Effects of environmental warming during early life-history on libellulid odonates

D. N. Frances[1,2], J. Moon[1] and S. J. McCauley[1,2]

[1]*Dept of Biology, University of Toronto Mississauga, Mississauga, ON, L5L1C6, Canada*

[2] *Dept of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, M5S3B2, Canada*

Corresponding author: Dachin N. Frances, Dept of Biology, University of Toronto Mississauga, Mississauga, ON, L5L1C6, Canada, email: dachin.frances@mail.utoronto.ca

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Abstract

Climate warming affects ectotherms globally yet we know little regarding the variability in species' responses to warming, particularly in early life stages. Additionally, intraspecific variation in response to warming is understudied but may determine species' resilience to warming. To assess how temperature affects egg development rate in co-occurring dragonfly species, we manipulated temperature (range: 22º -31º C) and measured time to hatching. Warming decreased egg development time across all species, indicating that while climate warming will advance hatching phenology, maintained synchrony in hatching order will likely not affect species interactions. Our second experiment examined early life history responses to warming in the dragonfly *Leucorrhinia intacta* (Hagen, 1861). We measured time to hatching, hatchling size, growth rate and survival at four temperatures (23º-30º C), including a treatment with increased thermal variation. Warming resulted in smaller hatchlings with increased growth and mortality rates, while higher thermal variation did not have effects different from those of warming alone. We observed significant intraspecific variation in the responses to warming in both egg development time and hatchling size and this variation was correlated with date of oviposition. High levels of intraspecific variation may be important in buffering populations from the effects of climate warming.

Key words:

Body size, climate change, development, ectotherm, life history, Odonata, survival

INTRODUCTION

Increasing temperatures resulting from climate change have had large ecological impacts across a broad range of taxonomic groups (Walther et al. 2002). In response to warming, organisms are becoming smaller (Gardner et al. 2011, Sheridan and Bickford 2011), altering the timing of life history events (Parmesan 2006), and shifting their range margins (Sunday et al. 2012). Ectotherms are especially vulnerable to the effects of climate change (Chown et al. 2010) because their body temperature and metabolic processes are tightly linked to environmental temperature, therefore warming directly influences ectotherm performance (Huey and Kingsolver 1989). Additionally, many ectotherms use abiotic cues such as changes in temperature to signal onset of life history events. For example, fish time their spawning (Genner et al. 2010) and bees break winter diapause (Forrest and Thomson 2011) in response to temperature signals. Because temperature has large effects on ectotherm life history and phenology, it is crucial to understand how these responses will be affected by a rapidly changing climate.

Shifts in phenology are one of the most commonly documented responses to climate change (Parmesan 2006). For example in freshwater systems, adult odonates (dragonflies and damselflies) are advancing the timing of their emergence from aquatic habitats earlier in the season (Hassall et al. 2007, Dingemanse and Kalkman 2008). Experimental warming of water temperatures has also been observed to result in earlier emergence in the libellulid dragonfly *Pachydiplax longipennis* (McCauley et al. 2015). Increasing temperatures can also hasten egg development rate, therefore advancing the timing of hatching (Howe 1967, Elliott 1978, Leggott and Pritchard 1985). While faster egg development in response to temperature is well documented, not all species respond in the same way and we still have little information about how much this response varies within and between species for many animals.

Understanding how rates of egg development are affected by temperature and how these may respond to climate warming is critical because for many ectotherms the timing of egg hatching is a key phenological event. The timing of egg laying and hatching determines the abiotic conditions (Visser and Holleman 2001) and the biotic interactions of juveniles (Rudolf and Singh 2013). Larval odonates are voracious predators and the order and relative timing in which species hatch can determine body size advantages (Rasmussen et al. 2014), a crucial force structuring species interactions in aquatic systems (Werner and Gilliam 1984). Unequal responses to warming could affect the rank order of hatching within groups of co-occurring species, thereby contributing to these body size advantages or disadvantages (Guo et al. 2009). These size changes induced by temperature could alter interactions between co-occurring species and ultimately create “winners and losers” in response to climate change (Cahill et al. 2012). As a general response, odonates have faster egg development when reared in higher temperatures (Pritchard et al. 1996) yet we know little about the plasticity in egg development in response to temperature found within co-occurring species . We addressed this gap by experimentally manipulating temperature and comparing the timing of egg hatching in four species of dragonfly (Odonata: Anisoptera) across temperatures from 22-31° C.

In ectotherms, smaller body size at maturity is a common effect of developing at higher temperatures because warmer conditions increase metabolic and developmental rates (Atkinson 1994, Sibly and Atkinson 1994). This effect is widespread with 75% of terrestrial and over 90% of aquatic ectotherms exhibiting this pattern (Atkinson 1995, Sheridan and Bickford 2011). Body size can affect dispersal ability (Bie et al. 2012), range size (Rundle et al. 2007), strength of trophic interactions (Rudolf 2011) and fitness (Sokolovska et al. 2000, Kingsolver and Huey

2008). However, many of these studies have focused on these effects in later ontogeny, while early life history stages may be equally or even more sensitive to temperature (Klockmann et al. 2016). Odonate body size at hatching has been under-reported in the literature and therefore it remains unclear whether faster egg development will lead to smaller hatchling size in this group. Body size at hatching or other early stages of development can determine the size and type of prey that animals can consume as well as their vulnerability to predators. Additionally, juvenile body size has been directly correlated with adult fitness for amphibians (Semlitsch et al. 1988) and some insects (Carroll and Hoyt 1986). Body size post-hatching is smaller when incubation temperatures are warmer as shown in reptiles (Gutzke and Packard 1987, Van Damme et al. 1992), snails (Collin and Salazar 2010), beetles (Ernsting and Isaaks 1997), soil arthropods (Liefting et al. 2010) and butterflies (Fischer et al. 2003), however the opposite pattern has been observed for one damselfly species (Van Doorslaer and Stoks 2005b). It therefore remains unclear how hatchling size is affected by temperature in other odonates. We addressed this question in our study by rearing eggs of a single dragonfly species in different thermal environments and measuring size at hatching.

Temperature can also affect ectotherm survival. While climate change is expected to increase environmental temperatures, most of these temperatures will likely remain below upper lethal limits of many species (Li et al. 2013). Therefore, mortality as a direct result of surpassing critical thermal limits is unlikely (Rohr and Palmer 2013). However, higher temperatures can increase mortality risk directly or through interactions with stressors such as pollutants, disease or other abiotic environmental changes (Folt et al. 1999, Sokolova and Lannig 2008, Deschaseaux et al. 2010, Janssens and Stoks 2013, Cole et al. 2016). Additionally, in many studies survival data are censored, measuring survival only at the end of development. Therefore it remains unclear at what stage higher temperatures are causing observed increases in mortality

(Klockmann et al. 2016). In one dragonfly species, higher mortality occurred when larvae were reared in warmer temperatures, however survival was only measured at metamorphosis (McCauley et al. 2015). The timing of mortality in odonates exposed to warming will influence aquatic food webs; mortality early in development has very different effects on the role of these predators in aquatic systems than if most of this mortality is occurring at or near metamorphosis. Therefore, we wanted to know if odonates experienced high rates of mortality during early stages of development when raised in warmer temperatures. Understanding at what stage odonates are most vulnerable to the effects of warming can also help direct future odonate conservation efforts.

We examined the effects of temperature on early life-history stages in odonates, an important group of predatory freshwater ectotherms, using a multi-level approach combining inter- and intraspecific comparisons. For the interspecific comparisons, we assessed how temperature affects egg hatching phenology across four species in the same family that co-occur in lakes and ponds in Eastern North America. We asked: does hatching time between species vary with increasing temperature, thus changing the order of hatching? We predicted more rapid egg development and thus earlier hatching in response to warming, however, we expected the magnitude of these responses to vary between species and lead to changes in the rank order of hatching.

There is a growing body of research indicating that variation within species can affect important ecological dynamics (Bolnick et al. 2011) such as the ability to colonize new habitats (Dibble et al. 2014), community interactions (Duffy 2010), and population stability and persistence (Agashe 2009), especially with environmental perturbations (Oney et al. 2013). For our intraspecific comparisons, we measured the degree to which responses to temperature varied both within and between clutches of the odonate species, *Leucorrhinia intacta* (Hagen, 1861).

Specifically, we quantified how temperature affected egg development time and size at hatching and then followed these larvae to assess the effects of temperature on rates of growth and survival during this critical early life phase. In addition to warming, we included one treatment with increased thermal variation because along with mean increases in temperature, increasing diel and seasonal fluctuations in temperature are expected to become more frequent with climate change (Easterling et al. 2000, Field 2012). A growing body of literature has examined ectotherm responses to fluctuating as opposed to constant temperatures and have found changes in physiology, stress tolerance, life history traits and fitness (Colinet et al. 2015). We wanted to know: i. how are early life history stages affected by warming and by increased thermal variability? ii. How much do these responses vary within a single species? Based on previous studies, we predicted that warming would increase egg development rate, reduce body size at hatching and increase growth and mortality rates (Pritchard et al. 1996, Suhling et al. 2015).

MATERIALS AND METHODS

Study system

Animals used in this study were collected from the Koffler Scientific Reserve, KSR (King City, Ontario, 44° 1' 47.136"N, 79° 32' 0.4662"W). Experiments were conducted in the lab at University of Toronto, Mississauga (UTM). In the first study, we used four odonate species (Anisoptera: Libellulidae): 1. *Celithemis elisa* (Hagen, 1861), 2. *Leucorrhinia intacta* (Hagen, 1861), 3. *Libellula luctuosa* (Burmeister, 1839), and 4. *Libellula pulchella* (Drury, 1770). Larvae of these species commonly co-occur in freshwater ponds in the study region (Paulson 2011). We chose these species because they are relatively common and dominant members of odonate communities in this region. Additionally, libellulids are the most diverse odonate family in these lentic systems. We selected species from this family that occur across a range of habitats, such as those with differing predators and habitat permanence (McCauley 2008). All of these species are univoltine in this region with a larval period lasting approximately nine months (Corbet et al. 2006).

Eggs of these species are typically laid in the beginning of June and oviposition continues for varying durations across the summer (Paulson 2011). These species are exophytic: eggs are laid on the water surface in clumps and then sink to the bottom and attach to the surface of algae or aquatic vegetation (Walker 1953, Corbet 1999). Eggs develop in the littoral zone of freshwater ponds and lakes—a shallow region that which tracks air temperatures closely (Schneider and Mauser 1996). Maximum air temperatures in the study region were 30.1º, 33.6º, and 32.8º C for June, July and August 2015, respectively (Environment Canada, retrieved 12 Dec 2016 from climate.weather.gc.ca). The 2050 climate prediction for this region is a + 2-2.5º C increase over the average current summer temperatures (IPCC 2012). Water has higher thermal conductivity than air, and therefore is more buffered from fine-scale variation in temperature, yet shallow waters such as the littoral zone can still warm and cool mirroring maximum and minimum air temperature (Abrahams et al. 2007).

Experiment 1: interspecific comparisons of egg development rate

For the first experiment, we collected eggs from five *C. elisa*, seven *L. intacta*, four *L. luctuosa* and four *L. pulchella* adult females caught at KSR. Females were captured with aerial insect nets either while mating or while flying in the vicinity of the ponds. Eggs were collected by dipping the females' abdomen into pond water-filled 120-mL plastic sample cups. After egg collection, we marked forewings of females with a permanent marker to avoid collecting from the same female more than once. Eggs were collected between 21 June and 22 July 2014.

We transported eggs in the water-filled sample cups to the lab at UTM on the same day as collection. They were kept cool and shaded during transit. We sorted eggs the following day after checking for signs of fertilization (eggs darken in color when fertilized). Using a split-brood design, we separated fertilized clutches of each female into four separate 350-mL plastic containers (AMAC © 2009 Plastic Products, Petaluma, California) with approximately 30 eggs per container. We randomly assigned egg containers to treatments and tanks so that eggs of each female were present in every temperature treatment. Treatment tanks were 20-liter glass aquaria. Each tank was filled with de-chlorinated, oxygenated water with submersible water heaters (Visi-Therm® Deluxe, Marineland Aquarium Products, Cincinnati, Ohio, USA) placed in every tank (for study design: Supplementary material Appendix 1 Fig. A1). We had four temperature treatments with means of: 22.2º C (± 0.61 SD), 24.9º C (± 0.43), 27.0º C (± 0.85), and 30.5º C (± 1.40). There were five replicates of each temperature treatment for a total of 20 treatment tanks. These treatments created a range of thermal environments similar to natural conditions in this region as well as simulating warmer temperatures that eggs may experience in the future with climate change (Feltmate and Thistlethwaite 2012). The highest temperature treatment used is well below the lethal limits recorded for odonates (Garten and Gentry 1976, Dallas and Rivers-Moore 2011). Photoperiod was set to 15L:9D to simulate day length in June in the study region. Data loggers (HOBO Pendant® Onset Computer Corporation, Cape Cod, Massachusetts, USA) recorded water temperature in the treatment tanks every four hours. This logging interval was chosen because the thermal inertia of water meant that a finer scale logging interval was not considered necessary. We visually inspected egg containers every day for newly hatched larvae. We counted hatchlings on the first and second day of hatching. By the second day, more than half of the larvae had hatched from the group (average for all treatments: 68.5% ± 0.2). For this reason, we recorded the second day of observed hatching as ‘day of hatching’ for the whole group.

Experiment 2: effects of warming on early life stages of *L. intacta*

For the second experiment, we measured the effects of temperature on embryonic development time, body size at hatching, growth rate and survival in a single species, *L. intacta.* We collected eggs from 10 mating *L. intacta* females near ponds at KSR using the same methods as above. We transported egg clutches to the lab at UTM on the same day as collection. Eggs were collected between 26 May and 9 June 2015. Treatment tanks were 20-liter glass aquaria filled with dechlorinated and oxygenated water and heated with submersible water heaters (Visi-Therm® Deluxe). Our experiment had three constant treatment temperatures: 23.4 ± 0.28º, 27.5 ± 0.54º, and 30.4 ± 0.45º C. Additionally, to explore the effects of thermal variability on larval performance, we had a treatment with a mean temperature of 27.4 ± 3.22º C, but manipulated variation by alternating between 23º and 30º C on a weekly basis. We chose this variable regime to simulate periodic heat waves that are becoming increasingly common with climate change (Rahmstorf and Coumou 2011). Data loggers (HOBO Pendant®) recorded water temperature every four hours in experimental tanks. Each temperature treatment was replicated four times for a total of 16 tanks. Photoperiod was variable in this experiment, however, larvae were exposed to light at least 8-hours per day.

Again, using a split-brood design, we divided clutches from 10 females into four equal groups and placed each group into a different thermal treatment, so that eggs from each female were included in every treatment (*n* = 10 for all treatments, except 27.4º C – variable, *n* = 9). Eggs were visually inspected every day for hatching. Again, we chose the second day of observed hatching as ‘day of hatching’ for each group. After a group hatched, we randomly selected 10 individuals from each group and photographed that sub-sample to estimate hatchling head width (Nikon D3200 HD-SLR camera, Tamron 90mm f2.8 macro lens). Head widths are a common metric used to measure body size in odonates (Corbet 1999). Next, the photographed larvae were individually placed into 100-mL plastic cups filled with dechlorinated, oxygenated water. Each cup was fitted with a polystyrene ring and floated in a water bath in the treatment tank (Supplementary material: Appendix 1 Fig. A2). Larvae were held separately to monitor individual growth rates (n = 40, 38, 39, and 36 larvae in 23.4º, 27.5º, 30.4º and 27.4º C – variable, respectively). We replaced water lost to evaporation every two days with dechlorinated, oxygenated water so that cups were always ~90% full.

Larvae were fed a diet of washed and rinsed *Artemia* nauplii in addition to small zooplankton (*Daphnia* species) twice weekly. This feeding regime is considered low compared to other odonate lab studies (see: Suhling et al. 2015), however we did observe treatment effects (see RESULTS), indicating that the feeding rate was sufficient to allow for growth and for us to observe the effects of temperature on growth. Additionally, food limitation may be quite common for larvae developing in ponds making the comparisons of growth responses across different feeding levels of interest. Waste that accumulated in the bottom of cups was removed weekly with 5-mL plastic pipettes to prevent hypoxia. We photographed all larvae again either after they had died, or at the end of the experiment. Head widths of larvae were measured from these photographs using Image J (U. S. National Institutes of Health, Bethesda, Maryland, USA), with a 3-centimeter ruler for calibration. Growth rate was calculated as the difference in head widths (ln-transformed), then divided by the time period to get a rate of mm x day^{-1} (Hoffman and Poorter 2002). This experiment lasted for 75 days between June and August 2015.

Statistical analyses:

We used a linear mixed effects model (LME) (package “lme4”, version 1.1-9) to analyze data from the first experiment and assess the effects of treatment temperature, species identity and the interaction between temperature and species on egg development rate (1/days to hatching). We included tank as a blocking variable. We evaluated the significance of each model term using log-likelihood ratio tests (logLRT) and eliminated factors with $p > 0.1$.

We analyzed data from our second experiment using a LME model to analyze the effects of treatment temperature on egg development rate for the species *L. intacta*, with female and oviposition date as random factors. Oviposition date was included to account for temporal heterogeneity in traits of eggs or larvae. We also used a LME model to analyze the effects of treatment temperature, female and the interaction between temperature and female on hatchling head width and larval growth rate. To determine the effects of temperature treatment on survival, we used a survival analysis using the package “survival” (version 2.38) and “coxme” (version 2.2-5). All analyses were performed in R version 3.2.3 (R Development Core Team 2016).

RESULTS

Experiment 1: interspecific comparisons of egg development rate

Increasing temperature significantly decreased egg development rates across all species (log-LRT: $X^2(1) = 76.81$, $p < 0.001$; Fig. 1, Table 1). We also found a significant effect of species identity on egg development rate (log-LRT: $X^2(3) = 35.48$, $p < 0.001$; Fig. 1, Table 1). *Celithemis elisa* had slower egg development compared to all other species (Tukey’s HSD for all: $p < 0.01$). We found no significant interaction between treatment temperature and species identity on embryonic developmental rate (log-LRT: $X^2(3) = 2.60$, $p = 0.46$; Fig. 1, Table 1). Tank was a significant predictor of egg development rate (log-LRT: $X^2(3) = 16.69$, $p < 0.001$; Table 1).

Experiment 2: effects of warming on early life stages of *L. intacta*

Similar to results in our first experiment, we found that increasing treatment temperature significantly decreased egg development rate (log-LRT: $X^2(3) = 52.90$, $p < 0.001$; Table 2). Eggs in the 30.4º C treatment developed the fastest (8.9 ± 1.0 days) compared to eggs developing in coolest treatments (mean for 23.4º C = 14.0 ± 1.1 days). All pairwise comparisons between treatments were significantly different except for eggs developing in 27.5º C – constant and 27.4º C – variable (Tukey's HSD: $p = 0.3$). In addition to treatment temperature, oviposition date also had a significant effect on egg development rate, with a trend of faster development at later oviposition date (log-LRT: $X^2(1) = 5.02$, $p = 0.03$; Table 2). This effect explained 55% of the total variation in egg development rate.

There was a significant effect of treatment temperature on hatchling head width (log-LRT: $X^2(3) = 25.84$, $p < 0.001$; Fig. 2, Table 2). Hatchlings reared at 30.4º C had the smallest head widths, with heads 7% smaller than hatchlings raised in 23.4º C. There was a nonsignificant trend towards larger head widths in larvae developing in 27.5º C – constant compared to head widths of larvae raised in and 27.4º C – variable (Tukey's HSD $p = 0.07$; Table A1), but for all other responses (growth rate and survival), we found no significant effects of developing in the variable compared to medium temperature treatment. Lastly, there was a significant female effect (log-LRT: $X^2(1) = 4.96$, $p = 0.03$; Table 2) as well as a significant interaction between female and temperature on hatchling head width (log-LRT: $X^2(1) = 6.26$, $p = 0.01$; Table 2).

Temperature had a significant effect on larval growth rate (log-LRT: $X^2(3) = 16.72$, $p < 0.001$; Fig. 3, Table 2). Growth rates were 29% faster in the 30.4º C treatments (0.029 ± 0.01 mm•day^{-1}), compared to the coolest treatment, 23.4º C (Tukey's HSD: $p = 0.04$; Table A1). We found no significant effects of the female (log-LRT: $X^2(1) = 2.43$, $p = 0.67$; Table 2) however, there was a marginally significant interaction between treatment and female (log-LRT: $X^2(1) =$

2.43, $p = 0.12$; Table 2) on growth rates. Growth rates were slowest in the intermediate 27.5º – constant and 27.4º C – variable treatments – a 39% and 33% reduction, respectively, compared to growth rates in 30.4º C.

Treatment temperature had a significant negative effect on survival (LRT: $X^2(3) = 38.21$, $p < 0.001$; figure 4). Larvae raised in 30.4º C experienced mortality sooner in the experiment (restricted mean: 16.1 ± 2.3 days (SE)) compared to larvae raised at 23.4º C (restricted mean: 40.2 ± 3.64 days (SE)).

DISCUSSION

We examined the effects of warming on odonates in two ways, through examining its effects on egg development rates in a suite of co-occurring, libellulid dragonflies and by comparing early life-history responses to warming in a single dragonfly species. Higher temperatures decreased egg development rates in similar ways across the four study species. Our study of the single species, *L. intacta,* found that temperature and growth rate were positively related, while size at hatching and survival rates decreased with increasing temperature. We also uncovered two sources of intraspecific variation within *L. intacta* responses to thermal conditions, differences between clutches of different mothers and to the date of oviposition. Our results provide a greater understanding into the effects of temperature on early life-history and performance in aquatic ectotherms.

The effects of temperature on inter- and intraspecific egg development rate

In our first experiment, we found that warming significantly accelerated hatching time in the four species we examined and responses between species did not differ (Fig. 1). While we expected accelerated egg development, the consistency with which all species responded to warming was interesting given previous observations that species' phenological responses to warming are often idiosyncratic (Guo et al. 2009, Diamond et al. 2011, Caradonna et al. 2014). Differential species responses to temperature could affect species interactions and therefore indirectly affect species abundances and community composition (Ohlberger 2013). By making direct comparisons of phenological responses to temperature we can increase our ability to successfully make predictions about the winners and losers of climate change and more broadly, how communities will be affected by warming climates (Ohlberger 2013). In our study, our results suggest that within libellulid dragonflies the acceleration of egg development in response to temperature may be remarkably consistent.

Timing of egg hatching is crucial in determining when species interact and can therefore have large effects on species interactions, for example intraguild predation (IGP). Perturbations that change the rank order of hatching between species, including differential species responses to temperature, could alter the structure of IGP interactions (e.g. reversing intraguild predator/prey roles), possibly altering population demographics (Guo et al. 2009) or even leading to the loss of certain species (Nakazawa and Doi 2011). The consistent response in egg development rate we found has important implications for this group in temperate regions where climate change is predicted to increase mean summer temperatures—the period in which these species' eggs develop (Paulson 2011). While increasing mean temperatures will accelerate egg development rates in all of these species, the current order of hatching times will be maintained. Among the species we studied, there was no shift in the rank order of time to hatching. These results suggest that interactions such as IGP, which are structured by body size, will remain relatively consistent even with future climate warming. While our interspecific comparisons captured a small but important portion of odonate life history, future studies should examine how similar these species remain in their responses to warming or if their responses diverge at later ontogenetic stages.

In our second experiment in which we measured early life-history responses to temperature in a single odonate species, *L. intacta*, we found that temperature accelerated egg development rates. However, we also found significant intraspecific variation in these developmental responses to temperature with approximately 55% of the variation explained by oviposition date. Eggs laid by females that emerged earlier in the season had faster development rates than eggs laid later in the season. Oviposition date is inherently tied to the female and therefore it remains unclear whether females that emerge earlier in the season lay eggs that develop faster, or if this effect is driven by environmental conditions. One hypothesis is that females that emerge earlier in the season have faster growth rates than females that take longer to develop and emerge later in the season. In turn, the eggs of these “fast” females may also have faster development rates. Given that oviposition date appears to explain much of the variation in egg development rate, future studies should explore how developmental responses of offspring from mothers emerging at different times in the season vary.

The effect of temperature on body size, growth rate and survival of *L. intacta*

In our second experiment, we measured several variables that relate to early larval performance, including hatchling head width—a measure of larval body size, as well as growth rate and survival. We expected that hatchling head width would be smallest in the warmest temperatures and our results support this prediction. Hatchling head width was inversely related to rearing temperature (Fig. 2). While our study did not control for the maternal environment, we were able to strictly control the environmental conditions for the duration of development. Our results conform to what prior studies have found for other taxa, however they differ from previous findings for odonates. A recent study found that hatchling size of a damselfly species was positively related to rearing temperature (Śniegula et al. 2016), while our study found an inverse relationship between these variables. Body size at hatching can affect the prey or resources the hatchlings can use and the types of predators they are vulnerable to (Werner and Gilliam 1984, Scharf et al. 2000). Future studies should examine the consequences of hatchling body size, specifically its role in performance at later stages of development.

We also found a nonsignificant trend towards smaller hatchling head width of larvae developing in 27.4º C - var compared to 27.5º - constant (Tukey's HSD: $p = 0.07$; Fig. 2). This may suggest that temperature variation can have effects different than more consistent warming but this remains unclear. As for the other responses (egg development, growth and mortality rate) we found no evidence that the constant and variable temperature treatment had differing effects on larvae (Tukey's HSD: $p > 0.10$). Overall, our results suggest that fluctuating temperatures may not have observable effects on insects during early stages of development. However, a growing body of literature examining the effects of increased thermal variation have found relationships between fluctuating temperature and life history traits and performance such as development time (Kingsolver et al. 2009), phenotype (Pétavy et al. 2004, Małek et al. 2015), survival (Ragland and Kingsolver 2008), and fitness (Estay et al. 2011). This suggests, and other work has shown, that the effects of increased thermal variation are cumulative and may have consequences at later life history stages. Vannote and Sweeney (1980) first pointed out that natural variation in stream temperatures can affect aquatic insect populations, that these effects can be mediated by factors aside from temperature induced mortality (e.g. effects of temperature on body size and fecundity), and that it can also affect species' geographic distributions. Their work may provide a useful template for future studies of the effects of climate change associated thermal variation on species and populations. Our work along with others demonstrate the complexity of thermal variation on life history processes and suggest that thermal variation should continue to be incorporated into future experiments to model the outcome of species' abilities to persist with future climate change (Vazquez et al. 2015).

We found that intraspecific variation in hatchling size was explained by the mother as well as by an interaction between temperature and mother. This suggests that body size may be influenced by other factors in addition to temperature; there may be heritable or maternal effects that underlies body size at hatching, thus generating a wide range of hatchling body size. This variation in hatchling size could reduce competition between individuals but also increase rates of cannibalism, as this phenomenon, like IGP, is facilitated by body size variation (Claessen et al. 2000). Taken together, our results imply that the developmental environment of eggs is important in determining body size at hatching and also driving hatchling body size variation between egg clutches of different mothers. Whether these variable responses between families are important in structuring interactions such as intraspecific competition and cannibalism should be explored further.

The general pattern we found of higher growth rates at warmer temperatures corresponds well with previous studies measuring the effects of temperature on odonate growth rates (Krishnaraj and Pritchard 1995, Pritchard et al. 2000, Nilsson-Ortman et al. 2014, Suhling et al. 2015) (Fig. 3). These studies have found that growth rates increase in warmer temperatures (except see: Van Doorslaer and Stoks 2005a), an expected result as ectotherm growth rates are known to scale allometrically with temperature (Angilletta et al. 2004). Faster growth rates are likely to underlie observed patterns of advancing phenology, such as earlier adult emergence in odonates (Hassall et al. 2007, McCauley et al. 2015). Whether accelerated growth rates in the context of a warming environment has net benefits or costs for populations will depend on the species and the ecological context in which these animals exist.

We found that temperature had a negative effect on larval survival at early stages of development (Fig. 4). Increases in temperature as a result of climate change could potentially add additional sources of mortality to populations that already have low larval survival (Cornell and Hawkins 1995, Hirst and Kiørboe 2002, Forster and Hirst 2012). Temperature appears to increase odonate mortality when larvae develop and metamorphose in heated conditions (McCauley et al. 2015). These types of studies, however, often do not track survival throughout development and therefore it remains unclear at what stage mortality is occurring. Our results suggest that temperature-induced mortality may occur at early stages of development. This is important for two reasons. First, increases in mortality at early life stages reduces the size of the population entering adult stages of development and therefore could influence population dynamics, as only adults reproduce. Second, an increase in mortality at early stages could change interactions between juveniles. With smaller population sizes, competition as well as cannibalism between individuals could decrease, thereby benefiting those individuals that survive in warmer conditions. It remains to be determined how mortality in early developmental stages will influence odonate populations and food web structure in these systems.

Conclusion

Our results demonstrate that early life history traits and performance are altered at higher temperatures, at both the intra- and interspecific levels. In our interspecific comparisons we found that all species decrease developmental rates in response to temperature, with no significant variation between species responses. We suggest that the absence of variation between species’ responses to warming means that hatching order and thus interspecific interactions between the species examined here will be maintained with future climate change. Our intraspecific comparisons found that egg development and growth rates were inversely related temperature, whereas hatchling size and survival increased with temperature. Egg development rate in responses to temperature varied between clutches of eggs laid at different dates. Hatchling size varied between clutches of different mothers. The high levels of intraspecific variation we observed in egg development time and hatchling size suggest that even with increased temperatures, populations of this species may be relatively more resilient to future climate warming.

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TABLE LEGENDS

Table 1: Results from the log-likelihood ratio tests on the effects of A) fixed and B) random factors on egg development rate. Factors with $p < 0.1$ were significant and included in the LME model.

Table 2: Results from the log-likelihood ratio tests on the effects of A) fixed and B) random factors on egg development rate, hatchling head width and growth rate. Factors with $p < 0.1$ were significant and included in the LME model.

FIGURE LEGENDS

Fig. 1: The effects of temperature on egg development rate in four odonate species: *C. elisa* (squares), *L. luctuosa* (triangles), *L. intacta* (diamonds), and *L. pulchella* (circles). Temperature means of these treatments were 22.2º, 24.9º, 27.0º, and 30.7º C. Error bars are ± 1 SE. Points are jittered on x-axis. *n* = 20, 21, 21, and 20 groups for each temperature, respectively.

Fig. 2: Head width (mm) of *L. intacta* hatchlings in constant (23.4º, 27.5º, 30.4º C) and variable (27.4º C - var) temperature treatments (*n* = 40, 36, 38 and 39 larvae, respectively).

Fig. 3: Growth rate ($\text{mm} \bullet \text{day}^{-1}$) of early instar *L. intacta* raised in constant (23.4º, 27.5º, 30.4º C) and variable (27.4º C - var) temperature treatments.

Fig. 4: Kaplan-Meier survival curves for the mean proportion of surviving *L. intacta* larvae in constant (23.4º, 27.5º, 30.4º C) and variable (27.4º C - var) temperature treatment over time (days). Different lines represent treatment temperatures.

TABLES

Table 1

Model and response variable		Predictor	df	χ^2	*p*
LME	A)	Treatment	1	76.81	<0.001
Egg development rate		Species	3	35.48	<0.001
		Treatment*Species	3	2.60	0.46
	B)	Female	1	0	1
		Oviposition date	1	4.28	0.39
		Tank	3	16.69	<0.001

Table 2

Model and response variable		Predictor	df	χ^2	*p*
LME	A)	Treatment	3	52.90	<0.001
Egg development rate	B)	Female	1	0	1
		Oviposition date	1	5.020	0.03
LME					
Hatchling head width	A)	Treatment	3	25.84	<0.001
	B)	Female	1	4.96	0.03
		Treatment*Female	1	6.26	0.01
		Oviposition date	1	0.30	0.58
LME					
Growth rate	A)	Treatment	3	16.72	<0.001
	B)	Female	1	0.19	0.67
		Treatment*Female	1	2.43	0.12
		Tank	1	0.48	0.49
		Oviposition date	1	0.83	0.36

FIGURES

Fig. 1

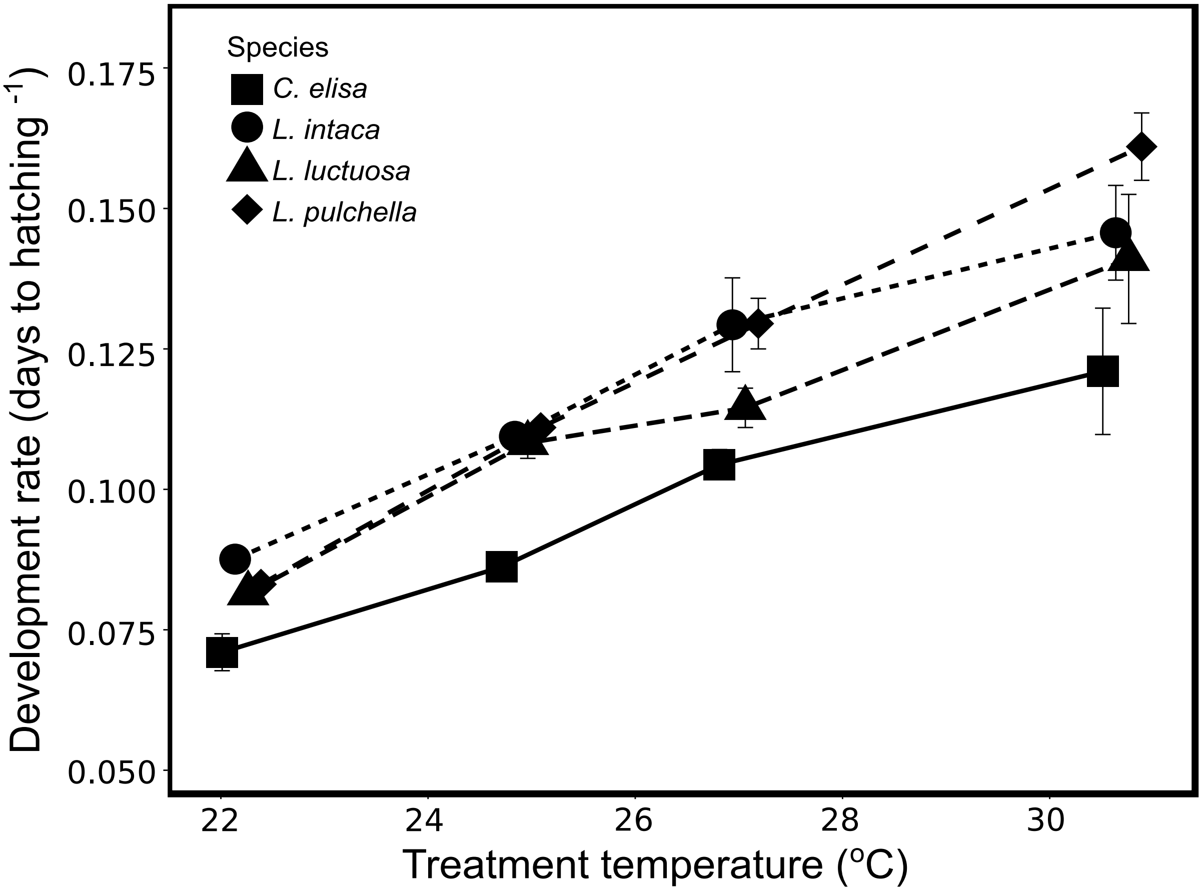
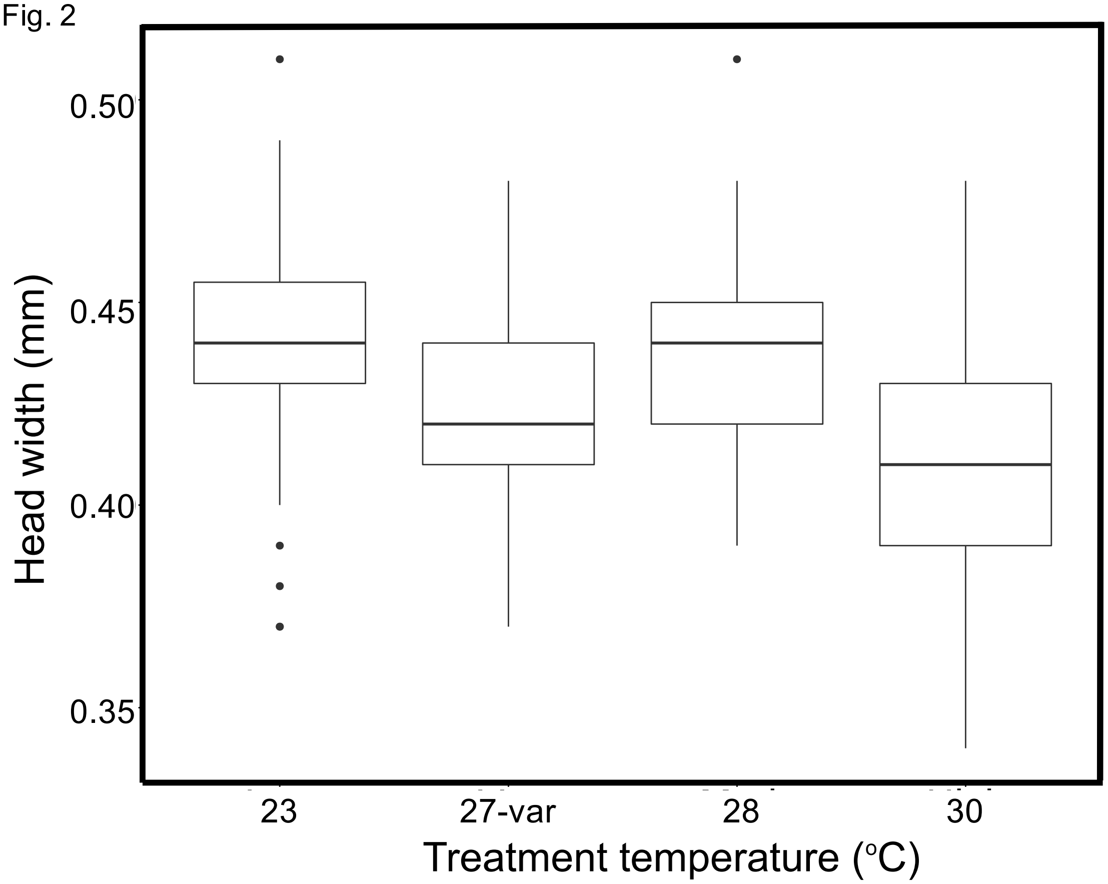
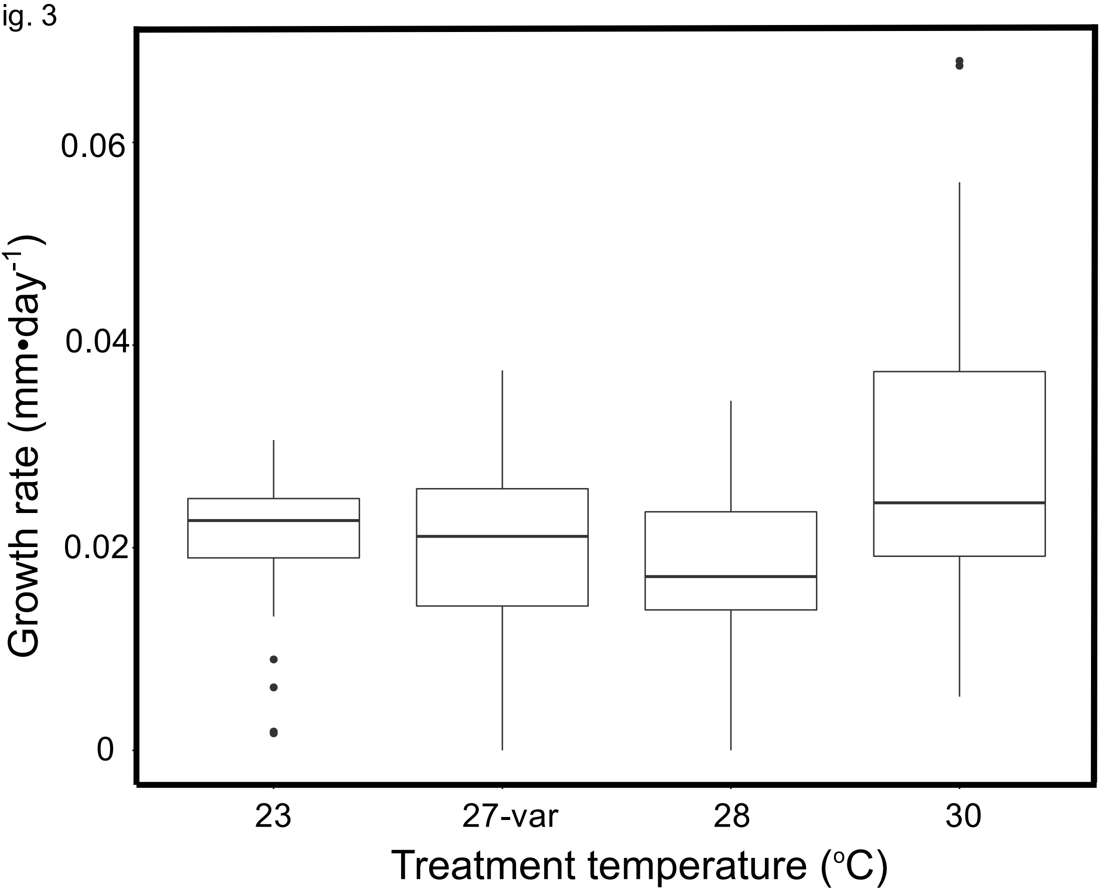


Fig. 2


Head width (mm)
0.50
0.45
0.40
0.35
23
27-var
28
30
Treatment temperature (°C)

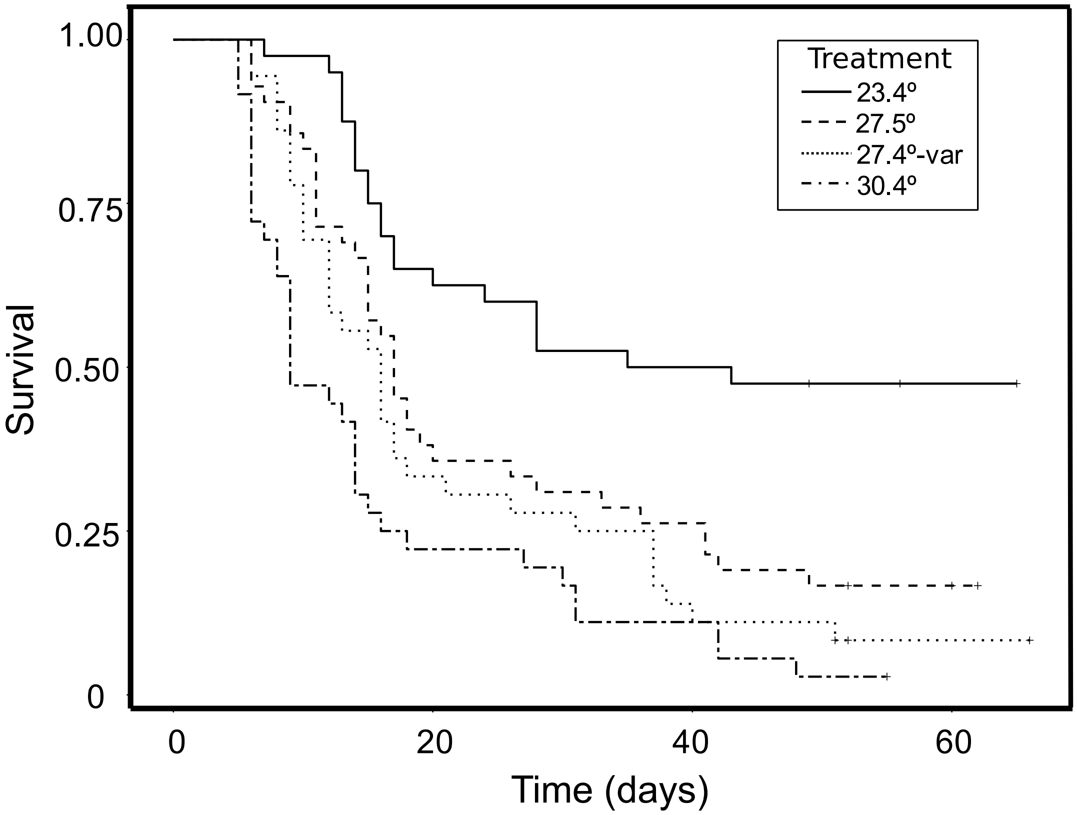
758

Fig. 3


0.06
0.04
0.02
0
Growth rate (mm•day-1)
23
27-var
28
30
Treatment temperature (°C)

759

Fig. 4


1.00
0.75
0.50
0.25
0
Survival
0
20
40
60
Time (days)
Treatment
23.4º
27.5º
27.4º-var
30.4º

760