{th} resulting in less heat transfer to the abdomen.

Observations of endothermic warm-up also show strong thermal coupling between head and thorax, since changes in T_h were large and mostly in parallel with changes in T_{th} . Instances when T_h showed evidence of independence from either T_{th} or T_a (No. 3 of Figs 2 and 3) suggest that this coupling was not entirely passive but involved a variable, active process such as hemolymph circulation. The evidence is indirect, however, and the irregularities in T_h were small, so no firm conclusion is possible. As with the situation in the field, transfer of heat to the head represents an important heat drain from the thorax at a time when maximal heat retention is clearly advantageous (HEGEL & CASEY, 1982; MAY, 1986) and again suggests that elevation of T_h is adaptive.

Changes in T_{ab} during warm-up were consistent with previous observations that heat transfer from thorax to abdomen is virtually nil during vigorous warming and that the restriction of heat exchange relaxed after completion of warming (HEINRICH & CASEY, 1978; MAY, 1976). Thus passive conduction through tissues to the abdomen is negligible, because otherwise T_{ab} would rise as T_{th} rose, and nearly all transfer is probably by circulation.

In some respects results from external heating experiments are the most interesting. The fact that T_{th} is lower and T_h and T_{ab} higher during heating of live than of dead specimens was expected, since circulation of hemolymph in life must carry some heat from the thorax to other body regions, in the absence of special mechanisms to retard heat flow (e.g. HEINRICH, 1976). Extreme differences, as in Figure 4, do suggest active augmentation of heat exchange to prevent thoracic overheating. In fact, elevation of T_{ab} , and therefore perhaps of T_h , in dead insects may have been entirely due to inadvertent heating of those tagmata or the surrounding air by the lamp, since during endothermic warm-up no passive heat transfer from thorax to abdomen occurred. Direct heating of the head gave no indication that the latter was cooled by increased circulation, but further experiments are needed.

During heat stress, stabilization or decline of T_{th} under constant external heat load is often correlated with increased T_{ab} (Fig. 4, and MAY, 1976), as

expected if head transfer to the abdomen is used to regulate T_{th} . The most remarkable features of Figure 4, however, are the abrupt drops in T_h , which are not obviously related to changes in T_{th} , T_{ab} , or T_a . Their functional significance, if any, is not clear, but they do strongly suggest that heat transfer to the head is under the insect's control, as found by HEGEL & CASEY (1982) in sphinx moths, and is to some degree independent of heat exchange with the abdomen. In turn this points to the possibility of an adaptive mechanism for control of heat exchange between head and thorax and conceivably for control of T_h itself. On the other hand, clamping the abdomen, thereby presumably occluding the dorsal vessel and interrupting circulation in general, also caused a rapid, partly reversible drop in T_h (Fig. 5). Thus it seems likely that the heat transfer mechanism to the head involves hemolymph circulation and requires an intact dorsal heart but is controlled in part independent of circulation to other regions.

ACKNOWLEDGEMENTS

This is New Jersey Agricultural Experiment Station Publication No. D-08155-19-85, supported by State and U.S. Hatch Act Funds.

REFERENCES

- BAIRD, J.M., 1985. A field study of thermoregulation in the carpenter bee *Xylocopa virginica* virginica (Hymenoptera: Anthophoridae). *Physiol. Zool.* (In press).
- CORBET, P.S., 1963. *A biology of dragonflies*. Quadrangle, Chicago.
- DORSETT, D.A., 1962. Preparation for flight by sphinx moths. *J. exp. Biol.* 39: 579-588.
- DURUZ, C. & F. BAUMANN, 1968. Influence de la température sur le potentiel de repos et le potentiel récepteur d'une cellule photoréceptrice. *Helv. Physiol. Pharmacol. Acta* 26: 341-342.
- HEATH, J.E., 1967. Temperature responses of the periodical "17-year" cicada, *Magicicada casinii*. *Am. Midl. Nat.* 77: 64-76.
- HEATH, J.E. & P.A. ADAMS, 1965. Temperature regulation in the sphinx moth during flight. *Nature* 205: 309-310.
- HEGEL, J. & T.M. CASEY, 1982. Thermoregulation and control of head temperature in the sphinx moth, *Manduca sexta*. *J. exp. Biol.* 101: 1-15.
- HEINRICH, B., 1970. Thoracic temperature stabilization by blood circulation in a free-flying moth. *Science* 168: 580-582.
- HEINRICH, B., 1971. Temperature regulation of the sphinx moth, *Manduca sexta* I. Flight energetics and body temperature during free and tethered flight. *J. exp. Biol.* 54: 153-166.
- HEINRICH, B., 1974. Thermoregulation in endothermic insects. *Science* 185: 747-756.
- HEINRICH, B., 1976. Heat exchange in relation to blood flow between thorax and abdomen in bumblebees. *J. exp. Biol.* 64: 561-585.
- HEINRICH, B., 1979. Keeping a cool head: honeybee thermoregulation. *Science* 205: 1269-1271.
- HEINRICH, B., 1981. *Insect thermoregulation*. Wiley, New York.
- HEINRICH, B. & T.M. CASEY, 1978. Heat transfer in dragonflies: "fliers" and "perchers". *J. exp. Biol.* 74: 17-36.
- MAY, M.L., 1976. Thermoregulation and adaptation to temperature in dragonflies (Odonata: Anisoptera). *Ecol. Monogr.* 46: 1-32.

- MAY, M.L., 1977. Thermoregulation and reproductive activity in tropical dragonflies of the genus *Micrathya*. *Ecology* 58: 787-798.
- MAY, M.L., 1979. Insect thermoregulation. *A. Rev. Ent.* 24: 313-349.
- MAY, M.L., 1984. Energetics of adult Anisoptera, with special reference to feeding and reproductive behavior. *Adv. Odonatol.* 2: 95-116.
- MAY, M.L., 1985. Thermoregulation. In: G.A. Kerkut & L.I. Gilbert, [Eds], *Comprehensive insect physiology, biochemistry and pharmacology*, Vol. 4, pp. 507-552. Pergamon Press, Oxford.
- MAY, M.L., 1986. Body temperature regulation and responses to temperature by male *Tetragoneuria cynosura* (Anisoptera: Corduliidae). *Adv. Odonatol.* 3 (In press).
- MAY, M.L. & T.M. CASEY 1983. Thermoregulation and heat exchange in euglossine bees. *Physiol. Zool.* 56: 541-551.