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Elevated temperatures alter competitive outcomes and body condition in southern Appalachian salamanders

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Abstract

Temperature elevation due to climate change is directly altering organismal performance and distributions, but the mechanisms behind these shifts require additional attention. Because small aquatic ectotherms are proposed to perform better at future climates, it is possible that competitive interactions in size-structured communities may also shift. To study the interactive effects of climate and competition on species performance, we evaluated body condition of small and large desmognathan salamanders at current and elevated temperatures in stream mesocosms, and characterized habitat use. *In situ* evaluation of capture locations demonstrated that the widespread and larger species, *Desmognathus conanti,* competitively excludes the smaller more narrowly distributed, *D. abditus,* from stream centers and cooler temperatures, but *ex situ* mesocosm experiments indicated an interaction between temperature and intra- versus inter-specific competition on *D. abditus* body condition. At current temperatures, *D. abditus* body condition increased in the presence of the larger *D. conanti,* but at elevated temperatures, *D. abditus* body condition tended to decline in the presence of the larger species relative to intraspecific competitors. We also noted that individuals at future temperatures prioritized growth differently than individuals at current temperatures by shifting allocations away from growth in length to growth in mass consistent with responses of other organisms to stressful conditions that could result in declining reproductive rates. This study demonstrates that processes in size-structured communities may interact with temperature to affect species' future success.

Introduction

Climate change can alter species performance, phenology and distributions (Walter *et al.*, 2002; Parmesan, 2006). Studies also suggest that ecological or phenological changes of organisms may shift interactions (e.g. mutualistic, predatory or competitive) among species (Araújo & Luoto, 2007; Van der Putten, Macel & Visser, 2010; Yang & Rudolf, 2010; Gibert & DeLong, 2014). Notably, predictions suggest that shifting climates may enhance performance of smaller, ectothermic organisms (Daufresne, Lengfellner & Sommer, 2009; Ohlberger, 2013). For example, if warm temperatures restrict species abilities to forage and elevates metabolic rates in ectotherms, then the energy balance of feeding and metabolic demands results in less energy to devote toward growth (Sinervo *et al.*, 2010). Multiple studies suggest and document a trend toward smaller body sizes in warmer climates (Sheridan & Bickford, 2011; Gardner *et al.*, 2011; Cheung *et al.*, 2013; Caruso *et al.*, 2014; Peterman, Crawford & Hocking, 2016; but see Grant, 2014) and another documents reduced diversity of size-structured food webs at elevated temperatures (Binzer *et al.*, 2016). Therefore, size-structured animal communities may organize and be regulated differently if smaller species begin to perform better than larger species (Werner & Gilliam, 1984; Polis, Meyers & Holt, 1989; Jonsson, 2014). Collectively, these studies indicate that climate warming interacts with processes governing community composition and may amplify or stabilize animal responses to climate change (Daufresne *et al.*, 2009; Sinervo *et al.*, 2010; Binzer *et al.*, 2016), but these responses vary with body size in inconstant ways necessitating more research to understand underlying mechanisms behind body-size shifts and population stability (Grant, 2014; Gibert & DeLong, 2014; Vasseur *et al.* 2014; Gibert *et al.*, 2016).

Outcomes of species interactions within a community may be altered due to species-specific responses to climate warming. Small ectotherms have physiological processes that are controlled by external environmental conditions that may make them susceptible to shifting thermal regimes (Spotila, 1972; Feder, 1983; Bernardo & Spotila, 2006).

In the southern highlands of the United States, salamanders in the family Plethodontidae have diversified to inhabit specific environmental gradients (Kozak & Wiens, 2010). Plethodontid species prefer microhabitats with high moisture content (e.g. streams, ravines, coves) because of their unique lungless anatomy and exclusive reliance on cutaneous respiration (Spotila, 1972; Feder, 1983). The high permeability of their skin also increases the susceptibility to desiccation at warm temperatures and/or low humidities (Spotila, 1972; Feder, 1983). Therefore, elevated temperatures may reduce above-ground activities of Plethodontids that limits foraging opportunities (Feder & Londos, 1984). Reduced foraging opportunities combined with higher metabolisms at warmer temperatures may suggest a mechanism behind trends in smaller body sizes (Feder & Londos, 1984; Caruso *et al.*, 2014; but see Connette, Crawford & Peterman, 2015). Ultimately, declining body sizes may alter the success of species interactions in size-structured communities if species respond differentially to warming climates (Walls, 2009; Caruso *et al.*, 2014). These changes in species interactions may intensify climate induced risk of endangerment (Urban, Tewksbury & Sheldon, 2012).

In headwater streams, *Desmognathus* species often represent the numerically dominant vertebrate taxon and as many as seven congeners can occupy the same region though competition and variable abiotic tolerances lead to spatial niche partitioning within stream reaches and surrounding terrestrial areas (Hairston, 1987; Peterman, Crawford & Semlitsch, 2008). The smallest species are more terrestrial and exhibit higher resistance to desiccation relative to the largest species that are highly aquatic (Littleford, Keller & Phillips, 1947; Ray, 1958; Houck & Bellis, 1972; Camp *et al.*, 2013; but see Luhring & Holdo, 2015); though recent work suggests high within species variation in desiccation rates (Riddell & Sears, 2015). Larger *Desmognathus* species tend to exclude smaller species to less aquatic and more terrestrial habitat zones (Hairston, 1987; Rissler, Wilbur & Taylor, 2004; Crawford & Semlitsch, 2007). In the absence of larger congeners, smaller species expand their niche space (i.e. competitive release) to occupy the areas toward the center of the stream (Hairston, 1987; Rissler *et al.*, 2004).

Amphibians represent the most threatened vertebrate taxon globally (Stuart *et al.*, 2004), and the southern highlands of the United States are an internationally recognized region of amphibian biodiversity (Stein, Kutner & Adams, 2000). Other studies reveal significant declines in Appalachian salamander abundance and project that climatically suitable habitat is quickly disappearing in the Southern Appalachian region (Walls, 2009; Milanovich *et al.*, 2010; Caruso & Lips, 2013; Currinder *et al.*, 2014). However, these studies overlook how climate change, and in particular warming, could affect species interactions and may mechanistically alter how communities are structured. Using the desmognathan community, we sought to evaluate how size-structured interactions may change with elevated temperatures. Specifically, we hypothesized that: (1) the larger species would depress growth rates of the smaller species consistent with competitive interactions and (2) future temperatures will minimize the effects of the larger species on growth by the smaller species. To address these hypotheses, we used stream mesocosms to evaluate competition between the smaller Cumberland Dusky Salamander *Desmognathus abditus* and the larger Spotted Dusky Salamander *Desmognathus conanti* that co-occur on the Cumberland Plateau at current temperatures and those elevated by 2°C to match predictions for 2100 (Isaak & Rieman, 2013; Van Vliet *et al.*, 2013). We supplemented our mesocosm experiment with field observations of stream habitat use by *D. abditus* and *D. conanti.* We predicted that *D. conanti* would exclude *D. abditus* to warmer, drier habitat further from the center of the stream.

Materials and methods

Study system

The *Desmognathus* genus contains species that exploit similar habitat but are able to coexist (Hairston, 1987). *Desmognathus conanti* is an abundant species across the southeastern United States and is found throughout elevational and latitudinal gradients, suggesting that it is a highly adaptable species at low risk of extinction due to climate change (Bernardo *et al.*, 2007). In contrast, *Desmognathus abditus* is a recently described species with a distribution limited to high elevations on the southern Cumberland Plateau of Tennessee (Anderson & Tilley, 2003). This distribution could be detrimental because *D. abditus* share these streams with other larger, more abundant species, such as *D. conanti*, that are predicted to respond less to climate change (Bernardo *et al.*, 2007)**.** Size-structured interactions observed between *D. conanti* and *D. ocoee,* a close relative to *D. abditus,* suggest that *D. conanti* could outcompete *D. abditus* (Organ, 1961; Folkerts, 1968). Because *D. abditus* already occurs in small, isolated populations, more studies are needed to establish how *D. abditus* will respond to higher temperature coupled with a competitive congener.

Competition experiment

We used a full factorial experimental design of intra- and inter-specific competition at current and elevated temperatures with four replicates per treatment. Animals were assigned to mesocosms to maintain a density of four individuals per mesocosm. Densities estimated for *D. conanti* on the Cumberland Plateau are lower than found elsewhere and range from 2 to 3 individuals per m^2 (Kirchberg *et al.*, 2016). Density estimates are unavailable for *D. abditus,* but field observations suggest that this is a reasonable assumption of density. Therefore, intraspecific treatments had four *D. abditus* individuals and interspecific treatments had two *D. abditus* and two *D. conanti.* We added 10 crickets (average length 6.4 mm) to each mesocosm weekly for the length of the experiment that lasted 6 weeks (42 days). Previous work suggested this length of time was sufficient to evaluate treatment effects within the mesocosms (Ennen, Davenport & Alford, 2016). At the end of the experiment, all individuals were removed from the mesocosms, identified, measured and weighed to assess outcomes of competition.

Desmognathus abditus ($N = 48$) and *D. conanti* ($N = 16$) were collected from a headwater stream in Laynes Cove, Tennessee where the species coexist. Salamanders were collected within 1 week. We turned cover objects and searched leaf litter along 200 m of the stream. We collected all *D. abditus* and *D. conanti* without obvious tail loss or regeneration to minimize confounding changes in growth associated with tail regeneration. Animals were housed individually in native stream water with a paper towel cover object for less than 1 week at the University of the South in a dark, 12°C environment prior to introduction to the stream mesocosms. We measured snout-vent length (SVL), total length (TL) and mass of each individual before using a stratified random approach to assign individuals to treatments. Because this guild is known for intraguild predation (Hairston, 1987), we only housed individuals together that were similarly sized to prevent stress associated with predation attempts. Salamanders were grouped by SVL to ensure that individuals were not housed in groups with substantial size differences (>5 mm SVL). Any *D. conanti* larger than 50 mm were released because they exceeded this size difference. Though *D. abditus* may be exposed to larger *D. conanti in situ,* this approach to housing ensured that we were evaluating changes due to competition rather than predation. After grouping, they were randomly assigned to a treatment (inter- or intra-specific competition and current or elevated temperature). Once groups of individuals were determined for each treatment, we individually marked all salamanders with visible implant elastomer (Northwest Marine Technology, Shaw Island, WA, USA) to monitor changes in morphological measurements and assess the outcome of competition. Groups were randomly assigned to mesocosms.

We conducted our experiment in 16 independent stream mesocosms at the Tennessee Aquarium Animal Care Facility (Ennen *et al.*, 2016). Each stream mesocosm was a recirculating system that consisted of a trial tank ($1.20 \times 0.60 \times 0.53$ m) that drained into a plastic sump with a pump that returned water to the trial tank. Water circulated at a rate of 0.6 L s^{-1} common to native streams and used in other mesocosm experiments (Resetarits, 1991; Lowe, Likens & Cosentino, 2006; Ennen *et al.*, 2016). Water depth was maintained using a standpipe set to 10 cm. Salamander escape was prevented by using a PVC cap with drilled holes (<1 mm^2) to cover the standpipe and window screen (1.44×1.58 mm) tightly secured to the mesocosm with binder clips. We randomly assigned a coarse mix of sand and gravel to form substrate and a narrow portion of land (<5 cm wide) within each stream mesocosm. Two cover objects of *c.* 0.09 m^2 were randomly assigned to each mesocosm with one placed fully in the water and the other on the land. Streams were filled with 176 L of dechlorinated water with additional water added throughout the experiment to counterbalance evaporative losses. Mesocosms were located in a greenhouse that maintained current temperatures close to those at the collection site (see Results). Mesocosms assigned to elevated temperature regimes had aquarium heaters (Aqueon 175 L aquarium heater; Aqueon, Franklin, WI) added to the sump to warm the water *c.* 2°C above current water temperature predicted by 2100 (Isaak & Rieman, 2013; Van Vliet *et al.*, 2013). Heaters were on a diel cycle so that they were on during the day and off for 9 h at night to mimic natural fluctuations in temperature. HOBO (Onset, Contoocook, NH) dataloggers were placed into each of the sumps to monitor water temperature at 15 min intervals.

In situ habitat characterization

To assess differences in habitat partitioning under current climate conditions between *D. abditus* and *D. conanti,* we surveyed two headwater streams in Laynes Cove, TN. We surveyed each stream twice before removing individuals from one of the streams for our mesocosm experiment in September 2016. Though we did not mark individuals to prevent resurveying them, stream amphibians have high temporary emigration rates suggesting that individuals come to the surface and are available for capture for very short periods of time (Cecala, Price & Dorcas, 2013). Both streams are steep with bedrock substrate and northern aspects. We surveyed 200 m reaches in each stream. We performed active surveys with 3–4 people and turned all rocks, logs, leaf litter and visually inspected crevices. When an individual was detected, they were captured for identification and quantification of SVL, TL and mass. At each capture location, we replaced any cover object and measured temperature using an infrared thermometer and relative humidity using a hygrometer. If individuals were found in water, we recorded 100% humidity. We also measured the distance of the capture location to the thalweg.

Data analysis

To evaluate performance of individuals among mesocosm treatments, we used differences in the scaled mass index pre- and post-experiment referred to as body condition (Peig & Green, 2009; Davenport & Lowe, 2016). We assessed the significance of our treatments using a linear mixed model implemented in R using the lme4 package with our random effect being an individual's mesocosm number (R Core Team 2013; Bates *et al.*, 2015). After review of the data, we performed *post hoc* analyses to determine the effect of temperature and competition on growth in SVL (referred to as length henceforth) and mass to evaluate whether changes in length or mass was driving the changes in body condition using a linear mixed model incorporating mesocosm number as a random effect. *Post hoc* Tukey honestly significant difference tests were used to evaluate statistical significance among treatments. *Post hoc* assessment of the normality of model residuals and the power of our non-significant analyses were performed for all linear mixed models. Significance was assessed at $\alpha = 0.05$.

To evaluate *in situ* habitat at current climate conditions, we used a MANOVA to evaluate if species identity altered capture location temperature, humidity and distance from thalweg. We standardized temperature and humidity by calculating z-score values for each variable and tested for normality (Shapiro Wilk's test) and equality of variances (Bartlett's test) before performing the MANOVA. The MANOVA was followed by *post hoc* one-way ANOVAs for each variable.

Results

Competition experiment

Mean water temperatures within our two *in situ* streams during this study period were 19.12 ± 0.04°C. Mean current mesocosm temperatures were 19.15 ± 1.43°C, while mean elevated mesocosm temperatures were 22.71 ± 2.29°C. Mean differences in water temperatures between current and elevated treatments were 2.56 ± 0.79°C. Although our current temperature treatment (*ex situ*) experienced greater water temperature variation (i.e. standard deviation) in than the two *in situ* streams, this *ex situ* treatment had a mean water temperature (19.15°C) that matched *in situ* mean water temperatures (19.12°C). Nearly all salamanders grew in length (SVL) and mass (Table 1), and we observed 95.8% survival. We found the carcasses of the two *D. abditus* individuals from two different mesocosms (one current and one elevated) that perished, and these individuals were excluded from our analyses. Data did not depart from normality (body condition: $w = 0.96$, $P = 0.17$; SVL: $w = 0.97$, $P = 0.26$; mass: $w = 0.95$, $P = 0.13$; random effects: $w = 0.94$, $P = 0.40$).

Table 1 Total change in body condition (scaled mass index), snout-vent length (SVL) and mass after 42 days at current and future temperature regimes for *Desmognathus abditus* and *Desmognathus conanti* and competitive treatment for *D. abditus*

	Competition	
Temperature	Intraspecific	Interspecific
D. abditus		
Body condition		
Current	−0.07 ± 0.05	0.03 ± 0.11
Elevated	0.19 ± 0.08	0.11 ± 0.10
SVL (mm)		
Current	5.0 ± 0.4	2.8 ± 0.9
Elevated	1.5 ± 0.5	2.9 ± 0.8
Mass (g)		
Current	0.26 ± 0.03	0.22 ± 0.05
Elevated	0.38 ± 0.05	0.35 ± 0.12
D. conanti		
Body condition		
Current	–	−0.01 ± 0.12
Elevated	–	0.16 ± 0.09
SVL (mm)		
Current	–	5.9 ± 1.0
Elevated	–	5.1 ± 1.2
Mass (g)		
Current	–	0.51 ± 0.05
Elevated	–	0.51 ± 0.07

All values represent means ±1 standard error.

We observed that the effects of competition on body condition of *D. abditus* were dependent on water temperature (Table 1; Fig. 1a). *Desmognathus abditus* increased in body condition for all treatments except intraspecific treatments at current temperatures where they declined. The effect of temperature on body condition was significantly different in intraspecific treatments but not interspecific treatments. Though not statistically significant in *post hoc* tests, *D. abditus* body condition tended to improve when competing with *D. conanti* at current temperatures. However, body condition increased less when competing with *D. conanti* at elevated temperatures. The random effect of mesocosm was 0.014 ± 0.120 (standard deviation [SD]), and the residuals were normally distributed ($w = 0.98$, $P = 0.46$). We note that a *post hoc* power analyses suggest that the test of the effect of competition may have been underpowered ($\beta = 0.47$).

Growth in length was significantly affected by temperature, but the effects of temperature were dependent on the competitive treatment (Table 2). Specifically, at current temperatures, *D. abditus* grew more in length at current temperatures in intraspecific treatments but not in interspecific treatments (Fig. 1b). Residuals of the linear mixed model for length were normal ($w = 0.964$, $P = 0.15$) with a well-powered analysis ($\beta < 0.01$) but positive random effects of mesocosm (0.43 ± 0.21 [SD]). Contrary to growth in length, *D. abditus* gained less mass at current temperatures than at elevated temperatures regardless of competitive treatment (Fig. 1c; Table 2). The random effect of mesocosm was 0.04 ± 0.19 (SD) for mass, and residuals of the linear mixed model for mass were normal ($w = 0.96$, $P = 0.10$). A *post hoc* power analysis indicated sufficient power to assess the interaction of competition and temperature ($\beta < 0.18$) but limited power to assess the effect of competition ($\beta = 0.39$).

In situ habitat characterization

We observed 46 individuals from both surveyed streams, including 28 *D. abditus* and 18 *D. conanti*. Species identity affected characteristics of their capture location ($\text{Pillai}_{\text{d.f.} = 3,41} = 0.177$, $P = 0.044$). *Desmognathus abditus* was found at higher temperatures (2.9 ± 0.21°C) than *D. conanti* (Fig. 1; $F_{\text{d.f.} = 1,43} = 7.20$, $P = 0.011$) though they did not differ in the humidity of their capture locations ($F_{\text{d.f.} = 1,43} = 0.001$, $P = 0.99$). On average, *D. abditus* was found 1.57 times further from the stream thalweg than *D. contanti* ($F_{\text{d.f.} = 1,43} = 4.438$, $P = 0.041$).

Discussion

Research suggests that plethodontid salamanders may respond negatively to warming temperatures (Walls, 2009; Milanovich *et al.*, 2010; Caruso *et al.*, 2014). We present two potential mechanisms (i.e. thermal stress and behavioral plasticity) to explain these changes. Although controversy exists about whether plethodontid body size is declining (Caruso *et al.*, 2014; Grant, 2014; Connette *et al.*, 2015), our results suggest that thermal stress may result in smaller body lengths consistent with results observed by Caruso

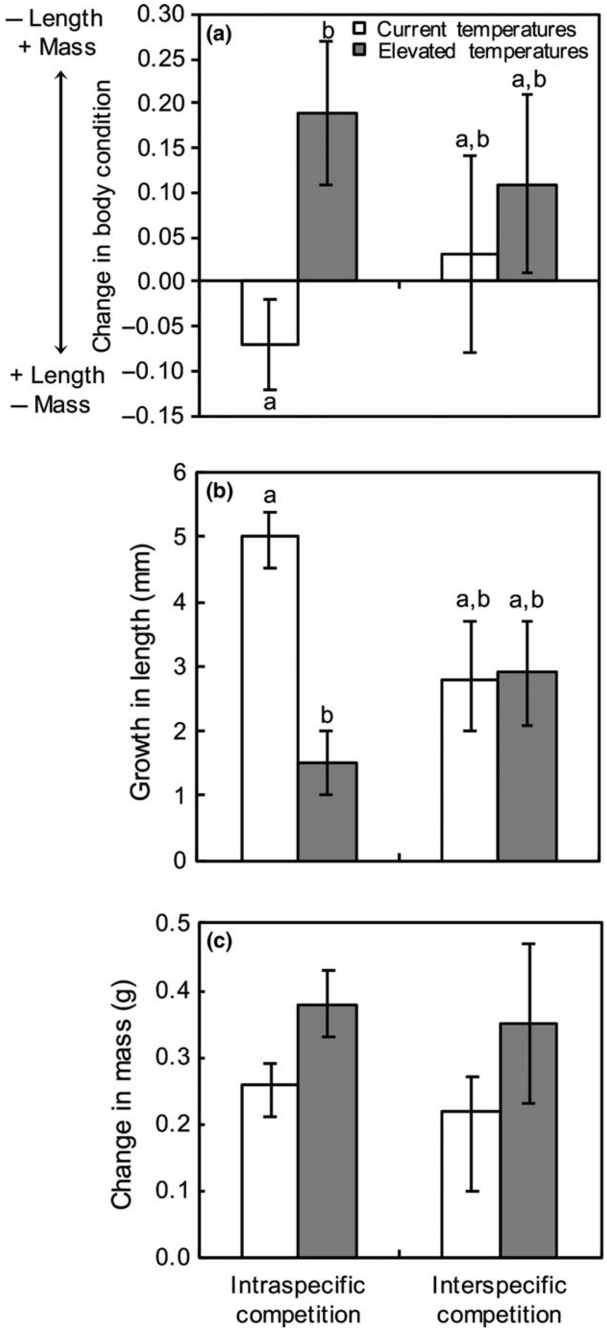

Figure 1 Mean change in body condition (a), snout-vent length (SVL; b) and mass (c) of *Desmognathus abditus* in response to temperature and competition treatments. Body condition is calculated using the scaled mass index. Displayed error bars represent ±1 standard error. Letters indicate significantly different results from a Tukey *post hoc* analysis. Though *D. abditus* added more mass at elevated temperatures (Table 1), Tukey *post hoc* analyses indicated that groups were not statistically different from one another.

Table 2 Statistical results of the mesocosm experiment evaluating the effects of competition and temperature treatments on *Desmognathus abditus* using linear mixed models to evaluate change in body condition, length (SVL) and mass

	d.f.	*t*	*P*
Body condition			
Competition	1	−1.42	0.165
Temperature	1	0.05	0.960
Interaction	1	2.09	0.044
Residuals	26		
Snout-vent length			
Competition	1	0.38	0.538
Temperature	1	13.34	<0.001
Interaction	1	7.96	0.004
Residuals	26		
Mass			
Competition	1	0.64	0.425
Temperature	1	4.68	0.030
Interaction	1	0.11	0.740
Residuals	26		

et al. (2014). However, we caution that our study occurred over short-time scales that may be offset *in situ* by behavioral plasticity. For example, salamanders in our stream mesocosms had no refuge from warm water temperatures. *In situ*, stream amphibians may be able to move into underground refugia and alter seasonal movement patterns unaccounted for in this study (Bailey, Simons & Pollock, 2004; Cecala *et al.*, 2013). Likewise, most amphibians alter activity patterns to avoid warm and dry temporal periods or spatial regions (Bailey *et al.*, 2004; Price, Browne & Dorcas, 2012). We recommend field surveys to determine if behaviors shift as predicted or if growth rates are related to thermal regimes *in situ* over longer time scales. Furthermore, rapid growth of salamanders in our mesocosms suggests that food availability may be higher than *in situ* limiting conclusions about the effects of competition on outcomes of *D. abditus.* We also observed an unexpected positive effect of our random effect, mesocosm, on snout-vent length. Two potential explanations exist for this pattern – variable growth potential of salamander groups and position of the mesocosms. It is unlikely that mesocosm position resulted in a positive relationship because mesocosms were numbered in a circle with the highest numbered mesocosm located adjacent to the lowest, but our data suggest a slight negative trend with larger numbered mesocosms housing individuals of smaller lengths. Smaller individuals may have had higher growth potential relative to larger individuals (Bruce, 2010).

Future temperatures are likely to have strong effects on the ecology and physiology of ectotherms (Hillman *et al.*, 2008; Sinervo *et al.*, 2010). By evaluating components of the composite body condition measurement, we observed that individuals changed energy allocations to growth that reflected different patterns. Higher metabolisms at higher temperatures predict that ectotherms should add less mass at elevated temperatures provided similar food resources (Hillman *et al.*, 2008; Sinervo *et al.*, 2010), yet we observed that they added the most mass at elevated temperatures. At high temperatures, plethodontid salamanders shift activity patterns to avoid surface activity where feeding occurs concurrently reducing foraging activity and therefore the potential to compensate for higher metabolic rates (Feder & Londos, 1984; Bailey *et al.*, 2004; Price *et al.*, 2012). The shift in growth allocation is consistent with high physiological stress. Prior studies on a sister species at its southern range limit described metabolic depression at temperatures only slightly higher than current environmental conditions (Bernardo & Spotila, 2006). At high stress levels, circulating cortisol levels increase and can inhibit reproduction when organisms tend to prioritize growth in somatic versus gonadal tissue (Chadwick, Nislow & McCormick, 2015). For amphibians and fish, length strongly predicts follicle number in females though the relationship may vary within and among species (Tilley, 1968; Bernardo, 1994). Although higher survival associated with greater mass and body condition may facilitate persistence (Roff, 1983), lower reproductive potential may decrease population growth rates under future climate conditions (e.g. Pankhurst & Van der Kraak, 1997). Alternatively, increase in mass may be reflective of high terrestrial prey availability in the mesocosms. We are unaware of any diet studies on *D. abditus* but studies of *D. conanti* suggest that they consume a mix of aquatic and terrestrial prey (Sites, 1978). Therefore, providing only high-quality terrestrial prey may have resulted in surplus energy storage (Álvarez & Nicieza, 2002). Overall, these data support conclusions that size and growth are plastic and conditional on local climates (Connette *et al.*, 2015; Peterman *et al.*, 2016).

At current temperatures, we expected to observe that the larger desmognathan salamanders would outcompete smaller species (Organ, 1961; Folkerts, 1968; Hairston, 1987). Our field results support these conclusions that similar species exhibit habitat partitioning due to competitive exclusion by the larger stream salamander species. *Desmognathus abditus* was found further from the stream center in areas of warmer temperatures, but humidity did not differ. At warmer temperatures, ectothermic animals will have higher metabolic rates that will require more resources to maintain healthy body condition (Dillon, Wang & Huey, 2010), and warmer temperatures suggest that water loss rates could be higher for *D. abditus,* possibly reducing their foraging time (Feder & Londos, 1984). Warmer environmental conditions may be offset for *D. abditus* because they may have higher resistance to desiccation (Houck & Bellis, 1972). Although water loss rates have not been assessed for *D. abditus,* its sister species, with similar ecological traits, *D. ochrophaeus*, has higher resistance to desiccation than more aquatic species (Houck & Bellis, 1972). *Desmognathus abditus* may have performed better when completing with *D. conanti* at current temperatures because of habitat partitioning observed *in situ,* but more research to describe habitat selection in mesocosms versus natal streams is necessary to address this hypothesis. Regardless, *in situ* measurements confirmed our predictions that competition with *D. conanti* currently excludes *D. abditus* from lower temperatures found closer to the stream center.

Competitor identity mediated the effect of temperature on *D. abditus* performance. As predicted for smaller ectotherms (Daufresne *et al.*, 2009; Ohlberger, 2013), *D. abditus* increased body condition more at elevated temperatures than current temperatures in intraspecific treatments though we caution that this conclusion depends on whether researchers compare body condition (present study), length or mass. Furthermore, limited power of analyses evaluating the effect of competitive interactions on body condition and mass suggest that larger sample sizes are needed to further evaluate the effect of competitor identity on *D. abditus* performance. However, the effects of temperature in interspecific treatments were minimized. At current temperatures, *D. abditus* body condition increased in interspecific treatments, whereas it declined at elevated temperatures supporting our predictions that the effect of *D. conanti* on *D. abditus* would decrease at warmer temperatures. We acknowledge that we do not have the habitat use data from our mesocosm study to evaluate whether *D. conanti* drove increased terrestrial movement of *D. abditus* nor did we isolate the intraspecific competition between *D. abditus* individuals in the interspecific treatments and recommend this for future studies. Shifts in competitive outcomes observed in this study may have resulted from a few potential mechanisms. Interspecific treatments also housed two *D. abditus* in addition to two *D. conanti,* which may result in more similar responses to temperature between intra- and inter-specific treatments because of the intraspecific interactions in both treatments. Secondly, despite limited sample sizes at current and future temperatures, *D. conanti* grew similarly if not better at elevated temperatures suggesting that their interaction strength on *D. abditus* was likely to remain similar regardless of temperature. *Desmognathus conanti* also has a large geographical and altitudinal range that implies that they may be more tolerant of warmer temperatures (Bernardo *et al.*, 2007; Strickland *et al.*, 2016). Similarly for terrestrial salamanders, a recent field study found that distributions and genetic contributions of a lower elevation species are expanding, while the distribution of the previously competitively superior high elevation species is contracting (Walls, 2009; but see Connette *et al.*, 2015). Collectively, these data suggest that small sizes combined with broad temperature tolerances will predict competitively superior species under new climate regimes.

In response to climate change, populations can adapt, move, or collapse (Sinervo *et al.*, 2010). Identifying the mechanism(s) responsible for determining which of these three responses occur within populations will allow for greater understanding of climate change's future impacts on biodiversity. In our study, we provide support for a mechanism related to thermal stress that causes short-term responses that minimize growth rates in body length of salamanders. Our findings are significant because current understanding of amphibian responses to climate change usually emphasizes desiccation and not temperature alone. Besides climate change, our results may predict salamander responses to physical and anthropogenic effects (e.g. elevation, forest removal, impervious surfaces; Sih, 2013; Peterman *et al.*, 2016) that create higher water temperatures in headwater streams. For example forest conversion to impervious surface increases local temperatures, and small-sized salamanders have been observed following riparian removal and urbanization of watersheds (Murphy *et al.*, 2016). Although the consequences of shifts in growth on salamander reproduction are currently undetermined, our results support the conclusion that any anthropogenic effects that induce a rapid increase in water temperature has the potential to alter competitive outcomes within aquatic ectothermic communities and affect long-term population dynamics through declines in reproductive rates (Urban *et al.*, 2012). As temperature elevation due to climate change alters species interactions and distributions, it is important to understand the current and potential future mechanisms of coexistence among species, and how species interactions might change in the future due to rising temperatures.

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