
DOES HABITAT DISTURBANCE AFFECT THE BEHAVIORS OF APPALACHIAN STREAM SALAMANDERS?

MARGARET BLISS AND KRISTEN K. CECALA¹

Department of Biology, University of the South, Seawee, Tennessee 37383, USA

Corresponding author, email: kkecala@seawee.edu

Abstract.—Riparian disturbance often yields stream amphibian declines, yet some populations persist at low densities in impaired ecosystems. Understanding behaviors of individuals that select to occupy degraded habitat provides important insight into amphibian declines and may identify effective targets for management. Our objective was to evaluate whether fine-scale habitat selection behaviors and responses to environmental cues differed between individuals inhabiting disturbed versus undisturbed habitats. Specifically, we evaluated habitat selection and movement biases by larval *Desmognathus quadramaculatus* (Black-bellied Salamanders) from streams with and without riparian forest cover to different habitat cues. In a laboratory setting, we observed habitat selection with respect to light, a potential predator, and refuge, and also recorded exploratory movement to determine if salamanders occupying deforested stream reaches exhibited bold behavioral syndromes. We found that salamanders did not exhibit correlated behaviors indicative of bold or shy behavioral syndromes, but individuals from deforested stream reaches were less responsive to light. Secondly, we evaluated reactive behaviors by exposing salamanders to different light regimes. Individuals from deforested reaches exhibited greater reactivity to match their habituated light regime. Individuals originating from deforested habitats had relatively poor body conditions, indicating that individuals from deforested streams may experience additional costs relative to those from forested habitats. Despite demonstrated declines in abundance of aquatic salamanders following riparian disturbance, our results indicated that individuals that exhibit high behavioral plasticity are capable of inhabiting altered stream habitats and may represent the future of populations in disturbed areas.

Key Words.—behavioral plasticity; deforestation; *Desmognathus*; personality; phototaxis; riparian

INTRODUCTION

Rapid and large-scale habitat alterations have detrimentally affected numerous taxa, but some species and individuals have adapted to thrive in these changed environments (Koolhaas et al. 1999; Sih 2013). Habitat selection behaviors presumably have evolved to maximize the fitness of an individual, and variation in behavioral traits within and among individuals may facilitate long-term persistence of a species in human-modified ecosystems (Schlaepfer et al. 2002; Crispo 2008; Manenti et al. 2013; Sih 2013). Population-level variability in behavioral traits depends on the underlying genetic diversity of individuals that interacts with ecological outcomes of behaviors (Drent et al. 2003; van Oers et al. 2003; Dall et al. 2004; Sih et al. 2004). Ultimately, behavioral variability in a population may increase the probability that some individuals will have traits or tendencies that facilitate persistence in degraded habitats. Further, evaluating behavioral differences of individuals from different habitats will improve management for long-term species persistence in human-modified ecosystems (Lima and Zollner 1996; Gordon 2011; Berger-Tal et al. 2011).

Behavioral syndromes describe correlated individual behaviors through time and across contexts (Dingle 2001; Dall et al. 2004). Correlated behaviors are often

found along gradients from bold to shy (Wilson et al. 1994; Sih et al. 2004) or reactive to proactive (Koolhaas et al. 1999; Sih et al. 2004). In rapidly changing environments, evolutionary theory would predict that bold and reactive individuals would respond faster and more favorably to novel ecological cues than shy or proactive counterparts thriving in stable habitats (Benus et al. 1991; Koolhaas et al. 1999; Sih et al. 2004). Bold and reactive individuals may provide an essential buffer to maintain demographic processes of dispersal and reproduction in modified ecosystems (Koolhaas et al. 1999). Additionally, individuals may also exhibit non-associative learning or habituation, the result of repeated exposure to a cue that results in neutral outcomes (Groves and Thompson 1970). This could allow individuals to ignore inconsequential cues and accurately respond to others, maximizing their fitness in novel habitats (Borenstein et al. 2008). One characteristic of reactive individuals is a high degree of behavioral plasticity, as they alter their responses to environmental cues that may ultimately provide them an advantage in human-modified ecosystems (Sih et al. 2004; Mery and Burns 2010).

Riparian disturbance is one form of anthropogenic change impacting southern Appalachian stream biodiversity (Kirsch and Peterson 2014; Cecala 2012; Cecala et al. 2014). Stream-associated amphibians live

under well-developed riparian canopies (Crawford and Semlitsch 2008); however, some streams remain occupied at low rates despite open canopies (Cecala 2012). Regions of limited canopy cover may represent poor habitat quality due to the high predator densities associated with human development (Chalfoun et al. 2002), smaller pools of basal resources resulting from canopy removal (Wallace et al. 1997), or thermal challenges to the physiology of stream-associated amphibians (Bernardo and Spotila 2006). Fine and intermediate scale behavioral studies suggest that low abundance and occupancy of stream-associated amphibians in these reaches may result from negative phototactic behavior (Cecala 2012) and limited movement across canopy gaps (Cecala et al. 2014). Nevertheless, these behaviors do not explain why some individuals choose to persist in these habitats while others avoid them.

This study aims to evaluate whether individuals occupying deforested stream reaches exhibit different behavioral traits than individuals from forested stream reaches, and if such individuals experience positive or negative effects of inhabiting those canopy gaps. We tested the following hypotheses: (1) individuals from deforested reaches would exhibit bolder and more reactive responses to cues than individuals from adjacent forested reaches; (2) individuals from canopy gaps would exhibit greater behavioral plasticity; and (3) individuals from deforested reaches would be smaller than predicted relative to forested stream reaches. Specifically, we evaluated larval *Desmognathus quadramaculatus* (Black-bellied Salamander) behavioral responses to a novel environment, refuge availability, light gradient, and predator to determine if individuals exhibited correlated behavioral syndromes. Individuals with bold or reactive personalities would be expected to explore novel ecosystems more, use refuge less, and locate themselves closer to light and a predator than individuals with shy or proactive personalities. We also evaluated reactivity of individuals by examining phototactic responses to light after being habituated to two different light regimes. We hypothesized that individuals from deforested reaches would exhibit a greater response to the light regimes; whereas, individuals from forested reaches would exhibit more fixed behavioral responses.

MATERIALS AND METHODS

Study organism.—We evaluated the behaviors of larval *D. quadramaculatus* because of their high abundance and broad distribution throughout the southern Appalachian Mountains (Peterman et al. 2008; Milanovich 2010). We selected larvae because they exhibit easily observable behaviors and have higher detection probabilities and fewer housing requirements

than adults. *Desmognathus quadramaculatus* larvae are associated with streams within the southeastern mountains of the United States with well-developed mid- and upper-story canopies and have been used in similar studies to evaluate salamander behaviors in response to disturbance (Peterman et al. 2008; Cecala 2012; Cecala et al. 2014).

Collection methods.—We collected *Desmognathus quadramaculatus* larvae (snout-vent length [SVL] 16–41 mm) from one fishless headwater stream in Macon County, North Carolina, USA (UTM 17S E288105, N3909668) and three fishless streams in Rabun County, Georgia, USA within the southern Appalachian Mountains (UTM 17S E276625, N3855797; E276231, N3856721; E278423, N3857720). These sites each had similar forested environments as well as canopy gaps (deforested) that were cleared in the 1920s for power-line rights-of-way that ranged from 13–85 m in width. Light levels under canopy cover were only 10% of light intensity in the canopy gaps (Cecala 2012). We collected salamanders from the stream within the canopy gap and within 30 m of forest upstream and downstream of the canopy gap and transported them back to Sewanee, Tennessee, USA, for behavioral experiments. We also captured 14 larval Spring Salamanders (*Gyrinophilus porphyriticus*), natural predators on *D. quadramaculatus* larvae (Petranka 1998), from one site in Jasper, Georgia, USA. Each *G. porphyriticus* (SVL 45–67 mm) co-occurred with *D. quadramaculatus* and was large enough to consume *D. quadramaculatus* larvae used in this study. We housed salamanders individually in native stream water with a paper towel cover object at 12° C with a 14:10 light:dark cycle with indirect sunlight (shaded windows) and fed blood worms (Chironomidae) *ad libitum*. Upon arrival to the laboratory, we processed the animals by weighing, measuring snout-vent and tail length, and noting if any part of the tail was missing.

Habitat selection trials.—We evaluated the behavior of 70 individual *D. quadramaculatus* larvae with 35 individuals originating from a deforested reach (canopy gap) and 35 from forested reaches. We first tested all individuals in our test enclosure to evaluate exploratory movement in a novel environment. For this experiment, we placed the animals halfway between the ends of the enclosure and observed them for 20 min, noting distance from the midpoint of the enclosure and how often they moved at least one body length. We filled 150 × 25 cm enclosures with aged tap water up to 2 cm deep and a sand substrate (initially washed with a 1% bleach solution), characteristic of their natal habitats. We added water between trials to maintain consistent water depth. We observed behaviors from 0800 to 1600 to reflect times when sunlight cues may influence behavior. We

shaded all windows in the room to eliminate extraneous light cues.

The initial selection trials were followed in a randomly determined order by our observations of their responses to a light gradient, refuge, and a predator. For light, refuge, and predator trials, we placed one salamander in the middle of the enclosure and monitored its position every 20 min throughout a 6-h interval. We tested our light and predator hypotheses by placing a light or a caged potential predator (*G. porphyriticus*; Petranka 1998) at one end of an enclosure and measured the distance the test individual located itself from the treatment. We used a compact fluorescent lamp to create a gradient from high light near the source to low light at the opposite end without imposing a thermal gradient (Cecala 2012). We randomly determined the position of light and predators for each set of trials. We used the same position for all enclosures within a time interval to prevent cross contamination of our light gradients. To examine use of refuges, we evenly-spaced four cobblestones of equal size throughout the enclosure and noted the frequency with which individuals were found under cover during our refuge experiment. We monitored salamander location as unobtrusively as possible to limit movement in response to our observations. For example, during the cover trials, we could often spot the tail of an individual protruding from the rock that allowed us to determine the position of the salamander without disturbing the cover object. However, if the salamander could not be spotted, we lifted one end of the cobblestones to confirm individual locations.

Habituation experiment.—We used 140 *D. quadramaculatus* larvae for this study with 70 originating from deforested reaches and 70 originating from forested reaches of the same streams in the previous experiment. Within one week of capture, we evaluated the habitat selection behavior of each individual in response to a light gradient using the protocol outlined above. We randomly assigned each individual to the experimental light or dark light regime ensuring that at least 30 of each habitat type was placed into each light regime. We housed both animal groups at 12° C, but we exposed individuals in the light regime to direct exposure to a compact fluorescent light for 14 h and kept them in the dark for 10 h each day that represented the summer light-dark cycle from their capture locations. We kept individuals assigned to the dark regime in complete darkness or the absence of light cues to maximize potential behavioral differences. Individuals experienced these light regimes for at least two weeks before we re-tested their habitat selection behaviors in response to a light gradient.

Data analysis.—We assessed body condition of salamanders from canopy gaps relative to those from the forest by evaluating size-corrected masses for all sampled individuals without tail loss. We obtained size-corrected masses from an ordinary least squares linear regression of log-transformed SVL and mass data (Green 2001; Schulte-Hostedde et al. 2005). For each individual, we calculated the residual of their mass from their predicted mass and determined that no linear relationship existed between the residuals and the log-transformed SVL (Green 2001). We tested whether residuals of size-corrected mass between the individuals from the canopy gaps or forests were different using a linear mixed model. We included capture site as a random factor and habitat type as a fixed factor. A likelihood ratio test was evaluated to determine the significance of habitat on body condition. We used an α of 0.05 to evaluate significance. We implemented all linear mixed models in R (R Development Corp Team 2014) using the lme4 package (Bates et al. 2015).

We used linear mixed models to evaluate the role of habitat type on habitat selection and movement of larval salamanders. For repeated observations of position, we averaged position values or used frequency of refuge use data for each individual. We included a random factor of capture site to account for any variability associated with the four different capture sites. We did not include a temporal blocking factor because we randomly assigned individuals to test days and treatments. We evaluated the significance of the fixed factor, forested or deforested habitat origin (habitat type) using likelihood ratio tests (Burnham and Anderson 2002). To evaluate whether larval salamanders exhibited behavioral syndromes, we tested whether mean behavioral responses to different cues and exploratory behavior were correlated within an individual using the Pearson correlation in R. We evaluated the normality of our data using the Shapiro test and adjusted the non-normal factor (frequency of cover use; $P = 0.026$) using an arc-sine transformation.

To evaluate the role of habituation in different light regimes, we designed a linear mixed model with capture site as a random factor. We evaluated the difference between the first observation before our treatment and the second observation after our treatment. We did not include a random factor of time because we were able to complete all observations for either the pre- or post-habituation trials within 3 d of one another. We evaluated fixed factors of habitat origin type (forested or deforested stream reach) and habituation environment (light or dark). The importance of habitat type and/or habituation treatment was evaluated by examining Akaike information criteria model weights and effect sizes of the predictors (Burnham and Anderson 2002). To determine if individuals exhibited correlated reactive behaviors, we performed a Pearson correlation between

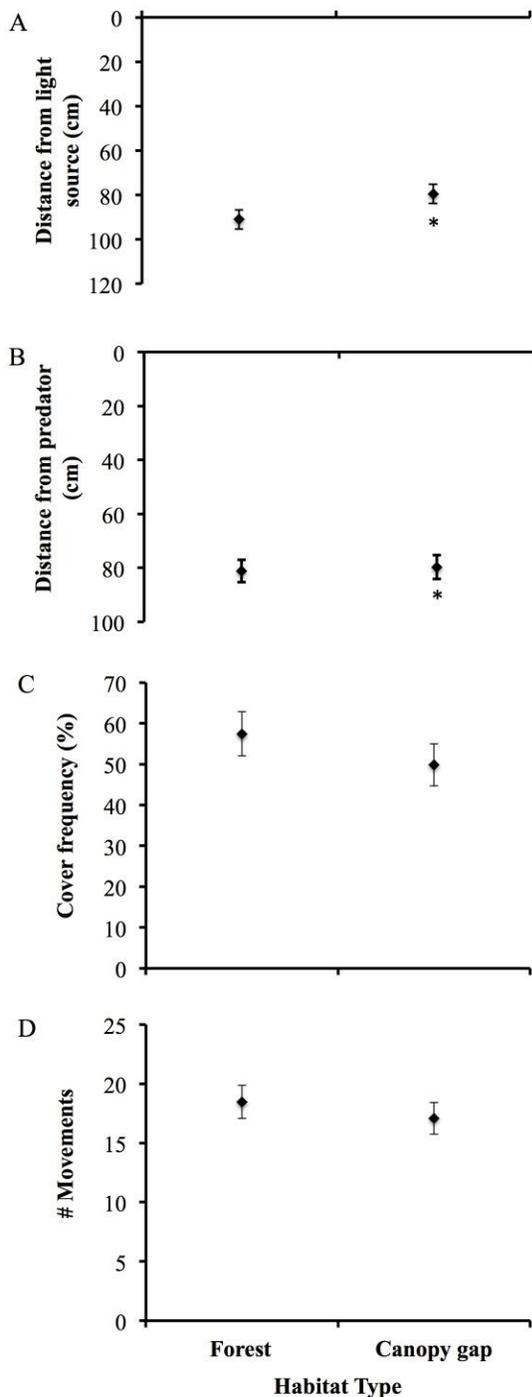


FIGURE 1. Habitat selection and movement behavior of larval *Desmognathus quadramaculatus* (Black-bellied Salamanders) from different habitat origins in response to light (A), a predator (B), cover availability (C), and a novel environment (D). An asterisk represents a statistically significant effect of habitat origin.

initial response to light and the difference between the pre- and post-treatment responses to light. We also conducted a Bartlett's test to determine if among-individual variability was similar between habitat types.

TABLE 1. Significance (*P*-values) of Pearson correlations (coefficient in parentheses) to assess whether larval *Desmognathus quadramaculatus* (Black-bellied Salamander) individuals exhibit correlated behaviors. The data indicate that exploratory movement, phototaxis, antipredator, and cover-use behaviors are not significantly correlated to one another.

	Movements	Light	Predator	Cover Use
Movements	-	0.59 (0.20)	0.78 (0.01)	0.11 (0.07)
Light	-	-	0.18 (-0.17)	0.48 (-0.09)
Predator	-	-	-	0.26 (0.02)
Cover Use	-	-	-	-

RESULTS

Individuals from deforested reaches were 12% smaller than individuals from forested reaches ($X^2 = 3.36$, $df = 1$, $P = 0.06$). Only 4% of individuals ($n = 3$ of 70) from forested reaches had tail injuries while 19% ($n = 13$ of 70) of individuals from deforested reaches experienced some degree of tail loss. On average, individuals from deforested reaches were found 15% closer to a light source ($X^2 = 7.78$, $df = 1$, $P = 0.01$, Fig. 1A), 2% closer to a predator ($X^2 = 5.36$, $df = 1$, $P = 0.02$, Fig. 1B), and spent 12% less time under cover relative to individuals from forested streams ($X^2 = 0.760$, $df = 1$, $P = 0.38$, Fig. 1C). Individuals from forested reaches were found to explore a novel enclosure 4% more than individuals from deforested reaches ($X^2 = 4.02$, $df = 1$, $P = 0.05$, Fig. 1D). Individual behaviors were uncorrelated among treatments (Table 1).

In our habituation models, the best-fitting model included only light regime as a predictive factor followed by a second model that included the additive effects of habitat type (Table 2). Individuals from deforested reaches housed in a dark environment selected habitat 13% further from the light source than they did immediately following capture (Fig. 2). Alternatively, individuals from deforested reaches housed in a well-lit environment selected habitat 20% closer to the light source than they did immediately following capture (Fig. 2). Individuals from the forested streams either did not alter their distance located from light or located themselves 5% closer to the light source following time spent in a dark environment (Fig. 2). Variance between habitat types was similar (post hoc Bartlett's test: $K^2 = 0.07$, $df = 1$, $P = 0.69$). Initial selection of distance from light was significantly correlated with the difference observed post-treatment ($r = 0.49$, $P < 0.01$).

TABLE 2. Model selection results of the generalized linear mixed model predicting larval *Desmognathus quadramaculatus* (Black-bellied Salamander) habitat selection based on the light regime (Light) and the habitat type (Habitat) where the individual was captured (forested or deforested stream reach) including a random effect of capture site. The generalized mixed models show that habitat type and the light habituation regime are significant factors in habitat selection among stream salamanders.

Model	K	AIC	Δ AIC	AIC weight
Light + capture site	4	2731.04	0.00	0.47
Light + habitat + capture site	5	2732.80	1.77	0.20
Capture site	3	2733.29	2.25	0.15
Light*habitat + capture site	6	2733.95	2.91	0.11
Habitat + capture site	4	2734.94	3.90	0.07

DISCUSSION

Despite collecting individuals from two distinct habitat types, larval *D. quadramaculatus* do not exhibit significant differences in exploratory or cover-use behavior upon capture, nor do individuals exhibit correlated responses to environmental stimuli. However, individuals from deforested reaches maintain positions closer to light sources and predators than those from forested reaches. Individuals from deforested reaches possibly experience negative consequences from inhabiting deforested zones as they have significantly lower body condition and experience tail injuries more frequently than their counterparts from nearby forested reaches. The most notable difference among individuals from forested and deforested reaches is the greater reactivity of individuals from deforested reaches to light regimes. Although not exhibiting behaviors associated with bold personalities, individuals from deforested reaches tend to exhibit reactive traits.

Individuals may inhabit deforested reaches because they exhibit more reactive personality traits or greater behavioral plasticity in response to environmental cues in a novel context. Deforested reaches are exposed to direct, unfiltered solar radiation; whereas, forested reaches have light filtered by dense mid-and upper-story canopies (Allan 2004; Caissie 2006). Negative phototactic behaviors by individuals from forested reaches would maintain their position within these forested reaches. Reduced reaction to and reliance on light cues may facilitate occupancy in deforested reaches (Cecala 2012; Mackey et al. 2014). Underlying personality differences in larval salamanders may explain variation in cue use. By exposing individuals from both habitat types to different light regimes, we observed that individuals from deforested reaches used cues that matched their light regime. For example, individuals from deforested reaches exposed to the light

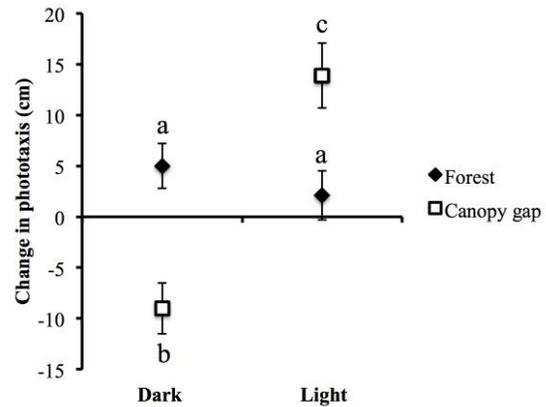


FIGURE 2. Change in phototactic behaviors displayed by two groups of larval *Desmognathus quadramaculatus* (Black-bellied Salamanders) exposed to different light regimes. Dark indicates that individuals were housed in near complete darkness while Light indicates that individuals were housed in a 14:10 light to dark cycle under a compact fluorescent bulb. Letters indicate significance of changes in phototaxis after two weeks.

regime later selected for brighter habitat patches whereas individuals from forested patches maintained their preferences through time. Likewise, individuals from deforested reaches selected darker habitats when held in the dark, whereas those from forested reaches selected locations slightly closer to light. These results suggest that individuals from deforested regions exhibited greater within-individual variation in behaviors, indicative of a reactive personality. Although habituation to light could explain positive phototactic behavior immediately following capture, rapid changes in phototactic behavior corresponding to the most recent exposure to light imply that habituation does not fully explain our results. Further evaluation of reactive traits in individuals from deforested reaches is necessary to confirm the reactivity hypothesis, but increased behavioral plasticity may confer success in altered ecosystems. Conversely, individuals with reactive personalities may experience a cost associated with learning to adapt to novel cues.

Multiple mechanisms may be responsible for reduced body condition of individuals from deforested reaches. Animals tend to locate themselves in patches with high resource availability and low predator risk and often use past experiences to detect these patches (Mathis and Unger 2011). Because recent studies propose that our study area is nearing the southern range limits of this species due to physiological limitations (Bernardo and Spotila 2006), high temperatures associated with deforested stream segments may exceed physiological tolerances (Caissie 2006). In deforested regions, salamander foraging may be reduced to avoid high temperatures or their physiology may be stressed. Body condition may also be altered in canopy gaps by limited access to preferred detritivorous macroinvertebrate prey

as stream basal resources shift from allochthonous to autochthonous sources (Hagen et al. 2010). Both environmental stressors could potentially result in the poor body conditions characteristic of salamanders from deforested streams used in this study if high temperatures result in high metabolic rates without sufficient resources to support those metabolic needs (Placyk and Graves 2001; Caruso et al. 2014). Finally, forest-field ecotones are often movement pathways for mesomammals or birds (Chalfoun et al. 2002), but it is unknown whether these organisms prey upon salamanders in canopy gaps. Increased rates of tail autotomy could represent increased predation risk in canopy gaps, but this hypothesis requires more research. Although individuals from canopy gaps consistently located themselves closer to predators, the difference was only 3 cm, which may or may not increase their predation risk. Increased predation rates may also alter foraging behavior including altered diurnal timing or increased stress, simultaneously reducing salamander body condition in deforested reaches (Bachman 1993; Lima 1998; Maerz et al. 2001). Reduced body condition and increased rates of tail autotomy may also represent costs associated with learning to respond to cues in a deforested context. More research is necessary to identify if salamanders exhibit evaluate behavioral shifts in response to different types of predators including avian or mammalian predators.

Despite negative consequences of occupying disturbed habitats, individuals persist in degraded stream reaches possibly due to positive habitat selection, exclusion from high-quality patches, or local adaptation to prefer these patches. Our study suggests that individuals with reactive personalities may be individuals that either select for degraded habitat patches or those that survive following habitat degradation. Alternatively, individuals may be forced to occupy deforested reaches from competitive interactions within forested reaches, or individuals located within gaps may be transient, moving or dispersing among forested reaches. We cannot exclude these potential mechanisms, as reduced body condition would also support these theories. Finally, if adults prefer these patches, offspring born in deforested reaches may be more likely to select these patches in the future; however, adult *D. quadramaculatus* in this region also exhibit negative phototaxis (Davis and Stamps 2004), and amphibian larvae apparently lack a natal preference induction period (Stamps and Krishnan 2014). Future studies evaluating whether individuals select degraded habitat or are forced into this habitat will help to determine the utility of managing canopy gaps for salamander persistence.

Why salamanders occupy canopy gaps is unclear and may be associated with a combination of factors. Increased behavioral plasticity associated with reactive personalities possibly explains why some larvae occupy

poor-quality habitat resulting in poor body condition. By demonstrating variability in responses to novel cues, individuals that maintain behavioral plasticity or reactivity are more likely to survive in modified landscapes (Koolhaas et al. 1999; Sih 2013; Osbourn et al. 2014). In unmodified ecosystems, fine-scale disturbance likely maintains a diversity of behavioral traits, yet in modified ecosystems, selection for behavioral traits that facilitate persistence in novel ecosystems may decrease the diversity of behavioral responses (Crispo 2008; Manenti et al. 2013). The long-term consequences of selection for particular behavioral traits may limit the ability of a population to respond to future change and requires further investigation.

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MARGARET M. BLISS is a senior Ecology and Biodiversity major at Sewanee: The University of the South from St. Louis, Missouri, USA. Her current research efforts are investigating behavioral shifts in amphibians resulting from ecological and environmental changes. Maggie is also a Canale Intern performing outreach and service with local high schools. (Photographed by Kristen Cecala).



KRISTEN K. CECALA is an Assistant Professor of Biology at Sewanee: The University of the South. She received her B.S. (2007) from Davidson College and Ph.D. (2012) from the Warnell School of Forestry and Natural Resources at the University of Georgia. She is broadly interested in understanding mechanisms contributing to changing ecologies and distributions of amphibians and reptiles due to environmental change. A strong proponent of undergraduate research, Kristen's undergraduate students are currently focusing on describing ecological patterns and processes occurring on the southern Cumberland Plateau. (Photographed by Janice Cecala).