Increased interspecific aggression between Appalachian stream salamanders at elevated temperatures

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Abstract: Community dynamics are often determined by size-dependent interactions. These interactions in aquatic ectothermic assemblages may be disrupted as ecosystems get warmer and organisms adapt to their warming environment by becoming smaller. Species will respond differently to rising temperature, so outcomes of inter-species interactions may change unpredictably. Stream salamander assemblages in the eastern United States are spatially partitioned by individual size, such that all species would prefer to occupy streams but larger species exclude smaller species to stream margins. Aggression by the larger species is probably one mechanism that contributes to this pattern, but we do not understand how temperature mediates these interspecific interactions. At multiple temperatures, we observed short-term interspecific interactions among 3 stream salamander congeners that exist along a body size gradient. We predicted that temperature would change the frequency and type of interspecific interactions. At current temperatures, we predicted that the largest species would frequently exhibit aggression but rarely exhibit escape behavior, and that the smallest species would rarely exhibit aggression and frequently exhibit escape behavior. Overall, we observed 3.8× more aggression at the warmest temperature. We also found that the largest species exhibited aggression most often, particularly towards the smallest species. However, the moderately-sized species fled most often. These fine-scale behaviors are consistent with observations of spatial habitat-partitioning in this assemblage. Our result that temperature increases aggression may indicate that warmer future thermal regimes may disrupt the interspecific interactions that currently shape ecological communities.

Key words: amphibians, behavior, climate change, coexistence, salamander assemblage, streams, temperature-mediated behavior

Climate change is already negatively affecting species distributions and how species interact with their ecosystems (Parmesan 2006, Boutin and Lane 2014, Caruso et al. 2014). Aquatic ectotherms may be among the taxa most affected by shifts in temperature (Daufresne et al. 2009, Forester et al. 2012, Naya et al. 2017). Notably, reductions in body size are predicted for these taxa, but species responses to warming may occur at different rates because of differences in physiology and behavior (Daufresne et al. 2009, Gardner et al. 2011, Sheridan and Bickford 2011, Riddell et al. 2018). The relative competitive ability of individuals within many aquatic and ectothermic assemblages depends primarily on size and physiological function (Ohlberger 2013, Reuman et al. 2014), so temperature-induced changes in body size might disrupt the outcomes of interspecific interactions within assemblages (Liles et al. 2017, Hoffacker et al. 2018).

Predictions about the success of individuals in future assemblages often rely on environmental relationships with demographic rates but fail to accurately predict patterns of change within assemblages (Sinervo et al. 2010). Inclusion of biological interactions can improve predictions, suggesting that they are overlooked but important processes regulating future communities (Sinervo et al. 2010). Because species and communities are often linked through predator–prey relationships, shifts in body size of even a single species within an assemblage can result in cascading shifts in body size of other community members and even entire food webs (Van der Putten et al. 2010, Cheung et al. 2013, Jonsson 2014). To date, most documented shifts have been towards smaller sizes because smaller prey requires additional searching and handling time for the same energetic intake (Van der Putten et al. 2010, Cheung et al. 2013, Jonsson 2014, Reuman et al. 2014).

Temperature is a key environmental regulator of behavioral patterns at both coarse and fine spatial and temporal scales (Biro et al. 2010, Pruitt et al. 2011). Ectotherms are well known for their ability to change their

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behavior based on temperature (Kearney et al. 2009, Strickland et al. 2016), so shifts in behavior associated with temperature may override or change how individuals interact with other species and their environment. For example, extended exposure to warmer temperatures limits lizard foraging and constrains metabolic functions including growth, maintenance, and reproduction (Hillman et al. 2008, Sinervo et al. 2010). In the same lizard system, Sinervo et al. (2010) found that competition with low-elevation congeners accelerated extinction rates of high-elevation species. This finding underscores the need to understand how temperature-induced behavioral changes affect how individuals behave and interact with other individuals. In a variety of species, temperature is correlated with bold behaviors, aggressiveness, and territoriality. Thus, increases in temperature may potentially increase the frequency and intensity of interactions among competitors (Stapley 2006, Biro et al. 2010, Pruitt et al. 2011, Clay and Gifford 2016). Determining the future of communities in novel climates requires identifying the behavioral mechanisms that maintain community stability at current temperatures and determining how biotic interactions change with abiotic gradients.

One ectotherm group that will probably respond quickly to changing environmental gradients such as temperature and precipitation are lungless salamanders because their anatomy and physiology require behavioral and physiological shifts in response to both major climatic variables (e.g., Hillman et al. 2008, Milanovich et al. 2010, Li et al. 2013, Caruso et al. 2014; but see Grant 2014, Connette et al. 2015). The current distributions of these salamanders are limited by warm temperatures (Grant et al. 2014, 2018). Furthermore, changing morphological and physiological traits may affect how species interact, which may influence their distribution and role within a community (Ohlberger 2013, Reuman 2014, Naya et al. 2017). Aggression is common in terrestrial lungless salamanders, and salamanders that are large or under competitive pressure are more aggressive (Nishikawa 1987, Mathis and Britzke 1999, Deitloff et al. 2009). Aggressive behaviors by these salamanders maintain their local territories, but they may also contribute to broader-scale species distribution patterns (Adams 2007, Gifford and Kozak 2012, Clay and Gifford 2016, Dallalio et al. 2017). In the southern Appalachian Mountains, large-bodied terrestrial salamander species occupy distinct elevation ranges (Nishikawa 1987, Clay and Gifford 2016). This pattern of spatial niche partitioning is probably maintained by the species that occupy high elevations and act aggressively towards individuals of other species when temperatures are warm (e.g., 20°C; Nishikawa 1987, Clay and Gifford 2016). However, similar relationships within a stream assemblage that co-occur across a broad elevation gradient have not been evaluated.

Semi-aquatic salamanders also demonstrate morphological and behavioral responses to climatic variables (Liles et al. 2017, Hoffacker et al. 2018). In desmognathan salamander communities, body size of congeners may regulate spatial partitioning of the aquatic to terrestrial gradient. In these communities, the largest species occupies the stream and excludes smaller species to more peripheral areas of the stream or even the terrestrial environment (Hairston 1981, Rissler et al. 2004, Hoffacker et al. 2018). In the absence of the largest species, the entire community shifts towards the stream center, confirming spatial exclusion by the largest species (Rissler et al. 2004, Liles et al. 2017, Hoffacker et al. 2018). However, it is unclear whether this spatial partitioning is a result of competitive or predatory interactions (Hairston 1986, Roudebush and Taylor 1987). Recent short-term trials have confirmed that larger congeners prefer aquatic habitats and perform better at current environmental temperatures than at elevated temperatures (Hoffacker et al. 2018). Notably, elevated temperatures increased the aquatic habitat use by a smaller species in addition to decreasing performance of the larger species. This change indicates that the elevated temperatures would alter the interactions between the 2 species (Hoffacker et al. 2018).

Understanding the relationships between abiotic and biotic drivers of habitat-use patterns and competitive outcomes requires characterizing interaction types and understanding how those interactions change along an environmental gradient. In this study, we used a size-structured stream salamander assemblage to evaluate how short-term interspecific interactions change along a thermal gradient. We hypothesized that, in a pair of 2 individuals of different species, aggressive behaviors by the larger species and escape or defensive behaviors by the smaller species would be most common. Aggression is linked to temperature in a number of animals (Thorp 1978, Anderson et al. 2000, Pruitt et al. 2011, Clay and Gifford 2016), but it has an inconsistent directional response. If aggression increases with temperature, it may indicate an increased tendency towards defense of a potentially limited resource. Conversely, if aggression decreases with temperature, it may indicate individuals are experiencing high stress levels and are, therefore, less willing to engage in territorial or resource defense.

METHODS

Salamander collection and maintenance

We collected 156 stream-dwelling salamanders in Monroe County, Tennessee. Specifically, we evaluated aggression of the stream salamander assemblage including *Desmognathus ocoee, D. monticola*, and *D. quadramaculatus* (*n* = 49, 49, and 58; snout-vent length [SVL] = 28–45 mm, 25–62 mm, and 31–45 mm, respectively). While these size ranges included adults of *D. ocoee*, it is possible that some individuals of *D. monticola* and *D. quadramaculatus* were juveniles. Together, these species form a well-studied example of a size-structured assemblage (Hairston 1987, Petranka 1998, Rissler et al. 2004, Hoffacker et al. 2018). *Desmognathus ocoee* is the smallest and most terrestrial of these 3 species and

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has morphological and physiological adaptations for terrestrial activity (Houck and Bellis 1972, Petranka 1998, Camp et al. 2007). Both *D. monticola* and *D. quadramaculatus* share morphological traits for aquatic activity, such as a keeled tail and keratinized toes. However, *D. monticola* is smaller as an adult, occupies a broader geographical range, and has a less specific habitat than *D. quadramaculatus* (Southerland 1986b, Petranka 1998).

We used visual encounter surveys to capture individuals from 3 streams in which all 3 species co-occur. We placed collected salamanders into an insulated chest cooler for transportation to the University of the South. Individuals were measured (SVL, total length [TL], and mass), and individually housed in an incubator at 18°C, 100% humidity, and a 12:12 photoperiod with indirect lighting. Tupperware enclosures included paper towels wetted with dechlorinated water. Individuals were fed 1 to 3 live crickets, depending on salamander size, at least once/w. Captive individuals grew 0.25–1.11 g over the 5-w period of captivity. Salamanders were kept for 4 d prior to initiation of behavioral observations that occurred intermittently over 4 w.

Interspecific interactions and temperature treatments

Individuals of different species were paired randomly, ensuring that interspecific pairs were of similar SVL (<5 mm difference) and that individuals were not paired together more than once. Pairing individuals of similar sizes prevented mortality or predation between individuals with large size differences. We did not consider sex when assigning pairs because a previous study found that sex did not affect interspecific interactions in this genus (Keen and Sharp 1984). Interspecific pairs were randomly assigned to a temperature, resulting in 20 to 24 successful pairs per species combination and temperature treatment. No individual was tested >3× during the course of the study, and all individuals were allowed to rest at least 48 h in between trials and fed at least 48 h before testing.

We evaluated behaviors of salamanders in incubators set to 15, 20, or 25°C and 100% relative humidity. Mean southern Appalachian Mountain stream temperatures in July range from 15.9 to 22.8°C (Cecala et al. 2017). Stream temperatures in this region are predicted to increase 2 to 3°C by 2100. Thus, the 15 and 20°C treatments represent current conditions, whereas the 25°C treatment is an estimate of future thermal conditions.

Test enclosures consisted of a sealed plastic box (36 × 23 × 5 cm) that housed 2 individuals initially separated by plastic dividers. We used Vaseline® to fill any gaps between the dividers to prevent pre-trial interactions. Each side of the enclosure contained a moist paper towel soaked in dechlorinated water, and enclosures were bleached and rinsed after every trial. Individuals from each pair were acclimated to one side of the test enclosure at the trial temperature for 48 h. After the acclimation period, we removed the divider between the pair of salamanders and monitored interactions between individuals remotely with a web camera for 30 min. Footage was scored immediately and stored for future reference.

Data scoring

We developed an ethogram to classify common behaviors observed during the salamander interactions. Common behaviors included fleeing, guarding, retreating, defensive approach with an arched head, biting, fighting, and chasing (Davis 2002). When an individual ran away from another, this behavior was marked as fleeing rather than a retreat, which was a slower, backwards walk. If one individual remained stationary in front of a corner or wall as the other approached, this behavior was marked as guarding. Behaviors were categorized by type: aggressive behaviors (biting, chasing, fighting), defensive behaviors (guarding, slow approach), and escaping behaviors (fleeing, retreating).

Some studies of salamander behavior rank the intensity of each behavior (e.g., Mathis and Britzke 1999, Clay and Gifford 2016), whereas others only evaluate singular behaviors to illustrate a category of behavior (e.g., bites as an indicator of aggression; Jaeger 1981, Deitloff et al. 2009). We elected to quantify all types of aggressive behaviors because our observations of wrestling and chasing did not always include biting and it was difficult to quantify biting during these behaviors. Thus, we recorded each physical contact as a single aggressive interaction with equal weight and analyzed the total number of aggressive interactions as a response variable. We used a similar approach for defensive and escape behaviors, and each behavioral type was converted to a frequency for data analysis.

Data analysis

Before we evaluated each response variable, we confirmed that behavioral frequencies were not associated with one another using Pearson correlations ($R^2 < 0.026$, $p > 0.086$), and that individual size did not affect the frequency of any of our behaviors using the quasi-Poisson regression described below ($\chi^2 < 1.48$, $p > 0.223$). We used R to perform all statistical procedures with an alpha of 0.05 to determine significance (R Project for Statistical Computing, Vienna, Austria). We evaluated whether linear regressions were significant with an analysis of deviance in the *car* package (Fox and Weisberg 2011). Our behavioral data departed from normality and were over-dispersed, so we used a quasi-Poisson regression with a log link function in the *MASS* package (Venables and Ripley 2002, Ver Hoef and Boveng 2007).

To address our primary hypothesis, we used 3 regression models to evaluate the effects of temperature and species on our dependent variables—the number of aggressive, defensive, or escape behaviors. We assessed model fit for

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these 3 models with the coefficient of determination between predicted and observed values and evaluated multicollinearity between species and temperature predictors using the variance inflation factor (variance inflation factors of models < 1.5). We used the package *multcomp* for Tukey post-hoc comparisons among species pairs and temperatures when these effects were significant (Hothorn et al. 2008).

Despite finding no correlations among behavioral frequencies, results from the analyses described above suggested the potential for associations among behaviors. For example, defensive behaviors could be associated with aggressive behaviors by an individual's partner. We used logistic regression models to evaluate if defensive or escape behavior by 1 individual depended on aggression by the other within 60 s. We also evaluated whether a defensive behavior precipitated an escape behavior in the same individual. To do this, we coded responses as associated (1) or unassociated (0).

RESULTS

We observed 19 instances of aggressive behavior, 17 instances of defensive behavior, and 45 instances of escape behaviors across all treatments. In predicting the frequency of aggressive, defensive, and escape behaviors by species pairs and temperatures, we found low to moderate fit dependent on the behavioral type (aggressive $R^2 = 0.23$, defensive $R^2 = 0.19$, and escape $R^2 = 0.12$).

The mean frequency of aggressive behaviors varied with treatment temperature ($\chi^2 = 4.67$, $df = 1$, $p = 0.031$; Fig. 1) and species identities ($\chi^2 = 8.10$, $df = 2$, $p = 0.017$; Fig. 2A). Aggressive behaviors were most frequent at the highest temperature. Aggression was less frequent at the lower temperatures (15 and 20°C; Fig. 1), and did not differ among these 2 treatments.

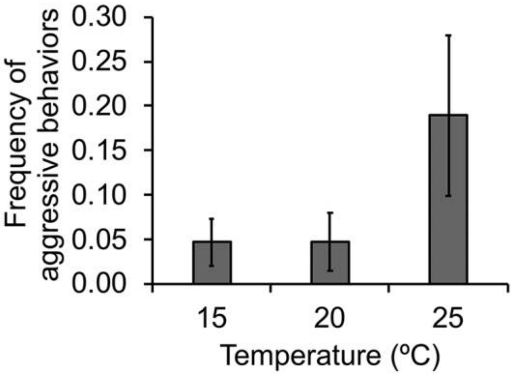

Figure 1. Mean (± 1 SE) frequency per trial of aggressive behaviors among all species pairs for each of 3 temperatures ($n = 20$–24 trials). No post-hoc comparisons were significant, but most aggressive behaviors occurred between the largest (*Desmognathus quadramaculatus*) and the smallest (*D. ocoee*) species. This species pair also had the highest increase in aggressive behaviors at 25°C.

The interaction between temperature and species identity modified aggressive behaviors slightly ($\chi^2 = 5.34$, $df = 2$, $p = 0.069$), but post-hoc analyses did not reveal any statistically-significant differences among pairwise comparisons. Aggressive behaviors of *D. quadramaculatus* and *D. ocoee* increased 5× between 20 and 25°C, whereas aggressive behaviors between *D. quadramaculatus* and *D. monticola* increased 1.3× between 20 and 25°C. Aggressive behaviors remained constant among temperatures in pairings of *D. monticola* and *D. ocoee*. The largest number of aggressive behaviors occurred between *D. quadramaculatus* and *D. ocoee*, and in these pairings *D. quadramaculatus* behaved aggressively most often. The fewest number of aggressive behaviors occurred between *D. monticola* and *D. ocoee*, and in these pairings only *D. ocoee* behaved aggressively. When *D. quadramaculatus* and *D. monticola* were paired, they each acted aggressively with approximately the same frequency.

The frequency of defensive behaviors also changed depending on species pair ($\chi^2 = 11.33$, $df = 2$, $p < 0.004$; Fig. 2B) and varied somewhat with temperature ($\chi^2 = 2.24$, $df = 1$, $p = 0.134$). The highest number of defensive behaviors occurred between *D. quadramaculatus* and *D. ocoee*, and *D. quadramaculatus* carried out most of the defensive behaviors in addition to the most aggressive behaviors. The lowest number of defensive behaviors occurred between *D. monticola* and *D. ocoee*, and in this pair the less aggressive species, *D. monticola*, was responsible for all the defensive behaviors. A weak interaction was observed between temperature and species pair ($\chi^2 = 3.57$, $df = 2$, $p = 0.168$), but post-hoc analyses revealed no significant pairwise differences.

The mean frequency of escape behaviors was marginally different among species pairs ($\chi^2 = 4.98$, $df = 2$, $p = 0.083$; Fig. 2C) but did not differ among temperatures ($\chi^2 = 0.394$, $df = 1$, $p = 0.532$). We observed a marginal interaction between species pair and temperature ($\chi^2 = 3.30$, $df = 2$, $p = 0.192$), but no post-hoc analyses identified significant pairwise differences. Most species pairs exhibited similar frequencies of escape behaviors across treatments, but *D. monticola* fled more frequently when paired with *D. quadramaculatus*.

While some species pairs appeared to have associated aggressive and defensive behaviors, logistic regressions revealed that individuals did not typically exhibit defensive ($\chi^2 = 0.330$, $df = 1$, $p = 0.566$) or escape ($\chi^2 = 1.87$, $df = 1$, $p = 0.171$) behaviors within 60 s of aggressive behaviors by their partners. However, escape behaviors were usually followed by defensive displays within an individual ($\chi^2 = 4.85$, $df = 1$, $p = 0.028$).

DISCUSSION

Short-term behavioral interactions within a semi-aquatic salamander community demonstrated behavior-specific responses to temperature. Aggressive behaviors were more common at warmer temperatures, but defensive and escape

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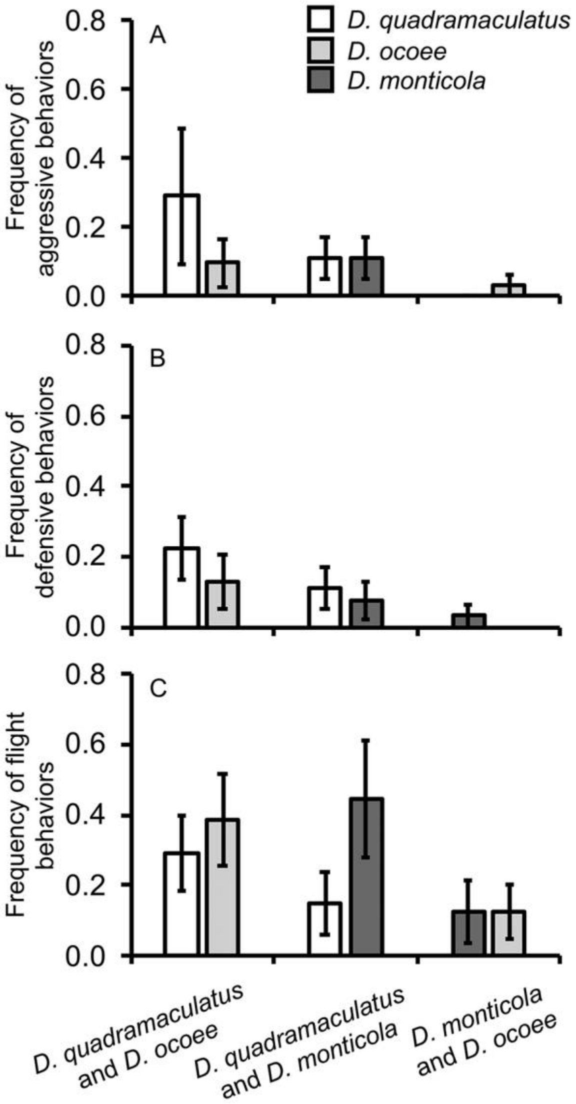

Figure 2. Mean (± 1 SE) frequency per trial of aggressive behaviors (A), defensive behaviors (B), and escape behaviors (C). Pairwise post-hoc comparisons did not reveal any statistically significant differences between species pair temperature trials.

behaviors did not have strong relationships with temperature. Individuals could increase rates of escape and defensive behaviors to minimize their risk of injury in response to increased aggressive behaviors, but we did not detect this pattern. Low to moderate fit of predictive models suggests that behavioral variability was high and additional patterns may be more detectable with larger sample sizes.

Two key experimental design choices could have introduced additional variance to our study—limited time to establish a territory and differences in species life stages. It is possible that 48 h was not sufficient for salamanders to establish a territory in the behavioral test enclosures. Lack of a territory could affect the frequency of aggressive and defensive behaviors. In this study, individuals of the largest species were probably juveniles potentially introducing additional variance into the study. Juvenile lungless salamanders exhibit territoriality and can, in some instances, be more aggressive than adults with established territories (Mathis and Britzke 1999, Osterhout and Liebgold 2010). However, body size and life stage affect aggressive behaviors and will probably also change as temperatures change (e.g., Daufresne et al. 2009, Caruso et al. 2014, Naya et al. 2017), so more research should investigate the interactions between body size, life stage, and aggression in stream-breeding plethodontids.

The present study describes short-term behaviors that may or may not be consistent with long-term in situ interactions among individuals. The dear enemy hypothesis would predict less aggression between nearby individuals through time (Jaeger 1981), or thermal stress may modify behaviors at the expense of maintaining territories (Tokarz 1987, Sgoifo et al. 1996, Schreck et al. 1997, Moore and Mason 2001). For example, at high temperatures or low humidity, terrestrial salamanders cease surface activity or alter habitat use (Spotila 1972, Feder and Londos 1984, Camp et al. 2013), which may reduce the time available to defend a territory. Furthermore, short-term interactions between *D. quadramaculatus* and *D. monticola* in this study did not match outcomes of a longer-term study of habitat use and competitive ability (Hoffacker et al. 2018). Increased aggression at warmer temperatures by *D. quadramaculatus* observed in this study would be expected to increase habitat partitioning through avoidance or escape behaviors by *D. monticola*. However, in the longer-term experiment, both species were found together in the water more often at warmer temperatures, and the winner of the competitive outcome switched from *D. quadramaculatus* to *D. monticola* at high temperature trials (Hoffacker et al. 2018). While *D. quadramaculatus* may initially exhibit higher levels of aggression in short-term interactions, this behavioral response may be minimized through time due to chronic stress (Tokarz 1987, Sgoifo et al. 1996, Schreck et al. 1997, Moore and Mason 2001) or adaptive responses (Jaeger 1981, Riddell et al. 2018).

We observed the highest frequencies of behavior and largest change in aggression in *D. quadramaculatus* relative to the other 2 congeners. Research has already demonstrated that closely-related congeners, like those observed in this study, have different aggression response relationships with temperature (Clay and Gifford 2016), and the thermal breadth and performance of species appear to be related to their distribution in the past and present (Bernardo et al. 2007, Gifford and Kozak 2012, Clay and Gifford 2018). Species that experience cooler and smaller thermal ranges may exhibit larger responses to warmer temperatures than those that experience warmer or broader thermal ranges (Bernardo et al. 2007, Gifford and Kozak 2012, Clay and Gifford 2018). Consistent with observations in this study, *D. ocoee* and *D. quadramaculatus* have ranges that are smaller, higher in elevation, and more restricted in latitude than *D. monticola* (Petranka

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1998, Camp and Tilley 2005) that may explain the highest levels of aggression between *D. ocoee* and *D. quadramaculatus*. Though species with larger body sizes, like *D. quadramaculatus*, have been repeatedly shown as more aggressive and competitively dominant, complex factors shape agonistic behaviors, including warm temperatures, that can induce more aggressive behaviors in smaller species like *D. ocoee* (Nishikawa 1987, Clay and Gifford 2016).

Interspecific behavioral interactions could be an important driver of community coexistence through selection for divergent phenotypes (Krzysik 1979, Nishikawa 1987, Adams 2007, Deitloff et al. 2009, Kozak et al. 2009). Species coexistence in this assemblage is best explained by the competitive exclusion principle (Hardin 1960, Hairston 1987, Rissler et al. 2004). Previous research suggests that aggression in stream-breeding lungless salamanders is common and helps to maintain behavioral avoidance and spatial niche partitioning (Keen and Sharp 1984, Southerland 1986a, b). Other studies have suggested that behavioral avoidance or escape may also be a result of intraguild predation, the most extreme outcome of aggression (Tilley 1968, Hairston 1980). However, salamanders are capable of modulating their behavior relative to the risk of predation (Cecala et al. 2015), and in situ predation rates appear to be very low (Camp and Lee 1996, Camp 1997). The escape response that we observed in this study might provide a behavioral mechanism to explain observed habitat partitioning. Escape from larger, more aquatic congeners would require individuals to flee towards terrestrial habitats (Roudebush and Taylor 1987, Camp 1997, Rissler et al. 2004). The tendency of smaller species to flee, combined with adaptations that minimize desiccation rates, allow smaller species to thrive in drier near-stream habitats and promote coexistence of closely-related species (Houck and Bellis 1972, Hairston 1987). Increasing the likelihood of agonistic behaviors at elevated temperatures may therefore strengthen selection pressure for small species to retain traits that improve terrestrial performance (Keen and Sharp 1984, Southerland 1986b, Hairston 1987, Deitloff et al. 2009), but more research is needed on the long-term impacts of exposure to high temperature conditions (Riddell et al. 2018).

More research is necessary to understand differences in thermal tolerances within and across species as well as community thresholds for competitive exclusion and species dominance. Differences in body size pose constraints on individual dynamics and can affect the strength and outcomes of community interactions (Werner and Gilliam 1984, Persson 1985, Liles et al. 2017, Hoffacker et al. 2018). Increasing aggression may contribute to accelerated declines of larger aquatic species if smaller species are favored and become competitively superior (Daufresne et al. 2009, Sheridan and Bickford 2011, Hoffacker et al. 2018), but short-term behavioral interactions may be misleading relative to long-term trends. Length of exposure to elevated temperatures may mediate outcomes of size-dependent interactions that could either enhance or weaken competitive exclusion contributing to cohabitation and diversity (Gilman et al. 2010, Riddell et al. 2018). This study demonstrates enhanced aggressive interactions between species under elevated temperatures and supports conclusions that processes structuring current communities could shift in unexpected ways in the future (Sinvervo et al. 2010, Dallalio et al. 2017, Hoffacker et al. 2018). Outcomes of species interactions are clearly tied to environmental gradients, and describing the connections between climate and community and population dynamics should be a priority moving forward to assess the implications for long-term community responses to climate warming.

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Author contributions: KEB and KKC designed the experiments, performed the research, analyzed the data, and co-wrote the manuscript.

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