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Assessment of upper thermal tolerances of naiads of two odonate families: Coenagrionidae and Libellulidae in Lake Kariba, Zimbabwe

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ABSTRACT

Thermal tolerances of Coenagrionidae and Libellulidae naiads in Lake Kariba, Zimbabwe, were determined using the critical thermal maximum (CTM) method. Eighty eight naiads were assessed, 44 from Coenagrionidae with two size classes, small (6.0 – 9.9 mm) and big (10.0 – 19.9 mm) and 44 from Libellulidae with two size classes, small (7.0 – 14.9 mm) and big (15.0 – 22.9 mm). Water temperature was increased at a mean rate of 0.5 ± 0.1ºC per minute until there was loss of locomotor capacity and motion. Temperatures at which the naiads stopped moving and responding to probing were recorded as the critical thermal maxima. The mean thermal tolerances of Coenagrionidae and Libellulidae naiads were 44.33ºC and 46.22ºC respectively. Regression analysis indicated that body size had no effect on thermal tolerance in Coenagrionidae ($P > 0.05$) but had an effect on Libellulidae ($P < 0.05$). Both families had high thermal tolerances though Libellulidae had a higher tolerance than Coenagrionidae. Anova revealed significant differences between the two families ($P < 0.05$). Understanding how temperature affects biological systems is a central question in ecology and evolutionary biology. Determination of upper thermal limits provides insight into the relative sensitivity of organisms to elevated temperatures hence to climate change.

Introduction

Global climate is swiftly changing, with poorly known consequences for biodiversity (Hogg et al., 1995). Temperature rises due to global warming are expected to have immense ecological consequences, including changes in the size, structure and functioning of ecosystems (Quinn, 1994). In particular, rising water temperatures have become a great concern on the survival of aquatic species especially invertebrates (Dallas and Rivers-Moore, 2008). It is well known that small changes in water temperature can have considerable consequences on freshwater invertebrates, affecting a wide variety of life history, behavioural and physiological responses. Food and feeding habits, reproduction and life histories, geographical distribution and community structure, movements and migrations, tolerance to parasites and diseases, and pollution of aquatic organisms can also be affected by changes in water temperature (Ward and Stanford, 1982).

The impacts of global warming on natural lakes are now beginning to emerge (Plinski and Jozwiak 1999; Ficke et al., 2007). For example Lake Kariba, Zimbabwe, has warmed by close to 2ºC since the mid-1960s and it is thought that this rise in lake temperature has caused a number of effects on aquatic organisms in the lake (Magadza, 2010). It is proposed that this warming has affected the food chain and productivity of the lake and, therefore, a decline in the pelagic fishery yield. Changes in lake thermal properties have also negatively affected plankton production (Ndebele-Murisa, 2011). Phytoplankton biomass and primary rates in Lake Kariba have declined by 95% and 57% since the last long –term phytoplankton study of 1986 to 1990 (Cronberg, 1997). Similar declines are reported in other Tropical African lakes and attributed to global warming. In turn, the reduced phytoplankton has led to a reduction in zooplankton biomass and palatable Cladocera and Copepoda species (Magadza, 1980; Marshall, 1982; Chifamba, 2000).

The effects of climate change on invertebrate immunology has received relatively little attention. Despite Odonates having been studied extensively in the field and in the lab, only one study has considered the impact of temperature on odonate immunity, in the context of variation in immune function across the flight season (Hassall and Thompson, 2008). This study clearly showed an increased melanotic encapsulation of mite feeding tubes at higher temperatures, which results from higher haemocyte counts at higher temperatures. The implications for this temperature-mediated immunity lie in the determination of range margins. At a certain threshold of immune function, the immune challenge presented by the pathogen community may result in too great a mortality. This would lead to the kind of small, unstable marginal populations that are found in nature (Hassall and Thompson, 2008).

Two methods are commonly used to determine the upper thermal tolerance of aquatic organisms. There is the lethal temperature method and the critical thermal maximum. The static or upper lethal temperature (ULT) method assesses the time to death at constant test temperatures (Fry, 1957). Cowles and Bogert (1944), introduced the concept of critical maximum temperature, which was defined as the temperature at which locomotor activity becomes disorganized and the organism loses its capacity to escape from possibly lethal conditions. In the critical thermal maximum method, temperature is gradually increased until an end point, a critical thermal maximum (CTmax), is reached. The end-points that have been used to define the CTmax include the loss of righting response, the onset of muscular spasms or convulsions, and heat paralysis or heat coma (Lutterschmidt and Hutchison, 1997[a, b]; Berrigan and Hoffmann, 1998). According to Lutterschmidt and Hutchison (1997[b]), the CTmax is an excellent index and standard for assessing the thermal requirements and physiology of an

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organism. The order Odonata is among the other species found in Lake Kariba affected by changes in water temperature. It is comprised of two suborders, the Zygoptera or damselflies and the Anisoptera or dragonflies (Schorr et al., 2007). The Odonata have a long history in the fossil record relative to other orders, with fossils present from the Lower Permian (Wootton, 1981). This fact, coupled with a range of adaptations which have enabled them to colonise temperate and sub-arctic habitats from their tropical origins (Pritchard and Leggott, 1987), make them ideally suited to surviving current climate change. Climate change brings with it unprecedented rates of increase in environmental temperature, which will have major consequences for the earth's flora and fauna. The Odonata represent a taxon that has many strong links to this abiotic factor due to its tropical evolutionary history and adaptations to temperate climates. Temperature is known to affect Odonate physiology including life-history traits such as developmental rate, phenology and seasonal regulation as well as immune function and the production of pigment for thermoregulation (Pritchard and Leggott, 1987). A range of behaviours are likely to be affected which will, in turn, influence other parts of the aquatic ecosystem, primarily through trophic interactions.

The water temperature in Lake Kariba rarely falls below 20ºC and in shallow waters of the lake, high temperatures of about 38ºC have been recorded (Phiri et al., 2011).The two Odonate families that is Libellulidae (dragonflies) and Coenagrionidae (damselflies) are the most commonly encountered families of order Odonata in Lake Kariba and since they are aquatic organisms (Hoell et al., 1998), their survival is determined by water temperatures. Therefore it is necessary to carry out this study to assess and have some understanding of the upper water thermal tolerances of these two families in Lake Kariba.

Small changes in water temperature can have considerable consequences for aquatic insects, affecting a wide variety of life history, behavioural and physiological responses. Lake Kariba has undergone changes in its thermal properties associated with global warming, which reflect in turn on its limnology (Timberlake, 2000). Analysis of decadal temperature changes in Zimbabwe revealed seasonal ranges of 0.25–0.7ºC per decade, with an annual mean of 0.36ºC indicating increasing temperatures (Boko et al., 2007). In essence, the lake has warmed by a mean of 1.54ºC between 1965 and 1990, equivalent to a warming rate of 0.62ºC per decade showing that the lake is warming at a faster rate (Parry et al., 2007). Whilst information on effects of temperature on organisms is plentiful in the Northern Hemisphere, there is an identified huge gap that exists in temperature-related data in Southern Hemisphere. Early studies of the upper temperature tolerances of aquatic invertebrates have mainly been centred in the USA (Garten et al., 1976). Odonata appear to be far more tolerant of high temperatures, with an average lethal temperature of 38ºC (Quinn et al., 1994). At the moment there is very little information on the upper thermal tolerance of Odonates in Lake Kariba, therefore this study seeks to assess the highest temperatures that can be tolerated by Libellulidae and Coenagrionidae naiads in the Lake Kariba.

Temperature changes associated with global climate change are expected to have immense ecological consequences, resulting in changes in the size and structure of populations, the species composition of communities, and the structure and functioning of ecosystems (Somero, 2005; Gilman et al., 2006; Pörtner and Knust, 2007). The determination of thermal tolerances of Libellulidae and Coenagrionidae naiads is thus essential for the development of an understanding of the possible impacts of climate change on distribution patterns, ecosystem structure and functioning of these species in Lake Kariba. Without baseline data on water temperature and the thermal requirements of aquatic organisms, it is extremely difficult to adequately manage aquatic ecosystems. It is thus critical that this knowledge gap be filled through comprehensive and integrated applied research programmes (Boubee et al., 1991). Arguably, estimating population and ecosystem level effects of climate change merely on the basis of large-scale patterns, without an understanding of organismal physiological responses, can result in erroneous predictions (Helmuth et al., 2005). Thus this research is of importance to researchers to improve their understanding on the physiological mechanisms underpinning thermal tolerance limits and the acclimatory capacity of those limits, if they are to predict the direct impact of climatic warming on biodiversity (Chown et al., 2004).

The study thus aimed at determine the effect of temperature increase on the thermal tolerance of two Odonate families, Libellulidae and Coenagrionidae in Lake Kariba, Zimbabwe. It also sought to determine whether there are differences in upper thermal tolerances between the two families and whether body size has an effect on thermal tolerance.

Materials And Methods

The study was carried out in basin 5 (Sanyati Basin) near the University Lake Kariba Research Station (UZLKRS) (16º 31.489′S, 28º 50.481′E). The experiments run for 15 days in January and 10 days in March 2012 at the University of Zimbabwe Lake Kariba Research Station.

Study area

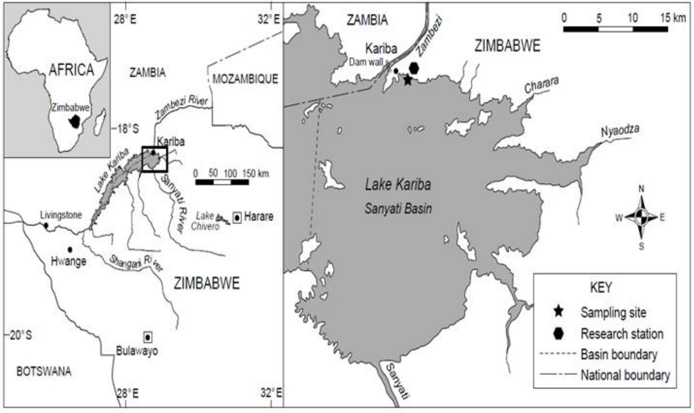

Figure 1. Map of Lake Kariba, Basin 5 showing the sampling site

Lake Kariba is located between 16.5^{o}S and 18^{o}S, and 27^{o}E and 29^{o}E (Magadza 2010), on the Zambezi River, about halfway between the river's source and mouth, and about 1,300 km upstream from the Indian Ocean. The lake lies along the border between Zambia and Zimbabwe. The Lake was filled between 1958 and 1963 following the completion of the Kariba Dam at its northeastern end, flooding a former gorge on the Zambezi River. Lake Kariba became a fascinating turmoil of ecological change, parts of which now teem with an abundance of flora and fauna in a striking and diverse terrain (Coche, 1968). Lake Kariba is divided into five geographical basins along its axis, namely Mlibizi (basin 1), Binga (basin 2), Sengwa (basin 3), Bumi (basin 4) and Sanyati (basin 5) (Coche, 1968). This study was undertaken in Sanyati basin.

Climate of study area

The climate is generally tropical with three reasonably distinguishable seasons. A hot rainy season from late November to March, a cool dry season from May to August and a very hot dry season from September to November. Annual rainfall ranges from 400mm in the valley to about 700mm on the plateau. Winter temperatures rarely go below 13^{o}C and day time temperatures hover at about 40^{o}C during the hot months (www.kariba.com/lake kariba.php). The water temperature in Lake Kariba rarely falls below 20^{o}C. In shallow waters of Lake Kariba, high temperatures of about 38^{o}C have been recorded (Phiri et al., 2011).

Ecology of the study area

The Lake's waters support more than 40 different species of fish in a rare example of a successful introduction of a non-native species to the lake that is the kapenta taken from Lake Tanganyika. Invertebrate biodiversity is not well known in the Zambezi Basin except for a few groups including dragonflies (Odonata), butterflies (Lepidoptera), freshwater molluscs, dung beetles (Coleoptera) and grasshoppers/crickets (Orthoptera), (Timberlake, 2000). The Zambezi Basin is renowned for its assemblage of large mammal species such as elephant, buffalo, giraffe, lion and, until recently, rhino. Compared to East Africa there is preponderance here of browsers rather than grazers as the basin is mostly woodland rather than highly productive grasslands associated with the East African Rift Valley (Timberlake, 2000).

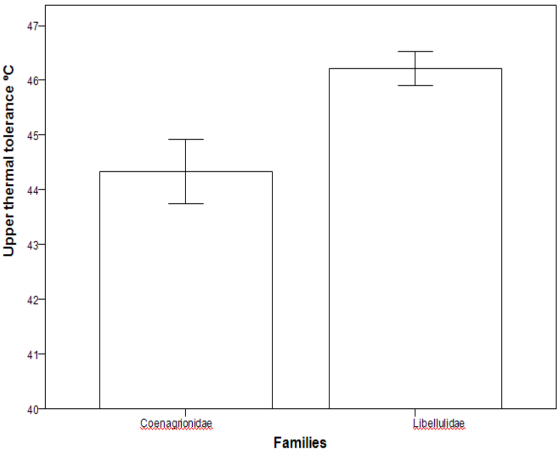

Figure 2. Thermal tolerances of Libellulidae and Coenagrionidae naiads

Collection Procedure

Libellulidae and Coenagrionidae naiads were collected from Lake Kariba, from shallow waters by sweeping macrophytes into a scoop net with a mesh size of 500µm. Two sizes classes, small and big per each family were assessed for thermal tolerance, The size classes were small (6.0 – 9.9 mm) and big (10.0 – 19.9 mm) for Coenagrionidae and small (7.0 – 14.9 mm) and big (15.0 – 22.9 mm) for Libellulidae (Table 1). There was equal replication of experimental units of 22 in each size class. The treatment for the all the experimental units above was a gradual increase in temperature at a rate of 0.5 ± 0.1ºC per minute.

Table 1. Summary of experimental units per each size class

	Coenagrionidae		Libellulidae	
Size class	(6.0 – 9.9 mm)	10.0 – 19.9 mm	7.0 – 14.9mm	15.0 – 22.9mm
Experimental units	22	22	22	22

Table 2: Mean thermal tolerances of Coenagrionidae and Libellulidae naiads

Family	Mean thermal tolerance of naiads	Number of samples
Coenagrionidae	44.33ºC	44
Libellulidae	46.22ºC	44

Relationship of thermal tolerance between Coenagrionidae and Libellulidae naiads

Libellulidae naiads had a higher thermal tolerance than the Coenagrionidae naiads (Figure 2). There was a significant difference ($p = 0.001$; $df = 1$; $F = 32.283$) in mean thermal tolerance between Libellulidae (46.22ºC) and Coenagrionidae (44.33ºC) naiads.

Effect of body size on thermal tolerances in Coenagrionidae naiads

Body size had no significant effect on the thermal tolerance ($p = 0.412$; $df = 1$; $F = 0.685$) of Coenagrionidae naiads. A plot of thermal tolerance against body size showed no clear trend ($r^2 = 0.016$) (Figure 3) indicating that body size has no effect on thermal tolerance.

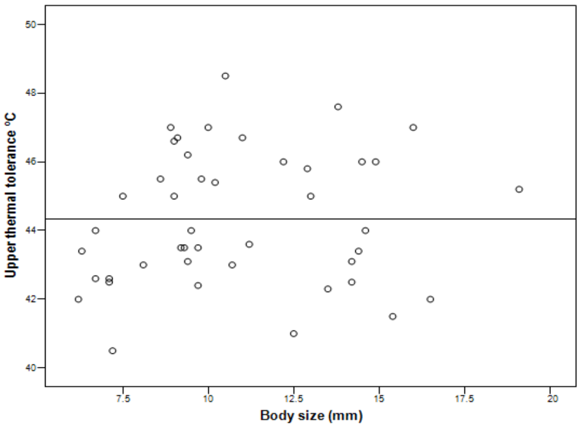

Figure 3. Relationship between body size and thermal tolerance in Coenagrionidae naiads

Effect of body size on thermal tolerance of Libellulidae naiads

Body size had a significant effect on the thermal tolerance ($p = 0.012$; $df = 1$; $F = 6.844$) of Libellulidae naiads. There was a positive correlation ship between thermal tolerance and body ($r^2 = 0.140$) (Figure 4). This shows that body size had an effect on thermal tolerance, with increasing tolerance as body size increased.

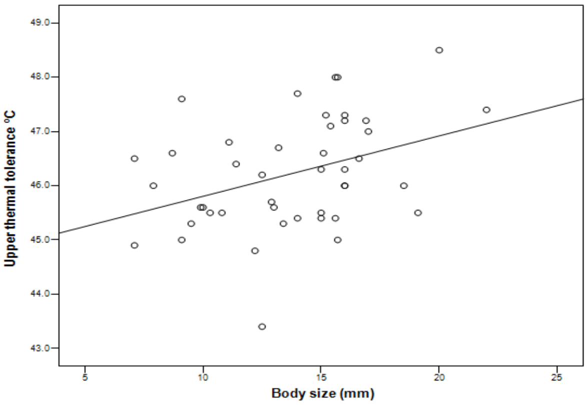

Figure 4. Relationship between body size and thermal tolerance in Libellulidae naiads

Discussion

Upper thermal tolerances of Coenagrionidae and Libellulidae naiads

Coenagrionidae and Libellulidae naiads have high upper thermal tolerances. Dallas and Rivers-Moore, (2012) confirmed that among other aquatic invertebrates, Odonates are less thermally sensitive. The Odonata have a long history in the fossil record relative to other orders, with fossils present from the Lower Permian (Wootton, 1981). This fact, coupled with a range of adaptations which have enabled them to colonise temperate and subarctic habitats from their tropical origins make them ideally suited to surviving current climate change (Pritchard, and Leggott, 1987). Of key importance in thermal tolerance research is the thermal history of the organism, where ambient stream temperatures influence the thermal sensitivity of a species, which may vary spatially and temporally (Dallas, and Rivers-Moore, 2012). Thus thermal history influences the adaption of Odonates to warm areas for example, Martin and Gentry (1974), found that nymphs of the dragonfly genus Libellula inhabiting a thermal effluent stream with elevated temperatures possess a greater thermal tolerance than those from a control stream, which had lower temperatures.

Pritchard (1982) and Pritchard et al., (1996) reviewed that the Odonata primarily originated from tropical environments and are adapted to warm conditions. Pritchard et al., (1996) also reviewed the development of aquatic insects eggs in temperate regions, and found that generally, Odonates oviposit into relatively warm water during summer and that the optimum temperature for embryogenesis and hatching is between 30ºC and 35ºC. Odonata larvae tolerate changes in water temperature through an enzymatic mechanism that promotes a fast physiological response

(Schott, and Brusven, 1980; Corbet, 1999). Pörtner (2002), highlighted that for most organisms not excluding Odonates, the biochemical processes that are necessary for their existence can only occur within a narrow range of temperatures, roughly between 0°C and 45°C. Within this temperature range, the rates of virtually all biological processes, from enzyme kinetics to species interactions and population growth rates, depend strongly on temperature (Angilletta, 2009; Daniel and Danson, 2010). This means that though Odonates have high thermal tolerances if temperatures exceed their upper thermal tolerances they will be greatly affected.

Relationship of thermal tolerance between Coenagrionidae and Libellulidae naiads

There was a difference in thermal tolerance between Coenagrionidae and Libellulidae naiads with Libellulidae having a higher thermal tolerance than the Coenagrionidae. Dallas and Rivers-Moore, (2012) recognised that thermal sensitivity is likely to vary within families with some more thermally sensitive than others as shown by this study. Peck (2002), also stated that temperature does not affect all organisms in the same way. There is strong evidence for selection of warmer pools in Odonates as stated by Hassall and Thompson, (2008). Libellulidae belong to the suborder Anisoptera. Anisoptera inhabiting deserts have been shown to exhibit substantially higher thoracic temperatures and thresholds for flight than congeners and conspecifics from cooler habitats, suggesting that a degree of adaptation to extreme thermal environments may be possible (Polcyn, 1994). Odonates exhibit thermoregulatory behaviours more commonly seen in endotherms. In particular, a number of species perform “wing-whirring”, which enables a build-up of metabolic heat originating in the flight muscles. At least one member of each American family of Anisoptera is capable of such behaviour and this can lead to warm-up rates of between 0.9 and 6.7°C.sec-1 (May, 1976). Regulation of body temperature is also performed through controlling circulation of haemolymph through the thorax and abdomen (May, 1976). However, some species are so adapted to their boreal habitat that they exhibit upper thermal thresholds for flight for example *Ischnura elegans* and *Aeshna caerulea* (Hilfert-Rüppell, 1998; Sternberg, 1997).

Angilletta (2009), highlighted some of the possible causes of differences in thermal tolerance between Libellulidae and Coenagrionidae. Adaptation to thermal heterogeneity frequently involves changes in the degree to which an organism’s performance depends on changes in body temperature. This is referred to as the thermal sensitivity or dependence of performance. Important performance traits include growth, development and locomotion. Thus, some organisms are able to maintain relatively constant levels of performance over a wide range of temperatures. These are referred to as thermal generalists (Angilletta, 2009). Others can only tolerate a very narrow range of temperatures, with even small changes in temperature causing major changes in performance. These are referred to as thermal specialists (Angilletta, 2009). This might explain why thermal regulation in dragonflies is more adavanced than that in damselflies and why Libellulidae have higher tolerances than Coenagrionidae.

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) making them to maintain higher thermal tolerances. The obelisk position orients the dragonfly’s abdomen directly at the sun, thereby reducing the surface area exposed to solar heating. Some dragonflies also point their wings forward and down in order to reduce exposure to sunlight and, perhaps, to reflect light and heat away from their bodies. The damselflies, because of their small size with body mass of approximately 70 mg as opposed to approximately 500 mg for *Libellula pulchella* and long narrow shape, are unlikely to retain a significant amount of metabolically generated heat (Marden, 1996) , and this may explain the reason they have lower thermal tolerance than Libellulids.

Effect of body size on thermal tolerances of Coenagrionidae naiads

There was no relationship between body size and thermal tolerance in Coenagrionidae naiads. Marsden (1985) and Agnew and Taylor (1986), found no relationships between body size and CTmax of some aquatic invertebrates such as amphipods and beach flea. Ernst et al., (1984), found that, within a species, younger stonefly nymphs did not have a significantly different CTmax from older ones. Banks and Thompson (1987) and Thompson et al., (2011), stated that the size of final-instar larvae is correlated with adult size in determination of longevity, fecundity and mating success in damselflies. This may support the hypothesis that body size does not affect thermal tolerance in Coenagrionidae.

Effect of body size on thermal tolerance of Libellulidae naiads

There was a positive linear relationship between thermal tolerance and body size in Libellulidae naiads. Thermal tolerance increased with increasing body size. Ernst et al., (1984), stated that studies differ in their observations of age/size effects, with some reporting no age effect, some others a positive effect and some others a negative effect. Garten and Gentry (1976) indicated that average body length of species of dragonflies appeared to affect their thermal tolerance, with larger species consistently exhibiting higher CTmax values. A positive relationship with size, suggests that younger nymphs are more sensitive to thermal stress than older ones Dallas and Rivers-Moore, (2012). For taxa that spend more than one year as aquatic nymphs, such as corydalids and dragonflies, it is possible that once individuals reach a certain stage, their sensitivity to thermal stress becomes relatively constant. Kingsolver and Huey (2008) confirmed a positive linear relationship between thermal tolerance and body size in Anisoptera, with bigger size positively correlated with mating success, fecundity, survival and development time (Rudolf, 2007), and for the outcome of competitive and aggressive encounters.

Thoracic temperatures of *Libellula pulchella* dragonflies during activity in the field were compared between age classes (Marden, 1996). Results showed that mature nymphs had higher and more precisely regulated thoracic temperatures of mean 43.6°C and range 38.7ºC – 49.9°C than young nymphs (Marden, 1996). *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 35ºC to 44°C) and 4°C (from 45ºC to 49°C), respectively, over the course of adult maturation (Marden, 1995).

Marden (1996), showed the abundance of mature nymphs around midday and that of younger nymphs early in the morning supporting the hypothesis that mature nymphs can tolerate high temperatures than younger nymphs. Marden (1996), highlighted that thermoregulation by *L. pulchella* dragonflies varied markedly with adult age and mature nymphs were more precise thermoregulators than younger nymphs. Maturational changes in the body temperatures experienced by *L. pulchella* dragonflies precisely match age-related changes in optimal body temperature.

In conclusion we can say that the Coenagrionidae and Libellulidae naiads have high thermal tolerances with Libellulidae having a higher tolerance than Coenagrionidae. Thermal tolerance increased as body size increased in Libellulidae while in Coenagrionidae thermal tolerance was not affected by body size.

However more research is required into the Odonata, not only because they represent an important part of many aquatic communities but also because this taxon's thermal sensitivity makes it a potential barometer for environmental change.

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