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ARTICLE

Context-dependent responses to light contribute to responses by Black-bellied Salamanders (*Desmognathus quadramaculatus*) to landscape disturbances

K.K. Cecala and J.C. Maerz

Abstract: Behaviour often regulates population responses to environmental change, but linking behavioural responses to population patterns can be challenging because behavioural responses are often context-dependent, have an instinctive component, and yet may be modified by experience. Black-bellied Salamanders (*Desmognathus quadramaculatus* (Holbrook, 1840)) occupy forested streams where dense canopies create cool, dark environments. Because riparian deforestation negatively affects salamander-population connectivity yet some individuals choose to persist in these gaps, we sought to evaluate whether phototaxis could explain these patterns and whether phototactic behaviour would be influenced by experience (capture from forested or deforested areas) or context (refuge type and availability). Our results demonstrated that larval *D. quadramaculatus* exhibited negative phototaxis, but that larvae from forested streams exhibited stronger negative phototaxis than individuals from deforested streams. Larvae also selected habitat closer to light when refuge was available. Our results show that light alters habitat use by larval *D. quadramaculatus*, but the magnitude of that effect depends on refuge availability and experience with well-lit conditions associated with forest removal. As human activities reduce canopy cover and refuge availability, negative phototaxis may be one explanation for behavioural barriers to movement. Ultimately, the ability of salamanders to exhibit behavioural plasticity will determine their potential for local adaptation facilitating persistence in the face of environmental change.

Key words: Desmognathus quadramaculatus, habitat selection, land-use change, light, phototaxis, Plethodontidae, riparian, substrate.

Résumé : Si les comportements régissent souvent les réactions de populations à des changements ambiants, il peut être difficile de relier les réactions comportementales à des motifs à l'échelle de la population parce que ces réactions dépendent dans bien des cas du contexte, comportent un élément instinctif, mais peuvent néanmoins être modifiées par l'expérience. Les grands desmognathes à ventre noir (*Desmognathus quadramaculatus* (Holbrook, 1840)) occupent des cours d'eau boisés où un couvert dense crée des milieux frais et sombres. Comme la déforestation des berges a une incidence négative sur la connectivité des populations de salamandres, mais que certains individus choisissent de demeurer dans les zones intercalaires, nous avons tenté de déterminer si la phototaxie pouvait expliquer ces motifs et si le comportement phototaxique serait influencé par l'expérience (capture dans des zones boisées ou déboisées) ou par le contexte (type et disponibilité de refuges). Nos résultats ont démontré que des larves de *D. quadramaculatus* présentaient une phototaxie négative, mais que les larves de cours d'eau boisés présentaient une plus forte phototaxie négative que les individus de cours d'eau déboisés. Les larves choisissaient également des habitats plus près de la lumière quand un refuge était disponible. Nos résultats montrent que la lumière modifie l'utilisation de l'habitat par les larves de *D. quadramaculatus*, mais que l'ampleur de cet effet dépend de la disponibilité de refuges et de l'expérience dans des conditions bien illuminées associées à la déforestation. Comme les activités humaines réduisent le couvert forestier et la disponibilité de refuges, la phototaxie négative pourrait constituer une explication des barrières comportementales aux déplacements. Ultimement, la capacité des desmognathes à faire preuve de plasticité comportementale déterminera leur potentiel d'adaptation locale facilitant la persistance en réponse à des changements du milieu ambiant. [Traduit par la Rédaction]

Mots-clés : Desmognathus quadramaculatus, sélection de l'habitat, changement d'utilisation du sol, lumière, phototaxie, pléthodontidés, rivulaire, substrat.

Introduction

Habitats vary in quality based on a number of factors that influence animal survival, growth, and reproduction (Werner and Anholt 1993), and it is widely accepted that habitat-selection behaviours have evolved to maximize an organism's fitness. Animals may accomplish this goal by responding to direct or indirect cues that maximize their fitness (Werner et al. 1983; Gilliam and Fraser 1987; Lima and Dill 1990; Brown et al. 1996; Roberts and Liebgold 2008). Although instinctive behaviours often guide animal responses to certain cues, these behaviours are only advantageous when the cue reliably indicates environmental conditions over long temporal scales (Borenstein et al. 2008). With fluctuating environmental conditions, habitat-selection plasticity would confer greater success than a fixed response (Borenstein et al. 2008). Population-level variability in habitat-selection behaviours results from variation in environmental context and individual experience (Gilliam and Fraser 1987; Davis and Stamps 2004; Benard and McCauley 2008; Dingemanse et al. 2010). Therefore, evaluating and predicting how a population responds to a change

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in one environmental cue requires examining how these responses interact with other changing environmental cues. Drawing ecological inferences about their responses to change can also be challenging because experience with contextual cues in heterogeneous environments can be highly variable among individuals (Lima and Zollner 1996; Gordon 2011). Consequently, comprehensive examinations of habitat-selection behaviours in response to multiple changing environmental cues are essential to predict how populations will respond to environmental change.

To evaluate behavioural shifts in an increasingly impacted ecosystem, we evaluated stream-breeding amphibians because they are beginning to respond to environmental change yet some individuals remain in disturbed habitats (Cecala 2012). Removal of riparian forest is commonly associated with urban and suburban developments. In addition to increasing sunlight penetration to the stream and warming stream temperatures (Paul and Meyer 2001; Walsh et al. 2005), riparian forest removal alters the availability of refuge by increasing flood magnitudes and erosion that flush leaves and small pebbles from the stream and fill in interstitial spaces created by cobble (Caissie 2006; Burcher et al. 2007). The creation of canopy gaps and edge habitat can also alter stream food webs by increasing primary productivity and increasing the presence of predatory mammals and birds (Crooks and Soulé 1999; Chalfoun et al. 2002). The loss of forest cover is known to affect behaviours such as dispersal of many forest-interior organisms (Schreiber and Graves 1977; Vistnes et al. 2004; Rittenhouse and Semlitsch 2006; Cecala et al. 2014), and the removal of forest canopy is associated with reduced amphibian diversity and abundance (Ash 1988, 1997; Ford et al. 2002; Willson and Dorcas 2003; Peterman et al. 2011; Cecala 2012). Finally, recent evidence suggests that deforested riparian zones may act as barriers to salamander movement along stream corridors (Cecala et al. 2014).

Despite the documented negative effects of anthropogenic habitat change, some individuals occupy impacted habitat (Cecala 2012; Sih 2013). Appalachian stream salamanders are adapted to cool shaded conditions of fully forested streams (Petranka 1998; Kozak and Wiens 2010), yet some individuals persist in stream reaches with deforested riparian zones (Cecala 2012). Studies have repeatedly demonstrated negative phototaxis in salamanders (Wilder 1913; Sugalski and Claussen 1997; Placyk and Graves 2001), but our observations of individuals in streams with deforested riparian zones is counter to predictions of this conserved behaviour. In this study, we seek to evaluate whether experience with well-lit conditions common to deforested stream reaches alters phototactic behaviour to explain this discontinuity. We infer experience from differences in larval sources related to losses of forest cover and that differences related to source-population experiences may include both learned or conditioned responses or local adaptation via selection for individuals less sensitive to the environmental cue. Because riparian forest removal is correlated with changes to stream geomorphology and therefore refuge availability (Burcher et al. 2007), we also assessed salamander phototactic responses in the context of refuge availability and common types.

The objective of this study was to examine the interactions between experience and context on the response of larval Black-bellied Salamanders (*Desmognathus quadramaculatus* (Holbrook, 1840)) to sunlight cues intensified following riparian forest removal. *Desmognathus quadramaculatus* forms the majority of larval salamander biomass in a diverse guild of streamside salamanders (family Plethodontidae) that are widely distributed throughout streams of the eastern United States (Petranka 1998; Peterman et al. 2008; Cecala 2012). We used a combination of laboratory and field experiments to examine microhabitat selection by larval *D. quadramaculatus* to determine if their experience with light (captured in forested or deforested reaches) or the environmental context of stream-refuge availability and type interacted to influence their behaviour. We hypothesized that (*i*) larvae would exhibit negative phototaxis by moving away from a light source, (*ii*) negative phototaxis would be greater in the absence of refuge, and (*iii*) individuals from deforested reaches would exhibit weaker negative phototaxis compared with individuals from forested reaches.

Materials and methods

Study organism

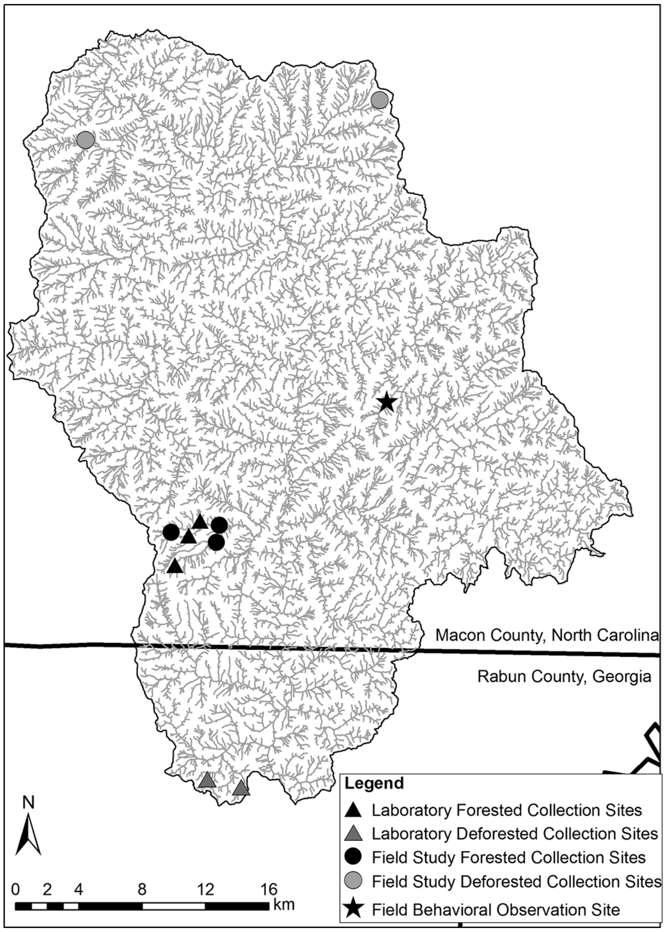
We selected to use *D. quadramaculatus* as our focal organism because this species represents one of the most aquatic and abundant headwater stream-breeding salamanders in the southern Appalachian Mountains (Petranka 1998; Peterman et al. 2008; Milanovich et al. 2015). This species belongs to the most diverse genus of stream salamanders and observations of their behaviours could be used to predict behaviours of other species (Petranka 1998). Previous research has demonstrated that occupancy of *D. quadramaculatus* declines with declining riparian forest cover and that riparian canopy gaps inhibit their movement (Cecala 2012; Cecala et al. 2014). Adult *D. quadramaculatus* lay 38–55 eggs that hatch in late summer (Petranka 1998). Larvae spend 2–4 years in streams before metamorphosis during which time they may move widely (>80 m upstream and downstream) and demonstrate site fidelity (Petranka 1998; Cecala et al. 2014). Upon metamorphosis, juvenile and adult *D. quadramaculatus* inhabit near-stream environments, remaining within 1–2 m of the stream channel (Peterman et al. 2008).

Laboratory behaviour experiment

Larval *D. quadramaculatus* were collected from fishless, headwater streams in the upper Little Tennessee River basin (Fig. 1). Salamander populations differentiate in headwater streams because of aquatic, upstream dispersal biases, suggesting that sampling of individuals from different headwater streams also samples different populations (Rissler et al. 2004; Grant et al. 2010; Lowe et al. 2012). We collected 180 individuals from three headwater streams in the fully forested Ball Creek watershed at the Coweeta Hydrologic Laboratory in Macon County, North Carolina. We collected 180 individuals from two stream reaches with deforested riparian zones within a watershed of Rabun County, Georgia, located approximately 10 km away from the Coweeta Hydrologic Laboratory (Fig. 1). Reaches were separated by approximately 0.6 km, exceeding any known dispersal distance for adult or larval stream salamanders (Lowe 2003). The deforested sites were selected because they were part of an ongoing study and had no other disturbance within the catchment besides a power-line right-of-way (Cecala et al. 2014). Individuals from the adjacent forested reaches were part of an ongoing study and unavailable for short-term removals. Local power companies have cleared and maintained these deforested riparian zones for at least the past 50 years, while the U.S. Forest Service has maintained forested habitat around the forested watersheds for the past 70 years (K.K. Cecala, unpublished data). These sites otherwise had similar physical and substrate attributes with the exception of canopy cover (Cecala 2012; Webster et al. 2012). Salamanders were captured opportunistically using dip nets and cover-object searches. Before behavioural observations were conducted, salamanders were held individually in containers with refuge, water from their source stream, and kept in a temperature-controlled room (15.5 °C) with a natural photoperiod from laboratory windows. Individuals were tested within 48 h of capture and subsequently released at their capture location within 1 week. Individuals were used for only a single treatment. This research complied with guidelines outlined by the Animal Behaviour Society and was approved by the University of Georgia Institutional Animal Care and Use Committee (A2009 09-168-A1).

We designed a full factorial experiment to determine the effects of light presence, experience, and context on the distance from a

Fig. 1. The upper Little Tennessee River Basin with animal collection sites identified by experiment and riparian habitat condition. Riparian conditions (forested or deforested) have been maintained for over 50 years at each location.



light source selected by salamanders. Factors included light presence or absence, refuge presence and type (i.e., context; sand only, sand and leaves, sand and cobble), and habitat type (i.e., experience; forested or deforested reach). Thirty individuals were tested for each combination of treatment conditions using a full factorial design. This study was performed in a temperature- and light-controlled room. Animals were observed individually in 150 cm × 25 cm enclosures constructed using a wood frame and inner pond liner to hold water. Each enclosure had a sand substrate soaked in a 1% bleach solution for 24 h before being rinsed for 10 min using tap water. Bleaching ensured that diseases were not transferred among individuals. We then introduced tap water for the experiment and allowed it to dechlorinate for 24 h before introducing each tested individual. At one end of each enclosure, a light source was placed with a low-heat-emitting lamp (compact fluorescent bulb) with wavelength peaks similar to those experienced by salamanders (400–700 nm; Makino and Dodd 1996). The light was either turned on for our light-presence trials or turned off for completely dark, light absent, trials. This light source provided a gradient from well-lit conditions close to the light source and low-light conditions at the far end of the enclosure. During dark trials, we used a red flashlight to indirectly light only the area of the enclosure necessary for us to search for the salamander. To examine the effects of context on behaviour, we tested salamanders in response to the absence of refuge (sand only) and in the presence of two types of commonly used refuge (leaves and cobble). Fifteen different objects (leaves or cobble) of equal size (<20 cm^2) were placed uniformly along the long, centre axis of the enclosure. Leaves were artificial craft leaves allowed to soak for 48 h to remove any excess dye. Cobble was collected from the local stream. Leaves and cobble were soaked in a 2% bleach solution for 24 h before being rinsed for 10 min prior to being placed in each enclosure. Each salamander was used only once within the study and was randomly assigned to a treatment. Animals were initially placed halfway between the high- and low-light regions to allow them to select to move either towards the light or away from the light. In dark trials, we placed individuals in the exact same location as the light trials. Initial placement in the middle of the enclosure allowed for positive or negative phototaxis to assess if individuals from deforested reaches exhibited positive phototaxis. After 1 h for acclimation to the enclosure, we measured distance from the light source every hour for 12 h. We tested 16 individuals simultaneously for 13 h per trial and repeated this process until all individuals were tested.

Field behaviour experiment

We collected 20 larval *D. quadramaculatus* from three forested headwater streams in the Ball Creek watershed of Macon County, North Carolina, and 20 larval *D. quadramaculatus* from a 65 m deforested power-line right-of-way located in Macon County, North Carolina, located approximately 50 km northeast from the watershed used in the "Laboratory behaviour experiment" above (Fig. 1). A different geographical location was used because access to the sites used in the laboratory experiment became limited; this provided an opportunity to evaluate whether behaviours observed in the laboratory experiment were consistent within the region. Individuals were captured using active surveys and housed in the same manner as in our "Laboratory behaviour experiment".

Salamander behavioural responses to sunlight were tested using a field enclosure. In-stream enclosures for this study were designed to allow stream water to pass through the enclosure and were placed in a stream lacking canopy cover to use natural-sunlight cues. Flow rates per hectare were 0.24–0.37 $\text{L}\cdot\text{s}^{-1}$, which is within the range of flow rates found at their capture locations. We used a 0.8 mm mesh wrapped around a PVC frame and added no additional substrate to the enclosure. Each of these enclosures was 150 cm × 25 cm and was set with a water depth <10 cm. We anchored enclosures by placing rocks outside the downstream edge of the enclosure. Enclosures were located at least 0.5 m from one another to reduce the availability of conspecific cues among enclosures. To create shade, we used four layers of shade cloth to shade half the enclosure to light levels similar to those found above a forested stream. Shade was randomly assigned to either the upstream or downstream half of the enclosure. Larval *D. quadramaculatus* were placed in the centre of the enclosure, and after a 1 h acclimation period, their distance from the shaded edge of the enclosure was recorded every hour for 12 h. Individuals were only studied once and the 13 h trials began by 0700 to ensure daylight for the length of the trial.

Data analysis

We used linear mixed models and multiple hypothesis testing to evaluate how context and experience altered habitat selection with respect to a light source (Bolker et al. 2009). Because we performed repeated observations of individuals, we used the mean distance individuals located themselves from the light source throughout our trials. We included a random factor for site to account for biases associated with capture location. We designed models using single predictors of light, context, or experience, as well as models that evaluated all interactions among these predictors. Using Akaike's information criteria corrected for small sample sizes (AIC_c), we ranked models from most likely to least likely (Akaike 1973; Hurvich and Tsai 1989; Burnham and Anderson 2002). We also calculated the R^2 of the best-fitting model to evaluate model fit to the data (Nakagawa and Schielzeth

Table 1. Model-selection results predicting habitat selection by larval Black-bellied Salamanders (*Desmognathus quadramaculatus*) with respect to light.

Model	*K*	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight
Light × experience × context	14	3555.07	0.00	1.00
Light × experience	6	3575.81	20.75	<0.001
Light + experience + context	7	3576.51	21.44	<0.001
Light × context	8	3577.55	22.48	<0.001
Light + experience	5	3586.60	31.53	<0.001
Light + context	6	3590.04	34.97	<0.001
Light	4	3599.35	44.28	<0.001
Experience + context	6	3635.62	80.55	<0.001
Experience × context	8	3637.96	82.89	<0.001
Experience	4	3643.95	88.89	<0.001
Context	3	3646.50	91.43	<0.001
Random factor only	3	3654.24	99.17	<0.001

Note: Akaike's information criteria corrected for small sample size (AIC$_c$) was used to assess the probability of model fit relative to the candidate models. Our three fixed factors included light (present or absent), experience (from forested or deforested stream reaches), and context (sand, leaf, or cobble substrate). Our random factor was the capture-site location.

Table 2. Effect sizes of treatments on habitat selection by larval Black-bellied Salamanders (*Desmognathus quadramaculatus*) with respect to light.

			95% CI	
	Effect size	SE	Lower	Upper
Light				
Light present	–28	4	–44	–12
Light absent	–1	3	–13	11
Context				
No refuge	–23	5	–42	–3
Leaf refuge	–10	5	–30	10
Cobble refuge	–8	4	–24	8
Experience				
Forested reach	–21	4	–37	–5
Deforested reach	–7	4	–23	9

Note: Positive values indicate positive phototaxis, whereas negative values indicate negative phototaxis. Larger absolute values indicate a larger effect of the treatment on salamander behaviour. Habitat indicates the capture location of the individual and suggests their experience with well-lit environments. SE is standard error and CI indicates the confidence interval for the estimate.

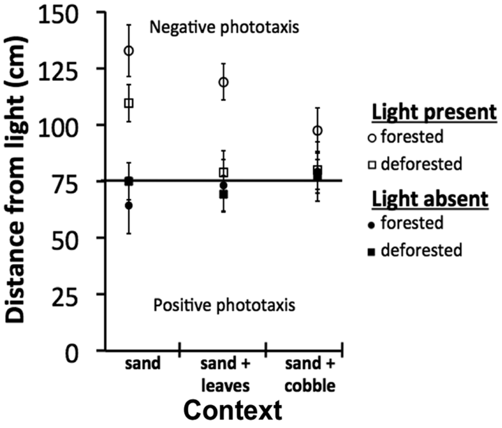
2013; Johnson 2014). We also used a Bartlett's test to determine if individuals from deforested reaches exhibited greater variability in habitat selection than individuals from forested reaches. For our field data, we also used the mean distance individuals positioned themselves from the sunlit end of the enclosure. We performed a linear mixed model with this data using experience as our fixed factor and capture location and location of the shaded portion of the enclosure (upstream or downstream) as our random factors. Models with and without the fixed factor were evaluated and ranked using AIC$_c$. We assessed all models using the lme4 package in R (Bates et al. 2011; Pinhiero et al. 2012; R Development Core Team 2012).

Results

Laboratory behaviour experiment

We recorded 4320 observations of 360 larval *D. quadramaculatus.* Model ranking indicated that the best-fitting model included all three factors of light presence, substrate type, and capture location and their interactions (Table 1). This model was ranked much higher than any derivative model (ΔAIC$_c$ ≥ 20.75), indicating that all three factors and their interactions were important for predicting where salamanders positioned themselves relative to light (Table 1). The best-fitting model had a marginal R^2 of 0.382 and a conditional R^2 of 0.390, indicating that the random factor of capture location only marginally improved model fit. Individuals were found 3 times farther from light if they came from forested reaches relative to deforested reaches (28 ± 4 cm; Table 2), and the presence of substrate caused salamanders to locate themselves 2.9 times closer to light when cobble was available (8 ± 4 cm) and 2.3 times closer when leaves were available (10 ± 5 cm; Table 2, Fig. 2). Individuals from deforested reaches used both leaves and cobble to position themselves closer to the light, whereas individuals from forested reaches only demonstrated a similar response when presented with cobble (Fig. 2). Larvae exhibited random movement in response to the absence of light, indicating that directional movement resulted from responses to our treatments. Individuals from deforested reaches had 1.3 times more variability in habitat selection relative to individuals from forested reaches ($K^2_{[1]} = 39.9$, $P < 0.001$).

Fig. 2. Mean (±1 SE) locations selected by larval Black-bellied Salamanders (*Desmognathus quadramaculatus*) with different experience with light in different environmental contexts. Salamanders either had little experience with a well-lit environment (i.e., those collected from fully forested sites) or they originated from deforested sites with little to no canopy cover and had prior experience with well-lit environments. Environmental context was manipulated by altering the presence and type of refuge. No refuge treatments had only sand substrate, whereas leaves and cobble were two different types of refuge typically used by salamanders in their natal environments. The solid horizontal line indicates the location where salamanders were initially placed. Any data point that includes this line within the error bars representing ±1 SE indicates a nondirectional response with respect to the location of the light source regardless of whether it was on or off.



Field behaviour experiment

We recorded 480 observations of 40 larval *D. quadramaculatus* in our field enclosures. Field observations of individual responses to sunlight indicated that capture location improved model fit predicting distance from the sunlit edge of the enclosure (habitat + random model: $K = 5$, AIC$_c$ = 370.6; random-only model: $K = 4$, AIC$_c$ = 401.7). The best-fitting model had a marginal R^2 of 0.488 and conditional R^2 of 0.571. Individuals from forested reaches were found under shade (26.8 ± 8.2 cm from shaded end) more often than individuals from deforested reaches. Individuals from deforested reaches were found in the sunlit areas and 3.7 times farther from the shaded edge than individuals from forested reaches (101.9 ± 9.3 cm).

Discussion

Habitat-selection behaviour of larval salamanders depended on the context in which the behaviour took place and was modified by the prior experience of individuals with deforested conditions. Negative phototaxis has been repeatedly demonstrated in salamanders (e.g., Wilder 1913; Sugalski and Claussen 1997; Placyk and Graves 2001), but this study characterizes plasticity in this behaviour that may affect how individuals distribute themselves within streams. These results are also consistent with studies demonstrating resistance among larval salamanders to move within streams across even relatively small forest canopy gaps (Cecala et al. 2014). Because the maintenance of local salamander populations is affected by within-stream larval and adult dispersals (Grant et al. 2010), factors that reduce the connectivity of streams within dendritic stream networks may negatively impact long-term salamander persistence (Grant et al. 2010). Land-use practices associated with loss of riparian forest are the primary drivers of siltation and reductions in leaf-litter inputs to streams, reducing the availability of refuge to stream organisms (Paul and Meyer 2001; Walsh et al. 2005; Burcher et al. 2007). Consequently, deforested reaches with little available refuge could inhibit within-stream movement to other forested patches, and negative phototaxis may be one behavioural explanation for reduced salamander abundance and movement following the loss of riparian forests (Cecala 2012; Cecala et al. 2014). Finally, behavioural differences associated with habitat origin may explain why some individuals persist in deforested stream reaches.

The environmental context of refuge availability suggests that the negative impacts associated with loss of riparian forest may be mitigated by the maintenance of in-stream refuges. In lit environments with cobble refuge, individuals from deforested reaches showed no directional phototactic behaviour that may reflect their ability to avoid light by moving underneath these objects. Despite the ability of all tested individuals to select the nearest available shaded environment provided by refuge, individuals from forested reaches selected refuge farther from the light source than individuals from deforested reaches and differentiated between leaf and cobble refuges. Because local stream-salamander abundance is often influenced by substrate (Barr and Babbitt 2002; Cecala 2012), our results imply that larval salamanders may persist in well-lit environments provided that these habitats continue to offer refuge. Unfortunately, streams with canopy gaps and cobble refuge are largely unavailable because riparian deforestation is strongly correlated with increased sedimentation and loss of cobble refuge (Burcher et al. 2007; Cecala 2012).

Several studies suggest that negative phototaxis by salamanders is a behaviour to avoid warmer, drier microhabitats that may be thermally stressful or have a higher desiccation potential (Sugalski and Claussen 1997; Placyk and Graves 2001). Plethodontid salamanders are particularly sensitive to desiccation from high temperatures and low moisture (Spotila 1972; Feder 1983). Larval salamanders are not vulnerable to increased dehydration risk in well-lit environments, so negative phototaxis is likely related to negative effects related to high UV-B radiation or higher water temperatures resulting from direct solar radiation (Blaustein et al. 2003; Caissie 2006). Salamanders exhibit metabolic depression at high temperatures that may be experienced in well-lit streams (Bernardo and Spotila 2006), which would favour negative phototaxis among larvae. Though studies of thermal limits and metabolic depression are only available for terrestrial life stages of salamanders, the higher mass-specific energy demand of larval salamanders likely makes them similarly sensitive to high temperatures (Hillman et al. 2009, but see Strickland et al. 2016). Preliminary data also suggests that larvae of this species use both temperature and light to select habitat (W. Noggle, unpublished data). Alternatively, the importance of negative phototaxis to prevent desiccation in terrestrial life stages and terrestrial woodland salamanders more generally may conserve the trait among aquatic salamander species and life stages (Plomin et al. 2000; Angilletta et al. 2002; Manenti et al. 2013).

Although salamanders show general negative phototaxis, our results demonstrate that prior exposure to well-lit environments tempers phototaxis. Although these sets of studies compared relatively few populations where regional adaptation uncorrelated with riparian condition may have occurred, the consistent results and trends among regions suggests that altered phototactic behaviours in deforested stream reaches is a more widespread phenomena, and further studies of individuals collected from additional streams confirm these results (Bliss and Cecala 2015; Supplementary material and Supplementary Fig. S1[1]). Two potential explanations for our observations are that selection favours individuals that are less sensitive to light or that larvae conditioned in well-lit environments become desensitized to light. For selection to favour individuals less sensitive to light, individuals with less light sensitivity must have higher success rates relative to more sensitive individuals when occupying deforested reaches. Relative to shaded streams, well-lit streams have increased autotrophic production that could increase larval prey availability (Bolnick et al. 2003; Riley et al. 2009; Hagen et al. 2010). Individuals willing to use well-lit environments may have access to more abundant resources and fewer competitors (e.g., Manenti et al. 2013). The simpler explanation for reduced negative phototaxis among salamander larvae from anthropogenic well-lit environments is that larvae become habituated to well-lit conditions. Habituation could exacerbate the negative effects canopy gaps on stream salamanders by causing individuals to increase the use of well-lit environments where temperature or other risks could increase larval mortality. Despite the potential for risks in deforested reaches, positive associative learning with increased prey availability may create positive reinforcement for reduced reliance on light cues. This study was unable to evaluate the relative contributions of habituation relative to associative learning or local adaptation. It is also possible that diminished negative phototaxis within the larval stage could be adaptive in certain contexts and facilitate persistence in or adaptation to novel ecosystems (Manenti et al. 2013). Preliminary evidence suggests that individuals in canopy gaps exhibit poor body condition relative to individuals from forested reaches, suggesting that more research is necessary to assess why individuals occupy this habitat and if decisions to occupy deforested reaches are maladaptive (Bliss and Cecala 2015). Similarly, increased variability of habitat selection by individuals from deforested streams could indicate differences in coping mechanisms employed by individuals remaining in deforested reaches (Sih 2013; Bliss and Cecala 2015).

Ultimately, the ability of salamanders to exhibit and maintain behavioural plasticity in response to novel cues dictates the long-term consequences of environmental manipulation. As ecosystems continue to change (Gardiner et al. 2008), evaluating the behavioural changes of organisms to specific environmental factors may provide manageable targets to prevent declines associated with maladaptive behaviours. In this instance, maintenance of high-quality refuge from light may facilitate long-term persistence of stream salamanders in deforested stream reaches. Because evolved responses to historically reliable cues may become

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[1] Supplementary material and Fig. S1 are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2015-0111.

diminished in altered environments (Schlaepfer et al. 2002), we must consider the context-dependent nature of behavioural and other proximate individual responses that ultimately shape population responses to environmental change.

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