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Author(s): Kristen K. Cecala, Will Noggle, and Seth Burns
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Negative Phototaxis Results from Avoidance of Light and Temperature in Stream Salamander Larvae

KRISTEN K. CECALA,[1] WILL NOGGLE, AND SETH BURNS

Department of Biology, University of the South, Sewanee, Tennessee USA

ABSTRACT. —**Forest removal is a global threat to amphibian diversity. Declines occur within these areas, but many amphibians also avoid moving into or through disturbed areas. Understanding which cues result in avoidance may provide targets for preservation of amphibian occupancy and population connectivity. Negative phototaxis is known from many amphibians, but light can serve as a cue or as a proxy for other environmental cues like temperature. This study sought to evaluate whether larval salamander habitat selection was influenced most by light or temperature cues. Because some individuals choose to remain in deforested habitat, we also assessed whether differences in habitat selection existed between individuals from forested and deforested habitat. Using a laboratory experiment, we found that salamanders use both light and temperature cues for habitat selection. Although salamanders demonstrated larger responses to temperature, they were willing to move into warmer habitats to avoid light. Individuals from deforested regions preferred brighter and warmer areas than individuals from forested regions although plasticity was higher with respect to light relative to temperature. We also noted that salamander thermal preferences were lower than daytime temperatures in small ($<$ 60 m) deforested regions. Overall, a combination of light and thermal cues following forest removal may contribute to avoidance of deforested regions, but more research is necessary to understand why some salamanders continue to occupy warm and bright-disturbed areas.**

Amphibian declines in North America are often linked to removal of forest cover (Cushman, 2006; Gallant et al., 2007; Tilghman et al., 2012). Declines documented in deforested regions are often attributed to changes in demographic rates, yet behavioral changes in response to changing cues are likely to be the proximal mechanisms for declines (Semlitsch et al., 2009). For example, some amphibians avoid moving into deforested areas decreasing immigration rates, but the specific cue leading to avoidance is unclear (e.g., Marsh et al., 2005; Rittenhouse and Semlitsch, 2006; Cecala et al., 2014). Land-cover change typically results in less complete canopy cover that allows greater penetration of solar radiation creating warmer and drier microclimates (Chen et al., 1999; Caissie, 2006; Brooks and Kyker-Snowman, 2008), increased exposure to ultraviolet B radiation (UVB; Brown et al., 1994; Blaustein et al., 1998), and changing food webs (Seastedt and Crossley, 1981; Ash, 1995; Hagen et al., 2010). Identifying which of these cues is prioritized for movement may allow for management strategies that encourage habitat use. For example, maintenance of coarse woody debris or retention of partial canopy cover may facilitate disturbed habitat use by juvenile amphibians (deMaynadier and Houlahan, 2008; Rittenhouse et al., 2008; Semlitsch et al., 2008)

Behavior and activity of amphibians often are regulated by exposure to light that creates diurnal cycles of activity or avoidance of movement in well-lit habitats (Sugalski and Claussen, 1997; Madison et al., 1999; Placyk and Graves, 2001). Several mechanisms have been proposed for movement regulation by light. First, amphibians have permeable skin that makes them susceptible to desiccation (Spotila, 1972; Feder, 1983). In well-lit habitats, temperatures are likely to increase, whereas humidity decreases accelerating desiccation rates (Spotila, 1972; Feder, 1983). Each of these changes in microenvironmental conditions could contribute to lower rates of movement to prevent desiccation (Feder and Londos, 1984). Second, although amphibians are ecothermic, they can experience metabolic depression at high temperatures (Bernardo and Spotila, 2006; Strickland et al., 2016). Avoidance of these areas may help to maintain optimal metabolic function. Finally, avoidance of UVB radiation that is common in areas with direct solar radiation prevents growth inhibition and decreased survival as a result of exposure to UVB (Blaustein et al., 1998). Avoidance of well-lit habitat may occur for primarily one or as a result of all of these factors, but these behaviors have different implications for management. Interactions may also exist among these factors for which environmental context may be particularly important (Garcia et al., 2009). For example, amphibians seeking warm temperatures to facilitate rapid growth may disregard cues related to UVB radiation (Bancroft et al., 2008). Alternatively, northern amphibian populations may be more willing to enter well-lit areas than southern populations because of the difference in temperatures experienced by these two geographical regions (Patrick et al., 2006, 2008; Tilghman et al., 2012). Similarly, individual differences in behavior may result in variation in cue prioritization associated with light (Cecala and Maerz, 2016).

The southern Appalachian Mountains are recognized as a global biodiversity hotspot for salamander diversity (Stein et al., 2000; Stuart et al., 2004), but declines have been documented in deforested regions (Ash and Bruce, 1994; Petranka et al., 1994; Crawford and Semlitsch, 2008). These declines include stream amphibian populations with demonstrated resistance to entering deforested stream reaches suggesting that avoidance of deforested areas may not be attributable to desiccation avoidance proposed for other species because of access to aquatic habitats (Todd and Rothermel, 2006; Cecala et al., 2014; Cecala and Maerz, 2016). Despite desiccation avoidance being a poor explanation for these behaviors, larval stream salamanders repeatedly demonstrate light avoidance (Bliss and Cecala, 2015; Cecala and Maerz, 2016), although individuals that continue to occupy deforested areas exhibit greater behavioral plasticity and decreased responsiveness to light cues (Bliss and Cecala, 2015). Avoidance of deforested areas may, therefore, be attributable to temperatures that exceed thermal preferences (Strickland et al., 2016). In fact, the elevation range limits of some species of seepage salamanders are hypothesized to be constrained by high temperatures (Bernardo and Spotila, 2006).

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[1] Corresponding Author. E-mail: kkcecala@sewanee.edu

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Furthermore, individuals persisting in deforested areas occur at lower body condition, suggesting either that individuals perform poorly in deforested areas or that individuals at low body condition with high behavioral plasticity select warmer habitat that could facilitate growth (Catenazzi and Kupferberg, 2013; Bliss and Cecala, 2015; Murphy et al., 2016).

In this study, we sought to evaluate whether behavioral responses to light were a proxy for responses to temperature to better understand why some individuals avoid deforested stream habitat. We designed a conflicting cue experiment to assess habitat selection with respect to thermal and light cues before placing them in conflict. In this treatment, we reversed the typical relationship between light and temperature with light corresponding to cool temperatures and shade corresponding to warm temperatures. We predicted that larval salamanders (*Desmognathus quadramaculatus* Holbrook, 1840; Black Bellied Salamanders) would prioritize movement toward cooler temperatures over movement toward shade. We also predicted that larval salamanders captured in deforested areas would prefer warmer temperatures and show less reaction to light cues relative to individuals from forested areas. Environmental stream temperatures were evaluated, and we hypothesized that thermal preferences of tested individuals would match mean environmental stream temperatures.

Materials and Methods

We evaluated behaviors of larval *D. quadramaculatus* because they are a common species of the southern Appalachian Mountains that decline following landscape disturbance (Petranka, 1998; Peterman et al., 2008; Surasinghe and Baldwin, 2015; Cecala et al., in press). We used larvae because they exhibit resistance to movement into riparian canopy gaps and do not forage on land (Petranka, 1998; Cecala et al., 2014). As large, easy to capture and observe larvae (Petranka, 1998; Peterman et al., 2008), *D. quadramaculatus* have also been used in previous phototaxic behavior studies (e.g., Bliss and Cecala, 2015; Cecala and Maerz, 2016; Liford and Cecala, 2017).

Desmognathus quadramaculatus larvae were captured from four locations in the Upper Little Tennessee River basin (locations described in Bliss and Cecala, 2015). Each location consisted of a canopy gap over the stream ranging from 13–85 m in length and adjacent forests. Sites were located at least 5 km from one another with a maximum distance of 50 km between sites. We collected 35 larval *D. quadramaculatus* from canopy gaps and 35 from adjacent forests. We housed salamander larvae individually in 2–3 cm of dechlorinated water with a paper towel as refuge at 12°C with a natural photoperiod. We fed thawed bloodworms to salamanders ad libitum every other day and tested them within 4 weeks of capture before being returned to their capture location. We used individuals once for each treatment, and we randomized the order in which individuals experienced each treatment. Treatments included no cues, light cues, temperature cues, or conflicting light and temperature cues.

To evaluate habitat selection in response to light and temperature, we used aluminum gutter with dimensions of 150 × 5 cm filled to a depth of 2 cm with dechlorinated water and a bleached sand substrate. We conducted trials in a room with indirect lighting that allowed for detection of the individual in trials where light gradients were not used. We created light gradients by setting a non–heat-emitting light bulb at one end of the enclosure (compact fluorescent [CFL] bulb with similar wavelength peaks experienced by salamanders; Makino and Dodd, 1996; Cecala and Maerz, 2016). We created thermal gradients by setting one end of the enclosure in an ice bath and the other end on a hot plate on the first setting. Thermal gradients ranged from 2–35°C. As needed, we added ice to the ice bath to maintain a minimum temperature of 2°C. In the absence of a thermal gradient, we conducted trials at room temperature (20°C). Our third treatment involved placing the light at the same end as the ice bath to place the two cues in conflict. Initially, we placed individuals in the center of the enclosure. We recorded the location of the individual from the light source or ice bath and the temperature of the location every 30 min for 6 h for a total of 12 records for each individual per treatment. We took measurements of temperature adjacent to the middle of the body to prevent disturbing the individual that could have induced it to change location. We bleached and rinsed enclosures between trials to remove any chemical cues that previous salamanders may have left.

To determine how temperature changed within canopy gaps and compare thermal preferences of individuals from canopy gaps and forests, we set two temperature-sensitive HOBO data loggers (UA-002-08 Pendant Temperature/Light Data Logger; Onset Computer Corporation, Bourne, MA) at each capture site. We attached data loggers to bricks and submerged one in the forest 5 m upstream of the canopy gap and one in the canopy gap 5 m before reentry into the forest. We set data loggers to collect water temperature at 15-min intervals for 2 weeks in August 2014.

We used linear mixed-effect models to determine whether treatment or habitat origin (deforested or forested reach) altered habitat selection with respect to distance from a light source or temperature. We added random effects of capture location and individual to account for individual or locational differences in habitat selection. We standardized the data to assess relative effect sizes of light and thermal cues (z-score). We ran two models with one evaluating distance from light or ice and another evaluating temperature. We also examined effect sizes of each treatment to evaluate the relative effects of light and thermal cues on habitat selection. We evaluated post hoc comparisons using Tukey honestly significant difference tests. We conducted all analyses in R using the "lme4" package (Bates et al., 2015; R Core Team, 2015).

After evaluating the data, we also tested whether habitat origin resulted in different response curves to temperature and light. Specifically, we evaluated whether individuals from deforested habitats selected a broader range of values than individuals from forested habitats. Using the repeated observations of individuals, we calculated the frequency with which individuals selected temperatures in 5°C categories in the temperature-cue–only treatment or distance from light in 30-cm categories in the light-cue–only treatment. We fit five common response curves (Gaussian, quadratic, Weibull, logistic, and log normal; Angiletta, 2006) to the data using TableCurve 2D (Systat Software, Inc.) and evaluated fit using the residuals (R^2). For distance from light, we evaluated the frequency with which individuals selected locations <120 cm from light and how often individuals selected the furthest distance away from light. If individuals from deforested reaches are more flexible and prefer well-lit habitat, we predict that they will select locations <120 cm more frequently and locations >120 cm less frequently than individuals from forested reaches. The best

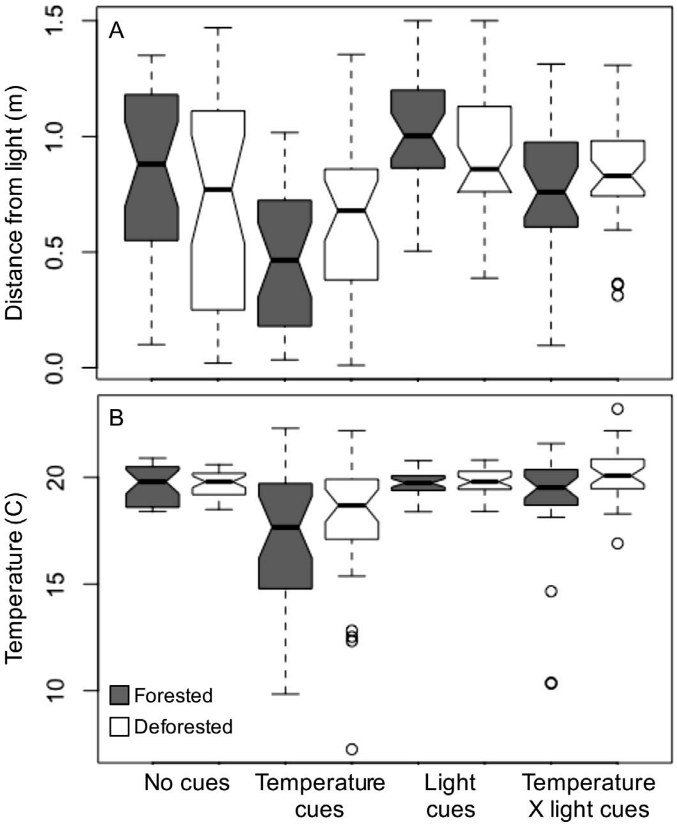

FIG. 1. Habitat selection results with respect to A) distance from light or ice bath and B) temperature for larval *Desmognathus quadramaculatus* individuals from forested and deforested stream patches. Boxplots reflect the mean, quartiles, and outlying values. When temperature and light cues were placed in conflict, that is where movement toward shade would require movement toward warmer temperatures, salamanders used both cues to locate themselves within light and temperature gradients.

fitting curve was used to estimate the mean, minimum, maximum, and 80% of temperatures each habitat type selected. If individuals from deforested reaches exhibited higher variance in habitat selection, we would expect that the 80% range would each be larger for individuals from deforested reaches relative to those from forested reaches.

RESULTS

Although we tested up to 35 individuals from each habitat type, only 29 individuals from forested reaches and 33 individuals from deforested reaches successfully completed all trials. We included only individuals who completed all trials for analyses. Most individuals that did not complete trials climbed out of the enclosure on more than one occasion during a treatment. Distance from the light source or ice bath was significantly affected by light cues ($F_{1,180} = 2.02$, $P = 0.034$) and thermal cues ($F_{1,180} = -2.93$, $P = 0.004$; Fig. 1A) but not by an interaction between light and thermal cues ($F_{1,180} = 1.02$, $P = 0.333$; Table 1). Marginal interactions were found between habitat origin and light cues ($F_{1,178} = 1.92$, $P = 0.058$) and habitat origin and thermal cues ($F_{1,178} = 1.87$, $P = 0.059$). Individuals from deforested reaches preferred locations brighter and warmer (inferred by distance from the ice bath) than individuals from nearby forested reaches. Thermal cues resulted in 1.4 times greater response relative to light cues (Fig. 1A).

Temperature selection was significantly affected by light cues ($F_{1,189} = -4.03$, $P < 0.001$), thermal cues ($F_{1,180} = -8.17$, $P < 0.001$), and an interaction between light and thermal cues ($F_{1.178} = 5.66$, $P < 0.001$; Fig. 1B). An interaction between habitat origin and thermal cues was found ($F_{1,178} = 2.10$, $P = 0.026$; Table 1). Individuals from deforested reaches preferred warmer habitats. Thermal cues resulted in 2.04 times greater response relative to light cues. The interaction of light and thermal cues resulted in a positive behavior response indicating overall movement toward warmer temperatures away from light (Fig. 1B).

We observed that stream temperatures within deforested reaches are frequently higher than in forested reaches (mean ± SE temperature difference = 0.73 ± 0.02°C) and during the day can increase by more than 5°C (range: −0.57–5.91°C; Fig. 2). Mean stream temperatures were 17.5 ± 0.02°C in the forested reaches and 18.2 ± 0.03°C in deforested reaches. The maximum observed stream temperature in the forest was 19.09°C and 22.72°C beneath canopy gaps.

Curve fitting to evaluate distance toward light supported the log normal curve for individuals from forested reaches ($R^2 = 0.94$) and the exponential curve for individuals from deforested reaches ($R^2 = 0.88$; Fig. 3A). Individuals from forested habitat were more likely to select distances >120 cm (50% of the time) relative to individuals from deforested habitat (25% of the time) while housed in our experimental enclosures (Fig. 3A).

TABLE 1. Statistical results of linear mixed models evaluating the influence of light and thermal cues on habitat selection (distance from light or ice bath; temperature) by larval *Desmognathus quadramaculatus*. We also evaluated the effect of the environmental condition of their capture location (forested or deforested).

Factor	Effect size	SE	df	*t*	*P*
Distance from light or ice bath					
Light cue	0.50	0.24	180	2.017	0.034
Thermal cue	−0.70	0.24	180	−2.926	0.004
Habitat origin	0.06	0.23	180	0.256	0.798
Light cue × thermal cue	0.31	0.34	178	1.023	0.333
Light cue × habitat origin	0.18	0.33	178	1.920	0.058
Thermal cue × habitat origin	0.61	0.33	178	1.874	0.059
Light cue × thermal cue × habitat origin	−0.71	0.46	174	−1.544	0.124
Temperature					
Light cue	−0.96	0.24	180	−4.031	<0.001
Thermal cue	−1.96	0.24	180	−8.168	<0.001
Habitat origin	−0.11	0.23	180	−0.468	0.640
Light cue × thermal cue	1.87	0.34	178	5.661	<0.001
Light cue × habitat origin	0.09	0.33	178	0.286	0.775
Thermal cue × habitat origin	0.76	0.33	178	2.133	0.026
Light cue × thermal cue × habitat origin	−0.59	0.46	174	−1.268	0.206

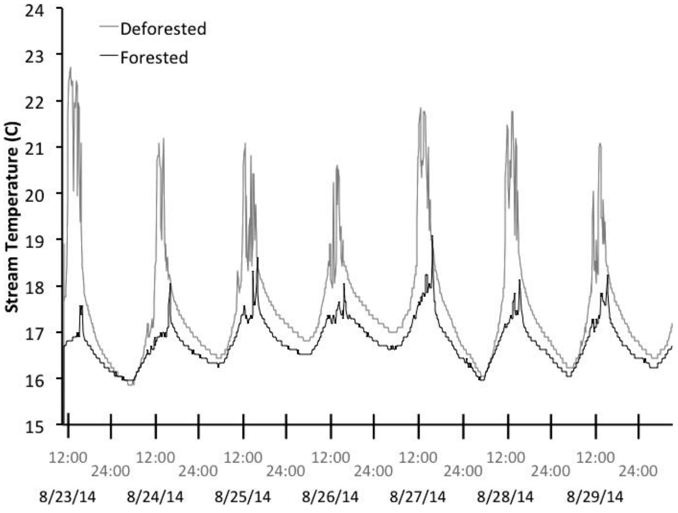

FIG. 2. Stream temperatures from an upstream-forested reach versus a downstream deforested reach. Stream temperatures within canopy gaps are on average 0.72 ± 0.02°C warmer than upstream forested reaches and can increase more than 5°C during the day. The canopy gap at this site is 55 m in length.

Individuals from deforested habitats also showed an increased tendency to select distances between 90 cm and 120 cm relative to individuals from forested habitat (Fig. 3A). Peaks at the lowest and highest values likely represent movement constraints resulting from resting in the corners of the test enclosure.

Curve fitting to evaluate temperature supported the logistic curve for individuals from forested reaches ($R^2 = 0.56$) and the Gaussian curve for individuals from deforested reaches ($R^2 = 0.64$). The curve width for individuals from forested reaches was slightly larger than those from deforested reaches (9.44°C and 9.14°C, respectively). This narrowed range was reflected in similar maximal temperatures or the temperatures at which individuals did not select to occupy (27.32°C and 27.89°C for individuals from forested and deforested reaches, respectively) but slightly higher minimum temperatures for individuals from deforested reaches (13.89°C) relative to individuals from forested reaches (12.12°C; Fig. 3B).

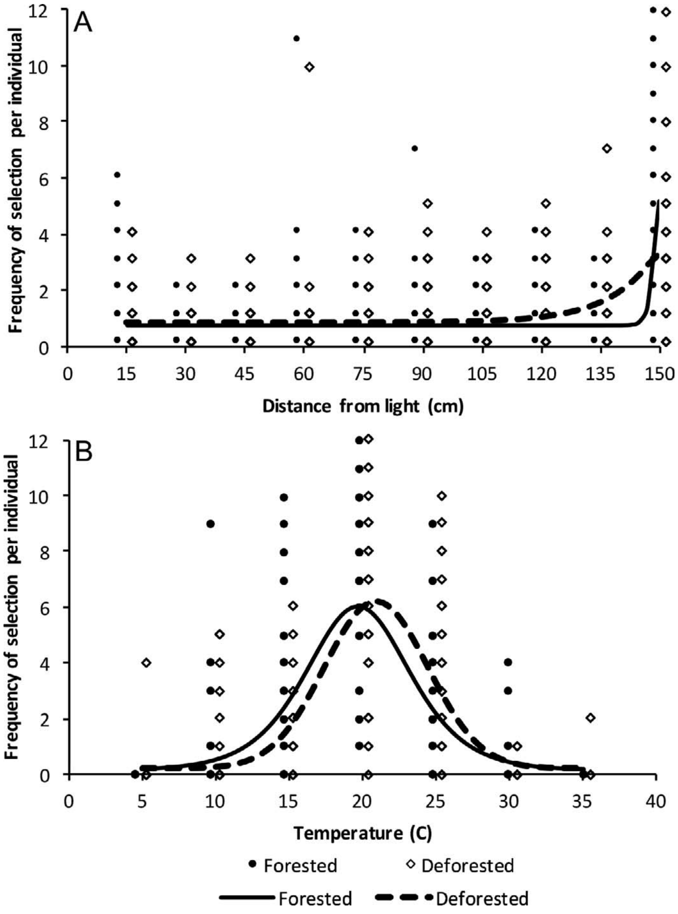

FIG. 3. Frequency with which individuals selected distance from light A) or temperatures B) during the 12 observations of habitat selection. Frequencies were obtained using 30-cm categories for distance from light in light-cue–only treatments and 5°C categories for temperature in temperature-only treatments. Individual selection frequencies are shown with their best fitting curve.

DISCUSSION

Stream habitats with different forested conditions result in habitats with a myriad of cues that individuals balance during habitat selection (e.g., Werner and Anholt, 1993; Bancroft et al., 2008; Ferrari and Chivers, 2009). Significant changes in the magnitude of light and thermal cues result from deforestation and drive avoidance of deforested regions (Ash and Bruce, 1994; Ward et al., 2008; Cecala et al., 2014). A previous study suggested that deforested areas that maintain rock or cobble refugia for salamanders may continue to provide high quality habitat for larval salamanders using phototaxis as a mechanism for assessment (Cecala and Maerz, 2016). The present study suggests that these regions are more likely to be avoided because of thermal cues, because these canopy gaps exceed thermal preferences by individuals from both forested and deforested reaches. Therefore, restoration of larval amphibian movement within riparian canopy gaps will require more extensive interventions to minimize differences in light and temperature experienced by individuals in deforested stream reaches. These data also highlight the need to better understand the thermal landscape of these organisms and evaluate how individuals balance competing needs to avoid physiologically challenging conditions and predation while finding resources to support larger size at metamorphosis that confers higher fitness (Werner and Anholt, 1993; Sears et al., 2011).

These data suggest that light is not simply a proxy cue for temperature and require additional consideration of mechanisms for why amphibian larvae would avoid light cues in the absence of thermal cues. First, light may make larval movements more likely to be detected by visual predators, and negative phototaxis may reduce depredation rates. In fact, individuals from deforested stream reaches were four times more likely to have experienced tail autotomy suggesting higher predation risks in well-lit and disturbed habitat (Bliss and Cecala, 2015). Second, as predators of stream invertebrates (Petranka, 1998; Peterman et al., 2008), negative phototaxis in stream amphibians may result in movement toward habitat with high biomass of allochthonous carbon and the invertebrates that contribute to leaf decomposition (Wallace et al., 1997; Hagen et al., 2010). A recent study found support for larval anurans using light and thermal cues as proxies for food quality (Catenazzi and Kupferberg, 2013). Third, although UVB radiation from CFL bulbs is low (Mironava et al., 2012), avoidance of light may reflect avoidance of UVB radiation (Blaustein et al., 1998). Finally, adult amphibians are also sensitive to light because of the risk of desiccation in the absence of permanent water, and this response appears to be strongest in salamanders relative to anurans (Sugalski and Claussen, 1997; Todd et al., 2006; Semlitsch et al., 2009). Therefore, larval avoidance of light may be attributable to persistent and conserved avoidance of light by salamander adults that carries over to the larval life stage (Sugalski and Claussen, 1997; Placyk and Graves, 2001; Semlitsch et al., 2009; Manenti et al., 2013).

Thermal cues do appear to be important for habitat selection. Habitat selection for temperature can override typical responses to cues like UVB radiation in larval anurans (Bancroft et al., 2008). Salamanders preferred temperatures within 0.5°C of mean observed temperatures of streams during the warmest part of the year suggesting that salamander larvae may acclimate to the thermal regime of their capture location (Angilletta et al., 2006; Kozak and Wiens, 2010). Preferred temperatures were also lower than those observed during the day in deforested areas. Because thermal preferences appear to be related to optimal physiological function (Strickland et al., 2016), salamanders that choose to enter or occupy deforested reaches may experience metabolic costs associated with high temperatures (Bernardo and Spotila, 2006; Gifford and Kozak, 2012; Gifford, 2016). This was demonstrated in our data by individuals from both habitat types selecting to avoid temperatures higher than 27.8°C, yet individuals from deforested reaches were less likely to select cooler temperatures (Fig. 3A). Bernardo and Spotila (2006) hypothesize that the elevation range limits of *Desmognathus* spp. are constrained by high temperatures. Therefore, reaches that experience high temperatures may be avoided more strongly in warmer regions of their range although individuals in this study were willing to select warmer temperatures to avoid well-lit regions. Additional insight into the degree of variability in thermal tolerances and preferences of stream amphibians may clarify conditions in which they will respond more negatively to losses in riparian forest cover (Tilghman et al., 2012; Gifford, 2016; Grant et al., 2016).

Behaviors observed in this study were over short temporal and spatial scales that could result in different behavioral traits than those observed over longer or larger scales. Notably, habitat origin affected habitat preferences with respect to light and temperature. Individuals from deforested reaches selected habitats that were brighter and warmer than their counterparts in adjacent forests. Although occupancy and density of larval salamanders declines in deforested stream reaches (Peterman and Semlitsch, 2009; Surasinghe and Baldwin, 2015; Cecala et al., in press), rarely is complete extirpation observed. Behavioral research suggests that individuals captured in deforested reaches tend to have more flexible behaviors that could cause them to change habitat selection priorities to match their current habitat, but whether they select for this habitat or adjust their behaviors after inhabiting this habitat is still unknown (Bliss and Cecala, 2015; Cecala and Maerz, 2016). Interestingly, this behavioral flexibility appears to be relevant to habitat selection with respect to light but not temperature (Bliss and Cecala, 2015; present study). As ectotherms, maintenance of body temperatures within an optimal range to maximize physiological functions may be less flexible than habitat selection with respect to other cues. Regardless, the thermal preferences of individuals from deforested reaches, although higher than individuals from forested reaches, are still lower than those observed for deforested areas, but individuals from both habitats had the ability to select habitat well above observed stream temperature maxima. During periods of time that temperatures exceed their optimal physiological function, individuals in deforested reaches may reduce their surface activity that could also reduce foraging time (Barbour et al., 1969; Spotila, 1972; Feder, 1983). Individuals captured in deforested areas tend to be at lower body condition than their forested counterparts (Bliss and Cecala, 2015), but again, biologists do not know whether individuals with poor body condition select for well-lit habitat or whether their poor body condition is a result of inhabiting well-lit habitat attributable to poor food resources (Hagen et al., 2010), higher metabolisms from warmer temperatures (Hillman et al., 2008), shifting foraging behaviors (Spotila, 1972; Feder, 1983), or a combination of these mechanisms. More research is needed to understand why some individuals persist in deforested areas.

Deforestation is a common result of human activities that has widespread effects on stream amphibian population size and connectivity in the southern Appalachian Mountains (Peterman and Semlitsch, 2009; Cecala et al., 2014; Surasinghe and Baldwin, 2015). This study suggests that avoidance of deforested areas by stream salamander larvae may be a result of individuals balancing light and thermal cues, although we acknowledge that more information about responses to UVB are necessary to completely understand trade-offs that larvae make in selecting habitat in and around riparian canopy gaps. The context-dependent nature of habitat selection decisions requires additional research into contextual or individual influences on decision-making processes. Research suggests that larval salamanders are capable of avoiding ecological traps associated with deforested areas (Liford and Cecala, 2017), but we encourage more research to understand whether low occupancy of stream amphibians in deforested reaches results from local extirpation because of ecological traps or demographic changes or results from avoidance of cues associated with deforestation.

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