

Predation risk shapes thermal physiology of a predaceous damselfly

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Abstract Predation risk has strong effects on organismal physiology that can cascade to impact ecosystem structure and function. Physiological processes in general are sensitive to temperature. Thus, the temperature at which predators and prey interact may shape physiological response to predation risk. We measured and evaluated how temperature and predation risk affected growth rates of predaceous damselfly nymphs (*Enallagma vesperum*, Odonata: Coenagrionidae). First, we conducted growth trials at five temperatures crossed with two levels of predation risk (fish predator present versus absent) and measured growth rates, consumption rates, assimilation efficiencies, and production efficiencies of 107 individual damselflies. Second, we used a model to evaluate if and how component physiological responses to predation risk affected growth rates across temperatures. In the absence of mortality threat, growth rates of damselflies increased with warming until about 23.5 °C and then began to decline, a typical unimodal response to changes in temperature. Under predation risk, growth rates were lower and the shape of the thermal response was less apparent. Higher metabolic and survival costs induced by predation risk were only partially offset by changes in consumption rates and assimilation efficiencies and the magnitude of non-consumptive effects varied as a function of temperature. Furthermore, we documented

that thermal physiology was mediated by predation risk, a known driver of organismal physiology that occurs in the context of species interactions. A general understanding of climatic impacts on ectothermic populations requires consideration of the community context of thermal physiology, including non-consumptive effects of predators.

Keywords Temperature · Predators · Consumption · Metabolism · Growth

Introduction

The threat of being eaten by a predator can drive diverse behavioral, morphological, and physiological responses in prey. Prey may reduce their foraging activity, shift habitat use, and induce structural defenses under predation risk (Lima 1998). These responses can alter the acquisition of food resources and elevate maintenance costs, thereby altering the conversion of assimilated food into biomass (Hawlena and Schmitz 2010a) and thus prey growth rates (e.g., Stoks and McPeck 2003; McPeck 2004; Benard 2004; Johansson and Andersson 2009; Higginson and Ruxton 2010; Stoks et al. 2012). Such non-consumptive predator effects can be more important for population dynamics than the direct mortality imposed by predators (McPeck and Peckarsky 1998; Pangle et al. 2007; Creel and Christianson 2008; Schmitz 2008; Preisser and Bolnick 2008) and can affect ecosystem structure and function (Hawlena and Schmitz 2010a, b; Hawlena et al. 2012).

Many of the processes involved in physiological responses to predators may be quite temperature sensitive, thus the environmental temperature at which predators and prey interact may shape these non-consumptive responses. Temperature accelerates biological reaction

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rates (Hochachka and Somero 2002) and drives organismal metabolic rates to increase exponentially (Gilluly et al. 2001). Consumption rates of food also tend to increase with warming to keep up with increasing demands for energy (e.g., Rall et al. 2010; Lemoine and Burkepile 2012). Elevated metabolic or survival costs under predation risk (Woodley and Peterson 2003; Sunardi et al. 2007; Beckerman et al. 2007; Hawlena and Schmitz 2010b) combined with increases in energy demand with warming may affect growth rates in profound ways, particularly because many organisms reduce their foraging and food intake rates in response to predation risk (reviewed in Lima and Dill 1990; Lima 1998).

To test this hypothesis, we experimentally measured how temperature and predation risk affected physiological processes involved with digestion and growth (relative consumption rate, assimilation efficiency, production efficiency, relative growth rate) and used a model to evaluate if and how component physiological responses to predation risk affected growth rates across temperatures. The physiological model determined relative growth rate as the difference between the rate of food assimilation and average daily metabolic rate (Ayres and Scriber 1994). Our focal species was the predaceous damselfly, *Enallagma vesperum* (Odonata: Coenagrionidae). Nymphs of this species display reduced growth rates in response to perceived predation risk from fish predators as well as visual contact with conspecifics (McPeck 1998, 2004).

Materials and methods

We conducted growth trials of *E. vesperum* nymphs in the presence or absence of a fish predator crossed with five temperature treatments during September 2012. These trials were conducted in environmental chambers (model 1-35 VL; Percival Scientific) set to 16, 18, 22, 26, and 30 °C with 13-h light:11-h dark (L:D) photoperiod. The experimental conditions matched the photoperiod regime and approximated temperatures in the ponds, but also included a higher temperature (30 °C) to try to capture the full range of the physiological response (Online Resource, Fig. 1). We used 16 °C as the lowest temperature based on constraints of the environmental chambers. We randomly reassigned temperatures to chambers every few days to avoid chamber effects and continuously monitored temperatures in each chamber using iButton temperature loggers (Maxim iButton model DS1921G). Each chamber contained predator and no-predator treatments and a preliminary experiment confirmed that results did not differ if the predator and no-predator treatments were in the same or different chambers.

Enallagma vesperum nymphs were collected from Stocker Pond (43°29'17.87"N, 72°06'36.13"W) in

Grantham, New Hampshire, USA between 23 August and 11 September 2012 and housed individually in 20-mL glass vials with pond water and a 2-mm wooden dowel for a perch. Each nymph was fed *Daphnia pulex* ad libitum every 2 days and maintained in an environmental chamber at 20 °C on a 13L:11D photoperiod until its first molt. After molting, individuals were moved to a new vial, randomly assigned to a temperature treatment, and held for 24 h without food at the assigned temperature to allow hardening of the exoskeleton, standardization of hunger levels, and adjustment to the new temperature. The following day, we measured fresh mass by blotting individuals dry on absorbent tissue and weighing them to the nearest 0.01 mg on a Mettler AT261 DeltaRange balance. Each nymph was then randomly assigned to either the predator or no-predator treatment within the temperature treatment. Vials with individuals from the no-predator treatment were placed in a tray containing cardboard dividers that visually isolated each nymph from the others. Vials with predator treatment individuals were floated in a 20-L aquarium containing one *Lepomis* sunfish (55–75 mm) by attaching a 45-mm-tall cylinder of 0.5-mm mesh to the opening of the vial with a small plastic cable tie and then attaching a small Styrofoam float to the mesh with a metal pin (see McPeck et al. 2001; McPeck 2004). This design allowed water to pass through the mesh and the nymphs had an unobstructed view of the fish predator and the other floating damselfly nymphs, providing both chemical and visual predator cues. Visual contact with conspecifics also elicits a mortality risk response (McPeck 1998). Each chamber had two 20-L aquariums with fish, and predator treatment individuals were frequently and haphazardly switched between the two to avoid a tank effect. Vials floating in tanks exchanged water with a larger pool versus vials housed in trays, but all vials were agitated during daily feeding and cleaning and thus differences in dissolved oxygen were unlikely. Furthermore, growth rates in previous experiments using the same design matched growth rates measured in the field in the presence or absence of a predator (McPeck 1998).

Once placed in respective treatments, experimental animals were fed *Daphnia* ad libitum daily for 4 days. We varied and recorded the number of *Daphnia* added (five to 35) based on how much each individual consumed in the previous 24 h and ensured that they were not food limited by giving each damselfly enough to recover at least two uneaten *Daphnia*. *Daphnia* were from a culture grown in three 1,000-L stock tanks placed outdoors. We size standardized the *Daphnia* by passing them sequentially through sieves and only using those retained between 0.71- and 1.00-mm sieve sizes to feed the damselflies. Each day we dried and weighed two samples of ten *Daphnia* to approximate the dry mass of *Daphnia* fed to the damselflies.

We collected fecal pellets and uneaten food and added new food to the vial every day of the trial. Twenty-four hours after the fourth day of feeding, we removed uneaten food and fecal pellets but kept the damselfly in the vial with no food for an additional 24 h to allow completion of digestive processes (Johnson et al. 1975). The following day we removed any last fecal pellets and measured final wet mass. Damselflies, their fecal pellets, and uneaten food were dried for at least 24 h at 60 °C and weighed to the nearest 0.001 mg on a Cahn C-35 microbalance. We successfully ran a total of 107 individuals, which yielded at least ten individuals per treatment. One individual in the 30 °C plus predator treatment died during the experiment. Mean (± 1 SE) temperatures were 16.0 (± 1.8), 18.1 (0.5), 22.1 (0.7), 25.8 (0.9), and 29.6 °C (1.1).

For each individual, we calculated relative growth rates as [(final dry mass) – (initial dry mass)]/[(4 days) \times (W_e^m)], where W_e is the exponential mean dry mass, which is the analog for average dry mass in systems with exponential growth (Gordon 1968; Ayres and Scriber 1994), and m is an allometric scaling factor that accounts for the effects of body size [$m = -0.33$ (Niven and Scharlemann 2005)]. Similarly, we calculated relative consumption rate as [(total dry mass of *Daphnia* given) – (total dry mass of all uneaten *Daphnia* material recovered)]/[(4 days) \times (W_e^m)]. Total dry mass (mg) of *Daphnia* given to each damselfly was calculated as the total number of *Daphnia* given over the 4-day period multiplied by the average dry mass of one *Daphnia*.

Assimilation efficiency, a unitless metric that describes the proportion of ingested food that is not lost as feces and thus available for cellular maintenance or growth, was calculated for each individual as [(total dry mass of *Daphnia* consumed) – (total dry mass of fecal pellets)]/(total dry mass of *Daphnia* consumed). Production efficiency, the ratio of biomass gain to assimilation was estimated as [(final dry mass) – (initial dry mass)]/[(total dry mass of *Daphnia* consumed) – (total dry mass of fecal pellets)]. We also estimated average daily metabolic rate for each individual with the assumption that this value represented the rate that assimilated food was expended for maintenance of cellular and metabolic processes (non-growth) (Ayres and Scriber 1994). Average daily metabolic rate was calculated as (relative assimilation rate) – (relative growth rate), where relative assimilation rate = (relative consumption rate \times assimilation efficiency).

We fit a set of models that described plausible responses of each of the five variables to changes in temperature. We did this separately for the no-predator and predator treatments to test if the form of the response differed due to predation risk. Candidate models included (1) an intercept-only model (i.e., no temperature effect), (2) a linear model, (3) an exponential model, and (4) a Gaussian model (PROC

NLIN, SAS version 9.4; Online Resource, Table 1). We compared these models with consideration of goodness of fit and corrected Akaike's information criterion (AICc) (Anderson 2008) and calculated the factor by which the rate changed over a given temperature range (Q_{10}), when appropriate.

For the damselflies without mortality risk, we used the model with the lowest AICc for relative consumption rate (RCR_T), assimilation efficiency (AE_T) and average daily metabolic rate ($ADMR_T$) as functions of temperature, T , to build a physiological model of relative growth rate (RGR_T) as a function of temperature, where,

$$RGR_T = [(RCR_T \times AE_T) - ADMR_T] \quad (1)$$

We then swapped in other plausible models for RCR_T , AE_T , and $ADMR_T$ to test their influence on RGR_T (e.g., a linear versus exponential model for RCR_T) and determined the final physiological model by calculating the sum of the squared differences between the model's predictions for relative growth rate for each temperature and the mean relative growth rate calculated from the actual data. Using the final physiological model, we analyzed how the measured physiological responses to predation risk influenced relative growth rate.

Results

In the absence of predation risk, damselfly relative growth rates exhibited a unimodal response to temperature (Fig. 1a). Relative growth rates increased with warming until reaching a maximum (± 1 SE) of 0.041 mg $mg^{0.33} day^{-1}$ (± 0.0053) at a temperature (± 1 SE) of 23.5 °C (± 0.98) and then began to decline. The Gaussian model was the only plausible model, based on AICc values, for this response (Fig. 1a; Table 1). Under predation risk, a linear model with a positive slope had the best fit given the data, but all four models were plausible (Fig. 1a; Table 1). Growth rates were generally lower under predation risk except at 30 °C (Fig. 1a) and the maximum relative growth rate (± 1 SE) estimated from the Gaussian model was 0.024 mg $mg^{0.33} day^{-1}$ (± 0.0047 ; Fig. 1a).

Relative consumption rates increased with increasing temperature in the no-predator and predator treatments (Fig. 1b). In the absence of fish, the best model given the data was the linear model, but the exponential model was also plausible (Table 1). When fish predators were present, the best and only plausible model given the data was the exponential model (Table 1). Relative consumption rates were similar in the two treatments but higher under predation risk at 30 °C (Fig. 1b). Q_{10} calculated from the exponential models were 1.7 and 2.5 for the no-predator and predator treatments, respectively.

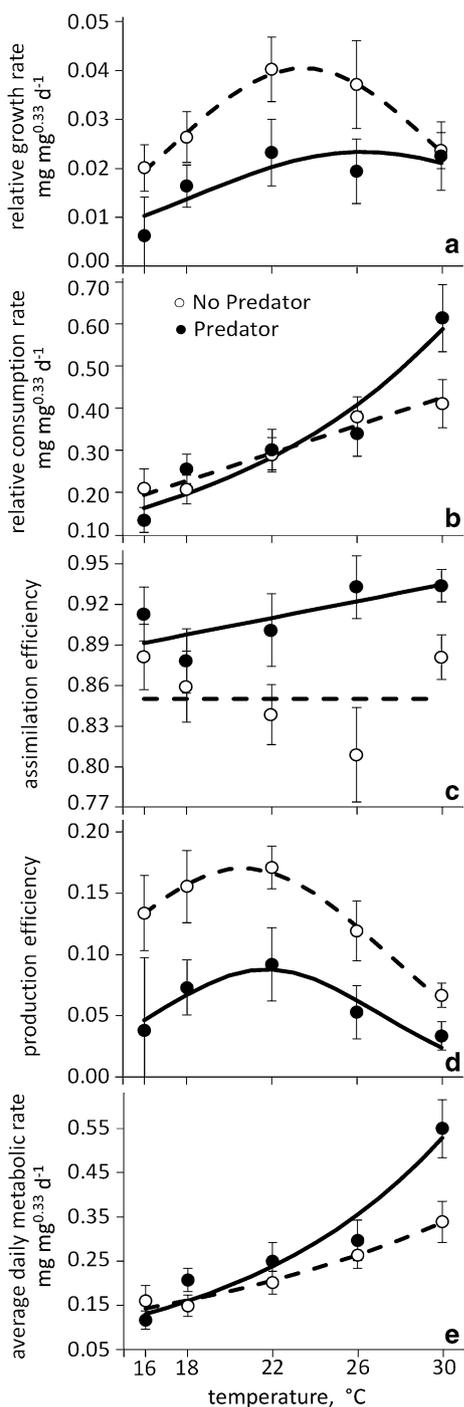


Fig. 1 Mean **a** relative growth rates, **b** relative consumption rates, **c** assimilation efficiencies, **d** production efficiencies, and **e** average daily metabolic rates of damselfly nymphs (*Enallagma vesperum*, Odonata: Coenagrionidae) at each temperature of each predator treatment (open no predator, filled predator). Bars indicate ± 1 SEM. Dashed lines (no predator) and solid lines (predator) are predictions from plausible models (Table 1) for **a** relative growth rates (Gaussian), **b** relative consumption rates (no predator, linear; predator, exponential), **c** assimilation efficiencies (no predator, intercept only; predator, linear), **d** production efficiencies (Gaussian), and **e** average daily metabolic rates (exponential)

Given the data for assimilation efficiency in the no-predator treatments, the best model was the intercept-only model with a mean assimilation efficiency (± 1 SE of temperature specific means) of 0.85 (± 0.03) across all temperatures, although the linear and exponential models were also plausible with the coefficients suggesting a decrease in assimilation efficiency with warming (Fig. 1c; Table 1). Under predation risk, damselfly assimilation efficiencies were generally higher compared to individuals in the no-predator treatments, and tended to increase with warming. The linear and exponential models were best, but the intercept-only model was also plausible (Fig. 1c; Table 1). The intercept-only model estimated a mean assimilation efficiency (± 1 SE of temperature specific means) of 0.91 (± 0.02) across all temperatures for individuals experiencing the threat of fish predation.

In the absence of mortality risk, the unimodal Gaussian model best described the thermal response of production efficiency, which increased to a maximum (± 1 SE) of 0.17 (± 0.020) at a temperature (± 1 SE) of 20.6 °C (± 1.05) and then began to decline (Fig. 1d). No other models were plausible (Table 1). Production efficiencies were lower under predation risk (maximum ± 1 SE estimated from Gaussian model, 0.089 ± 0.025) and showed a unimodal response as well (Fig. 1d), but all four models were plausible and the intercept-only model had the lowest AICc (Table 1).

In both treatments, average daily metabolic rates increased with warming and the best model given these data was the exponential model (Fig. 1e; Table 1). The linear model was also plausible for the no-predator treatment (Table 1). Q_{10} calculated from the exponential models were 1.8 and 2.7 for the no-predator and predator treatments, respectively. Individuals experiencing predation risk had a higher estimated average daily metabolic rate at the highest temperature (30 °C).

For damselflies not under threat of predation, the physiological model for RGR_T based on the models with the lowest AICc for relative consumption rates (linear), assimilation efficiency (intercept only), and average daily metabolic rate (exponential) resulted in a function for RGR_T that had the lowest sum of squared differences between predicted and measured growth rates (Fig. 2a: Online Resource, Table 2, Eq. 1). If individuals experiencing predation risk diverted more assimilated food into non-growth pathways but did not alter their relative consumption rate or assimilation efficiency, relative growth rates would have fallen to below 0 above 23 °C (Fig. 2b, dotted line). Relative consumption rate did increase faster with warming under predation risk and could have promoted positive relative growth rates until above 24 °C (Fig. 2b, long dashed line). Elevated assimilation efficiency under predation risk (0.91 versus 0.85) maintained positive relative

Table 1 Corrected Akaike's information criterion (AICc) values for each of the four candidate models (Online Resource, Table 1) fit to relative growth rate, relative consumption rate, assimilation efficiency, production efficiency, and average daily metabolic rate in the no-predator and predator treatments

Response	Model	AICc	
		No predator	Predator
Relative growth rate	Intercept only	-406.8	-405.6
	Linear	-405.4	-405.9 ^a
	Exponential	-405.2	-405.4
	Gaussian	-409.0 ^a	-404.3
Relative consumption rate	Intercept only	-192.0	-150.9
	Linear	-204.9 ^a	-176.1
	Exponential	-204.6	-178.3 ^a
	Gaussian	-202.9	n/a
Assimilation efficiency	Intercept only	-255.5 ^a	-279.6
	Linear	-253.8	-280.2
	Exponential	-253.9	-280.2 ^a
	Gaussian	n/a	n/a
Production efficiency	Intercept only	-264.7	-246.2 ^a
	Linear	-267.2	-244.3
	Exponential	-266.7	-244.3
	Gaussian	-269.7 ^a	-244.3
Average daily metabolic rate	Intercept only	-225.9	-165.4
	Linear	-242.7	-195.0
	Exponential	-243.5 ^a	-198.4 ^a
	Gaussian	n/a	n/a

n/a Model did not converge

^a Lowest AICc value for each of the five responses

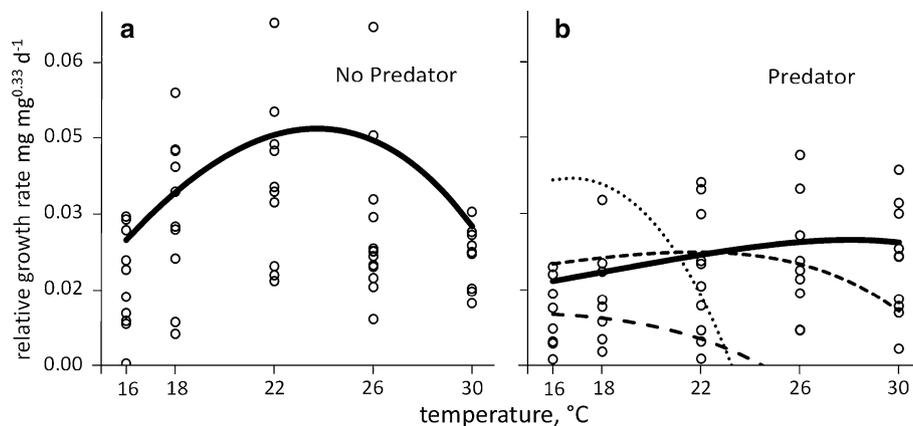


Fig. 2 Observed (*open circles*) and modeled (*solid lines*) relative growth rates across temperatures in the **a** no-predator and **b** predator treatments. **b** *Dotted line* represents the effects of elevated costs associated with mortality risk on relative growth rates without compensatory effects of altered consumption rates and assimilation efficiencies. Changes in consumption rates alone (*long dashed line*) did not dras-

growth rates across all temperatures (Fig. 2b, short dashed line), but the linear increase in relative growth rate with warming more closely matched the shape of the measured growth rate data (Fig. 2b, solid line). For damselflies experiencing predation threat, the physiological model for RGR_T based on the models with the lowest AICc for relative consumption rates (exponential), assimilation efficiency (linear/exponential), and average daily metabolic rate (exponential) also resulted in a function for RGR_T that had the lowest sum of squared differences between the predicted growth rates and actual growth rate data (Fig. 2b, solid line), with the linear model for assimilation efficiency having a slightly lower difference value (Online Resource, Table 2, Eq. 2).

Discussion

Damselfly growth rates were shaped by temperature and predation risk. When measured in the absence of mortality risk, damselfly growth rates had a unimodal response to increasing temperatures, a pattern that is typical across diverse ectothermic taxa (Kingsolver 2009). In the predator treatments, growth rates were generally lower and the typical peak shape of the thermal response was less apparent. All four models were plausible, including the intercept-only model that is indicative of no temperature effect. Thus, the response of growth rates to changes in temperature were less pronounced when a predator was present. Measuring and analyzing the component physiological processes

tically increase relative growth rates but elevated assimilation efficiency (constant at 0.91) increased growth rates to above zero across all temperatures (*short dashed line*). A linear increase in assimilation efficiency with warming significantly improved model fit to the data (*solid line*; Online Resource, Table 2)

involved with digestive physiology allowed us to disentangle some of the mechanisms driving these patterns.

In the absence of predation risk, the physiological model for damselflies that best fit the unimodal experimental data suggested consumption rates that increased linearly, assimilation efficiencies that were invariant, and metabolic rates that increased exponentially with warming. Increases in consumption rates with warming are quite general in insects (e.g., Thompson 1978; Kingsolver and Woods 1997; Kingsolver and Woods 1998) and other ectothermic taxa (see Englund et al. 2011; Lemoine and Burkepile 2012) and have been attributed to increasing demands for energy from increasing metabolic rates (Rall et al. 2010; Lemoine and Burkepile 2012). Temperature invariance of assimilation efficiency is attributed to warmer temperatures that cause an increase in gut enzyme activity that balances faster gut-passage time (Harwood 1979; Chen et al. 2003). Insensitivity of assimilation efficiency to temperature has been reported in other ectotherms (Ayres and Scriber 1994), but is not universal (see review in Lawton 1970). The initial increase in growth rates up until about 23.5 °C (± 0.98 °C) likely resulted from greater intakes of food and increasing proportions of that food going into biomass production (production efficiency). Above 23.5 °C, growth rates began to decrease as metabolic demands began to outpace consumption rates (higher Q_{10}) and less of the assimilated food was put into biomass. Although we did not directly measure metabolic rate, other studies have demonstrated that mismatches in the thermal sensitivity of metabolic versus consumption rates cause declines in growth rates at high temperatures (Lemoine and Burkepile 2012).

Lower growth rates under predation risk were not explained by a reduction in food intake rates (McPeck 2004) even though that is a commonly observed response to predation risk (Lima and Dill 1990). Consumption rates were generally similar in the predator and no-predator treatments but the rate of change in consumption with increasing temperature was higher under predation risk (Fig. 1b). The highest consumption rates were measured at 30 °C when a fish predator was present, possibly due to additive or synergistic effects of predators and temperature on their demand for energy. These elevated consumption rates may explain why the growth rates of individuals experiencing predation risk at 30 °C were similar to the growth rates measured in the no-predator treatment at that temperature.

The lower growth rates in the predator treatments were also not explained by assimilation efficiency. In the no-predator treatments, assimilation efficiency was 0.85 across temperatures, a value commonly reported for carnivorous insects (Lawton 1970; Rall et al. 2010), but it was higher when a predator was present [mean = 0.91 (McPeck 2004)] and actually increased with warming. In previous studies,

damselflies experiencing predation risk consumed similar amounts of food over a 4-day period as individuals feeding in the absence of predator cues (McPeck 2004), but in the absence of mortality risk, damselflies tended to eat larger amounts at once versus slowly eating for the duration of the trial. Slower eating may lead to a less full gut and thus greater extraction of nutrients and higher assimilation efficiency. Damselflies under predation risk were eating about the same or more food as individuals without mortality risk and had higher and increasing assimilation efficiencies, but still gained less mass over the 4-day period (Figs. 1a, 2).

Production efficiencies were lower under predation risk indicating that a smaller proportion of the assimilated food was being put into biomass production. Our model rested on the assumption that food that did not go into biomass production went into non-growth pathways such as cellular maintenance and metabolic costs (average daily metabolic rate). Average daily metabolic rate changed more rapidly with warming under predation risk with the highest rates estimated at 30 °C, but differences between the predator and no-predator treatments were less apparent at the lower temperatures. Some studies have directly measured increases in metabolic rates under predation risk (Woodley 2003; Sunardi and Manatunge 2007; Beckerman et al. 2007; Hawlena and Schmitz 2010b) that possibly support functions that increase survivorship (Wingfield et al. 1998; Hawlena and Schmitz 2010b; Thaler et al. 2014). For example, Slos et al. (2009) found evidence that threatened damselflies produce stress proteins that may correlate with anti-predator behavioral traits. Direct measurements of metabolic rates and the biochemical and hormonal changes induced by mortality threat would help disentangle the underlying mechanisms that drive behavioral and physiological responses to stress in invertebrates (Slos and Stoks 2008; Slos et al. 2009).

Our results were consistent with previous studies of damselflies (McPeck 1998; Stoks and McPeck 2003; McPeck 2004) and other prey species (e.g., Benard 2004; Johansson and Andersson 2009; Higginson and Ruxton 2010) that showed a reduction in prey growth rate under predation risk, but in this study we also showed that the magnitude of these non-consumptive effects varied as a function of temperature and in the opposite direction of our predictions. Maintenance and survival costs associated with mortality risk were partially offset by changes in consumption rates and higher assimilation efficiencies (Fig. 2b). At the lowest temperature in our study (16 °C), growth rates were reduced by 70 % when a fish predator was present (calculated as the percent change in the mean experimental values; Fig. 1a). At the middle temperature (22 °C), growth rates were reduced by 42 %. At 30 °C, the reduction in growth rates under predation risk was only 5 %, likely because of the high consumption rates and high assimilation efficiencies measured in damselflies experiencing

predation risk at this temperature. Environmental temperature may control the magnitude of non-consumptive effects (Barton 2009; Barton et al. 2010) but not necessarily in predictable ways.

Predation risk, a known driver of organismal physiology, ultimately constrained the response of growth rate to changes in environmental temperature. Most studies measure the effects of temperature on growth rate and other physiological processes in a laboratory setting where all other factors are held constant, although interactions between temperature and food quality have been documented (e.g., Ayres and Scriber 1994; Kollberg et al. 2013). Measured temperature effects are projected onto natural populations to reach conclusions about changes in species distributions and abundances (e.g., Deutsch et al. 2008), even as mediated through species interactions (Vasseur and McCann 2005; O’Conner et al. 2011), but the growth rates we measured in the lab have never been measured in nature because individuals of this species never occur in habitats without predators (McPeck 1998; McPeck, personal observation). Given the general global increases in temperature and consequent changes in biological communities, we propose that a general understanding of climatic impacts on ectothermic populations requires consideration of the community context of thermal physiology, including non-consumptive effects of predators.

Author contribution LEC conceived the idea. LEC, MAM, and MPA generated hypotheses and designed experiments. LEC performed the experiments, analyzed the data, and wrote the manuscript. MAM and MPA provided input on modeling and multiple versions of the manuscript.

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