

RESEARCH ARTICLE

The metabolic, locomotor and sex-dependent effects of elevated temperature on Trinidadian guppies: limited capacity for acclimation

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SUMMARY

Global warming poses a threat to many ectothermic organisms because of the harmful effects that elevated temperatures can have on resting metabolic rate (RMR) and body size. This study evaluated the thermal sensitivity of Trinidadian guppies (*Poecilia reticulata*) by describing the effects of developmental temperature on mass, burst speed and RMR, and investigated whether these tropical fish can developmentally acclimate to their thermal conditions. These traits were measured following exposure to one of three treatments: 70 days at 23, 25, 28 or 30°C (acclimated groups); 6 h at 23, 28 or 30°C following 70 days at 25°C (unacclimated groups); or 6 h at 25°C following 70 days in another 25°C tank (control group). Body mass was lower in warmer temperatures, particularly amongst females and individuals reared at 30°C. The burst speed of fish acclimated to each temperature did not differ and was marginally higher than that of unacclimated fish, indicative of complete compensation. Conversely, acclimated and unacclimated fish did not differ in their RMR at each temperature. Amongst the acclimated groups, RMR was significantly higher at 30°C, indicating that guppies may become thermally limited at this temperature as a result of less energy being available for growth, reproduction and locomotion. Like other tropical ectotherms, guppies appear to be unable to adjust their RMR through physiological acclimation and may consequently be susceptible to rising temperatures. Also, because larger females have higher fecundity, our data suggest that fecundity will be reduced in a warmer climate, potentially decreasing the viability of guppy populations.

Key words: beneficial acclimation hypothesis, climate change, developmental plasticity, oxygen consumption, temperature–size rule, thermal tolerance.

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INTRODUCTION

There is growing recognition that responses to global warming will vary among species (Harrington et al., 1999; Nilsson et al., 2009) and perhaps even among populations of the same species (Pörtner et al., 2008; Eliason et al., 2011). With the average global air temperature projected to increase by 1.8–4.0°C by 2099 (IPCC, 2007), identifying thermally sensitive groups and the traits that determine their vulnerability is a crucial endeavour for biologists (McKinney, 1997; Williams et al., 2008). Ectothermic organisms, such as fish, are physiologically dependent on their thermal environment, with high temperatures having a wide range of effects including increased metabolic demands, reduced body size, protein denaturation, increased developmental rates and the loss of locomotor performance (Atkinson, 1994; Somero and Hofmann, 1997; Taylor et al., 1997; Gillooly et al., 2001; Blanckenhorn and Hellriegel, 2002). Describing the capacity of ectotherms to avoid these deleterious effects *via* physiological or evolutionary responses will be key in understanding the potential biological impacts of climate change.

Acclimation is a mechanism by which individuals can shift their thermal window of performance through changes in the functional capacity of all levels of biological organization (reviewed in Kassahn et al., 2009; Hofmann and Todgham, 2010), providing ectotherms with some degree of independence from the far-reaching effects of temperature. Two distinct types of response are reversible acclimation and developmental acclimation. Reversible acclimation

refers to a physiological adjustment made in response to a chronic change in a single environmental variable (Prosser, 1986), whereas developmental acclimation includes all phenotypic, often non-reversible changes induced by an organism's developmental environment (Angilletta, 2009). Consideration of the adaptive significance of acclimation has led to the beneficial acclimation hypothesis (Leroi et al., 1994), which posits that all acclimation responses enhance fitness such that individuals acclimated to a certain environment will always outperform unacclimated individuals in that environment. Support for this hypothesis, however, is generally weak, particularly in studies of developmental acclimation (Wilson and Franklin, 2002; Angilletta, 2009). Instead, optimal conditions for development tend to exist, such that individuals that develop at certain temperatures outperform individuals reared at other, non-optimal temperatures, in any thermal environment (e.g. Huey et al., 1999; Gibert et al., 2001).

In fishes, the effect of increased temperature on aerobic metabolism has been highlighted as a crucial factor determining the ability of a species to cope with rising temperatures (Pörtner, 2001; Pörtner and Knust, 2007; Farrell et al., 2008; Pörtner and Farrell, 2008). In ectothermic organisms, the thermal dependence of metabolism causes resting metabolic rate (RMR) to increase in warmer temperatures. This elevation of RMR is harmful to an ectotherm because less energy is available for somatic growth and reproduction as the minimum metabolic requirements increase with temperature (Gillooly et al., 2001; Sogard and Spencer, 2004).

Moreover, an elevated RMR reduces aerobic scope (i.e. the difference between resting and maximal rates of oxygen intake) (Fry, 1947) when there is not a corresponding increase in maximum metabolic rate. For example, the aerobic scope of several coral reef fish species was reduced by nearly 50% in elevated temperatures mainly because of increases in their RMR (Nilsson et al., 2009). Because increased energetic demands and reduced aerobic scope can limit an organism's persistence in elevated temperatures (Pörtner and Knust, 2007), acclimation responses involving partial or complete compensatory adjustments of RMR would be highly beneficial.

Thermal specialization is thought to trade-off with physiological plasticity, such that species from thermally stable environments have low compensatory capacities compared with those living in variable conditions (Huey and Hertz, 1984; Somero et al., 1996). Indeed, results from studies on tropical fish support this thermal specialization hypothesis (e.g. Tullis and Baillie, 2005; Nilsson et al., 2009; Nilsson et al., 2010), with stenothermal reef fish generally displaying no capacity for metabolic acclimation. However, such studies usually allow only a brief acclimation period (i.e. a few days or weeks) and occur within a single life stage, neglecting the potential for developmental acclimation. A recent study (Donelson et al., 2011) found that the tropical fish *Acanthochromis polyacanthus* was able to make compensatory reductions of its RMR through developmental acclimation to temperatures that were 3°C warmer than current conditions. Such disagreement warrants further study of developmental plasticity as a means to overcome temperature change in tropical ectotherms.

The Trinidadian guppy (*Poecilia reticulata*) is a small tropical fish native to northeastern South America and the Caribbean, where they inhabit shallow, freshwater streams and pools, and play a key role in shaping aquatic ecosystems (Bassar et al., 2010). In Trinidad, the average air temperature fluctuates by ~2°C throughout the year, while daily air temperatures fluctuate by ~10°C (weatheronline.co.uk). Changes in air temperature generally induce similar changes in the water temperature of shallow streams, although the magnitude of the change is often reduced (Pilgrim et al., 1998; Caissie et al., 2001). Because the waters in which guppies reside currently average 25°C (Houde, 1997), guppies probably do not naturally experience water temperatures beyond 20–30°C. Their habitat is warming, however, as the average air temperature in Trinidad has increased by about 1.5°C in the past 60 years (Singh, 1997) and is projected to increase by 0.94–4.18°C by the end of the current century (IPCC, 2007). Physical barriers, such as oceans, prevent dispersal from Trinidad, meaning guppies will have to respond physiologically or genetically in order to cope with elevated temperatures. Having evolved in relatively stable thermal conditions, guppies are predicted to be physiologically inflexible according to the thermal specialization hypothesis. Indeed, heat stress affects commercially raised guppies by increasing growth rate yet decreasing adult length, mass, survivorship and fecundity (Dzikowski et al., 2001; Karayucl et al., 2008). However, guppies have previously demonstrated an ability to adjust their critical thermal limits (Chung, 2001) and energy allocation (Auer, 2010) in response to environmental stress, suggesting they may not be as vulnerable to temperature change as typically would be predicted for a tropical ectotherm.

The aim of this study was to investigate the thermal sensitivity and developmental plasticity of Trinidadian guppies in the context of climate change. To do so, we investigated the effects of developmental temperature on body size, resting oxygen consumption rate (a measure of RMR) and burst swimming speed (an organism-level performance

trait), and examined guppies' ability to make compensatory adjustments of RMR and burst speed in different thermal conditions. Because guppies have previously demonstrated a capacity for phenotypic plasticity, we predicted that they would make partial or complete compensatory adjustments (*sensu* Precht et al., 1973) of these two traits upon thermal acclimation.

MATERIALS AND METHODS

The experiments followed ethical guidelines from the Canadian Council on Animal Care as reviewed and approved by the Animal Use Subcommittee at the University of Western Ontario. Guppies (*P. reticulata* Peters 1859) used in this experiment were descendants of fish that were collected in 2003 from a tributary of the Paria River (10°44'42"N, 61°51'42"W) in Trinidad. The established laboratory population has been kept at 25±3°C to simulate mean natural conditions (Houde, 1997). The experiments described here were conducted from October 2010 to March 2011. Fish were held in 250 l stock tanks in the Freshwater Ecology Research Facility at the University of Western Ontario, kept on a 12h:12h light–dark cycle, and fed twice daily to satiation with TetraMin flake food and brine shrimp. Adult females were individually separated into 10 l tanks with the temperature set at 25°C until they gave birth. At this point, the adult females were removed from the tanks, leaving only their offspring, and the water was set to one of four temperatures: 23, 25, 28 or 30°C. With 15 families of fish (median brood size=5) kept at each temperature, the newborn fish were left to develop in their thermal conditions for an acclimation period of 70±10 days. Guppies were able to mature in this 70 day period, having a generation time of 2–3 months (Reznick and Endler, 1982).

To determine the compensation response of guppies, oxygen consumption and burst speed were measured for three treatment groups: acclimated, unacclimated and control (Fig. 1). The acclimated group consisted of fish measured following long-term (70 days) exposure to 23, 25, 28 or 30°C. The unacclimated group was composed of 25°C-acclimated fish measured following short-term (6 h) exposure to 23, 28 or 30°C. A pilot study found 6 h to be sufficiently long to detect changes in metabolic rate following a temperature change. The control group consisted of 25°C-acclimated fish measured following short-term (6 h) exposure to another 25°C tank, thereby controlling for any handling effects in the unacclimated treatment. The control temperature was 25°C because this simulates current natural conditions, and the conditions the guppies were kept at in the laboratory prior to the experiment.

Oxygen consumption

Closed-box respirometry techniques and the Winkler titration method (see Strickland and Parsons, 1968) were employed to measure rates of resting oxygen consumption (\dot{M}_{O_2}). Respirometers were made using 600 ml glass jars lined with a single rubber tube for water extraction and covered with a thin sheet of closed cell foam to prevent oxygen diffusion into the water. Using an initial water volume of 380 ml, five fish of the same family that had been starved for 24 h prior to trials were placed into each respirometer at their test temperature. The fish were left undisturbed in the respirometers for 30 min prior to trials. During the trials, 60 ml water samples were taken from the respirometers at time 0, 30 and 60 min. Covering around the respirometers prevented the fish from being visually disturbed throughout the trials, and the rubber tubing allowed water to be extracted from the respirometers without compromising the resting status of the fish. The dissolved oxygen content (in mg O₂ l⁻¹) at each time point was determined by adding manganous sulphate and alkaline iodide to the water samples to

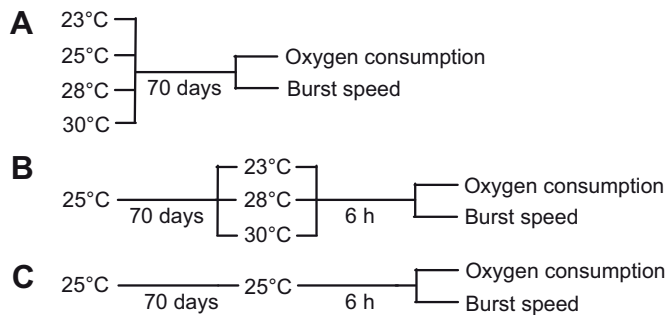


Fig. 1. Experimental design to determine the compensation response to temperature change of guppies (*Poecilia reticulata*). Fish were subjected to one of three thermal treatments: (A) acclimated group acclimated to 23, 25, 28 or 30°C; (B) unacclimated group acclimated to 25°C then briefly exposed to 23, 28 or 30°C; or (C) control group acclimated to 25°C then briefly exposed to another 25°C tank. Oxygen consumption and burst speed were measured following the indicated exposure times.

form a precipitate of $\text{MnO}(\text{OH})_2$, adding concentrated sulphuric acid to reduce the iodide ions to iodine, and then measuring the amount of iodine present by titrating the solution to its endpoint using 0.01 mol l^{-1} sodium thiosulphate (Strickland and Parsons, 1968). The oxygen content ($\text{mg O}_2 \text{ l}^{-1}$) of each water sample was calculated as:

$$\text{O}_2 \text{ content} = (8000 \times V_{\text{Na}_2\text{S}_2\text{O}_3} \times M_{\text{Na}_2\text{S}_2\text{O}_3}) / V_{\text{H}_2\text{O}}, \quad (1)$$

where $V_{\text{Na}_2\text{S}_2\text{O}_3}$ is the volume of titrated sodium thiosulphate used, $M_{\text{Na}_2\text{S}_2\text{O}_3}$ is the molarity of the sodium thiosulphate solution, $V_{\text{H}_2\text{O}}$ is the volume of the water sample, and 8000 is the molar mass (mg mol^{-1}) of oxygen divided by four (i.e. the number of iodine molecules present for every one molecule of oxygen). These methods have been shown to yield measures of dissolved oxygen content with an accuracy of $\pm 0.05 \text{ mg l}^{-1}$ (Markfort and Hondzo, 2009). From these measurements, mass-specific oxygen consumption rates ($\mu\text{g O}_2 \text{ min}^{-1} \text{ g}^{-1}$) were calculated. Following trials, fish were lightly anaesthetized with approximately $10 \text{ mg}/50 \text{ ml}$ of MS-222 (Sigma-Aldrich, St Louis, MO, USA), weighed to the nearest mg, and returned to their experimental tanks. Using these methods, a total of 57 trials were performed.

Burst speed

Maximum burst swimming speed throughout individuals' entire escape response was measured using methods similar to those described previously (Chappell and Odell, 2004). A total of 191 trials were performed in which guppies were placed individually into a circular aquarium (30 cm diameter) filled with approximately 4–5 cm of water and maintained at the fish's test temperature. Guppies were left undisturbed in the tank for 4 min, after which a stimulus (a 50 g metal cylinder) was dropped into the water to elicit an escape response. The response was recorded using a Sony HDR-XR200V video camera (Tokyo, Japan) placed directly above the aquarium. If a fish did not respond to the first stimulus, a second stimulus was released 3 min after the first. If no response was made after the second stimulus, the individual was removed from the study (10 individuals were removed). Oufiero and Garland demonstrated that these methods yield burst speeds that are highly repeatable for individual guppies, indicating that they represent actual measures of organism performance (Oufiero and Garland, 2009).

Burst speed was quantified using methods similar to those described elsewhere (Breckels and Neff, 2010). Images (captured at 30 frames s^{-1}) were extracted from the videos using Picture Motion

Browser software (Sony). Using the tip of each fish's rostrum as the tracking point, x - and y -coordinates in a two-dimensional plane were determined for each fish in each image using NIH ImageJ software (<http://rsbweb.nih.gov/ij>) and the distance travelled between consecutive frames was calculated. Because of the effects of temperature on size and the strong influence of size on swimming speed (Wardle, 1975), burst speed was quantified in body lengths per second (BL s^{-1}), a commonly used index of fish burst speed that controls for the effects of size (Domenici and Blake, 1997).

Statistical analysis

Body mass at the end of the experiment for fish reared in the four different temperatures was compared using ANCOVA, with temperature and sex as fixed factors and age as a covariate, as well as a Tukey's *post hoc* test. In the \dot{M}_{O_2} and burst speed analyses, the four acclimated groups were compared using ANOVA with temperature as a fixed factor, as well as a Tukey's *post hoc* test. The acclimated and unacclimated groups at 23, 28 and 30°C and the 25°C-acclimated and control group were also compared using ANOVA with acclimation as a fixed factor. Sex was used as a second fixed factor throughout the burst speed analysis. A paired *t*-test was also conducted to evaluate the repeatability of \dot{M}_{O_2} measurements between 0–30 min and 30–60 min. All statistics were performed using PASW STATISTICS 18.0 software (Chicago, IL, USA), and all means are reported ± 1 s.e.m.

RESULTS

Body mass

Temperature had a strong effect on the mass of guppies, with size significantly decreasing in warmer temperatures for both sexes ($F_{3,122}=9.82$, $P<0.001$; Fig. 2). Females showed more variation in body mass than males (coefficient of variation CV of 40.3% versus 17.4%), ranging from 0.017 to 0.158 g compared with 0.028 to 0.086 g in males. On average, females were significantly larger than males (0.071 ± 0.003 and 0.055 ± 0.001 g, respectively; $P=0.003$); however, this difference was reduced with increasing temperature from 25°C (34% larger at 25°C compared with only 7% larger at 30°C; Fig. 2). The age of guppies at the time of measurement did not have a significant effect on body mass ($F_{1,122}=2.91$, $P=0.091$).

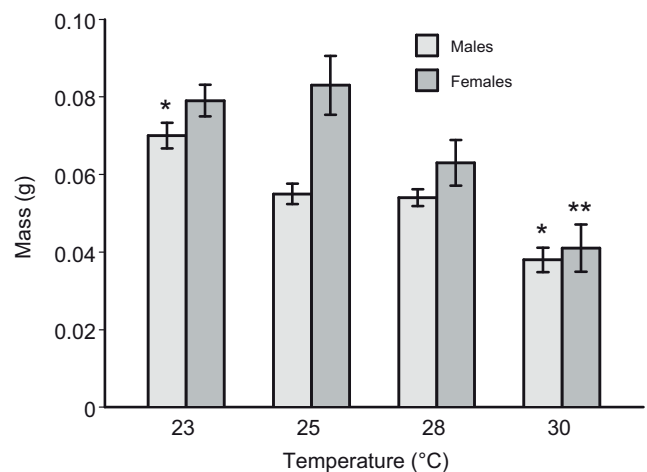


Fig. 2. Body mass (mean ± 1 s.e.m.) in different developmental temperatures of male and female guppies (*P. reticulata*). Fish were reared in 23°C ($N=44$), 25°C ($N=33$), 28°C ($N=35$) and 30°C ($N=19$) water and weighed when they were 60–80 days old. * $P<0.01$, ** $P<0.001$ (compared with 25°C values for the same sex).

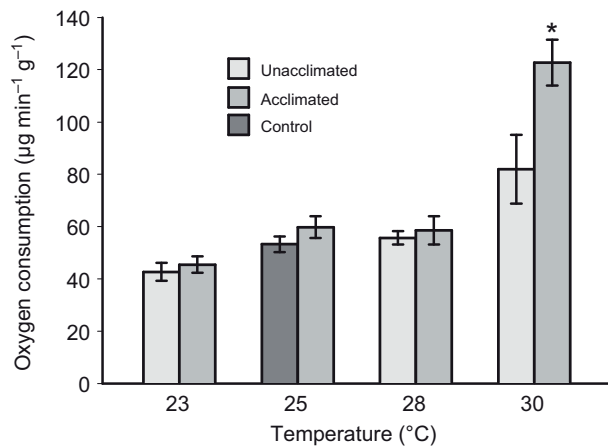


Fig. 3. Mass-specific oxygen consumption rates (mean \pm 1 s.e.m.) of acclimated, unacclimated and control groups of guppies (*P. reticulata*). To determine guppies' compensation response, oxygen consumption rates of acclimated groups (23°C, $N=15$; 25°C, $N=11$; 28°C, $N=8$; 30°C, $N=7$) were compared, as were those of acclimated and unacclimated ($N=4$ for each temperature) groups at 23, 28 and 30°C, and the control ($N=4$) and 25°C-acclimated fish. The asterisk indicates a significant difference ($P<0.001$) from other acclimated groups according to ANOVA. There were no significant differences between acclimated and unacclimated groups or between the control and 25°C-acclimated groups.

Resting oxygen consumption

Guppies reared at 30°C had significantly higher mass-specific \dot{M}_{O_2} than those reared at 23, 25 and 28°C ($F_{3,37}=40.9$, $P<0.001$; Fig. 3). \dot{M}_{O_2} was not significantly different between acclimated and unacclimated fish ($F_{1,40}=0.392$, $P=0.535$) or between the control and 25°C-acclimated fish ($F_{1,13}=0.809$, $P=0.385$; Fig. 3). These trends were also observed when absolute oxygen consumption rates ($\mu\text{g O}_2 \text{ min}^{-1}$) were compared. There was considerable inter-family variation in \dot{M}_{O_2} , with an average CV of 23.9% across acclimation temperatures. Measurements of \dot{M}_{O_2} were not significantly different between 0–30 min and 30–60 min (paired $t=1.557$, d.f.=56, $P=0.125$), and the ratio of males to females used in each trial did not differ between treatments ($F_{7,49}=0.793$, $P=0.597$) and showed no relationship with \dot{M}_{O_2} (Pearson's $r=-0.072$, $P=0.596$).

Burst speed

Fish reared at all four temperatures ($N=131$) did not differ in their burst swimming speed ($F_{3,123}=0.677$, $P=0.568$; Fig. 4), which ranged from 19.1 to 76.1 BL s^{-1} (mean of $41.3 \pm 0.987 \text{ BL s}^{-1}$). These values were higher than the burst speed of unacclimated fish ($N=35$), which ranged from 18.8 to 49.4 BL s^{-1} ($34.3 \pm 1.21 \text{ BL s}^{-1}$). Indeed, there was a significant effect of acclimation on burst speed ($F_{1,129}=12.1$, $P=0.001$), with unacclimated fish having a slower speed than acclimated fish at 23, 28 and 30°C (Fig. 4). The burst speed of 25°C-acclimated fish was not different from that of the control group ($F_{1,44}=0.384$, $P=0.539$), indicating that there were no significant handling effects in the unacclimated treatment. Inter-individual variation in burst speed was high, with an average CV of 27.0% across acclimation temperatures. Similar trends were found when absolute speeds (cm s^{-1}) were compared, with no differences between acclimation temperatures ($F_{3,123}=1.45$, $P=0.232$) and acclimated fish generally swimming faster than unacclimated fish (51.9 ± 1.33 versus $47.9 \pm 1.97 \text{ cm s}^{-1}$, respectively). There was no significant effect of sex on burst speed ($F_{1,179}=2.34$, $P=0.127$).

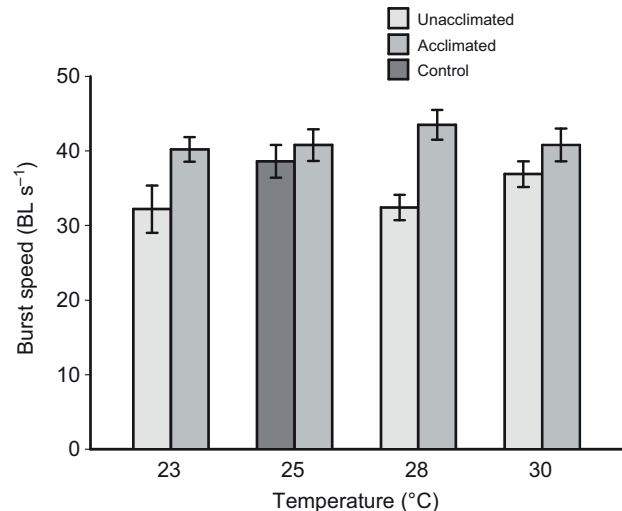


Fig. 4. Burst speed (mean \pm 1 s.e.m.) of acclimated, unacclimated and control groups of guppies (*P. reticulata*). To determine guppies' compensation response, the burst speed of acclimated fish (23°C, $N=44$; 25°C, $N=33$; 28°C, $N=35$; 30°C, $N=19$) was compared, as was that of acclimated and unacclimated (23°C, $N=8$; 28°C, $N=12$; 30°C, $N=15$) fish at 23, 28 and 30°C, and the control ($N=15$) and 25°C-acclimated fish. Acclimated fish had a significantly higher burst speed ($P=0.001$) than unacclimated fish according to ANOVA. There was no effect of temperature on the burst speed of acclimated fish.

DISCUSSION

Describing the thermal sensitivity and phenotypic plasticity of organisms is key in determining which species are most threatened by climate change (Williams et al., 2008). In this study, we found that guppies were unable to adjust their metabolic rate through developmental acclimation to 30°C, as resting rates of metabolism were higher than those at lower temperatures and similar in acclimated and unacclimated fish. Guppies also had reduced body mass in warmer developmental temperatures, following the temperature–size rule (Atkinson, 1994). However, although significant changes occurred at 30°C, there were virtually no differences in resting metabolic rate between fish exposed to 23–28°C. Furthermore, guppies showed complete compensation in terms of their burst locomotor performance, as the burst speed of acclimated fish was similar in all temperature treatments and was always higher than that of unacclimated fish. Indeed, our findings for guppies adhered to the beneficial acclimation hypothesis (Leroi et al., 1994): in a given temperature, fish reared at that temperature consistently outperformed fish that were reared at another temperature. Previous studies have similarly demonstrated such enhanced burst swimming performance among acclimated fish (Beddow et al., 1995; Johnson and Bennett, 1995; Carey and Franklin, 2009). Our findings suggest that guppies possess the ability to maintain certain aspects of their physiological condition in the face of changing environmental temperatures, provided some critical threshold is not crossed. This tipping point appears to be between 28 and 30°C.

Reduced body size has been proposed as a universal response to climate warming in both ectothermic and endothermic species (Gardner et al., 2011; Sheridan and Bickford, 2011). There are two fundamental rules of physiological ecology that can explain this response in ectothermic organisms. First, the temperature–size rule (Atkinson, 1994) posits that animals develop faster and achieve smaller body sizes when they develop in warmer

temperatures. Second, the temperature–metabolic rate rule (Gillooly et al., 2001) states that ectotherms have higher metabolic demands in elevated temperatures, meaning organisms must consume more energy in order to achieve a given body size when it is warmer. Because the guppies in our study were fed to satiation, the reduction in size that we observed at 30°C appears to have been a direct, unavoidable consequence of warm temperatures, and not caused by an inability to meet increased metabolic demands. These thermal effects on growth are likely to be even more severe in the wild, because individuals will have to consume more energy in resource-limited environments in order to prevent further reductions in size. Like many other species (Sheridan and Bickford, 2011), guppies will probably be smaller in size in a warming climate.

Thermal sensitivity is thought to be enhanced in large individuals, such that thermal windows for growth and aerobic performance are narrower for large than for small individuals (e.g. Linton et al., 1998; Rodnick et al., 2004). Indeed, Pörtner and Knust found that large North Sea eelpout (*Zoarces viviparus*) experienced reduced growth and abundance at earlier temperatures than did small eelpout (Pörtner and Knust, 2007). In our study, females were more thermally sensitive than males, decreasing in body size more sharply when reared in temperatures warmer than their mean environmental temperature of 25°C. Because female guppies are larger than their male counterparts, this result is in line with the above-mentioned findings and suggests that female guppies may be more susceptible to warming temperatures than are males. Moreover, this enhanced sensitivity of females may be problematic for the stability of guppy populations because female fecundity decreases with decreasing body size in guppies (Reznick and Endler, 1982; Herdman et al., 2004). The same may hold true for other ectothermic species that similarly exhibit female-biased sexual size dimorphism. In fact, warming temperatures over the past two decades are highly correlated with decreased female size, fecundity and survival in the common toad (*Bufo bufo*), possibly explaining some of the recent, widespread declines of amphibian species (Reading, 2007).

Our study of a tropical, freshwater fish revealed dissimilar acclimation of burst locomotor performance and resting metabolic rate in physiologically relevant temperatures. The inability of guppies to lower the increased energetic demands at 30°C may limit their ability to tolerate this temperature because less energy would be available for growth, reproduction and locomotion. This temperature corresponds to the maximum temperature that guppies are likely to experience in their current natural conditions, meaning the projected warming will increase their exposure to this temperature and may consequently reduce the viability of guppy populations. Furthermore, our findings are consistent with the notion that thermal sensitivity is enhanced in large individuals. This size-dependent sensitivity may have adverse consequences for guppies and other species in which females are the larger sex, as female fecundity may be reduced and population stability then jeopardized as temperature increases. Studies examining the evolutionary relationship between temperature, fecundity and abundance are now needed to determine whether these species are in fact particularly susceptible to global warming and thus require enhanced conservation efforts.

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