

# Riparian disturbance restricts in-stream movement of salamanders

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## SUMMARY

1. Long-term population persistence or population rescue require dispersal from other source populations. Barriers to movement can effectively fragment and isolate populations, reducing persistence and recolonisation. For stream organisms that depend heavily on movement within dendritic networks, research is needed to identify and estimate the effects of such barriers on connectivity.
2. We used capture–mark–recapture of displaced larval and adult salamanders to estimate return rates across gaps (length 13–85 m) in the riparian canopy and thus to assess the fragmentation of salamander populations within otherwise fully forested catchments.
3. Relative to salamanders in fully forested reaches, displaced salamanders were 86% less likely to return to their capture location when required to cross gaps in the canopy as short as 13 m, and the likelihood of return declined with increasing gap length. The effects of gaps on return rates were consistent among life stages and for up- and downstream movement.
4. Our study suggests that riparian disturbance can reduce permeability to salamanders, even in the absence of additional land-use change. Because anthropogenic features, such as roads and powerlines, frequently cross small streams, the accumulation of apparently small land-cover changes has the potential to reduce continuous populations to small fragments with limited connectivity.

*Keywords:* behaviour, connectivity, dispersal, fragmentation, phototaxis

## Introduction

Animal responses to environmental change depend upon the effects of that change on demographic processes (Mills, 2007). Immigration buffers populations against extinction and increases recolonisation rates, thereby promoting long-term persistence and increasing species occupancy across the landscape. Although barriers to immigration are known to reduce resilience and long-term persistence of populations (Brown & Kodric-Brown, 1977; Pulliam, 1988; Frankham, 2005; Holland & Hastings, 2008), identifying the mechanisms limiting dispersal can be difficult (Ims & Hjermann, 2001; Nathan, 2001; Wiens, 2001; Lowe & Allendorf, 2010). Relatively minor environmental changes potentially affect dispersal behaviour differently for various ages or size classes of individuals (McPeck & Holt, 1992; Stamps, 2001; Haughland & Larsen, 2004).

In physical networks such as streams, animals may select to move along the stream or terrestrially between stream branches (Fagan, 2002; Lowe, 2002; Grant, Lowe & Fagan, 2007). The latter may be physiologically challenging or include habitats that do not provide all the necessary resources for an animal, such as refuge from environmental conditions or predators (Grant *et al.*, 2007, 2010). Therefore, animals most often disperse along streams due to the low habitat resistance offered by this pathway (reviewed in Grant *et al.*, 2007, 2010). Consequently, in-stream barriers may be particularly effective in limiting connectivity among habitat patches (Fagan, 2002). Barriers to movement within streams can be physical obstacles (e.g. waterfalls, culverts and dams; Carlsson & Nilsson, 2001; Neraas & Spruell, 2001; Novinger & Rahel, 2003; Blakely *et al.*, 2006), biological (e.g. predators such as stocked fish; Fraser, Gilliam & Yip-Hoi, 1995; Ruzzycki, Beauchamp & Yule, 2003) or

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abiotic conditions (e.g. high-temperature or high-light conditions; Bozinovic, Calosi & Spicer, 2011). These conditions often interact with the behaviour of animals to create barriers to movement (Wofford, Gresswell & Banks, 2005; Blakely *et al.*, 2006). For example, if species avoid high light or predators, some stream reaches may be impassible even where there are apparently no physical obstacles (deMaynadier & Hunter, 1999; Todd & Rothermel, 2006).

For species restricted to small, forested streams, gaps in the canopy created by human land use could act as barriers to movement. Several studies have shown that large-scale deforestation for agriculture, residential and commercial purposes can impede movement of aquatic organisms (Eikaas *et al.*, 2005; Didham *et al.*, 2012; Seger *et al.*, 2012). However, the effects of small (but often abundant) gaps associated with road crossings, etc. are largely unstudied. Such effects may be prevalent in the southern Appalachian Mountains, for instance, where land-use conversion generally occurs along stream corridors (Wear & Bolstad, 1998). Although this region remains largely forested, the southern Appalachians are undergoing extensive residential development, including expansion of roads and installation of rights-of-way for a growing population (Kirk, Bolstad & Manson, 2012). This region also has a diverse stream fauna, including salamanders (Stein, Lutner & Adams, 2000), and recent research demonstrates declines of aquatic species due to reduced riparian canopy cover (Kirsch, 2011; Cecala, 2012).

Streams with well-developed over- and mid-storey canopies are deeply shaded (Kozak & Wiens, 2010). Salamanders in such streams disperse most frequently along aquatic pathways, and this can be important for long-term population persistence (Lowe, 2003; Grant *et al.*, 2010). However, little information is available on how movement along these pathways may be altered by development. In human-modified landscapes, salamander occupancy is highest in streams connected to others and with forested riparian zones (Grant, Green & Lowe, 2009), while decreasing riparian cover is correlated with low salamander occupancy, even within reaches in otherwise well-forested catchments (Cecala, 2012). Similarly, both abundance and small-scale movements decline with removal of the canopy (Spotila, 1972; Ash, 1997; Ford *et al.*, 2002; Cecala, 2012). Collectively, these studies suggest that small-scale riparian forest loss may be a mechanism of stream fragmentation that reduces salamander dispersal, abundance and occupancy.

Our goal was to estimate the effect of small canopy gaps on salamander movement within streams. Specifically, we sought to estimate the probability of salamanders crossing canopy gaps as a function of gap length.

We focussed on the movement of the black-bellied salamander (*Desmognathus quadramaculatus*) across canopy gaps ranging in length from 13 to 85 m, and we took advantage of the tendency for plethodontid salamanders to return when displaced (Madison 1969; Marsh *et al.*, 2004). We hypothesised that animals displaced across a canopy gap would have a lower probability of returning than those displaced inside an intact forest corridor. Furthermore, we hypothesised that movement probability would be negatively correlated with gap length.

## Methods

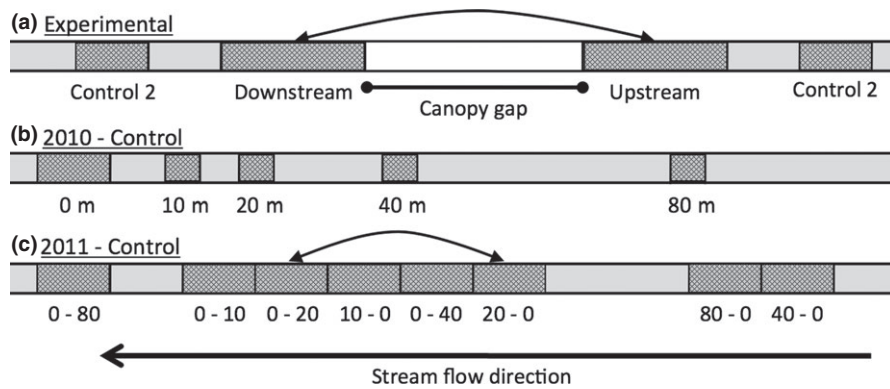
### *Study organism*

We focussed on *D. quadramaculatus* because several of their traits are well suited to this study, and it is one of the most abundant and widely distributed species within this region (Peterman, Crawford & Semlitsch, 2008; Milanovich, 2010). The larval period of *D. quadramaculatus* lasts 2–4 years, and larvae, juveniles and adults generally remain within streams and adjacent stream banks (Peterman, Crawford & Semlitsch, 2008). Individuals are highly philopatric, with linear home ranges of c. 1 m where they occupy the same cover objects or burrows throughout their life (Camp & Lee, 1996; Peterman *et al.*, 2008). These traits all lead to high detection of individuals within small areas (Koenig, VanVuren & Hooge, 1996; Pollock *et al.*, 2002). In addition, the large size of *D. quadramaculatus* adults allowed us to mark them with passive integrated transponders, improving our ability to detect adult movement (Hamed, Ledford & Laughlin, 2008; Connette & Semlitsch, 2012).

### *Experimental methods*

To compare movements across canopy gaps and forested stream reaches, we established six experimental streams with canopy gaps between 13 and 85 m of stream length and two continuously forested control sites in May 2010 (Fig. 1). Canopy gaps were all created by transmission power line rights-of-way. During this study, no active management of the power lines occurred, such as mowing or herbicide application. Generally, we surveyed sites twice per week depending on accessibility and landowner activities, for a total of 40–49 surveys per site between May–September 2010 and May–October 2011.

At each gap site, we identified the boundaries of the canopy gap as the edge of the tree canopy and designated 20 m reaches up- and downstream of the canopy gap (Fig. 1a). We collected individuals from the 20-m



**Fig. 1** Study design of experimental canopy gap sites (a) and control sites in 2010 (b) and 2011 (c). The shift between 2010 and 2011 control designs did not overlap as suggested in this diagram but, using the same stream reach, we were able to maintain surveys of the 2010 transects in 2011. The shaded transects indicate that they were forested reaches. Non-shaded regions indicate canopy gaps located above the stream. Cross-hatching reflects stream reaches sampled for salamanders. Canopy gaps (13–85 m in length along the stream channel) were formed by cleared rights-of-way bisecting our study streams. The bidirectional arrow in (a) represents how individuals were moved across canopy gaps; the bidirectional arrow in (c) represents how individuals were moved between paired transects at our control sites.

transect downstream of the canopy gap, then marked and translocated these animals to the upstream transect, and vice versa. All transects were sampled for unmarked and marked individuals. Marked individuals were released at their capture location, whereas unmarked individuals were marked (see below) and released on the opposite side of the canopy gap.

We developed two types of controls. The first was designed to evaluate return probability in two fully forested streams. In 2010, we delineated a 10-m downstream transect with 5 m transects located 10, 20, 40 and 80 m upstream from the upstream edge of this downstream transect (Fig. 1b). We collected unmarked individuals in the 10-m downstream transect, marked and translocated them to randomly assigned upstream transects. Unmarked individuals captured in the upstream transects were captured, marked and translocated to the larger downstream transect (Fig. 1b). Because of low sample sizes in 2010, we shifted our design in 2011 to four paired 10-m transects with pairs located 10, 20, 40 and 80 m apart (Fig. 1c). At control sites in 2011, unmarked individuals were captured and translocated up- or downstream to their paired transect. We also continued to monitor transects from 2010 for marked individuals. Our second control was to evaluate whether translocation altered survival and detection. Therefore, we developed 12 additional 10-m forested control transects where individuals were captured and marked but not translocated. To provide the closest comparison, we created these transects in forested areas up- and downstream of our study area at each experimental site (Fig. 1a).

We captured salamanders in each transect using leaf litter bags (in the channel) and active surveys of the

stream and bank (Marsh, 2009). We set  $25 \times 40$  cm leaf litter bags at a density of  $1 \text{ m}^{-1}$  stream length and checked them weekly during our sampling periods by removing the bag from the stream and placing it in a bin filled with water before gently agitating it to dislodge any organisms. Water, debris and organisms were then poured through a net to detect larval, juvenile and adult *D. quadramaculatus*. After larval and juvenile salamanders were captured, we batch marked individuals by site, transect and date with visual implant elastomer (Northwest Marine Technology; Bailey, 2004). Upon recapture, individuals received a second mark that allowed us to develop individual capture strings. We recorded snout-vent length, life stage and capture location for all recaptured animals.

Most new individuals were identified by life stage, but some captured early in the 2010 season were not categorized, nor were they ever recaptured. Because these marked-but-not-recaptured individuals could not be assigned to either life stage, they could not be included in estimation models without a correction. Otherwise, our models would underestimate the number of individuals displaced, causing a positive bias in estimates of return probability. To prevent this positive bias, we used the ratio of larvae to juvenile captures to determine the number of these capture strings that should have been assigned to either the larval or juvenile group. After assessing the ratio for each transect surveyed, we then randomly assigned the appropriate number of individuals without a recorded life stage to the larval or juvenile group.

We detected adult *D. quadramaculatus* by performing weekly nocturnal surveys of streamside burrows within

each transect during our sampling period. We housed captured *D. quadramaculatus* adults separately in Tupperware containers with stream water and leaves from their capture location and brought them back to the laboratory for marking. We anaesthetised individuals with a buffered 500 mg L<sup>-1</sup> solution of MS-222 before injecting them with a passive integrated transponder (PIT tags; 8.5 mm long and 2.1 mm diameter, TX148511B; BioMark, Boise, ID, USA; Peterman & Semlitsch, 2006; Hamed *et al.*, 2008; Connette & Semlitsch, 2012). We monitored individuals for 24 h to ensure full recovery from anaesthesia and to prevent loss of the PIT tag, then translocated and released these animals. Resighting of adult *D. quadramaculatus* was conducted by detection of the PIT tag via an RFID detection system (BioMark FS-2001F-ISO Reader and portable antenna; Connette & Semlitsch, 2012). Because these tags have an estimated detection range of <20 cm underground, these surveys were conducted in the morning to allow for detection of the PIT tag before salamanders moved too far underground to be detected by the antenna (Connette & Semlitsch, 2012).

#### Statistical analysis

We used Cormack–Jolly–Seber multistate models implemented in Program MARK to test whether return rates differed for individuals returning across canopy gaps and those moving through the forest (Cormack, 1964; Jolly, 1965; Seber, 1965; Hestbeck, Nichols & Malecki, 1991; Brownie *et al.*, 1993; Table 1). We used an information theoretical approach to determine the relative support for each of our hypotheses regarding the influence of intervening habitat type, life stage, and direction and distance of translocation (see below; Burnham & Anderson, 2002). To evaluate the plausibility of each model, we used Akaike's information criterion (AIC; Akaike, 1973) corrected for small sample sizes with the small-sample bias adjustment in Program MARK (White &

Burnham, 1999). We calculated AIC<sub>c</sub> weights for each candidate model and ranked these models from highest to lowest weight to allow us to draw inferences on the best supported models given our data. We tested the goodness of fit of the global, time-dependent model in program UCARE (Choquet *et al.*, 2009).

Because many of our sampling events resulted in few or no captures, particularly during nocturnal surveys for adults, we collapsed our sampling events into 14 occasions encompassing the 2010 and 2011 seasons (Grant *et al.*, 2010). Most of our sampling was in June and July, requiring us to form two sampling occasions for these months to incorporate recaptures of recently marked animals within each month improving our model resolution. We adjusted the intervals among sampling occasions in Program MARK to reflect this variation. To avoid overparameterisation of our models and to improve confidence in our parameter estimates due to low observed return rates, we assumed that all monthly parameter estimates were constant temporally (Williams, Nichols & Conroy, 2002). This simplifying assumption improved our power to detect differences in return probability, given that a fully time-dependent model would have 384 parameters (which would exceed the number of returning individuals). Because we employed consistent effort during surveys, and since previous studies of stream salamanders have found that detection remains constant throughout late spring–early autumn (Peterman *et al.*, 2008; Cecala, Price & Dorcas, 2009), this seems a biologically reasonable simplification of our models.

Generally, we used a sequential modelling approach to determine the most parsimonious model for our data. We represented survival and capture probabilities most effectively by testing for differences: (i) among life stages, (ii) between translocated and non-translocated individuals, (iii) by direction of translocation and (iv) between individuals translocated within a forested stream versus across a canopy gap. After identifying the

**Table 1** Hypotheses associated with each variable included in our candidate models

Variable	Abbreviation	Hypothesis	Support
Intervening habitat type	Gap	Salamanders are less likely to return to their capture location when they need to move through a canopy gap because of their behavioural avoidance of high light habitats.	Rittenhouse & Semlitsch (2006) and Todd <i>et al.</i> (2009)
Life stage	Stage	Stream salamander life stages have different dispersal probability with juveniles more likely to disperse than larvae or adults.	Grant <i>et al.</i> (2010)
Translocation direction	Direction	Stream salamanders move upstream more frequently than downstream.	Lowe (2003), Cecala <i>et al.</i> (2009) and Grant <i>et al.</i> (2010)
Translocation distance	Distance	Salamanders are more likely to return when displaced shorter distances.	Madison (1969)

models with the greatest support for survival and capture probability, we used those models to test our specific hypotheses about the influences on salamander return probability.

We designed subsequent models to evaluate evidence that return rate was either similar or different between our control and experimental sites (i.e. forested versus open canopy). We first examined whether model selection results indicated support for models considering each site individually or for grouping sites into control and gap models. Because models indicated little support for considering each site separately ( $\Delta\text{AIC}_c = 1996$ ), we grouped sites into control or gap models. To model return probability, we had three potential states for each individual: 'not translocated' (detection transects), 'captured upstream' and 'captured downstream'. We assigned new individuals to the state (i.e. place) at which they were released. For example, individuals captured in the downstream transect were assigned to the upstream transect where they were released after marking. The transition probability reflects the probability that an individual returns to its capture location while accounting for whether, and in which direction, it was displaced. Because no individual moved among the translocation and control transects at our experimental sites (Fig. 1a), we fixed the transition probability to and from the control transect at zero.

Because the probability of successful movement often varies among salamander life stages (Grant *et al.*, 2010), we tested explicitly whether life stages had different return rates by examining support for models that grouped all life stages together relative to models including each life stage separately (Table 1). The majority of recaptured individuals did not progress to the next life stage during our study. Therefore, we did not allow individuals to transfer between life stages in our models.

Stream salamanders tend to move upstream, making them more likely to return up- than downstream (Lowe, 2003; Cecala *et al.*, 2009; Grant *et al.*, 2010; Table 1), and salamander return probability often increases with decreased displacement distance (Madison, 1969; Marsh *et al.*, 2004; Table 1). We used model selection results to assess support for transition probabilities that varied between the captured-upstream and captured-downstream states, or for considering these two groups together. We also included a normalised individual covariate representing the displacement distance for each individual corresponding to the canopy gap width for experimental sites or the predetermined translocation distance for control sites. For individuals captured and

released within the detection transects, we set the translocation distance to zero. Before including the influence of translocation distance on return probability, we first examined model support for all permutations of our hypotheses regarding the effects of a canopy gap, life stage and translocation direction. Based on the top two models only, we then designed two additional models to include the influence of translocation distance on return probability and evaluate support for this final hypothesis (Table 1).

## Results

We captured and marked 1398 larval, juvenile and adult *D. quadramaculatus*. Of these, 1148 individuals were translocated, with 814 of those translocated across a canopy gap (for a more detailed breakdown of sample sizes see Table S1 in Supporting Information). The mean time interval between translocation and detection of individuals that had returned to their original capture location was shorter for adults ( $1.79 \pm 0.54$  months; mean  $\pm 1$  SE) than for larvae or juveniles ( $3.5 \pm 0.45$  months,  $4.38 \pm 1.10$  months, respectively), and neither the direction nor distance of translocation appeared to influence the return interval. Using the 3G, M and Jolly Move model fit tests in UCARE, we failed to reject any of the hypotheses and therefore concluded that our models demonstrated reasonable fit to our data (3G statistic =  $38.1_{\text{d.f.}=45}$ ,  $P = 0.76$ ; M statistic =  $18.7_{\text{d.f.}=13}$ ,  $P = 0.13$ , JMV statistic =  $56.8_{\text{d.f.}=58}$ ,  $P = 0.52$ ). Similarly, our  $\hat{c}$  (0.996) indicated neither under- nor over-dispersion of our data.

The most parsimonious model for survival allowed this parameter to vary among life stages, control versus gap sites and whether individuals were translocated or not (Table 2). The most parsimonious model for capture probability depended on variation among life stages, control versus gap, translocated or non-translocated, and translocation direction (Table 2). Although survival and capture probabilities depended on these factors, 95% confidence intervals were broadly overlapping, preventing us from drawing robust conclusions about the influence of life stage and canopy gaps on survival and capture probabilities (Table 3).

The presence of canopy gaps was the most important variable influencing return probability (Table 4). The model including the presence of canopy gaps was 2.4 times better than the next best model at predicting return probability. The second best model included the influence of translocation distance on return probability (Table 4). All other models had  $\Delta\text{AIC}_c$  values much lar-

**Table 2** Model selection results for survival and capture probability to determine the most parsimonious model to describe the salamander populations surveyed in this study

Model	K	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> weights
<b>Survival</b>				
Habitat × Stage × State	23	2717.92	0.00	1.000
Habitat × Stage × State × Direction	29	4019.20	1301.28	0.000
Stage × State × Direction	28	4031.01	1313.08	0.000
Habitat × State × Direction	26	4031.64	1313.71	0.000
State × Direction	24	4037.49	1319.57	0.000
Habitat × Stage	28	4050.57	1332.65	0.000
Habitat	27	4072.74	1354.82	0.000
Stage	26	4074.49	1356.56	0.000
Constant	24	4080.05	1362.13	0.000
<b>Capture probability</b>				
Habitat × Stage × State × Direction	23	2717.92	0.00	1.000
Habitat × Stage × State	26	4026.89	1308.97	0.000
Habitat × State × Direction	22	4029.87	1311.95	0.000
Stage × State × Direction	25	4036.21	1318.29	0.000
State × Direction	22	4049.08	1331.16	0.000
Habitat	21	4056.44	1338.52	0.000
Stage	22	4067.73	1349.81	0.000
Constant	20	4067.96	1350.03	0.000

Models use hypotheses defined in Table 1. State represents whether individuals were translocated or not.

ger than 2.0, indicating that they had little support given our data (Table 4).

Probability of return ( $\pm 1$  SE) was 7.03 times larger along forested streams than along streams that required crossing a canopy gap ( $0.146 \pm 0.023$  versus  $0.021 \pm 0.004$ , respectively). Return probability across a canopy gap declined with increasing gap width, but the model indicated a positive relationship between displacement distance and homing probability along fully forested streams (Fig. 2). This positive relationship is an artefact of including control animals that were not

translocated. Low-capture probability for this group at translocation distances of zero relative to translocated individuals biased the intercept of this curve to lower values than those observed at larger translocation distances. Therefore, we conclude that it is most likely that return probability is uncorrelated with translocation distances used in this study. In streams with a canopy gap, return probability was  $>0.1$  when canopy gaps were  $<8$  m, but declined to  $<0.01$  when canopy gaps were  $>80$  m. Although models that allowed return probability to vary by life stage received little support, graphical interpretations suggested that larval return probability across gaps may be lower than juveniles and adults (Fig. 3). Similarly, because of limited information for adults not translocated or with a translocation distance equal to zero, the model projected an increasing rate of return for adults with increased translocation distance, but it is more likely that this relationship is consistent for the translocation distances used in this study.

## Discussion

Even relatively small riparian canopy gaps evidently act as barriers to the movement of larval and adult black-bellied salamanders. These results are consistent with studies of terrestrial and wetland breeding amphibians that show similar behavioural resistance to moving into canopy gaps (reviewed in Cushman, 2006; Semlitsch *et al.*, 2009), but our study suggests that this behavioural avoidance can serve to fragment populations of stream salamanders because dispersal is strongly biased to linear, within-stream movements (Grant *et al.*, 2010). Our data from displaced individuals indicate that a population upstream of a canopy cap would be, on average, 86% less likely to receive immigrants than an upstream population with a continuous canopy along the stream. Our results demonstrate that any canopy gap, even as

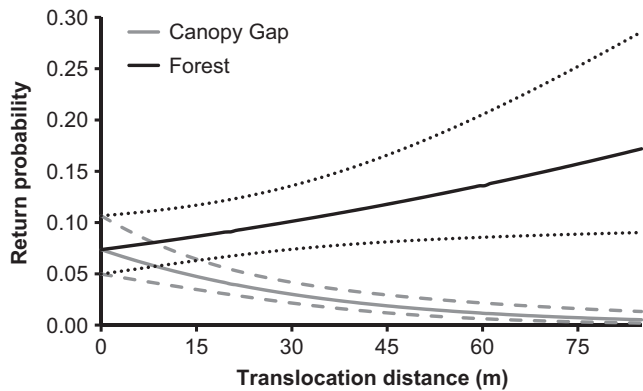
**Table 3** Parameter estimates for survival and capture probability from the most parsimonious model

	Translocated			Not translocated					
	Larvae	Juveniles	Adults	Larvae	Juveniles	Adults			
<b>Survival</b>									
Forest	$0.71 \pm 0.08$	$0.54 \pm 0.22$	$0.46 \pm 0.23$	$0.31 \pm 0.07$	$0.48 \pm 0.14$	$0.42 \pm 0.46$			
Canopy gap	$0.55 \pm 0.03$	$0.76 \pm 0.04$	$1.00 \pm 0.00$	–	–	–			
<b>Capture probability</b>	Upstream return			Downstream return			Not translocated		
	Larvae	Juveniles	Adults	Larvae	Juveniles	Adults	Larvae	Juveniles	Adults
Forest	$0.10 \pm 0.03$	$0.12 \pm 0.10$	$1.00 \pm 0.00$	$0.12 \pm 0.04$	$0.11 \pm 0.09$	$0.79 \pm 0.83$	$0.25 \pm 0.08$	$0.14 \pm 0.07$	$0.55 \pm 0.50$
Canopy gap	$0.23 \pm 0.04$	$0.09 \pm 0.02$	$0.04 \pm 0.02$	$0.19 \pm 0.03$	$0.12 \pm 0.03$	$0.06 \pm 0.02$	–	–	–

Values represent parameter estimates  $\pm 1$  SE.

**Table 4** Results of model ranking procedures describing our hypotheses about the factors that may influence return probability of *Desmognathus quadramaculatus*

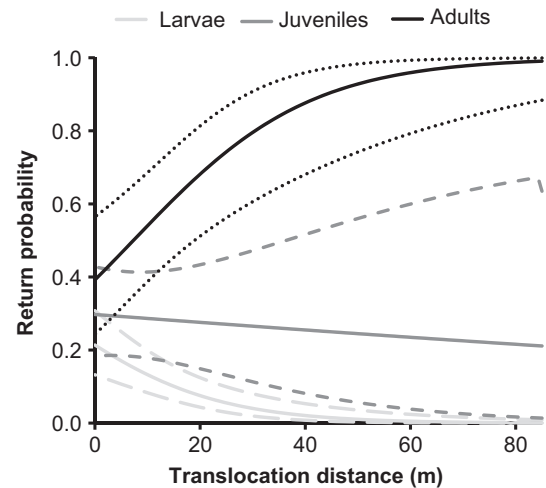
Model	K	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> weight	Hypothesis
Gap	23	2718	0.00	0.705	Return probability varies depending on the presence or absence of a canopy gap
Gap × Distance	26	2720	1.74	0.295	Return probability varies depending on the presence or absence of a canopy gap and return distance
Gap × Stage × Distance × Direction	31	4010	1291.82	<0.001	Return probability varies depending on the presence or absence of a canopy gap, life stage, and return distance and direction
Gap × Stage × Direction	29	4019	1301.28	<0.001	Return probability varies depending on the presence or absence of a canopy gap, life stage and return direction
Gap × Stage	27	4030	1311.72	<0.001	Return probability varies depending on the presence or absence of a canopy gap and life stage
Stage × Direction	27	4042	1323.67	<0.001	Return probability varies depending on the life stage and return direction
Stage	24	4044	1325.83	<0.001	Return probability varies depending on the life stage
Gap × Direction	24	4050	1332.48	<0.001	Return probability varies depending on the presence or absence of a canopy gap and return direction
Direction	23	4074	1356.04	<0.001	Return probability varies depending on the return direction



**Fig. 2** Probability of return is reduced if homing individuals are forced to move through a canopy gap to return to their capture location, and this probability in altered habitats declined as the return distance increased. Although it appears that return probability increases with translocation distance along forested streams (i.e. control sites), this is an artefact of the model because capture probability was greater for translocated individuals than for non-translocated individuals. Return probability reflects the joint probability of surviving and returning. Dashed lines indicate 95% confidence intervals surrounding the estimates.

short as 10 m of channel length, negatively affects salamander movement within streams and that gaps >80 m may completely fragment stream populations (<1% of displaced individuals likely to return). Because of these reduced dispersal rates and low occupancy probability associated with low canopy cover (Cecala, 2012), fragmented stream salamander metapopulations may be at increased risk of local extinction (Grant *et al.*, 2010).

We do not yet know the mechanisms by which canopy gaps over streams impede stream salamander movement. In terrestrial habitats, dispersing amphibians



**Fig. 3** Probability of return across a canopy gap for each life stage. Larvae were least likely to return across a canopy gap, and this relationship declined with increasing translocation distance. Juvenile and adult return probabilities remained relatively constant in relation to distance, but juvenile return probability was higher than that for larvae and lower than for adults, with much greater variability. Although the model suggests that adult return probability is positively related to translocation distance, this relationship is probably due to a small sample size of non-translocated adults (translocation distance is zero) and low survival associated with those individuals (Table 4; Table S1). Return probability reflects the joint probability of surviving and returning. Dashed lines indicate the 95% confidence interval surrounding the estimates.

often orientate towards forest and move slower within deforested regions (deMaynadier & Hunter, 1999; Rothermel & Semlitsch, 2002; Rothermel, 2004; Rittenhouse & Semlitsch, 2009). Because deforested areas tend to be hotter and drier, desiccation risk is commonly proposed to explain reduced amphibian movement in deforested

terrestrial habitats (Rittenhouse & Semlitsch, 2006; Crawford & Semlitsch, 2008; Todd *et al.*, 2009). However, desiccation risk does not explain the apparent reluctance of stream salamanders to cross canopy gaps within aquatic habitat and additional mechanisms must be involved. Laboratory and field behavioural studies indicate that this species selects habitat of low light intensity, suggesting that the reluctance to cross gaps may be due to negative phototaxis (Cecala, 2012). Streams passing through canopy gaps may warm rapidly, and these areas are known to act as corridors and habitat for predatory mammals and reptiles (C. R. Jackson, per. comm.; King, 1939; Chalfoun, Thompson & Ratnaswamy, 2002). Negative phototaxis would ensure that individuals remain within their preferred thermal range or reduce the risk of predation (King, 1939; Chalfoun *et al.*, 2002; Bernardo & Spotila, 2006).

For organisms that rely on stream habitats, undisturbed stream corridors should have high permeability relative to pathways across watersheds ('divides'). Despite the common perception that streams are relatively continuous and homogenous with respect to movement (see discussion in Roberts & Angermeier, 2007), our results show that even small canopy gaps (that may have little influence on the physical structure of the stream) can dramatically reduce habitat permeability for aquatic animals. Because overland pathways of movement will be physiologically challenging, if not impossible, for some stream fauna, management of riparian zones is critical for maintaining connectivity in human-influenced regions. For example, a two-lane road in our study region requires a 20-m right-of-way free of trees (North Carolina Department of Transportation, 2012). Our results suggest that such a gap would reduce salamander movement across that section of stream by 56%. Moreover, although dispersal capability often varies among life stages, our results indicate that movement by all life stages was negatively affected by the presence of a canopy gap.

Although our study quantified return probability rather than natural dispersal *per se* (Nathan, 2001), the results provide insight into the dispersal of highly aquatic stream salamanders in disturbed and fragmented regions. Plethodontid salamanders have been repeatedly demonstrated to home when displaced (Madison, 1964; Marsh *et al.*, 2004). Because salamanders expend energy defending and maintaining a territory and are highly philopatric, the motivation of individuals with established territories to return to their capture location through a canopy gap is likely to be higher than for naturally dispersing individuals (Camp & Lee, 1996). There-

fore, the negative effects of canopy gaps on dispersal may be greater than observed here. Similarly, observed return rates within our control streams were equivalent to upstream dispersal rates observed for congeners in undisturbed habitats (Grant *et al.*, 2010). Future studies should document the proximate mechanisms underlying these movement patterns and determine the long-term effects of isolation by canopy gaps on population persistence.

Much evidence shows that large-scale land-use change can alter the distribution and abundance of forest-dwelling taxa (e.g. Bender, Contreras & Fahrig, 1998; Sutherland, Meyer & Gardiner, 2002; Welsh & Lind, 2002), but our study demonstrates that the small scale of canopy gaps belies their impact on movement dynamics in stream networks. The density of road networks in the eastern United States, and often-weak regulation regarding development around headwater streams, suggests that streams may be bisected frequently by canopy gaps for a variety of purposes (Fahrig & Rytwinski, 2009). The accumulation of these small land-use changes and their effects have the potential to limit connectivity among populations even in the absence of significant habitat alteration.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Number of individuals marked, the number of recaptures, and the number of individuals that returned and were detected at their capture location distributed between habitat types and translocation distances.

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