# DEPENDENCE OF FLIGHT BEHAVIOR AND HEAT PRODUCTION ON AIR TEMPERATURE IN THE GREEN DARNER DRAGONFLY *ANAX JUNIUS* (ODONATA: AESHNIDAE)

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## Summary

The large, endothermic dragonfly *Anax junius* regulates the temperatures of its thorax ($T_{th}$) and head ($T_h$) during flight. At high ambient temperature ($T_a$) it is able to dispose of excess heat from the thorax by increasing hemolymph circulation to the abdomen, but recent evidence suggests that heat loss to the abdomen is largely passive at $T_a < 30\,^{\circ}$C. Nevertheless, these insects continue to regulate $T_{th}$ and $T_h$ at least down to 20 $^{\circ}$C and probably at much lower values of $T_a$. As $T_a$ declines, *A. junius* glide less, probably fly faster when feeding, and increase their wingbeat frequency when patrolling. Presumably as a result of these behavioral changes, heat production, and thus inferred flight metabolic rate, is inversely proportional to $T_a$. This is the first demonstration based on field data that an insect regulates body temperature while flying by altering heat production.

Key words: *Anax junius*, Anisoptera, body temperature, flight metabolism, green darner dragonfly, heat exchange, thermoregulation.

## Introduction

Insect flight metabolism is of interest to comparative physiologists because of its high intensity and its relationship to muscle function and because it provides a source of heat for endothermic body temperature regulation during flight (Casey and Ellington, 1989; Casey, 1992*b*). It is difficult, however, to measure the metabolic rate of most insects under conditions closely resembling natural flight. Heinrich (1971*a*) showed that tethered or otherwise-supported insects may reduce flight effort below levels characteristic of free flight. Most credible data pertain to hovering flight in a small, closed container. Only one study (Ellington *et al.* 1990) has successfuly measured oxygen consumption during steady forward flight by bumblebees in a wind-tunnel. Hence, measurements are generally possible only under conditions that prevent expression of many flight behaviors and are possibly affected by aerodynamic anomalies in a confined space. In addition, many insects do not hover under such experimental conditions.

Flight metabolism is largely a function of aerodynamic requirements, which are, in turn, determined primarily by the morphological characteristics of each insect. Measurement of variation stemming from changes in flight performance has been possible, however, in only a few instances; for example, differences in load carriage (Heinrich, 1975) and flight speed (Ellington *et al.* 1990) in bumblebees. A possible non-aerodynamic influence on flight metabolism is variable environmental temperature. Many large insects that are good

fliers regulate their thoracic temperature endothermically (Heinrich, 1993). Since vertebrate endotherms respond to reduced $T_a$ by increasing heat production, Heath and Adams (1965) proposed that endothermic sphinx moths similarly increase flight metabolic rate at low $T_a$ in order to maintain $T_{th}$. However, Heinrich (1971*a,b*) demonstrated that *Manduca sexta* regulate $T_{th}$ by controlling heat loss *via* hemolymph circulation to the abdomen and not by changes in metabolic rate. Unwin and Corbet (1984) subsequently hypothesized that bumblebees might increase wingbeat frequency, and thus flight metabolic rate, at low $T_a$, but Joos *et al.* (1991) failed to confirm this. However, recent reports indicate that both flight metabolic rate and wingbeat frequency are reduced at high $T_a$ in honeybees (Harrison *et al.* 1994; Roberts *et al.* 1994).

Sphinx moths and bumblebees are relatively heavy-bodied insects that do not glide and probably must expend a large fraction of their total available power to stay aloft. Dragonflies, in contrast, characteristically have much lower wing loading, although some species are highly endothermic. I proposed (May, 1976, 1991*b*) that these insects are more likely than most moths and bees to be able to exploit variable heat production as a mechanism of thermoregulation, but this suggestion has remained speculative.

Data in this paper show that wingbeat frequency and flight speed may decline while the proportion of time spent gliding increases with increasing $T_a$. I also provide estimates of heat

production by *Anax junius* (Drury) under field conditions that permit computation of flight metabolic rate and indicate that the latter is higher at low than at high $T_a$. Since heat loss *via* the abdomen is evidently augmented principally at $T_a \geqslant 30\,°C$ (May, 1995), control of heat production may be the primary mechanism of regulation of thoracic temperature at low $T_a$.

## Materials and methods

### Flight behavior and velocity

Flying *Anax junius* were video-taped with a Panasonic PV-22 Palmcorder at $60\,\text{frames}\,s^{-1}$ during migratory flights at Crescent Beach, St Johns County, Florida, USA (29°40′N, 81°15′W), on 4–5 September 1993, and during feeding flights at Alachua County, Florida (29°40′N, 82°15′W), on 4 December 1993, and Cape May, New Jersey, USA (38°55′N, 74°55′W), on 18 October 1993. During video-taping, I measured $T_a$ and solar radiation intensity as described by May (1995); I estimated wind direction and either measured wind speed using a Dwyer Wind Meter pith ball anemometer or estimated it subjectively. Tapes were analyzed using a Panasonic NV-8950 variable-speed video recorder. In addition, I made many qualitative observations of flight behavior at Crescent Beach from 1982 to 1993 and at Cape May from 1991 to 1993.

To determine the proportion of time spent gliding, I selected tape sequences showing flights in which wing movements were clear, then played these at 5 or $9\,\text{frames}\,s^{-1}$. Total flight duration and duration of gliding (no wing movement) were timed with stopwatches. Flight velocity was estimated from flight sequences in which the image of the dragonfly was in good focus and its length on the monitor was at least 15 mm and changed by less than 10 % during the course of the measured flight, indicating that the flight path was approximately normal to the line of sight; no length change occurred during most selected flights, but if it did, velocity estimates were adjusted accordingly within the flight. The tape was advanced frame-by-frame and the position of the insect's head marked on an acetate overlay. Velocity was calculated in terms of apparent body lengths per second, then converted to $m\,s^{-1}$ by assuming that mean body length is 7.5 cm (May, 1991*a*).

### Wingbeat frequency

Wingbeat frequency of *A. junius* was measured in the field using an optical tachometer (Unwin and Ellington, 1979) and recorded on a Realistic CTR-85 cassette recorder. Feeding *A. junius* fly in irregular patterns, often at low light intensity, when the tachometer was ineffective, so frequency data were obtained only from males patrolling in sunlight at mating rendezvous sites. Even so, most records were no more than 1 s in duration. After each recording, environmental conditions were measured as above. I also recorded wingbeat frequency in male *Epitheca* (*Tetragoneuria*) *cynosura* (Say), a much smaller species that commonly hovers or flies very slowly at rendezvous sites, so that longer records were possible.
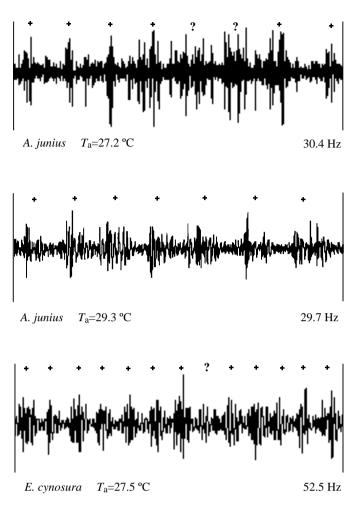


Fig. 1. Optical tachometer records of wingbeat frequencies of patrolling males of *Anax junius* and *Epitheca cynosura*; plus signs indicate positions of individual wingbeat records, question marks indicate the inferred positions of unclear beats. Duration of each record is 0.25 s.

Recorded data were visualized using the SoundEdit sound analysis program on a Macintosh II computer. Series of wingbeats were selected from the tachometer records that were clear enough to give unambiguous frequencies to within 1 Hz (Fig. 1); generally at least seven wingstrokes were included, although in two cases only four strokes could be used. Within some sequences, some individual wingbeats produced weak or indistinct records (Fig. 1), probably because of variation in reflection of light due to changes in position or wing twisting. The data included a great deal of high-frequency noise, while the wingbeat frequencies are near the lower limit for audible sound. This made automatic frequency analysis difficult, so records were printed and wingbeats counted by hand.

### Body temperature and heat production

Temperatures of the head ($T_h$), thorax ($T_{th}$) and abdomen ($T_{ab}$) were measured in the field by netting dragonflies during flight and piercing each tagma in rapid succession (<15 s) with a thermocouple probe (May, 1995). I also recorded air temperature ($T_a$) and solar radiation (*SR*); in this paper only data from individuals feeding at dusk or dawn, at radiation

intensities below $60\,\mathrm{W\,m^{-2}}$, and usually below $10\,\mathrm{W\,m^{-2}}$, are considered. Data were only taken during periods when, despite careful observation, I saw no evidence that any dragonflies alighted on vegetation. Thus, I assume that flight was continuous and that all individuals were at thermal equilibrium, although I often could not directly observe those that I caught for more than a few seconds. All specimens used for calculation of heat loss rates were killed, dissected and the head, pterothorax and abdomen each weighed to $0.001\,\mathrm{g}$.

Heat exchange coefficients ($C_h$, $C_{th}$, $C_{ab}$, in $\mathrm{min^{-1}}$) were determined from cooling curves measured in intact, dead specimens at several wind velocities in a small wind-tunnel (data reported in May, 1995). Coefficients for the head and abdomen were corrected for heat transfer from the thorax (which always remained warmest during cooling and thus retarded the cooling of the other tagmata) as also described by May (1995).

The assumption of thermal equilibrium requires that heat production = heat loss. Heat loss ($\mathrm{d}H/\mathrm{d}t$, in $\mathrm{W\,g^{-1}}$) from the entire insect was calculated as the sum of losses from each tagma, assuming Newtonian heat transfer (Casey, 1992$a$; May, 1991$b$). Thus:

$$\mathrm{d}H/\mathrm{d}t = [SC_h(T_h - T_a) + SC_{th}(T_{th} - T_a) + SC_{ab}(T_{ab} - T_a)]/60, \quad (1)$$

where $S$ is the specific heat of dragonfly body tissue (approximately $3.3\,\mathrm{J\,g^{-1}\,^{\circ}C^{-1}}$; May, 1979) and the divisor 60 corrects values from $\mathrm{min^{-1}}$ to $\mathrm{s^{-1}}$. Heat exchange coefficients were determined from the measured mass of each tagma and assumed flight speed; the latter was estimated from the relationship between flight speed and $T_a$ during feeding, given below.

## Results

### Flight behavior and velocity

Feeding flights at all sites were erratic in direction and encompassed areas a few tens of meters across. In Florida, four or five individuals flew at heights of $1.5\,\mathrm{m}$ or less in a sheltered clearing about $30\,\mathrm{m}$ in diameter in still air with occasional perceptible gusts. In New Jersey, many more individuals were present at each of two sites: at about $1$–$7\,\mathrm{m}$ above a lawn approximately $200\,\mathrm{m}$ north of beach dunes (wind speed was approximately $4.5\,\mathrm{m\,s^{-1}}$ from the south on the beach but was nearly still with gusts up to $2.5\,\mathrm{m\,s^{-1}}$ at $2\,\mathrm{m}$ height where video-taping occurred), and at about $1$–$3\,\mathrm{m}$ over fields bordered at distances of $10$–$200\,\mathrm{m}$ by woods or tall hedgerows (wind speed $0$–$3\,\mathrm{m\,s^{-1}}$). Frequent course changes, apparently in response to prey, and occasional prey captures could be seen, but none of these *A. junius* appeared to be feeding on localized prey swarms. At the second of these sites, a few males flew in much more localized patterns along the edges of the woods, with frequent hovering and generally slower flight than other individuals; I termed this 'patrolling' because it resembled flight at mating rendezvous sites. A single such male was video-taped.

Migratory flights, observed and video-taped over beach dunes and scrub in Florida, were mostly oriented south-south-east, parallel to the beach, with few course changes. They began at about $07{:}00\,\mathrm{h}$ Eastern Daylight Savings Time (sunrise was at $07{:}05\,\mathrm{h}$) and ended quickly when a fresh south-easterly sea breeze arose at about midday. Some feeding occurred, especially later in the morning ($T_a=31$–$32\,^{\circ}C$) when flights were less strongly directional. On 4 September, wind conditions remained nearly calm all morning. On 5 September, a light, intermittent westerly breeze, roughly perpendicular to the usual flight course, arose at about $09{:}30\,\mathrm{h}$ ($T_a=28$–$29\,^{\circ}C$), then became steadier (approximately $2\,\mathrm{m\,s^{-1}}$) from the south-west from about $10{:}30\,\mathrm{h}$, after which many dragonflies flew slightly into the wind, moving gradually inland from the beach.

An exceptional local flight pattern occurred during the migratory flights. Over a single clump of palmetto (*Serenoa repens*), roughly $10\,\mathrm{m}$ in diameter, from $11{:}00$ to $11{:}30\,\mathrm{h}$ on 4 September, about $20$–$30$ individuals flew rapidly and very erratically. They seemed to be feeding, although prey were not observed. Because of the appearance of their flight, I designate the activity as 'frantic feeding'.

No significant relationship existed overall between $T_a$ and flight speed (Fig. 2). Within different flight types, however, speed was negatively correlated with $T_a$ for both typical feeding (i.e. excluding 'patrolling' and 'frantic feeding') and migratory flights. In addition, previously reported data on speed during feeding (May, 1991$a$) are consistent with such a relationship (Fig. 2). Migratory flight was directional, and wind velocity increased during the morning as $T_a$ increased, so the changes in ground speed recorded on video tape could have been affected by wind. This objection would not apply to feeding flights, despite the occurrence of light wind, because
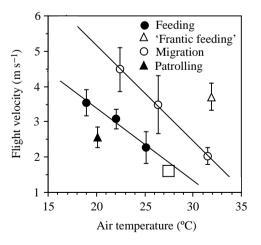


Fig. 2. Flight velocity ($v$), estimated from video tapes of *A. junius* during various activities described in the text, as a function of air temperature ($T_a$); error bars are $\pm 1$ S.E.M. The open square represents flight velocity from May (1991$a$) at an estimated $T_a$. The overall regression of $v$ on $T_a$ is not significant ($r^2=0.013$, $P=0.206$, $N=127$), but regressions for normal feeding ($v=7.31-0.196T_a$, $r^2=0.208$, $P=0.0003$, $N=59$) and migration ($v=10.56-0.271T_a$, $r^2=0.662$, $P<0.0001$, $N=36$) categories are significant.
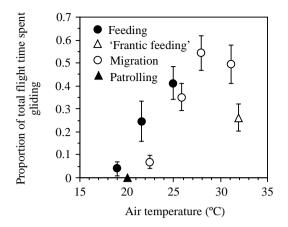
Fig. 3. Proportion of total flight time spent gliding, estimated from video tapes of flying *A. junius*, as a function of $T_a$. Data shown are untransformed and error bars are ± 1 S.E.M.; correlations and tests of significance were performed on arcsine–square-root transformed data. The overall correlation is significant ($r=0.674$, $P<0.0001$, $N=123$), as are those within the feeding and migration categories ($r=0.746$, $P=0.0001$, $N=36$ and $r=0.776$, $P<0.0001$, $N=66$, respectively).

wind velocity and direction were not correlated with $T_a$ and flight headings were highly variable relative to wind direction. In any case, as $T_a$ increased, mean air speed did not increase and during feeding flights very probably decreased. Thus, *A. junius* do not, as a rule, fly faster as a means of augmenting convective cooling in the situations observed here. Nevertheless, flight speed may sometimes be high at high $T_a$, as seen in the 'frantic feeding' episode, or low at low $T_a$, as in 'patrolling'.

The proportion of time aloft devoted to gliding, as opposed to flapping flight, was strongly correlated with $T_a$, not only within different modes of flight but also for the entire data set (Fig. 3). As with velocity, effects of $T_a$ may be confounded with effects of wind during the migration, but this is unlikely to have been the case during normal feeding. The 'frantic feeding' flight was again anomalous, with considerably less gliding than predicted by $T_a$. No gliding was recorded in the single patrolling individual.
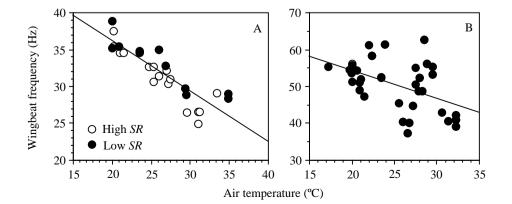
Quantitative data on flight behavior are from only a few days of recording and do not cover the full range of flight behaviors

of which *A. junius* are capable. They are generally in accord, however, with qualitative observations. Flights at dawn and dusk were generally rapid and erratic, with little or no gliding. These characteristics of crepuscular flights were especially exaggerated at $T_a<20–22\,°C$ (individuals may fly in near darkness at $T_a=15\,°C$). Similar fast, 'jerky' or 'bouncing' flight during feeding at dusk has been reported previously (Corbet, 1963) and can occur even in bright sunshine at $T_a<22\,°C$; I observed one female flying extremely rapidly shortly after sunrise at $T_a=7\,°C$ ($SR=300\,W\,m^{-2}$). Visible gliding sometimes occurred in bright sunshine at $T_a=20–21\,°C$, but only when many individuals were basking on vegetation and making relatively short flights and thus not regulating $T_{th}$ by endothermy alone (see Corbet and Eda, 1969).

Gliding and slower flight usually became obvious at $T_a=23–25\,°C$ under sunny conditions in the morning, but after sunset usually were no longer evident even when $T_a$ exceeded $25\,°C$. Under warmer conditions, apparent velocity declined while gliding became more frequent. In very warm weather ($T_a\geqslant33\,°C$), these dragonflies often gave the impression of almost hanging in the air and gliding nearly continuously except when turning or chasing prey or conspecifics; this behavior was observed at $T_a$ values as high as $39\,°C$ ($SR=400–600\,W\,m^{-2}$). Only during the single 'frantic feeding' event recorded here did unusually rapid flight occur at high $T_a$.

### Wingbeat frequency

Wingbeat frequency declined markedly and significantly in patrolling male *A. junius* as $T_a$ and $SR$ increased (Fig. 4A). These data were obtained over several years and sites, under variable wind conditions. Wind velocity was not usually measured but did not appear to be correlated with $T_a$, nor was flight heading related to wind direction. Wingbeat frequency is related to size (May, 1981), but the individuals for which frequency was measured in the field could not generally be collected for morphological measurements. Size may vary seasonally (Penn, 1951); in particular, the very earliest individuals, which were probably migrants from the south, may have been smaller than those that emerged locally later in the summer (M. L. May, personal observations). However, the month of collection did not significantly influence frequency. Wingbeat frequency also declined significantly with increasing



Fig. 4. Wingbeat frequency ($n$) as a function of $T_a$ in *A. junius* (A) and *E. cynosura* (B). Regressions lines are $n=49.9-0.686T_a$, $r^2=0.762$, $P<0.0001$, or $n=59.4-0.735T_a-0.0108SR$, $r^2=0.892$, $P<0.0001$, for both $T_a$ and solar radiation ($SR$) for *A. junius* (only the first of these is shown) and $n=69.5-0.758T_a$, $r^2=0.234$, $P=0.0032$, for *E. cynosura*. Each point is a value for one individual.
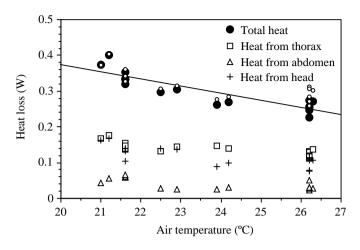
Fig. 5. Calculated whole-animal heat loss (d$H$/d$t$; equation 1) of individual *Anax junius* during crepuscular feeding flights. Filled circles, total heat loss; squares, heat loss directly from the thorax; crosses, heat loss from the head; triangles, heat loss from the abdomen. Least-squares regression of total heat loss (solid line) is: d$H$/d$t$=0.777−0.0201$T_a$, $r^2$=0.790, $P$<0.0001, $N$=16). The small open circles represent total heat loss if losses from the abdomen are assumed to increase linearly from values equal to those shown at $T_a$=21 °C to twice those shown at $T_a$=26.5 °C.
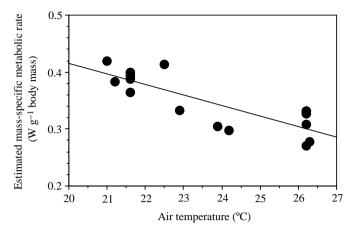


Fig. 6. Estimates of mass-specific flight metabolic rate (*MR*) of individual *A. junius* during crepuscular feeding flights, calculated as described in the text, as a function of $T_a$. The least-squares regression (solid line) is *MR*=0.781−0.0183$T_a$, $r^2$=0.683, $P$<0.0001.

$T_a$ in *E. cynosura* males (Fig. 4B), although the correlation was weaker.

### Heat exchange and T$_a$

At $T_a$ between 20 and 30 °C and SR<60 W m$^{-2}$, $T_{th}$ and $T_h$ were strongly elevated above $T_a$, while $T_{ab}$ was elevated by less than 3 °C; for all three body temperatures, the degree of elevation above $T_a$ was negatively correlated with $T_a$ (see Fig. 8 in preceding paper; May, 1995), so overall non-evaporative heat loss must likewise decline as $T_a$ increases. I obtained complete body temperature and mass data for 16 individuals under conditions of negligible solar radiation, over a $T_a$ range of 21.0–26.5 °C. 'Dry' heat loss, calculated from equation 1, is shown for these individuals in Fig. 5, along with the loss calculated for each tagma. All data were collected during typical crepuscular feeding flights with no perceptible wind. Estimates assume that flight speed declined with increasing $T_a$ using the relationships given in Fig. 2. Heat loss from the thorax accounted for 46.5 % and from the head 39.8 % of the total loss, while loss from the abdomen was only 13.6 %. Furthermore, total heat loss declined significantly as $T_a$ rose, by about 30 % over the 5.5 °C range. Energy metabolism was estimated from these data by adding estimates for evaporative heat loss and mechanical work. I calculated the former by assuming that air was inspired at 50 % relative humidity (*RH*) and $T_a$ and expired at 100 % *RH* and $T_{th}$ and that ventilatory exchange rate was 1.21 g$^{-1}$ h$^{-1}$ (Weis-Fogh, 1964). Work was estimated by assuming that the maximum work rate was 100 W kg$^{-1}$ flight muscle and that flight muscle constituted 86 % of thoracic mass (May, 1991*a*). The resulting estimates of mass-specific metabolic rate appear in Fig. 6 and, like dry heat loss, are negatively correlated with $T_a$. If work and evaporative heat loss are constant, as assumed here, they will not affect the slope of metabolic rate on $T_a$. If they are not independent of $T_a$, they probably increase as $T_a$ decreases: evaporation because of the increasing elevation of $T_{th}$ and $T_h$ above $T_a$, work because of the reduction in gliding and probable increase in wingbeat frequency and/or flight velocity. Thus, the assumption of constant values is most likely to make the caclulated slope less negative than the true relationship.

### Discussion

A combination of quantitative and qualitative data provide strong support for the conclusions (1) that flapping is increasingly replaced by gliding under conditions of high heat load, although the effect of environmental temperature can be overridden to meet other flight demands; and (2) that flight speed does not increase with $T_a$, varies according to the function of flight, and probably declines as the proportion of time spent gliding increases during feeding. Heat production must decline as more time is spent gliding, in accordance with calculated values (Figs 5, 6). Nonetheless, although the overall evidence is strong, the arguments are indirect and require assumptions that need examination.

Variation in ambient wind velocity complicates the interpretation of the flight behavior data. Wind velocity was not measured during every observation and could not be measured at the exact moment and location where individual dragonflies were flying. For feeding flights, however, wind speed was probably not an important factor in the relationships between flight speed and the proportion of time spent gliding with $T_a$. Aside from the facts that flight headings showed no preferred direction relative to the wind and that wind velocity was apparently uncorrelated with $T_a$, as already noted, I often observed progressive, qualitative changes in flight behavior clearly uncorrelated with changes in wind speed or direction.

It is also unlikely that the observed increase in gliding reflects the use, as an energy reduction strategy, of thermals or slope soaring (Gibo, 1981). The data on which calculations of heat production are based were taken at dusk under nearly windless conditions, so neither explanation could have applied. During video-taping of feeding, flying individuals were not confined to small areas where convective or slope lift would be likely, nor were groups concentrated in such areas, and many individuals flew at low and constant height. In addition, sunlight intensity was generally low, wind intermittent, and upwind slopes and obstructions absent, all conditions inconsistent with thermal or slope soaring. During migration, flight was nearly constant in direction and height (except when insects actually passed over an obstacle) and again, therefore, not consistent with behavior expected during either form of soaring. It is possible, however, that some qualitative observations on hot, sunny days may have included dragonflies taking advantage of either or both phenomena.

Polcyn (1988) suggested that at extremely high $T_a$ in the Mojave Desert of California, dragonflies, including *A. junius*, increase their flight speed to augment convective cooling. Under an intense radiant heat load, body surface temperatures might approach core temperatures, enhancing the effectiveness of convection, but in more moderate conditions this strategy may be less effective. Heat loss is relatively insensitive to increasing air speed above about $1\,\mathrm{m\,s^{-1}}$ (May, 1995), and very fast flight must entail increased heat production; for example, Heinrich and Casey (1978) found that flight was curtailed in some dragonflies at high $T_a$.

Wingbeat frequency in *A. junius* in the field was similar to, but more variable than, that recorded in the laboratory at levels of $T_{th}$ characteristic of flight (May, 1981), but within the range reported by Rüppel (1989) for *Anax imperator* during variable flight maneuvers. Wingbeat frequency is positively correlated with flight speed in *Locusta migratoria* (Baker *et al.* 1981), so frequency reduction at high $T_a$ in *A. junius* is consistent with the inference that flight speed declines, although the data pertain to different flight modes. Frequency is also presumably correlated with heat production, so the observed reduction with increasing $T_a$ again implies that heat production declines as environmental heat load rises.

Whether temperature-correlated change in frequency occurs during flights other than patrols at mating rendezvous sites is uncertain. The opportunity to reduce heat production by extensive gliding may be less in patrols than during feeding or migratory flights; modulation of wingbeat frequency might provide an alternative to gliding. However, both tactics could be used during all flights. In any case, elevation of wingbeat frequency at low $T_a$ is consistent with a general strategy of adaptively changing heat production in the face of changing heat load.

Computed rates of heat loss during feeding flights directly suggest alteration in flight metabolic rate in response to changes in $T_a$. The 30 % reduction from 21 to 26.5 °C corresponds satisfactorily to the approximately 25 % reduction in the proportion of flapping flight (from about 80 % to about 60 % of total flight time; Fig. 3) over the same temperature range. The validity of such calculations rests, however, on the appropriateness of equation 1. Stavenga *et al.* (1993) validated a three-compartment model of heat loss in a blowfly (an insect that does not regulate $T_{th}$ endothermically) that reduces to equation 1 under conditions of thermal equilibrium. Casey (1992*a*), in contrast, suggested that equation 1 may underestimate heat loss, especially at high values of $T_a$, in insects that regulate $T_{th}$ because, in the abdomen particularly, temperature is not uniform and temperature gradients are not constant owing to alterations in hemolymph flow in order to unload heat from the thorax. In the present case, however, the very slight elevation of $T_{ab}$ seems to preclude much active heat transport to the abdomen over the $T_a$ range considered here (May, 1995). Even if heat loss from the abdomen doubled between 21 and 26.5 °C (Fig. 5) and flight speed were constant, the correlation of total heat loss with $T_a$ would be significant ($P<0.005$) and negative, although the reduction over the 5.5 °C range would be diminished to about 15 %.

Comparison of estimated values of energy metabolic rate with those measured respirometrically by Polcyn (1988) also supports the validity of this approach. He found mean mass-specific metabolic rate of *A. junius* to be $0.48\,\mathrm{W\,g^{-1}}$ body mass, compared with the mean from Fig. 6, at $T_a<23$ °C, of $0.39\,\mathrm{W\,g^{-1}}$ body mass; these correspond to 1.01 and $0.86\,\mathrm{W\,g^{-1}}$ thoracic mass, respectively. Similar calculations for the smaller Anisoptera, *Epitheca cynosura* (May, 1987, 1995) and *Gynacantha nervosa* (Rambur) (M. L. May, unpublished
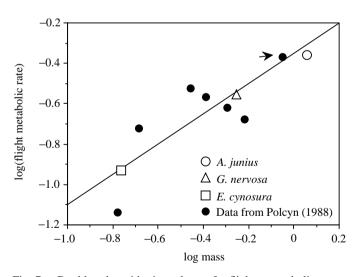


Fig. 7. Double logarithmic plot of flight metabolic rate ($\mathrm{W\,kg^{-1}}$ body mass) *versus* mass (g) for dragonflies. Open symbols represent estimates, based on calculations of heat budgets as described in the text, for *A. junius* ($N=16$; this study), *E. cynosura* ($N=9$; May, 1987) and *Gynacantha nervosa* ($N=9$; M. L. May, unpublished data). Data from Polcyn (1988) are based on mean $O_2$ consumption during flight in closed containers of *Tarnetrum corruptum*, *Erythemis simplicicollis*, *Tramea lacerata*, *Libellula luctuosa*, *Libellula saturata*, *Aeshna multicolor* and *Anax junius* (listed in order of increasing body mass). The arrow indicates his point for *A. junius*. The solid line is the least-squares regression for Polcyn's data.

data) also seem to correspond well with Polcyn's (1988) data (Fig. 7).

Among other insects, only honeybees have been shown by means of respirometry to reduce flight metabolic rate at high $T_a$ (Harrison *et al.* 1994; Roberts *et al.* 1994). Data adequate to calculate an approximate heat budget in flight are available for *Manduca sexta* (Hegel and Casey, 1982) and for euglossine bees (May and Casey, 1983). For *M. sexta*, in which the rate of $O_2$ consumption is known to be independent of $T_a$, the calculated rate of heat loss also is independent of $T_a$ and, assuming a work output of $90\,\mathrm{W\,kg^{-1}}$ muscle mass (Stevenson and Josephson, 1990), metabolic rate for a 2.2 g moth is 0.371 W, or 87 % of the value estimated from $O_2$ consumption measurements. Hegel and Casey (1982) and Casey (1992*a*) concluded that metabolic rate was underestimated at high $T_a$, but their calculation was based on an erroneous regression of $T_h$ on $T_a$ (May, 1995).

Re-analysis of the data of May and Casey (1983) on euglossine bees indicates that in large pubescent bees (*Eulaema* spp. and *Eufriesia* spp.) calculated heat budgets are again independent of $T_a$ and lead to estimates of metabolic rate of 97–109 % of rates of $O_2$ consumption. In *Euglossa* spp., comparable estimates range from 100 to 127 % of $O_2$ consumption rates but are negatively correlated with $T_a$. The reduction is only about 7 % between 20 and 30 °C, however, approximately one-sixth the predicted decline of about 43 % over a comparable range in *A. junius* (Fig. 6).

Although heat budgets clearly must be applied cautiously to field data, the evidence for their validity in the case of *Anax junius* appears compelling. At $T_a$ above about 30 °C, these dragonflies modulate heat loss by controlling hemolymph circulation from the thorax to the abdomen (Heinrich and Casey, 1978; May, 1995), much as in sphinx moths or bumblebees. At lower ambient temperatures, however, there is no evidence for variable heat transfer to the abdomen during flight. Instead, the insects evidently fly more steadily, and probably more rapidly, thereby increasing heat production to maintain high $T_{th}$ and $T_h$ in the face of declining $T_a$. Although activity is generally curtailed at $T_a$ below about 18–20 °C, this strategy can enable them to remain on the wing at temperatures below 10 °C (M. L. May, personal observation).

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