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ARTICLE

Does riparian disturbance alter stream amphibian antipredator behaviors?

A.N. Liford and K.K. Cecala

Abstract: Ecological traps occur when a species makes maladaptive habitat-selection decisions. Human-modified environments including deforested riparian habitats can change how organisms respond to environmental cues. Stream amphibians alter their habitat selection in response to abiotic cues associated with riparian clearing, but little research exists to determine if behavioral shifts to abiotic cues may make them more susceptible to predation. To evaluate if deforested habitats create ecological traps, we studied habitat-selection behavior of larval Black-bellied Salamander (*Desmognathus quadramaculatus* (Holbrook, 1840)) when given conflicting environmental cues. We also evaluated the potential for learning or adaptation to cues in deforested reaches by evaluating individuals from forested and deforested reaches. We anticipated that individuals from deforested reaches would make adaptive antipredator choices when presented with well-lit habitat, whereas individuals from forested reaches would select shaded habitat closer to a predator. We found that habitat origin, light, and predator presence all interacted to influence habitat selection. Although individuals from forested habitats selected shaded environments, all observed individuals adaptively avoided a predator. Individuals from deforested reaches were more willing to enter well-lit habitat to avoid the predator. Despite documented declines of salamanders associated with forest removal, it appears that individuals are capable of making adaptive antipredator decisions in degraded habitats.

Key words: behavioral adaptation, Black-bellied Salamander, canopy gaps, cues, deforestation, *Desmognathus quadramaculatus*, ecological trap, habitat selection.

Résumé : Les pièges écologiques se produisent quand une espèce prend des décisions de sélection d'habitat se traduisant par une mauvaise adaptation. Les milieux modifiés par les humains, y compris les habitats riverains déboisés, peuvent modifier les réactions d'organismes aux signaux ambiants. Si les amphibiens de cours d'eau modifient leur sélection d'habitat en réponse à des signaux abiotiques associés au déboisement des zones riveraines, peu de travaux sont disponibles pour déterminer si des changements comportementaux en réponse à des signaux abiotiques pourraient les rendre plus vulnérables à la prédation. Afin d'évaluer si les habitats déboisés créent des pièges écologiques, nous avons étudié le comportement de sélection d'habitat de larves de salamandre à ventre noir (*Desmognathus quadramaculatus* (Holbrook, 1840)) en présence de signaux ambiants contradictoires. Nous avons aussi évalué le potentiel d'apprentissage ou d'adaptation à des signaux dans des tronçons déboisés en évaluant des individus issus de tronçons boisés et déboisés. Nous anticipions que les individus de tronçons déboisés feraient des choix adaptatifs antiprédateur en présence d'un habitat bien éclairé, alors que les individus de tronçons boisés choisiraient un habitat ombragé plus près d'un prédateur. Nous avons constaté que l'origine de l'habitat, la lumière et la présence d'un prédateur interagissaient toutes pour influencer la sélection d'habitat. Si les individus issus d'habitats boisés choisissaient des milieux ombragés, tous les individus observés évitaient le prédateur de manière adaptative. Les individus issus de tronçons déboisés étaient plus disposés à entrer dans un habitat bien éclairé pour éviter le prédateur. Malgré les baisses documentées des salamandres associées au déboisement, il semble que les individus soient capables de prendre des décisions d'adaptation antiprédateur dans des habitats dégradés. [Traduit par la Rédaction]

Mots-clés : adaptation comportementale, salamandre à ventre noir, ouvertures du couvert, signaux, déboisement, *Desmognathus quadramaculatus*, piège écologique, sélection d'habitat.

Introduction

All animals perceive and use cues from their environment to inform decisions about important behaviors such as habitat selection or breeding (Woodward et al. 2001; Rittenhouse et al. 2004; Cayuela et al. 2014). Changes to an environment can result in altered or novel cues causing maladaptive decisions based on incorrect perceptions of habitat quality (Boal and Mannan 1999; Woodward et al. 2001; Sih et al. 2011). This concept is referred to as an ecological trap, a situation where an animal chooses to inhabit a degraded or low-quality habitat over a high-quality habitat based on misleading environmental cues (Schlaepfer et al. 2002; Battin 2004). Although certain cues may have been formerly correlated with a particular outcome, rapidly changing environments may cause disconnect between cues and outcomes (Schlaepfer et al. 2002), resulting in decreased survival and fitness. For example, gravestones can emit the same horizontally polarized light as smooth water, causing dragonflies to be attracted to gravestones for oviposition rather than water surfaces (Horváth et al. 2007). Ecological traps fit into the framework of source–sink dynamics as an attractive sink, a low-quality habitat that is preferentially chosen (Battin 2004). Ecological traps have been noted in birds (Dwernychuk and Boag 1972; Woodward et al. 2001; Boal and Mannan 1999), sea turtles (Witherington 1997), insects (Kriska et al. 1998;

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Horváth et al. 2007), and amphibians (D'Amore et al. 2009; Ward-Fear et al. 2009). As humans continue to modify habitat, ecological traps provide one potential mechanism for population declines (Sih et al. 2011).

Riparian forest removal is responsible for declines of aquatic species including stream amphibians (Darveau et al. 1995; Jones et al. 1999; Peterman and Semlitsch 2009), and those declines may in part be due to shifting cues (Sih et al. 2011; Cecala and Maerz 2016). Following forest removal and the subsequent increase in light, streams often experience changes in temperature regimes (Brown and Krygier 1970), increased UVB radiation (Kelly et al. 2003), and greater autochthonous production (Hagen et al. 2010). At warmer temperatures, salamanders in the southern Appalachian region approach metabolic depression resulting from thermal stress (Marangio 1975; Bernardo et al. 2007). In addition to changed abiotic factors, stream food webs may also shift to include more mesopredators that use forest ecotones as movement pathways (Darveau et al. 1995; Chalfoun et al. 2002). Ultimately, riparian forest removal results in warm, dry habitats for which salamanders are poorly adapted (Crawford and Semlitsch 2007; Peterman et al. 2011). Larval salamanders that persist in these degraded environments often have higher rates of injury and lower body condition than those from forested reaches (Bliss and Cecala 2015).

Previous research has shown that riparian forest gaps act as movement barriers for stream salamanders owing to negative phototaxis (Cecala et al. 2014; Cecala and Maerz 2016), a well-conserved behavior among a wide variety of amphibians that may be a mechanism for avoiding stressful habitats (Garcia et al. 2004; Greenberg 2001). It has also been observed that individuals from deforested and forested stream reaches all exhibit negative phototaxis, but that individuals from deforested reaches respond less strongly to light cues than do individuals from forested reaches (Bliss and Cecala 2015; Cecala and Maerz 2016). Because amphibians are capable of moving away from canopy gaps (Lowe 2003; Cecala et al. 2009, 2014), behavioral shifts by individuals selecting well-lit habitat may represent habituation to light cues, associative learning with light cues, or different behavioral syndromes of individuals that occur in deforested habitat (Sih et al. 2011; Bliss and Cecala 2015). Regardless, consistent negative phototaxis suggests that individuals could prioritize response to light cues over responses to other cues. Larger salamanders and other fish use similar refugia as larval salamanders, exposing larval salamanders to high risk of predation (Semlitsch 1987; Sih et al. 1992; Petranka 1998), which represents one potential consequence of different habitat-selection behaviors in canopy gaps (Bliss and Cecala 2015; Cecala and Maerz 2016). If negative phototaxis causes salamanders to prioritize movement away from light towards refuge over predator cues, then negative phototaxis in well-lit canopy gaps could prove to be an ecological trap and provide a mechanistic understanding for why occupancy of salamanders decline in deforested streams (Grant et al. 2016).

To determine whether canopy gaps serve as an ecological trap, we used behavioral observations in a field experiment using larval Black-bellied Salamander (*Desmognathus quadramaculatus* (Holbrook, 1840)), a large plethodontid salamander. The larvae were given conflicting cue sets to discover which cue would be prioritized, predator or shade. Conflicting cue sets are created by pairing cues so that movement away from one cue necessitates movement towards another cue, thus requiring individuals to prioritize one cue over another for habitat selection. We tested larval *D. quadramaculatus* behaviors in a sun-lit enclosure in response to shade, the presence of an intraguild predator, and both cues in conflict. Because some *D. quadramaculatus* individuals persist in degraded environments with open canopies, we also tested for potential behavioral differences between individuals experienced with well-lit environments (deforested) and those collected from fully forested streams (forested) where they were likely inexperienced with well-lit environments (Cecala and Maerz 2016). We hypothesized that larval *D. quadramaculatus* would exhibit negative phototaxis and predator avoidance. If riparian canopy gaps act as ecological traps, then we would expect that individual responses to light would exceed responses to predators as they prioritize negative phototaxis. Finally, we hypothesized that experience with well-lit environments would result in consistent predator avoidance despite the presence of light.

Materials and methods

Study species

Desmognathus quadramaculatus is a large plethodontid salamander endemic to the southern Appalachian Mountains (Petranka 1998). They exhibit a 2–3 year larval period where they grow to be one of the largest and most abundant larval salamanders in the region, making them easy to detect and observe in a behavioral study (Peterman et al. 2008). Adult salamander behaviors are influenced by light and humidity (Spight 1968; Spotila 1972; Feder 1983), but by studying larvae, we remove the conflicting influence of humidity to isolate the impact of light cues. As a predator, we used larval Spring Salamander (*Gyrinophilus porphyriticus* (Green, 1827)) because they are frequent intraguild predators and are likely to use similar refuges as larval *D. quadramaculatus* (Petranka 1998).

Field experiment

Desmognathus quadramaculatus larvae were captured from four fishless locations in the Upper Little Tennessee River basin. Each location included a canopy gap over the stream ranging from 13 to 85 m in length and adjacent fully forested stream locations. Sites were located at least 5 km from one another with a maximum distance of 50 km between sites. We collected 80 larval *D. quadramaculatus* from streams with canopy gaps and 80 from forested areas immediately upstream and downstream from the canopy gap. Though individuals were captured close together spatially, previous work has documented behavioral differences between individuals captured from canopy gaps and adjacent forests (Bliss and Cecala 2015; Cecala and Maerz 2016), and behavioral data in the laboratory and the field document resistance to movement into or through well-lit habitat or canopy gaps (Cecala et al. 2014; Cecala and Maerz 2016). We also collected 10 *G. porphyriticus* to serve as predators. Each captured *G. porphyriticus* was large enough (>45 mm snout–vent length (SVL)) to consume the *D. quadramaculatus* larvae used in this study (21–37 mm SVL). 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 tested individuals within 48 h of capture and released individuals at their capture location within 1 week. Larval *G. porphyriticus* were not fed for 48 h prior to experimentation. Larval *G. porphyriticus* were fed thawed blood worms every 2 days.

In-stream enclosures for this study were designed to allow stream water to pass through the enclosure and placed in a stream lacking canopy cover to use natural sunlight cues. The site where behavior was evaluated was located approximately halfway between the capture locations in another fishless stream (Upper Hickory Knoll Creek; Kirsch and Peterson 2014). We used a 0.8 mm mesh to form the enclosure boundaries and added no additional substrate to the enclosure. Each of these enclosures was 150 cm × 25 cm and was set with a water depth less than 10 cm. To create our shaded treatment, we used four layers of shade cloth to shade half the enclosure to light levels similar to those found above a forested stream (approximately 1500 lx). Predator treatments were created by placing a single larval *G. porphyriticus* in a small mesh enclosure measuring 25 cm × 5 cm. This enclosure was necessary to prevent predation and direct physical interference by the *G. porphyriticus* individual. The enclosure was clipped to the assigned end of the enclosure using a binder clip.

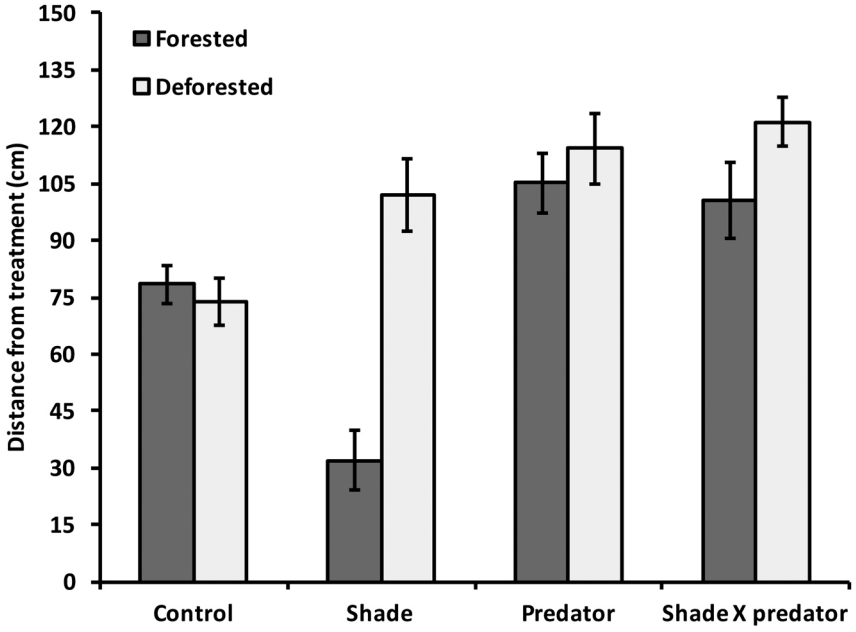
Each treatment was randomly assigned to either the upstream or the downstream half of the enclosure. We tested the responses

Table 1. Results of a linear mixed model evaluating the effects of shade, predator, and habitat origin on habitat selection in larval Black-bellied Salamanders (*Desmognathus quadramaculatus*).

Variable	Estimate	Standard error	df	*F*	*P*
Habitat origin	−5	10	1, 152	0.19	0.664
Shade	−46	11	1, 152	1.43	0.233
Predator	27	11	1, 152	19.15	<0.001
Habitat origin × shade	74	15	1, 152	23.69	<0.001
Habitat origin × predator	15	15	1, 152	0.82	0.368
Shade × predator	36	16	1, 152	0.93	0.338
Habitat origin × shade × predator	−60	22	1, 152	8.47	0.004

Note: Random effects in this model included capture location, direction of treatment, and individual.

Fig. 1. Mean (±1 SE) distance that larval Black-bellied Salamanders (*Desmognathus quadramaculatus*) selected relative to the presence of shade, a predator, and habitat origin (canopy gap or forest).



of 20 individuals from deforested reaches and 20 individuals from forested reaches to no-cues, shade-only, predator-only, and shade-and-predator treatments. Conflicting cues of shade and predator were created by placing the predator and the shade treatment on the same side of the enclosure. Individual *D. quadramaculatus* larvae were placed in the center of the enclosure, and their position relative to either the shaded edge of the enclosure or the predator was visually recorded every subsequent hour for 12 h using measurements on the side of the enclosures. In the no-cues treatment, we quantified distance from the downstream end of the enclosure. Individuals were only studied once, and trials began by 0700 to ensure daylight for the length of the trial in July 2011.

We evaluated the distance that larval *D. quadramaculatus* selected relative to shade and predators using a linear mixed-effects model. We included random effects of capture site and the treatment orientation (upstream or downstream). Repeated observations of individuals were achieved by including a random effect for individual. Fixed effects included presence or absence of a predator and shade and habitat origin (forested or deforested reach). We used package lme4 in program R (R Core Team 2015) and estimated *F* ratios using the Satterthwaite approximation using package lmerTest.

Results

We recorded 1920 observations of 160 individuals (80 from forested streams and 80 from deforested streams). Residuals were centered at 0.097 (75% range of −0.51 to 0.49). Variance associated with site was zero, but the direction of treatment and individual had variances of 1.24 ± 0.035 and 10.65 ± 0.33, respectively. Linear mixed models revealed that predator presence was the only single factor that influenced larval habitat selection ($F_{[1,152]}$ = 19.15, P < 0.001; Table 1, Fig. 1). Significant interactions were observed between habitat origin and the availability of shade ($F_{[1,152]}$ = 23.69, P < 0.001) and the three-way interaction between shade and predator presence and habitat origin ($F_{[1,152]}$ = 8.47, P = 0.004; Table 1, Fig. 1). Habitat origin did not have a significant interaction with predator presence, suggesting similar antipredator behaviors regardless of experience with light ($F_{[1,152]}$ = 0.816, P = 0.368; Fig. 1), nor was a significant interaction found between shade and predator presence ($F_{[1,152]}$ = 0.926, P = 0.338). Individuals from deforested reaches selected unshaded habitat and moved farther away from a predator into unshaded areas than individuals from forested reaches (Fig. 1).

Discussion

Our results indicated that canopy gaps do not act as an ecological trap for stream salamanders. Despite persistent behaviors

that cause salamanders to avoid light cues (Marangio 1975; Angilletta et al. 2002; Manenti et al. 2013), larval *D. quadramaculatus* made adaptive decisions in the presence of conflicting cues, choosing to move towards light rather than towards a predator, despite the suboptimal microhabitat that light presumably represents. We did observe a difference between predator avoidance behavior in salamanders from deforested reaches and those from forested reaches, with individuals from canopy gaps venturing farther towards light to escape a predator. However, antipredator behavior was prioritized over light avoidance in all cases, suggesting that predator avoidance is a stronger cue even for individuals not accustomed to bright light conditions.

Although infrequently observed, positive phototaxis is one mechanism to avoid predation in these systems but may also have other positive effects for salamander larvae. For example, positive phototaxis may result in habitat selection of warmer areas that could accelerate rates of growth and time to metamorphosis that may be adaptive in aquatic environments with high predator densities (Marangio 1975; Werner 1986; Beachy 1995; Ihli and Beachy 2016). Rapid growth could be a useful adaptation for acquiring resources before other larvae metamorphose, or for avoiding stream drying (Semlitsch et al. 1988; Beachy 1995). Conversely, accelerated development may result in individuals transforming at smaller sizes, which has been documented to negatively affect long-term fitness (Werner 1986). The occupancy of habitat typically avoided by other individuals is another possible advantage to positive phototaxis (Fretwell and Lucas 1970; Gilroy and Sutherland 2007). Canopy gaps could represent an undervalued habitat, the inverse of an ecological trap in which some individuals avoid a habitat because of a negative cue such as light (Gilroy and Sutherland 2007). In this scenario, canopy gaps may hold untapped resources or space that other organisms are reluctant to capitalize on because of the warmer, drier habitat. For example, small gaps may maintain allochthnonous resources that are supplemented by autochthonous production that increase basal carbon resources in canopy gaps (Hagen et al. 2010). Individuals able to override adverse behaviors to light may ultimately have an advantage over individuals that remain in forested areas.

Although positive phototaxis in this context is adaptive, in other contexts, it may be detrimental to fitness. For example, salamanders inhabiting canopy gaps have poorer body conditions than their forested counterparts (Bliss and Cecala 2015) and may be at higher risk of predation (Darveau et al. 1995). Ultimately, these changes could result in lower survival and reproductive rates culminating in population decline (Tilghman et al. 2012; Grant et al. 2016). An adaptation for positive phototaxis also may mean higher risk of lethal or sublethal effects of ultraviolet radiation. Ambient levels of UVB have been proven to have negative effects on larvae and egg masses (Blaustein et al. 1995; Nagl and Hofer 1997), especially in shallow, well-lit areas. Little research is available on the UVB effects on high-elevation stream amphibians in the eastern United States and what role it plays in light avoidance behaviors (but see Garcia et al. 2004). One potential defense against radiation is developing darker coloration (Belden and Blaustein 2002; Garcia et al. 2004), which may provide a mechanism for the continued persistence of individuals in canopy gaps where they might otherwise be unable to grow or survive due to UVB radiation. Although coloration was not noted in this study, it would be informative for future studies to examine whether individuals inhabiting canopy gaps tend to have darker skin color compared with those inhabiting fully forested habitats. In addition to UVB radiation, increased temperature can push salamanders to their physiological limits with a warmer and drier microclimate resulting in high stress and potentially lower fecundity (Bernardo and Spotila 2006).

Common to other studies, prior experience with light cues altered habitat-selection choices (Bliss and Cecala 2015; Cecala and Maerz 2016). We found that habitat origin did have a significant influence on habitat selection within the enclosure, with individuals from deforested stream reaches selecting areas closer to light and farther from a predator than did individuals from forested reaches. Our results suggest that prior experience with light or phenotypic plasticity results in changes to responses of individuals, allowing them to occupy previously unsuitable microhabitat. This may signal habituation to light or positive associative learning to light cues (Borenstein et al. 2008; Sih et al. 2011; Cecala and Maerz 2016). Alternatively, maternal effects or genetic differences cannot be excluded, though we suggest that maternal effects are unlikely because adults exhibit strong avoidance of light gaps and individuals were collected over short spatial scales where reproductive isolation is unlikely (Cecala et al. 2014). Previous research suggests that behavioral differences associated with reactive personalities (Bliss and Cecala 2015) may be most associated with assortative mating for behavioral flexibility or reactivity (Laubu et al. 2016). Regardless of the mechanism behind behavioral differences associated with habitat, the behaviors displayed by stream salamanders from disturbed habitat may result in increased fitness in human-modified ecosystems (Sih et al. 2011). Adaptation to novel ecosystems requires rapid and adaptive responses to changing cues and environments, but more research is needed to assess why habitat-selection differences exist between animals captured from disturbed and intact habitats and whether their abilities to adapt are equivalent (e.g., Bliss and Cecala 2015).

Our study indicates that despite documented declines of stream salamanders in open canopy areas (Tilghman et al. 2012; Grant et al. 2016), some individuals are able to persist in these degraded environments and make adaptive antipredator decisions. We acknowledge that adaptive decisions made in our study may be a result of the fine-scale nature of these behavioral observations. Although headwater streams in the southern Appalachians tend to have complete canopy cover, small areas of sunlight may reach the stream resulting in a mosaic of shaded patches within forested streams. Therefore, positive phototaxis on a fine scale may simply reflect an individual's willingness to move into an unsuitable area temporarily and may not reflect the same mechanisms that indicate avoidance of large-scale gaps (Cecala et al. 2014). Although studies in this system have documented declines in occupancy rates and poor body condition (Bliss and Cecala 2015; Cecala 2012), the present study suggests the potential for successful adaptation by stream amphibians to fine-scale canopy gaps.

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