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# AGE-RELATED VARIATION IN BODY TEMPERATURE, THERMOREGULATION AND ACTIVITY IN A THERMALLY POLYMORPHIC DRAGONFLY

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## Summary

**Thoracic temperatures ($T_{th}$) of *Libellula pulchella* dragonflies during activity in the field were compared between age classes and with laboratory measures of optimal thoracic temperature for flight performance ($T_{th,opt}$; a trait that varies during adult maturation in this species). Newly emerged adults (tenerals) had mean $T_{th}$ values during flight (34.5 °C; range 29–40 °C) that did not differ from their mean $T_{th,opt}$ (34.6 °C; range 28.5–43.8 °C). Mature adults had higher and more precisely regulated thoracic temperatures (mean $T_{th}$ 41.7 °C; range 37.5–45.2 °C), which were somewhat lower than their mean $T_{th,opt}$ (43.6 °C; range 38.7–49.9 °C). Among matures, behaviors requiring the highest levels of flight exertion (aerial copulation; mate guarding; escalated territorial contests) caused an elevation of $T_{th}$ above that of concurrently sampled individuals engaged in routine flight (mean $T_{th}$ difference 1.3 °C), which raised mean $T_{th}$ to a level that was not significantly different from $T_{th,opt}$ (42.5 *versus* 43.5 °C). Compared with tenerals, matures spent more time flying, made longer-duration flights and showed a more restricted pattern of daily activity. Sympatric *Anax junius* dragonflies that regulate $T_{th}$ endothermically had a uniform pattern of activity across the entire day, i.e. occupied a broader ecological niche than that of *L. pulchella*. These results support the hypotheses that optimal body temperature evolves to match the elevated body temperatures that occur during exercise and that the ecological benefits of an expanded niche are a secondary benefit rather than a primary selective force during the evolution of homeothermy and high body temperatures.**

Key words: dragonfly, thermoregulation, *Libellula pulchella*, behavior, thermal sensitivity.

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## Introduction

*Libellula pulchella* dragonflies (Odonata; Libellulidae) undergo a novel maturational change in the thermal sensitivity of their flight performance (Marden, 1995). Measurements of vertical force production during tethered flight show that optimal thoracic temperature and upper lethal temperature increase by an average of 9 °C (from 35 to 44 °C) and 4 °C (from 45 to 49 °C), respectively, over the course of adult maturation. This shift accompanies an approximate doubling of body mass and a threefold increase in flight muscle mass. Seasonal changes in ambient temperature appear to be unrelated to this transition in thermal physiology, for mature and teneral (newly emerged) adults overlap broadly in their seasonal occurrence, and calendar date fails to explain a significant component of the variation in thermal sensitivity.

One hypothesis for the utility of this unusual physiological transition involves the sudden change in thermal environment between aquatic larvae and terrestrial adults (dragonflies lack a pupal stage, emerging directly from nymphs to adults). Libellulid nymphs are sedentary bottom-dwellers in ponds where the water temperature rarely, if ever, exceeds 30 °C. In contrast, flying adults routinely experience thoracic temperatures that exceed 40 °C (Pezalla, 1979). Thus, teneral adults may represent a necessary transitional stage between cool-adapted nymphs and hot-adapted mature adults, even though their relatively cool-adapted thermal physiology might be suboptimal (i.e. a developmental constraint). This hypothesis would be supported by data showing that field thoracic temperatures of tenerals and matures are not significantly different and that tenerals tend to be active with thoracic temperatures greater than their optimal thoracic temperature.

Alternatively, tenerals and adults might differ in behavior and heating/cooling characteristics and may experience widely divergent body temperatures. In that case, the maturational transition in thermal sensitivity might represent a plastic trait that fine-tunes performance physiology to age-specific differences in the internal thermal environment (i.e. optimization rather than a suboptimal constraint). This hypothesis would be supported by data showing maturational changes in behavior and thoracic temperature, and a close correspondence at all ages between field thoracic temperatures and optimal thoracic temperatures.

Here we examine age-related changes in behavior and thoracic temperature in *L. pulchella* dragonflies in order to test these hypotheses, as well as to examine general hypotheses for the evolution of thermal sensitivity and thermoregulation.

## Materials and methods

*Libellula pulchella* Drury dragonflies were studied at two field sites in Centre County, Pennsylvania, USA, during the summer of 1994. Newly emerged adults (tenerals, varying in adult age from a few hours to perhaps 2–3 days) were distinguished from matures by their relatively weak fluttering flight, glossy wings, absence of white pigmentation on their wings and dorsal abdomen, and their softer exoskeleton.

Thoracic temperatures ($T_{th}$) were measured by capturing flying *L. pulchella* dragonflies (or in the case of some tenerals, within a few seconds post-flight because their flights are exceedingly brief) in an insect net and, within approximately 5 s of capture, inserting a fine-gauge thermocouple into the thorax (Physitemp MT-26 needle microprobe connected to a BAT-12 thermocouple thermometer). Immediately after each measurement of $T_{th}$, the thermocouple was wiped dry and ambient temperature in the shade at a height of 1 m ($T_a$) was recorded. Samples of $T_{th}$ included both the first individuals to become active on cool mornings and individuals active at midday on the hottest days of the summer. Thus, our data represent as closely as possible the entire range of ambient temperatures at which *L. pulchella* adults were active.

To determine the effect of high-exertion flight on $T_{th}$ of mature males, we captured individuals that were engaged in aerial copulation, mate guarding and escalated territorial contests. Aerial copulation occurs following a brief chase wherein one or more males pursue and overtake a female that has approached the shoreline of a pond. The male that succeeds in grasping the female then supports most or all of her weight for approximately 2–10 s during copulation. Following copulation, the male releases the female within his territory, then makes rapid back-and-forth flights above her while she oviposits. During this period of post-copulatory guarding, the male intercepts and repels other males that attempt to rush in and abduct the female. Escalated territorial contests occur independently of mating. They are triggered by an intruding male that ignores the usual 'resident-wins' convention (Waage, 1988) and persists in a challenge against a territorial male. Escalated contests involve a high-speed chase around the entire periphery of the pond (i.e. far outside the boundaries of a single territory) and last for approximately 10–120 s (see Pezalla, 1979, for a fuller description). Whenever we obtained a $T_{th}$ measurement from a male engaged in one of these high-exertion activities, we then measured $T_{th}$ from a nearby mature male engaged in routine territorial patrolling flight (average time between paired $T_{th}$ measurements 242 s). These experiments were carried out only on clear, sunny days when there was no chance that intermittent clouds could significantly alter thermal conditions in the interval between paired $T_{th}$ measurements.

Thermal conductance of *L. pulchella* dragonflies was determined from measurements of passive cooling. Three mature and three teneral adults were killed by freezing, and a fine-gauge thermocouple was implanted in the approximate center of the thorax. The thermocouple was secured with glue, after which the dragonfly was heated to 45 °C, then suspended by the thermocouple wire in still air at room temperature within a covered styrofoam box. Thoracic temperature and ambient temperature (measured from a second thermocouple hanging inside the box) were monitored using an A-D converter (MacLab). Cooling constants were derived from slopes of linear regressions of the natural logarithm of the difference between $T_{th}$ and $T_a$ as a function of time. Cooling constants were multiplied by the specific heat of tissue ($3.47\,\mathrm{J\,g^{-1}\,°C}$; Bartholomew, 1981) to yield an estimate of thermal conductance.

Maturational changes in the thoracic temperatures that can be attained by *L. pulchella* dragonflies during passive heating (basking) were examined by gluing freshly killed (frozen) individuals in typical basking postures onto a thin forked stick (approximately 0.5 cm diameter). The stick was then mounted in the field so that the long axis of the body of each dragonfly was approximately perpendicular to oncoming sunlight. This experiment was carried out on two clear, sunny, calm days; on each day, we used two tenerals and two matures, mounted so that one of each age group occupied each fork of the stick. At 10 min intervals over a period of 1–2 h, a thermocouple was inserted into the thorax of each dragonfly, and thoracic temperature was recorded. Wounding caused by thermocouple insertion must elevate the rate of evaporative heat loss; therefore, these data are likely to underestimate the actual $T_{th}$ attained by basking.

Censuses of daily activity of dragonflies were obtained by conducting standard walks along the shore of a pond and through the surrounding scrubby vegetation in which *L. pulchella* adults forage. A walk of approximately 200 m was taken every 20 min from either 08:00 to 15:20 h or 08:00 to 20:00 h during 7 days in June and July of 1995. We counted as 'active' all *L. pulchella* tenerals and matures that were flying or were perched in an exposed location (i.e. scanning for prey during intermittent foraging). A few of the tenerals in these counts were flying away from the water following adult emergence; however, the vast majority were older tenerals engaged in intermittent foraging. Newly emerged tenerals that were not yet flight-capable were not included in these counts. On two separate days in July, counts were made of sympatric *Anax junius* dragonflies (Odonata; Aeshnidae). Both of these species disappear from the study sites when they become quiescent; while inactive, they perch inconspicuously in dense vegetation. Thus, our censuses represent counts of the 'active' subset of the population even though not all individuals counted were flying.

Flight activity was recorded during continuous 8 min observations of individually marked dragonflies. These samples were taken sporadically over times spanning early morning to late afternoon on 10 clear days. Marking was accomplished by blowing a small amount of fluorescent powder onto the abdomen of a dragonfly through a 1 m long blowpipe (Marden, 1989). This eliminated the need to capture and handle the dragonflies, and their behavior appeared to be unaffected by this procedure. Observations of tenerals were limited to those individuals engaged in intermittent foraging, i.e. older, flight-capable individuals. Data were collected by two observers; one watched the dragonfly and called out behavioral transitions (perching *versus* flying), while the other noted times and recorded data in a notebook.

## Results

Thoracic temperatures of flying tenerals (29–40 °C, $N=31$; Fig. 1) were very different from those of matures during routine (38–44 °C, $N=41$) and high-exertion (40–45 °C, $N=31$) flight. Analysis of covariance (ANCOVA) showed that age ($P<0.0001$), ambient temperature ($P<0.0001$), exertion level ($P=0.002$; exertion for tenerals was always considered 'routine') and the interaction between age and ambient temperature ($P=0.008$) all had significant independent effects on $T_{th}$. The slope of a regression line relating thoracic temperature to ambient temperature was approximately three times steeper for tenerals than for matures during routine flight (Fig. 1; 0.35 *versus* 0.13; this difference is significant according to the interaction between $T_a$ and age class in the ANCOVA described above). Thus, matures were markedly more 'hot-blooded' and homeothermic.

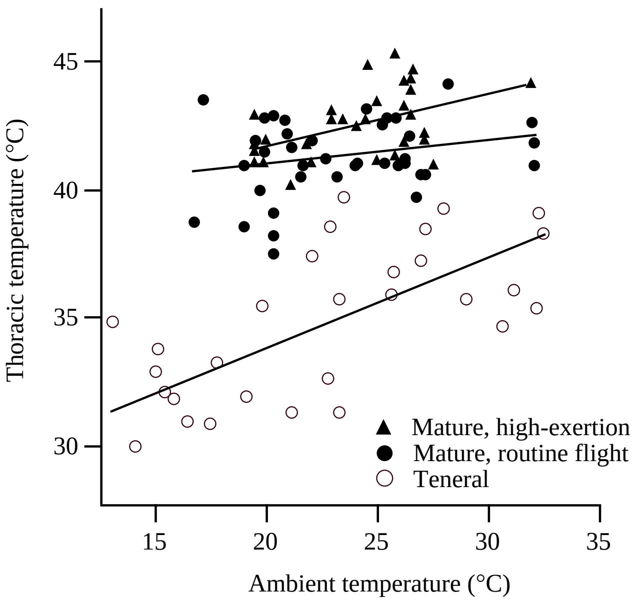

Fig. 1. Thoracic temperature of mature and newly emerged *Libellula pulchella* dragonflies as a function of ambient air temperature. The regression equation for matures during routine patrolling flight is: $T_{th}=0.125T_a+38.2$ ($N=41$, $P=0.06$, $r^2=0.09$); that for matures during high-exertion flight (defined in text) is: $T_{th}=0.197T_a+37.8$ ($N=31$, $P=0.008$, $r^2=0.22$); and that for tenerals is: $T_{th}=0.351T_a+26.8$ ($N=31$, $P<0.0001$, $r^2=0.51$).

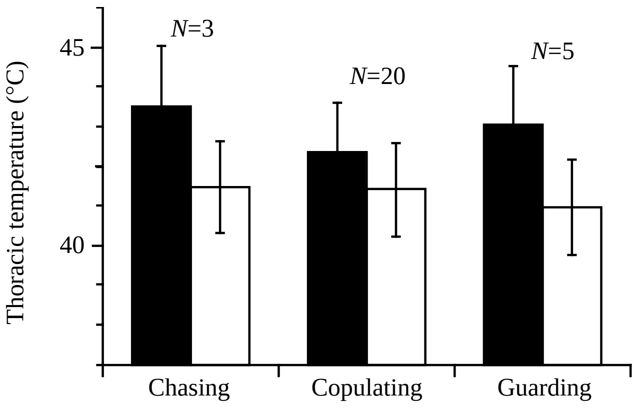

Fig. 2. Mean (±S.D.) thoracic temperature of mature males engaged in three types of high-exertion flight (black bars) compared with that of males engaged in routine territorial patrolling (white bars). These data were collected in a paired fashion; that is, each measurement of $T_{th}$ from a high-exertion flight was followed within minutes by a measurement of $T_{th}$ from another territorial male at the same site engaged in routine patrolling flight. Pooling data across all of these behaviors shows a significant effect of high-exertion flight ($P<0.001$).

Thoracic temperatures of mature males were significantly affected by their level of flight exertion. $T_{th}$ of males engaged in routine territorial patrolling was significantly lower than that of paired males (sampled within a few minutes from the same site) engaged in aerial copulation, mate guarding or escalated territorial contests (Fig. 2; $N=28$ pairs; mean difference 1.3±1.75 °C, S.D., $P<0.001$). The highest $T_{th}$ from any of the dragonflies that we sampled (45.2 °C) was from a mature male involved in a highly escalated territorial contest (i.e. a high-speed chase).

Thermal conductance during passive cooling for teneral *L. pulchella* dragonflies is approximately three times greater than for matures (Fig. 3; mean values = 150.2 *versus* 49.4 $\mathrm{J\,g^{-1}}$ body mass $\mathrm{°C\,h^{-1}}$; $P=0.02$). Surface area is nearly identical between tenerals and matures; however, they differ greatly in body mass (mean body mass 552 mg for matures, 350 mg for tenerals; Marden, 1995) and therefore heat content, which in turn affects their rates of temperature change.

Equilibrium temperatures of freshly killed dragonflies placed in basking positions in sunshine also showed a significant difference with age ($P=0.002$). Matures equilibrated at thoracic temperatures of 27–39 °C (mean 34.0 °C; $T_a$ range 20–25 °C), whereas simultaneously sampled tenerals ranged in $T_{th}$ from 26 to 36 °C (mean 31.7 °C). This result is somewhat surprising, considering that external dimensions undergo little change during adult maturation (despite the large change in body mass) and that matures are lighter in coloration. However, the immature cuticle of tenerals may be more permeable and thus create more passive evaporative cooling. Greater evaporative cooling in tenerals might also explain why the age-related difference in thermal conductance is proportionally greater than the difference in mass.

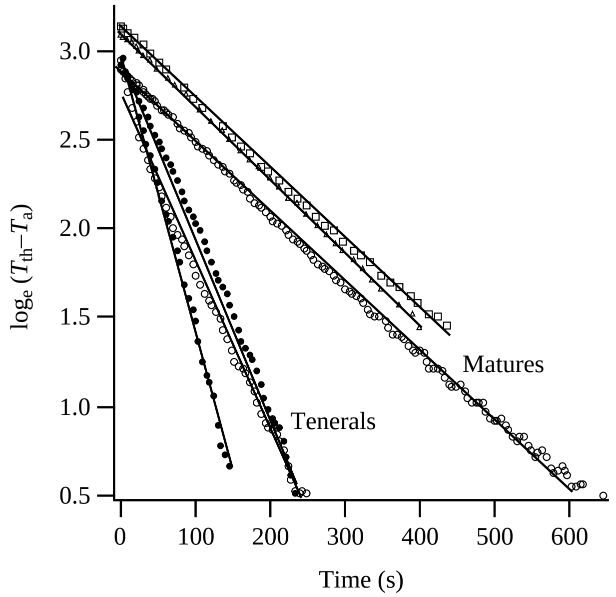

Fig. 3. Passive cooling rate of freshly killed mature and teneral *L. pulchella* dragonflies for three individuals of each age. Least-squares regression lines are fitted to the data for each individual.

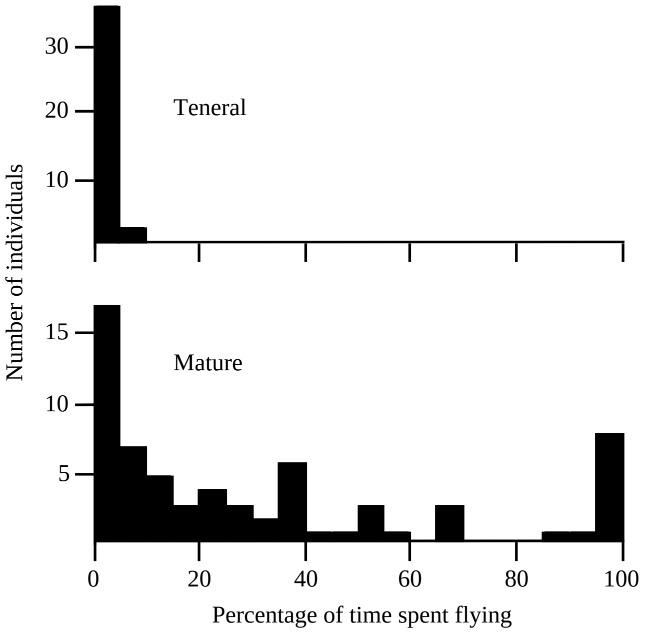

Fig. 4. Percentage of time spent flying by teneral and mature *L. pulchella* dragonflies during continuous observations (480 s) of marked individuals ($N$=39 tenerals, 66 matures; $T_a$=20–32 °C for tenerals, 18–30 °C for matures).

Mature and teneral *L. pulchella* dragonflies differed tremendously in their level of flight activity. During continuous observation of marked individuals (480 s periods), tenerals spent an average (±s.d.) of only 1.7±2.1 % of the time flying (Fig. 4; $N$=39), with an average flight duration of 3.1±1.1 s ($N$=127 flights, maximum 5.7 s). In contrast, mature males spent an average of 32.4±33.5 % of the time flying (Fig. 4; $N$=66), with an average flight duration of 82.2±154.9 s ($N$=370). More than 10 % of matures spent the entire observation period (480 s) in continuous flight. Percentage of time spent flying by tenerals was not significantly related to ambient temperature ($P$=0.10; $T_a$ range 20–32 °C), whereas matures showed a distinct peak in flight activity at intermediate $T_a$ (all observations of ‘100 % time in flight’ occurred at 23–26 °C). Excluding relatively inactive individuals (less than 10 % time in flight), matures showed a significant convex relationship between percentage time in flight and $T_a$ ($P$=0.015, $r^2$=0.19, $N$=44; $T_a$ range 20–31 °C), a pattern which has previously been observed for *L. saturata* (Heinrich and Casey, 1978).

Censuses of dragonflies perched during intermittent foraging or flying showed that age groups differed in their daily distribution of activity. The abundance of tenerals as a function of time of day was not significantly different from a uniform distribution (Fig. 5; $\chi^2$=29, $P$>0.25) and was weakly affected by $T_a$ ($P$=0.03, $r^2$=0.02). Abundance of matures showed a significant peak around midday ($\chi^2$=316, $P$<0.001) and was more strongly affected by $T_a$ ($P$<0.0001, $r^2$=0.15). Tenerals showed a greater tendency to be present early in the morning, and neither age class was frequently present in the evening hours. The abundance of *A. junius*, a large endothermic sympatric dragonfly (Fig. 5C), did not vary significantly with time of day ($\chi^2$=14, $P$>0.9) or $T_a$ ($P$=0.28) and was much greater than that of *L. pulchella* during late evening and dusk.

## Discussion

Unlike large dragonflies in the family Aeshnidae, libellulid dragonflies cannot generate heat endothermically by shivering, nor can they increase the rate of heat loss from the abdomen by increasing blood circulation (Heinrich and Casey, 1978). Libellulids achieve thermoregulation behaviorally by varying both their posture in relation to sunlight and the amount of time they spend flying (May, 1976; Heinrich and Casey, 1978). The present study adds further detail by showing that thermoregulation by *L. pulchella* dragonflies varies markedly with adult age. Tenerals tend to have much lower $T_{th}$ values than do matures, and this difference is apparently caused by their reduced tendency to heat up during basking, their more rapid rate of cooling (Fig. 3), and their lack of endogenous heating (i.e. they spend very little time flying; Fig. 4).

Maturational changes in the body temperatures experienced by *L. pulchella* dragonflies precisely match age-related changes in optimal body temperature. Mean field $T_{th}$ of active tenerals is not significantly different from their $T_{th,opt}$ (Fig. 6; 34.5 *versus* 34.6 °C; $P$=0.96; $T_{th,opt}$ data from Marden, 1995). Furthermore, active tenerals in the field show a range of $T_{th}$ variation (29–40 °C) that corresponds closely to the broad plateau of peak performance that they show over the same range of muscle temperatures (Fig. 6). In contrast, matures are more precise thermoregulators, maintaining active $T_{th}$ between 37.5 and 45.2 °C. Mean $T_{th}$ of flying matures is significantly

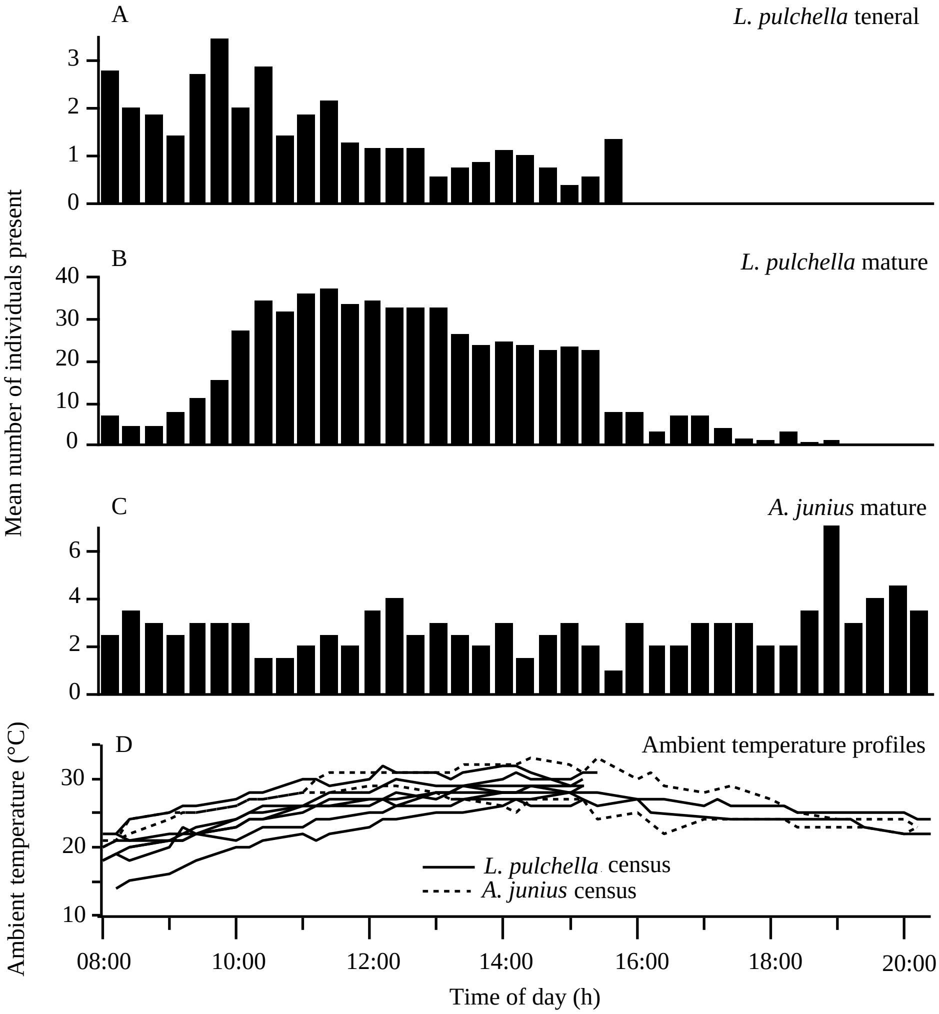

Fig. 5. Mean number of active *L. pulchella* and *A. junius* dragonflies in scrub habitat surrounding ponds and along pond margins. *L. pulchella* observations are from 7 days in June and July 1994; *A. junius* data are from 2 days in July 1994. These days varied somewhat in temperature profile (traces in D), but each had predominantly clear, sunny weather.

lower than their $T_{th,opt}$ (Fig. 6; 41.7 *versus* 43.6 °C; $P$=0.003). However, when data for field $T_{th}$ of matures is restricted to those individuals ($N$=31) engaged in the most vigorous forms of flight (aerial copulation, mate guarding and escalated territorial contests), there is no difference between field $T_{th}$ and $T_{th,opt}$ (42.5 *versus* 43.5 °C; $P$=0.13).

For matures, the difference between mean $T_{th}$ and $T_{th,opt}$ probably serves the important function of allowing a thermal safety margin, i.e. the ability to maintain high performance during exercise-induced hyperthermia. For males especially, aerial copulation, mate guarding and escalated territorial contests are important components of reproductive fitness (Marden, 1989), and these behaviors cause a significant increase in $T_{th}$ (Fig. 2). We have only a small sample of $T_{th}$ measurements from males involved in high-speed chases that constitute escalated territorial contests ($N$=3; they are exceedingly difficult to catch at such times), but one of these measurements showed a $T_{th}$ of 45.2 °C. Given our small sample size, it is unlikely that this measurement represents an extreme value; thus, $T_{th}$ during high-speed chases is likely to rise even higher than 45 °C.

Territorial contests have been studied extensively in the damselfly *Calopteryx maculata*. These damselflies, because of their small size (body mass is approximately 70 mg as opposed to approximately 500 mg for *L. pulchella*) and long narrow shape, are unlikely to retain a significant amount of metabolically generated heat, and their escalated territorial contests can last for up to an hour. The male with greater fat reserves almost always wins (Marden and Waage, 1990; Marden and Rollins, 1994). *L. pulchella* males retain metabolic heat during their much briefer contests (which last from a few seconds to perhaps as long as 2 min), and we suspect that these contests may be thermal ‘wars of attrition’ wherein the outcome is based on the ability to tolerate the highest $T_{th}$. Thus, the spectacularly right-shifted thermal sensitivity curves of mature *L. pulchella* males (Fig. 6) might be the physiological equivalent of peacock’s tails, i.e. a trait that has evolved in response to sexual selection and the social environment.

It is illuminating to consider results from this study with respect to the largely untested body of hypotheses for the evolution of thermal sensitivity and thermoregulation. One evolutionary model (Heinrich, 1977) states that animals accumulate heat during intense activity, especially at high ambient temperatures. Because natural selection for maximal performance capacity should be most pronounced during intense activity (i.e. prey capture, predator evasion,

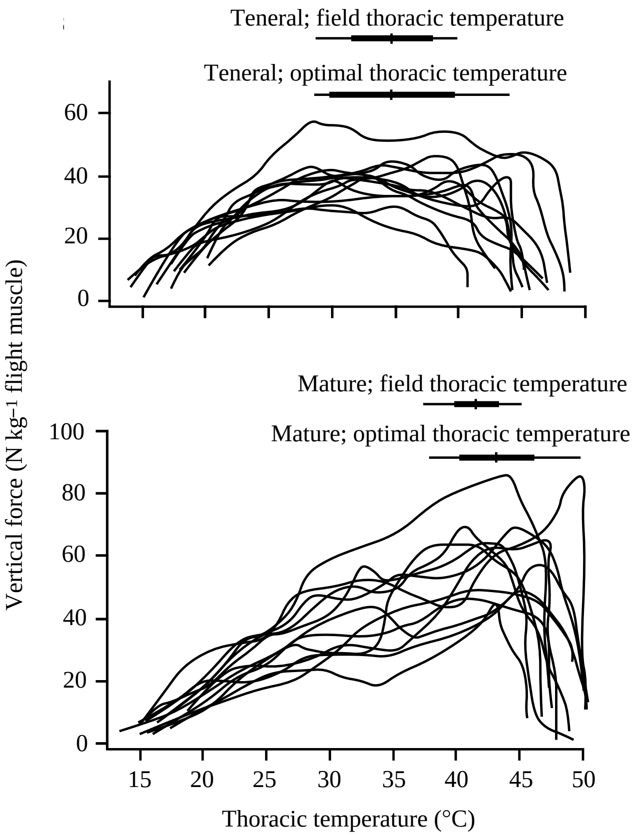

Fig. 6. Field thoracic temperatures ($T_{th}$) of *L. pulchella* dragonflies in comparison with previously obtained measures (Marden, 1995) of their optimal thoracic temperatures ($T_{th,opt}$) and thermal sensitivity curves. Horizontal bars show the mean (vertical cross near center) ±1 s.d. (thick bar) and range (thin bar). Traces show the upper limit of vertical force production as a function of thoracic temperature for 12 teneral and 12 mature *L. pulchella* adults (data from Marden, 1995).

competitive interactions), optimal body temperature should evolve to match the high body temperatures experienced during exercise-induced heat loading. These predictions are supported by our data from *L. pulchella*, in which exercise brings about a significant rise in body temperature.

Heinrich's model goes on to state that, if performances at high and low temperatures are inversely correlated (as may occur in *L. pulchella*, although this result is somewhat ambiguous; Marden, 1995), then the evolution of a high optimal body temperature may subsequently impose selection for thermoregulatory ability, so that low body temperatures can be avoided. Thus, the evolution of homeothermy might be a stepwise process, in which the initial stage is evolution of a high optimal body temperature in a relatively heterothermic species, and the final stage is homeothermic regulation of body temperature by physiological mechanisms (i.e. endothermy and variable heat loss) as opposed to behavioral mechanisms. Stages in this process appear to be exemplified by the diversity of thermal physiology in dragonflies. If we assume that dragonflies were primitively heterothermic and incapable of endothermy (i.e. the primitive condition for insects in general; Heinrich, 1993), then the teneral stage in *L. pulchella* exemplifies a relatively primitive physiological condition, whereas the mature stage in *L. pulchella* represents a more derived condition (i.e. high optimal body temperature, with homeothermy accomplished *via* behavioral mechanisms).

An alternative hypothesis for the evolution of homeothermy emphasizes the role of ecological opportunity as a primary driving force (Crompton *et al.* 1978; Block *et al.* 1993). This hypothesis assumes that, in a population of organisms that vary in their ability to thermoregulate, the more homeothermic individuals should be able to exploit a broader range of habitats or activity periods. The opposite pattern occurs in *L. pulchella*, in which activity of tenerals is relatively uniform with respect to time of day, whereas activity of the more homeothermic matures is significantly clumped around midday (Fig. 5) and is more strongly temperature-dependent. Thus, improved homeothermy in *L. pulchella* dragonflies is accompanied by a niche contraction rather than a niche expansion. A niche expansion has occurred in *A. junius*, whose endothermic warming and variable cooling (Heinrich and Casey, 1978) permit uniform activity throughout the day (Fig. 5), including periods of heavy clouds and even rain (such behavior is rarely or never seen in large libellulids). Expansion of activity into evening hours has special ecological significance, for it is then that a large amount of feeding occurs when many dipterous insects are swarming (Corbet, 1963). If we assume that endothermic warming is the most derived condition in dragonflies, and that endothermic dragonflies evolved from behavioral thermoregulators such as *L. pulchella*, then homeothermy in dragonflies probably first evolved in response to selection on thermal sensitivity of performance physiology, with endothermy and an accompanying niche expansion occurring secondarily.

It is not presently possible to map dragonfly thermal physiology onto a phylogenetic tree for the group and thereby make stronger inferences about evolutionary changes. A recent study of evolutionary transitions in the thermal physiology of billfish (Block *et al.* 1993) contains such a phylogenetic analysis, but presents no data concerning the thermal sensitivity of billfish brain or eye function, or heat loading during intense activity at warm ambient temperatures. Thus, there are presently no studies that contain all of the elements necessary to determine unambiguously the selective pressures and sequence of evolutionary events that have led to homeothermy; however, the diversity of thermal physiology, behavior and ecology that exists among insects suggests that this may be an especially fertile group in which to seek such answers.

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