

# LARGE-SCALE CHANGES IN THERMAL SENSITIVITY OF FLIGHT PERFORMANCE DURING ADULT MATURATION IN A DRAGONFLY

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## Summary

Newly emerged adult dragonflies are physiologically immature in a number of ways, including the mass, ultrastructure and biochemistry of their flight muscles. In *Libellula pulchella* dragonflies, adult maturation of flight muscle is accompanied by striking changes in thermal physiology. Vertical force production during fixed flight attempts in newly emerged adults (teneral) shows a broad plateau of near-peak performance, first attained at cool thoracic temperatures (typically 28–34 °C) and maintained up to thoracic temperatures of 40–45 °C [mean optimal thoracic temperature (OTT)=34.6 °C; mean upper lethal temperature (ULT)=45.3 °C]. In contrast, fully mature

adults show narrow thermal sensitivity curves, wherein peak performance is approached only within a few degrees of the thermal optimum, which invariably occurs at hot thoracic temperatures (38–50 °C; mean OTT=43.5 °C; mean ULT=48.6 °C). These changes in the shape and position of thermal performance curves are compared with predictions from hypotheses for the evolution of thermal sensitivity.

Key words: insect, temperature, ontogeny, dragonfly, *Libellula pulchella*, Odonata, phenotypic plasticity.

## Introduction

Most large flying insects engage in some form of thermoregulation, presumably in order to achieve body temperatures that optimize flight performance. How insects accomplish thermoregulation is fairly well understood in terms of the mechanisms involved (reviewed in Heinrich, 1993); however, we have only a general understanding of how temperature affects performance. Few data precisely define (i.e. within 1–5 °C) optimal body temperatures for flight (e.g. Esch, 1976; Barnes and Laurie-Ahlberg, 1986; Coelho, 1991) or show how steeply performance degrades at sub- and supra-optimal temperatures. Furthermore, we know very little about intraspecific variation in thermal sensitivity of insect locomotor physiology. Insect body temperatures are typically reported as means or as individual data points on a regression of body temperature *versus* ambient temperature, with variation around the mean or the regression line treated explicitly or implicitly as error. This practice may overlook important variation among genotypes or age groups that regulate different body temperatures. Previous studies that have sought intraspecific variation in the thermal physiology of insect flight performance have been richly rewarded (Watt, 1977, 1983, 1992; Watt *et al.* 1983, 1985, 1986; Carter and Watt, 1988; Laurie-Ahlberg *et al.* 1985; Barnes and Laurie-Ahlberg, 1986).

Here, a dragonfly species (*Libellula pulchella*) is examined for age-related variation in the thermal sensitivity of flight

performance. Forthcoming papers will describe age-related changes in the biochemistry and contractile performance of flight muscle, and how body temperatures of *L. pulchella* in nature vary as a function of age and activity.

## *Libellula pulchella*

Many dragonflies in the family Libellulidae (Odonata: Anisoptera) begin adult life at approximately half of their eventual mature body mass (Marden, 1989; Anholt *et al.* 1991) (Fig. 1). Hypertrophy of the flight musculature (an increase in cell size and mitochondrial elaboration) constitutes a large portion of this growth. Striking changes in behavior accompany these trends in body mass and muscle development. Newly emerged (teneral) libellulids spend little time in flight; they are primarily sit-and-wait predators in early successional habitats surrounding their natal ponds. In contrast, during territorial defense and mating, mature libellulids are among the most active animals on earth, spending up to 100% of their time in vigorous flight (J. H. Marden, in preparation).

While perched, libellulid dragonflies adjust their body temperatures behaviorally by altering their body orientation with respect to sunlight (May, 1976). They are unable to warm themselves by shivering, and they are not able to transfer excess heat actively from their thorax to their abdomen as do endothermic insects, including dragonflies of the family Aeshnidae (Heinrich and Casey, 1978; Heinrich, 1993). Heat



Fig. 1. (A) An adult *Libellula pulchella* emerging from the nymphal stage. (B) A mature adult male.

generated as a by-product of flight metabolism during prolonged flight can accumulate in the thorax, as indicated by the high thoracic temperatures ( $T_{th}$ ) of *L. pulchella* males defending territories ( $T_{th} > 40^{\circ}\text{C}$ ; Pezalla, 1979; J. H. Marden, in preparation) and the curtailment of flight activity at high ambient temperatures in *L. saturata* (Heinrich and Casey, 1978).

The life history of libellulid dragonflies is thus characterized by an increasing tendency to experience high body temperatures as maturation progresses. In temperate-zone species, nymphs are probably never exposed to water temperatures in excess of  $30^{\circ}\text{C}$ . Teneral adults are rarely (if ever) exposed to thoracic temperatures in excess of  $40^{\circ}\text{C}$  (J. H. Marden, in preparation). Mature adults routinely experience thoracic temperatures in excess of  $40^{\circ}\text{C}$ , reaching at least  $45^{\circ}\text{C}$  during brief episodes of peak exertion (Pezalla, 1979; J. H. Marden, in preparation).

The combination of dramatic adult myogenesis, accompanied by predictable maturational changes in behavior and body temperature, led to the hypothesis that *L. pulchella*

may undergo a change in thermal physiology during adult maturation. Here this hypothesis is tested by examining age-related changes in the thermal sensitivity of locomotor performance in *L. pulchella*.

#### Materials and methods

*L. pulchella* Drury adults were collected at numerous sites in Chittenden County, Vermont; Madison County, New York; and Centre County, Pennsylvania, during the summers of 1991–1994. Immediately after capture, they were placed in an insulated cooler that was maintained at  $10\text{--}15^{\circ}\text{C}$ . Dragonflies were maintained in the laboratory in a humidified incubator at  $17^{\circ}\text{C}$  for 1–48 h prior to use in flight experiments.

Dragonflies were attached to a force transducer, and mean vertical force production during brief flight attempts was measured over a wide range of thoracic temperatures. The force transducer consisted of a thin metal plate made of high-carbon steel (a portion of a razor blade), clamped at one end, and a rigid glass rod (a 1.5 cm segment of a  $5\ \mu\text{l}$  microcapillary

tube) that extended horizontally from the other end. Four foil strain gauges (Omega Engineering, HBM 3/120 LY11) were bonded to the metal plate and were connected in a full-bridge configuration to a bridge amplifier (World Precision Instruments TBM4). Dragonflies were glued by their ventral thorax with quick-setting epoxy resin to the distal end of the glass rod, with their head pointing towards the strain gauges and their body aligned parallel to the rod. Wings could beat in an unobstructed manner, with the potential for a full stroke amplitude of 180°. Dragonflies fixed to the force transducer made spontaneous flight attempts or they were stimulated to attempt flight by gently pinching their legs or abdomen with fine forceps.

The force transducer had an unloaded resonant frequency of approximately 1 kHz, which dropped to as low as 200 Hz when dragonflies were attached. Wingbeat frequencies of the dragonflies (approximately 15–100 Hz depending on temperature and wingbeat kinematics; see Fig. 2) were well below the loaded resonant frequency of the transducer, so that resonance was not pronounced. The transducer showed a linear relationship between static load and electrical output over a wide range of forces ( $r^2=0.99$  from 0 to 15 g static loads, with resolution approaching 10 mg).

A fine-gauge thermocouple implanted in the dorsal thorax and connected to a Physitemp Bat-12 thermocouple thermometer was used to monitor thoracic temperature. Thoracic temperature was varied by surrounding the dragonfly with a copper cooling coil (removed prior to flight attempts) or raised by heating with an infrared lamp. The following sequence of thoracic temperatures was used: flight attempts were initially recorded at a  $T_{th}$  equivalent to room temperature (22–24 °C), then  $T_{th}$  was raised progressively to 40 °C (rate of change was approximately 1 °C min<sup>-1</sup>).  $T_{th}$  was then lowered to 15 °C, and again raised to 40 °C.  $T_{th}$  was then lowered again

to 15 °C, then raised until the dragonfly could no longer beat its wings (typically around 46–50 °C; this temperature was defined as the upper lethal temperature). The experiment was then terminated. In this way, flight attempts over replicate temperature series were obtained for each individual over most sublethal temperatures. A comparison of the first *versus* the second temperature series for 10 individuals sampled early in the study showed a high degree of repeatability of both mean and maximal performance at specific temperatures, with no indication of a performance change between replicate series. The total number of flight attempts averaged 223±90 per individual (s.d.; total  $N$  dragonflies=37; total  $N$  flight attempts=8240).

Signals from the force transducer (*via* the bridge amplifier) and the thermocouple were converted to 12-bit digital information (AD Instruments, MacLab/8) and fed into a Macintosh computer, where they were monitored in real time with software emulating a chart recorder (AD Instruments; Chart) at a sampling frequency of 1 kHz. At the conclusion of each experiment, force data were calibrated by loading the quiescent dragonfly with known weights. The software used this calibration to convert the data to force units. Portions of each flight attempt that were well away from stimulus artifacts (forces arising from pinching the dragonfly) and which included at least three full wingbeat cycles were selected (Fig. 2), and from these data the software integrated the area under the curve and corrected for the baseline to yield the mean vertical force. Force data were divided by flight muscle mass (established by post-experiment dissection and weighing; Marden, 1989) and are reported as N kg<sup>-1</sup> flight muscle (Marden, 1987, 1994). Note that all measures of force production were obtained by integrating from peak to peak over several wingbeat cycles. None of the analyses uses peak instantaneous force (*i.e.* peaks of the raw traces in Fig. 2).

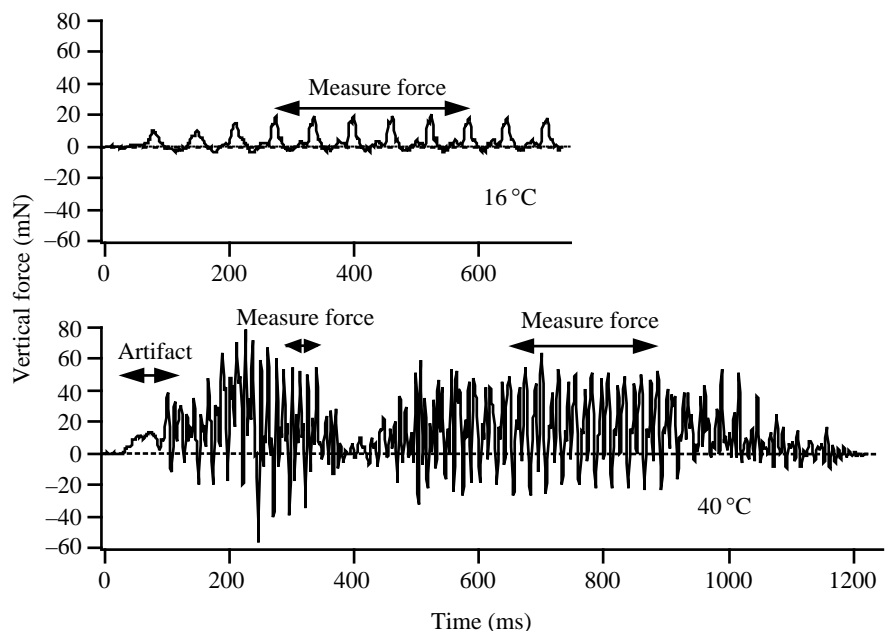


Fig. 2. Samples of raw traces of vertical force production during flight attempts by dragonflies attached to a force transducer. Mean vertical force was measured from peak to peak over stable portions of the traces, as indicated by the double-headed arrows. The portion of the record labeled artifact indicates forces arising from stimulating the dragonfly with forceps. Note the diversity of waveforms even within a single flight attempt; this is caused by dragonflies switching among different wingbeat kinematics.

### Characterizing relative maturity

*L. pulchella* adults increase in body mass from approximately 300–400 mg at emergence to as much as 700 mg at maturity (see Table 1; see Anholt *et al.* 1991, for additional data). However, body mass alone is not an accurate measure of relative maturity, because variation among individuals in exoskeletal size (fixed when the cuticle hardens shortly after adult emergence) limits the potential for mass gain during maturation. Thus, a better index of relative maturity, particularly with regard to muscle development, is given by residuals from a regression of the cube root of thorax mass on hindwing length (units= $\text{mg}^{-3}$ ; a value of 0 indicates the approximate midpoint of adult maturation). This quantity indicates the degree to which flight muscle has developed within an exoskeleton of fixed dimensions and is used throughout this report to quantify relative maturity (abbreviated as RM).

## Results

### Raw data for thermal sensitivity of flight performance

Examples of distributions of vertical force as a function of thoracic temperature are shown in Fig. 3. These distributions varied both within and among individual dragonflies in the amount of apparent submaximal effort. Over certain parts of the temperature range, individuals showed consistently maximal effort, whereas the same individual often showed a wide range of effort over another temperature range (for example, compare the evenness of effort at 15–25 °C with the variation in effort at 30–50 °C for the RM=0.06 and 0.29 individuals in Fig. 3). Note also that few force measurements fall far above the overall distribution, as would result from substantial measurement error or if maximal effort was only rarely exerted. Peak performance (the maximum vertical force observed during any one flight attempt) averaged  $55 \pm 17 \text{ N kg}^{-1}$  (S.D.;  $N=37$ ) for the entire sample and  $62 \pm 16 \text{ N kg}^{-1}$  ( $N=25$ ) when teneral ( $\text{RM} < -0.40$ ) were excluded. These values agree closely with the maximum load-lifting capacity measured for mature dragonflies in free-flight experiments ( $59.9 \text{ N kg}^{-1}$ ; Marden, 1987). To summarize, the abundance of apparent submaximal effort, the lack of outliers for maximal force and the agreement of global force maxima with data obtained using other methods indicate that the relationship between vertical force production and thoracic temperature is best characterized by measures that describe the upper bound of the force distribution (i.e. rather than by temperature-specific means, which would be biased by submaximal effort towards artificially low values). Traces that outline the upper bound of the force distribution (i.e. all data are contained beneath the trace) for each of the 37 individuals tested are shown in Fig. 4.

### Age-related change in thermal sensitivity of flight performance

Optimal thoracic temperature (OTT; the temperature at which peak performance occurred) became dramatically hotter during adult maturation (Figs 3–5;  $\text{OTT} = 5.57\text{RM} + 40.5$ ,  $r^2 = 0.50$ ,  $P < 0.0001$ ). Peak performance (PP) and upper lethal

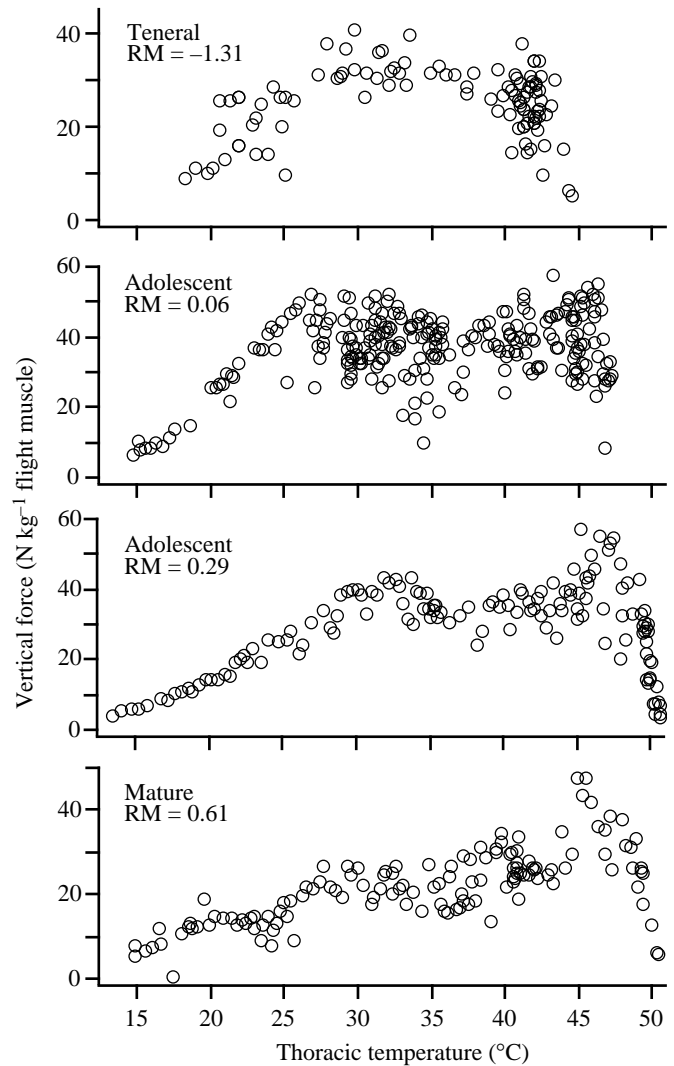


Fig. 3. Distributions of vertical force production as a function of thoracic temperature for four representative *Libellula pulchella* dragonflies. Each point represents a single flight attempt; each plot shows all flight attempts made by an individual. Relative maturity (RM) of each individual is indicated by the residual from a regression of the cube root of thorax mass (mg) on hindwing length (cm).

temperature (ULT) also increased significantly with maturity (Fig. 5;  $\text{PP} = 13.96\text{RM} + 54.9$ ,  $r^2 = 0.31$ ,  $P < 0.001$ ;  $\text{ULT} = 1.80\text{RM} + 47.0$ ,  $r^2 = 0.25$ ,  $P = 0.002$ ). Mean ULT (45.3 °C) exceeded mean OTT (34.6 °C) by about 10 °C in tenerals, whereas this 'safety margin' shrank to about 5 °C at full maturity (mean ULT 48.6 °C, mean OTT 43.5 °C; difference between ULT and OTT =  $-3.8\text{RM} + 6.5$ ,  $r^2 = 0.29$ ,  $P < 0.001$ ). For two mature individuals, there was no distinguishable difference between OTT and ULT; that is, their performance dropped from maximal to zero within a few tenths of a degree.

### Age-related change in the shape of thermal performance curves

Tenerals ( $\text{RM} < -0.40$ ) showed a broad plateau of near-peak performance that was first attained at cool temperatures

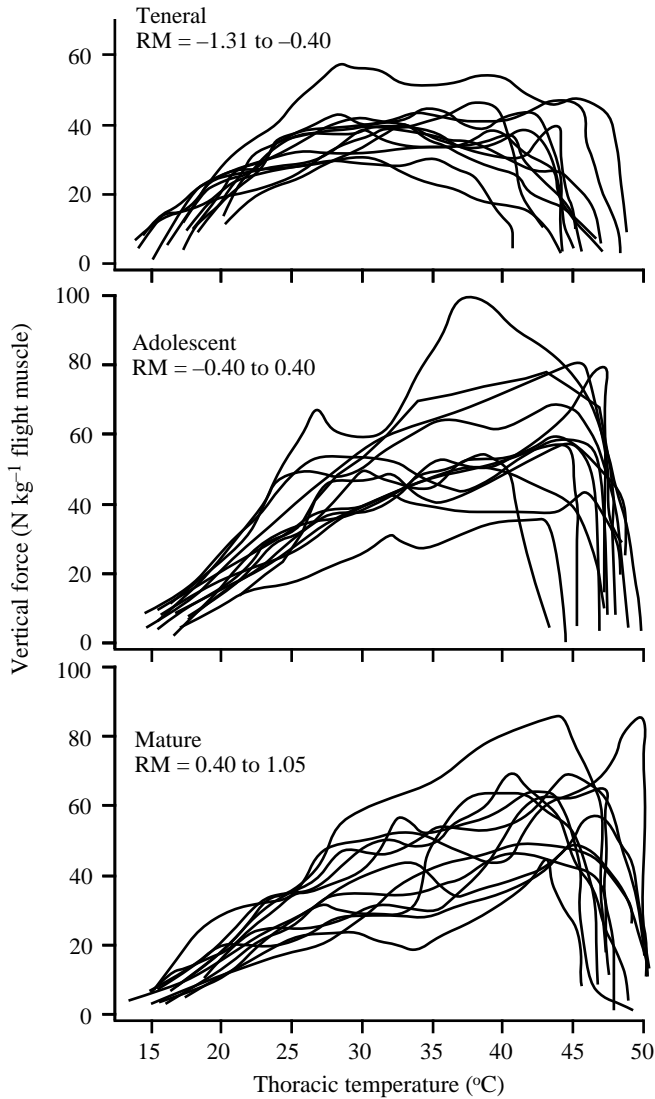


Fig. 4. Traces outlining the upper limit of vertical force production as a function of thoracic temperature for each of the 37 individual *Libellula pulchella* dragonflies tested. Curves are divided among three age categories, based on relative maturity (RM; defined in Fig. 3 legend and text).

(typically 28–34 °C; Fig. 4). In contrast, fully mature adults (RM>0.40) had narrower thermal sensitivity curves, where peak performance was usually approached only within a few degrees of OTT, which invariably occurred at very hot temperatures (38–50 °C; Fig. 4). Mature and especially adolescent (−0.4<RM<0.4) individuals sometimes displayed two distinct performance peaks (Fig. 3), one at cool temperatures (generally 28–34 °C) and one at hot temperatures (40–50 °C).

The minimum temperature for the initiation of flight attempts did not vary as a function of age; all age groups initiated flapping at approximately 15 °C (Fig. 4). However, performance at cool temperatures, as indicated by peak performance at 28–34 °C (chosen because this temperature

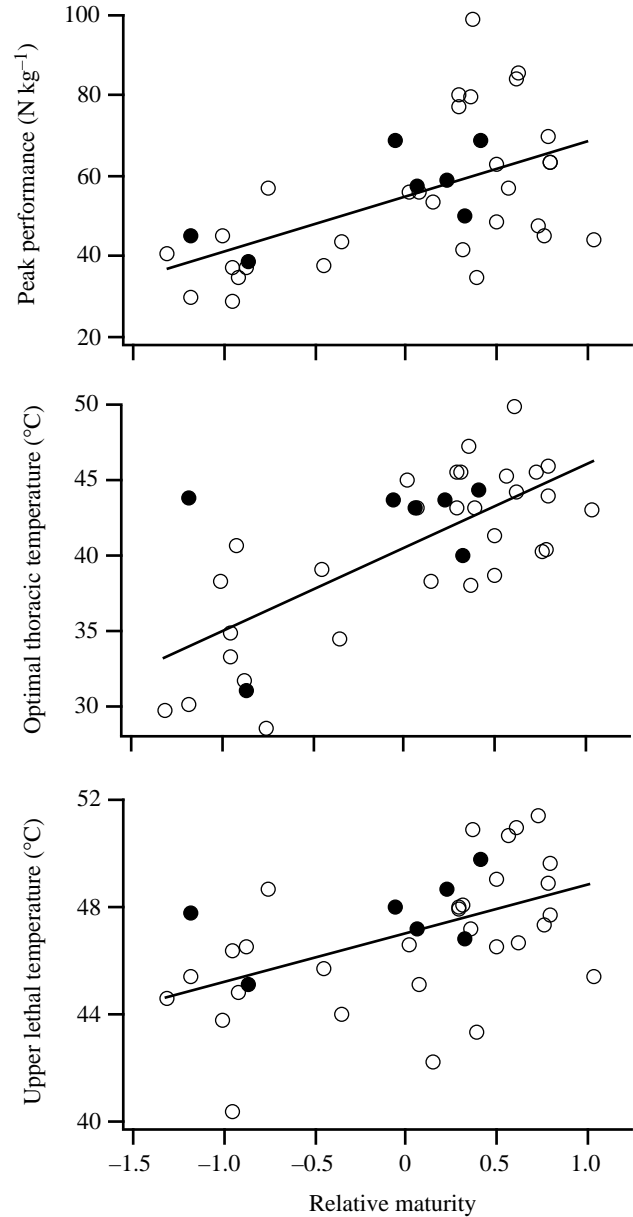


Fig. 5. Variation in thermal sensitivity characteristics as a function of relative maturity (defined in Fig. 3 legend and text). Open circles represent males; filled circles represent females. Sexes are pooled for all statistical analyses.

range contains the cool-temperature performance peak in double-peaked distributions; Fig. 3) and by the rate of rise in performance from 15 to 25 °C (slope of a line fitted to the upper bound of vertical force values over the 15–25 °C temperature interval for each individual), showed a convex relationship with relative maturity (Fig. 6; PP at 28–34 °C=−1.7RM−10.9RM<sup>2</sup>+47.5,  $r^2=0.15$ ,  $P=0.07$ ; slope at 15–25 °C=−0.5RM−1.1RM<sup>2</sup>+3.1,  $r^2=0.21$ ,  $P=0.02$ ). In contrast, peak performance at hot temperatures (40–50 °C) increased in a linear fashion with increasing maturity (Fig. 6; PP at 40–50 °C=18.8RM+52.5,  $r^2=0.41$ ,  $P<0.0001$ ).

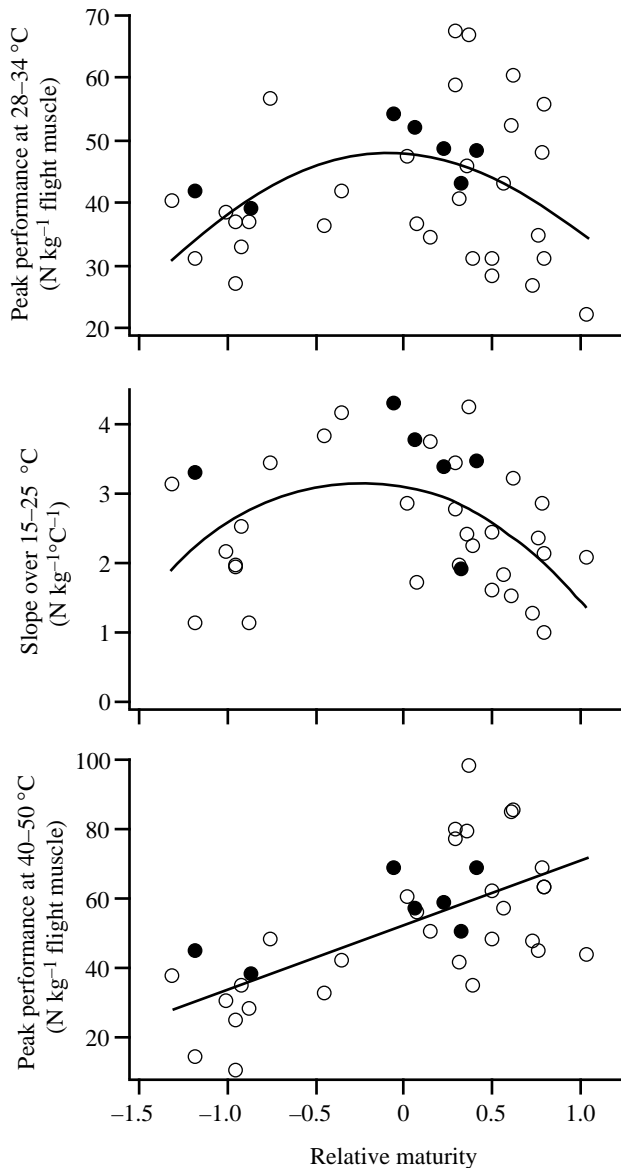


Fig. 6. Variation in flight performance over specific temperature ranges as a function of maturity (defined in Fig. 3 legend and text). Symbols are as in Fig. 5.

#### Gender effects

Females (seven of the 37 individuals sampled, spanning an age range from teneral to fully mature; Table 1) did not differ significantly from males in any of the above analyses. Females followed the same maturational trajectory of thermal sensitivity as did males, with the exception that females did not achieve the same degree of hypertrophy of thoracic muscle as did males [Table 1; i.e. they did not progress beyond the 'adolescent' stage of relative maturity as measured here, even though four of these females were fully mature in terms of body mass and ovarian development. Marden (1989) shows details of gender differences in maturational growth of libellulid dragonflies.] Females did not become as extreme as males in their thermal sensitivity characteristics (Figs 5, 6).

Table 1. Mean body and thorax mass of *Libellula pulchella* dragonflies according to relative maturity

Age	<i>N</i>	Body mass (mg)	Thorax mass (mg)
Teneral			
Male	10	350±38	151±25
Female	2	312±36	130±10
Adolescent			
Male	9	483±54	263±18
Female	1	478	227
Mature			
Male	11	552±54	325±30
Female	4	632±63	257±25

Values are means ± S.D.  
Relative maturity is explained in the text.

#### Discussion

*L. pulchella* dragonflies undergo a striking shift in thermal sensitivity of locomotor performance during adult maturation. This transition involves increases in peak performance, optimal thoracic temperature and upper lethal temperature (Fig. 5) as well as changes in the overall shape of the thermal sensitivity curve (Figs 4, 6). Cool-temperature performance declines as maturation progresses beyond the adolescent stage (Fig. 6), and cool-temperature performance relative to overall performance declines steadily throughout maturation.

The age-related shift in thermal sensitivity of flight performance in *L. pulchella* adults matches an age-related shift in the body temperatures that these dragonflies experience in nature (J. H. Marden, in preparation). Thoracic temperatures of teneral flying in the field range between 29 and 40 °C, whereas mature adults fly with thoracic temperatures of 38–45 °C. These age-specific ranges of field thoracic temperature correspond almost exactly with the age-specific ranges of optimal thoracic temperature for flight performance (Fig. 5).

The exact time course of adult maturation in *L. pulchella* is uncertain, but for other libellulids of similar size and life history, adult maturation requires about 2 weeks, during which rapid growth occurs (Marden, 1989). Adult emergence in *L. pulchella* occurs over a period of about 2 months (June and July), during which mature adults are present at nearly all times. Thus, teneral and mature adults are not separated seasonally, and it is unlikely that maturational changes in thermal physiology result from acclimation to seasonal changes in the thermal environment. Season (coded as the number of days after June 1 that a dragonfly was used for experiments; range=7–110 days) did not contribute significantly to relative maturity as an explanatory factor for either optimal thoracic temperature or upper lethal temperature (for season,  $P=0.78$  and  $0.96$ , respectively). Moreover, field measurements of thoracic temperature show wide differences between teneral and mature adults, even when these data are obtained from equivalent microsites (J. H. Marden, in preparation). For example, at an ambient temperature of 20 °C, thoracic temperature averages 34 °C in teneral *versus* 41 °C in

mature adults. Thus, it appears that the maturational shift in thermal sensitivity of flight performance in *L. pulchella* occurs independently of seasonal trends in ambient temperature and is either an acclimation response to an increasing trend in internal temperature (caused in part by an increase in metabolic heat retention as thoracic mass and flight duration increase) or is a more or less 'fixed' tendency that anticipates predictable changes in the internal thermal environment.

A close match between age-specific optimal thoracic temperature and the range of body temperatures experienced during flight indicates that the thermal physiology of *L. pulchella* flight muscle tracks a maturationally changing thermal environment. A similar phenomenon occurs in altricial nestling birds, where thermoregulatory competence improves with age, and nestlings undergo an ontogenetic shift in both body temperature ( $T_b$ ) and thermal sensitivity of neuromuscular performance (Choi and Bakken, 1990). In contrast, interspecific studies of lizards have sometimes found relatively little adjustment of optimal body temperature to different thermal environments, even though there appears to have been ample time for such an evolutionary change to occur (Huey and Bennett, 1987; Autumn *et al.* 1994). It is not presently clear why certain lizards, over evolutionary time scales, do not generally make the sort of adjustments in thermal physiology that individual dragonflies and birds undergo during a time scale of days (but see above citations for a discussion of possible reasons why the thermal physiology of lizards is conservative).

Evolution of the shape and position of thermal performance curves is a subject of considerable research interest (reviewed in Huey and Kingsolver, 1989, 1993), and thermally polymorphic *L. pulchella* dragonflies provide a novel way to examine the problem. Statistical difficulties of interspecific studies (the comparative phylogenetic approach) are avoided, as well as questions about the relevance of laboratory selection experiments to natural settings. One hypothesis from evolutionary models is that shifting to a higher optimal body temperature can have correlated effects on performance at low temperatures. In *L. pulchella*, the minimum temperature for the initiation of flight attempts (analogous to the lower critical temperature in studies of ectothermic vertebrates) does not change during the maturational shift to higher optimal thoracic temperature (Fig. 4). However, other indices of cool-temperature performance do change in a correlated, but complex, fashion. Cool-temperature performance first increases with maturity and increasing OTT among teneral and adolescents (Fig. 6; this may reflect an overall increase in performance as the musculoskeletal system matures), then decreases among mature adults. The latter effect supports hypotheses that performances at high and low temperatures are inversely correlated (Somero, 1975; Heinrich, 1977; Huey and Kingsolver, 1989, 1993). There is also a significant positive relationship between peak performance and OTT ( $PP=0.09OTT^2-5.15OTT+117.4$ ,  $r^2=0.28$ ,  $P=0.004$ ), which supports the hypothesis that 'hotter is better' (Hamilton, 1973; Bennett, 1991). Thermal breadth (TB; range of  $T_{th}$  over which performance is within 80% of maximal; Huey and Stevenson,

1979) decreased significantly with maturity ( $TB=-3.9RM+10.7$ ,  $r^2=0.20$ ,  $P=0.006$ ) and was inversely related to peak performance ( $PP=1.03TB+65.9$ ,  $r^2=0.13$ ,  $P=0.03$ ), as predicted by the 'jack-of-all-temperatures' hypothesis (Huey and Kingsolver, 1989). However, thermal breadth did not have a significant effect ( $P=0.19$ ) in a multivariate model that examined the simultaneous effects of TB and OTT on peak performance.

To my knowledge, there have been no previous reports of age-related changes in the thermal physiology of locomotor performance in insects, and it is not presently clear if this phenomenon is likely to be rare or widespread. Among insects with holometabolous development (i.e. a pupal stage), the adult emerges in very nearly its final form and, except for the ovaries, undergoes little bulk increase in tissue mass. For fully differentiated tissues, there may be little opportunity for large-scale changes in thermal physiology. Nevertheless, many insects undergo age-related changes in behavior, which may lead to large-scale changes in average and extreme body temperatures. For example, we know that the thoracic temperatures of insects engaged in activities such as territorial competition, foraging, predation, hive defense and mating often exceed 40°C (May, 1976; Bartholomew and Heinrich, 1978; Heinrich, 1979; Heinrich and Buchmann, 1986; Pezalla, 1979; Baird, 1986), and hotter individuals tend to be more successful (Heinrich and Bartholomew, 1979; Chappell, 1984). When this type of activity is restricted to a certain age class, we might expect commonly to find shifts in peak performance temperature and upper lethal temperature. A knowledge of these physiological changes might be important for understanding the ecology and behavior of many types of insects.

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