Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

Context-dependent dispersal directionality in a headwater stream salamander

ERIC L. LYONS

eric.lyons@umontana.edu

University of Montana

WINSOR H. LOWE

University of Montana

Research Article

Keywords: capture-mark-recapture, context-dependence, dispersal costs, dispersal directionality, salamanders

Posted Date: July 9th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-10251741/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Additional Declarations: No competing interests reported.

Abstract

Background

Dispersal is an integral component of population dynamics that comes with both fitness costs and benefits. Behavioral adaptations that minimize dispersal costs, such as non-random directionality, occur across taxa. However, most studies on directionality focus on single-risk (or single-benefit) systems even though organisms are likely subject to multiple co-occurring risk factors that may influence directionality in different ways.

Methods

Here, we used 12y of spatially explicit capture-mark-recapture data to investigate variation in dispersal directionality based on the spatial location of individual salamanders (*Gyrinophilus porphyriticus*: *n* = 1,375). Each summer, we conducted weekly surveys across 1000m of three independent headwater streams to quantify movement dynamics based on life history stage.

Results

We found that adult, but not larval, salamanders are more likely to disperse upstream in downstream reaches, and more likely to disperse downstream in upstream reaches, consistent with our initial expectations given the risk landscape present in these systems. Specifically, we found that adult salamanders in the furthest upstream portions of the stream are approximately 1.68 times more likely to disperse downstream than those at the base of the stream, which were more likely to disperse upstream.

Conclusions

Regardless of direction, the proportion of salamanders that dispersed was consistent across three populations, suggesting that dispersal propensity is unrelated to dispersal directionality. Our results suggest that context-dependent directionality may represent a common source of individual-level variation in dispersal behavior for this species. Assessments of context-dependent directionality in other species may improve models of animal movement.

BACKGROUND

Dispersal — the permanent movement away from one location and settlement in another — occurs across a wide range of taxa and directly influences the abundance and distribution of species. At an individual level, dispersal is an adaptive response to environmental heterogeneity, allowing dispersers to escape environments poorly suited to their phenotype (Bowler & Benton, 2005). Dispersers are also less likely to mate with close relatives or compete with kin for shared resources (Pusey & Wolf, 1996),

improving the fitness of themselves and their offspring. However, dispersal comes with costs (Bonte et al., 2012). For example, actively dispersing individuals are often more susceptible to predation, incur energetic costs of movement, and spend time that could otherwise be invested in acquiring resources or searching for mates (Alberts & Altmann, 1995; Klarevas-Irby et al., 2021). When the fitness benefits of dispersal are high, selection may act to minimizefig these costs, maintaining dispersal in a population.

There are many ways to reduce the costs of dispersal (Bonte et al., 2012), but less attention has been paid to directionality as a cost-reduction strategy. Once an organism departs from its initial location, it necessarily disperses in a direction. Directionality, whether absolute (e.g., north v. south) or relative to habitat features (e.g., upstream v. downstream), can be either random or non-random (Armsworth & Roughgarden, 2005). Random directionality is risky. For example, an individual that randomly disperses into an area with more predators or fewer refuges increases their chances of being eaten (Vucetich et al., 2002). An individual in the same habitat that instead deliberately dispersed away from predators (i.e., in a non-random direction) would experience higher likelihood of survival during and after movement, providing fitness benefits and mitigating the costs of dispersal (Kim & Choi, 2020).

Dispersal itself is a behavioral response to multiple co-acting forces (Rogers et al., 2019), so we should expect that directionality is also likely to be influenced by multiple factors (Fig. 1), including the life history stage of the individual (Bilton et al., 2001). However, most studies on non-random directionality are restricted to single-risk (or single benefit) systems (e.g., Gardiner & Hill, 2004). In part, this is probably related to the difficulty of distinguishing the effects of co-occurring risk factors in two- and three-dimensional landscapes, where continuous variation in movement directions can obscure subtle changes in directional bias (Liu et al., 2003). As a result, we do not know the degree to which these and other observed patterns of directionality are a result of multiple co-occurring risk factors.

Streams provide an excellent opportunity to investigate how competing risk factors shape the directionality of dispersal in natural populations. Streams, particularly headwater streams, are characterized by fine scale environmental heterogeneity (Gomi et al., 2002; McGuire et al. 2014), increasing the likelihood of overlapping risk factors. Additionally, the linear nature of streams restricts dispersal to a single axis of movement (i.e., upstream or downstream), allowing for a clear distinction between dispersal directions. This restriction also overcomes the logistical challenges associated with tracking dispersal in two- and three-dimensional space because the probability of detecting a dispersal event (i.e., recapturing an individual after it disperses) does not decline with movement distance (Koenig et al., 1996).

Here, we used a headwater stream salamander (*Gyrinophilus porphyriticus*) to investigate how competing risk factors influence dispersal directionality. We used twelve years of spatially explicit capture-mark-recapture data from three headwater streams to test whether specific environmental variables influenced the likelihood of an individual dispersing upstream or downstream based on their initial capture position. Brook trout (*Salvelinus fontinalis*) are predators of *G. porphyriticus* (Resetarits, 1995) and occur throughout the downstream reaches of the study streams, becoming most abundant near the

mainstem confluence (Warren et al., 2008). Also, exceptionally high flow events (i.e., floods) are more common in downstream reaches (Galster, 2007), and *G. porphyriticus* survival and adult recruitment both decline after high flow events (Cochrane et al., 2024a). In contrast, the upper reaches of the study streams are much more likely to dry out for all or part of the summer months (Cochrane & Lowe, 2025), increasing the likelihood of desiccation for both adult and larval salamanders (Bruce, 1972; Feder, 1983). Together, these competing risk factors – fish and floods in downstream reaches versus drying in upstream reaches – led us to predict that salamanders in downstream reaches should be more likely to disperse upstream and salamanders in upstream reaches should be more likely to disperse downstream. In testing these predictions, we also included conspecific density as an explanatory variable based on evidence of its effects on dispersal behavior from diverse taxa, including amphibians (Cayuela et al., 2019).

Because directionality can only be assessed in individuals that do disperse, we assessed variation in dispersal propensity (i.e., the likelihood of dispersal, regardless of direction) as a function of the same factors. For example, rather than causing individuals to disperse downstream, stream drying may simply prevent individuals from dispersing at all by eliminating aquatic movement corridors (Malish et al., 2023). Similarly, we might expect competitively inferior individuals to be driven out of high-quality habitat where conspecific density is high (Waser, 1985), leading to higher dispersal propensities in these areas. Lastly, because moving with the flow of water is easier than moving against the flow of water (McElroy et al., 2012), we investigated the relationship between dispersal distance and dispersal behavior.

METHODS

Study species and study site

Gyrinophilus porphyriticus is a lungless salamander (family Plethodontidae) that occurs along the Appalachian uplift in the eastern United States. The larval period lasts approximately four to eight years, and adults can live to be around 20 years old (Cochrane et al., 2024). *G. porphyriticus* occupy a home range of approximately 4m of stream channel length, and dispersal is uncommon (Cochrane & Lowe, 2025). Both larval and adult *G. porphyriticus* disperse, and dispersal distances vary widely among individuals of both stages (Addis & Lowe, 2020). *G. porphyriticus* also exhibit homing behavior, which minimizes the confounding effect of involuntary displacement (i.e., downstream drift) on dispersal research (Cochrane et al. 2024a). In the absence of fish, *G. porphyriticus* occupy the top trophic level in the stream, preying on macroinvertebrates as well as other salamanders (Bayer & Lowe, 2021).

The Hubbard Brook Experimental Forest is located in New Hampshire, USA. We conducted this research in three first-order streams there: Bear Brook, Paradise Brook, and Zigzag Brook (Appendix S1: Figure S1). All three streams flow into the mainstem of the Hubbard Brook, a tributary of the Pemigewasset River. We sampled two 500m reaches in each stream. Downstream reaches began at the Hubbard Brook mainstem confluence. Upstream reaches ended at weirs where long-term hydrologic data are collected

and above which sampling is restricted (Bormann & Likens, 1979). Distance between these reaches is 400m in Bear Brook, 250m in Paradise Brook, and 500m in Zigzag Brook (Addis & Lowe, 2020).

Capture-mark-recapture surveys

We conducted surveys for *G. porphyriticus* using capture-mark-recapture methods in June-September of 2012–2015 and again in 2018–2021. Each field season, we conducted nine surveys in each stream, resulting in 72 surveys per stream across all years. In each survey, researchers walked the two 500-meter study reaches in a stream, flipping one haphazardly-selected cover object per meter of stream channel length to find salamanders (Heyer et al. 2014). From 2012–2015, we marked salamanders with visual implant elastomer (Northwest Marine Technology, Inc., Anacortes, Washington, USA). From 2018–2021, we marked salamanders (including recaptured salamanders with elastomer tags) with 8mm PIT tags (Hecere Electronic Col, Ltd., Quanzhou, China). We also recorded the life history stage and capture position for each individual. Capture position was the distance (m) upstream from the Hubbard Brook mainstem where the salamander was captured. Life history stage was identified based on gill presence (in larvae) or absence (in adults). Metamorphosing salamanders were treated as larvae because they had not yet lost their gills. Larvae with snout-vent length < 35mm (< 2 years old) could not be marked. In 12 years of sampling, 5008 *G. porphyriticus* individuals were marked in the three study streams. Of those, 1375 were recaptured over the course of the study: 484 in Bear Brook, 491 in Paradise Brook, and 400 in Zigzag Brook. Capture positions ranged from 2-1384m from the mainstem in Bear, 5-1249m in Paradise, and 30-1500m in Zigzag.

Telemetry surveys

To improve recapture rates of marked salamanders, we surveyed stream reaches using a PIT-tag reader in June-August of 2022–2025 (HPR Plus reader, BP Lite portable antenna, Biomark Inc., Boise, ID, USA). Each year, we conducted nine surveys in each stream, resulting in a total of 36 surveys per stream across all years. Researchers walked upstream, continuously scanning the streambed between bankfull edges until a PIT tag was detected. Upon detection, a second researcher began searching for the marked salamander in that area, spending a maximum of two minutes searching to minimize the disturbance to the habitat. We re-scanned captured individuals to confirm their identity. To check for individuals that moved out of the study reaches, we also surveyed the channels between the downstream and upstream study reaches in each stream six times in 2022. Unmarked salamanders could not be detected with these surveys.

Quantifying dispersal traits

We quantified dispersal distances of recaptured individuals as the net distance moved (meters of stream channel length) over the study period (i.e., the distance between initial and final capture positions, consistent with prior studies; e.g., Addis & Lowe, 2020). We then used dispersal distances to assign

dispersal propensities. Dispersal propensity is the discrete emigration response (i.e., stay v. leave) that differentiates dispersers from non-dispersers in natural populations (Turchin, 1998). In *G. porphyriticus*, we know from prior studies that home ranges are approximately $4m^2$ on average and that dispersal tends to be both unidirectional and permanent (Addis & Lowe, 2020; Cochrane & Lowe, 2025). Therefore, individuals with dispersal distances > 4m were quantified as dispersers, and individuals with dispersal distances ≤ 4m were quantified as non-dispersers. Upstream dispersers were defined as salamanders that moved more than 4m upstream from their initial capture position, while downstream dispersers were defined as salamanders that moved more than 4m downstream from their initial capture position. Because detection probability is unrelated to movement distance in linear streams (Koenig et al., 1996), we assumed that capture probability did not differ depending on dispersal status. Individuals that were marked but never recaptured were excluded from analyses. Individuals were assumed to have dispersed in the year of recapture, even when there were multiple years between recaptures. Unless otherwise stated, all analyses in this paper were conducted using R version 4.4.2 (R Core Team, 2024).

Quantifying predation risk

To quantify *S. fontinalis* densities along the study streams, we set minnow traps (Danielson, Morehead City, North Carolina) without bait every 25m of stream channel length in downstream reaches. Traps were deployed in the stream 48h before each survey began and removed from the stream following the survey to minimize bycatch (Munro, 1974). Each trap was checked regularly from mid-June to late August: nine times (weekly) in 2022–2024 and six times (biweekly) in 2025 due to logistical constraints. All captured fish were placed in plastic containers filled with stream water. Fish were marked by clipping the adipose fin and given a unique combination of elastomer tags. We calculated the number of unique individuals captured at each position as an index of predation risk along the streams. A fish index score was assigned to each salamander based on the index associated with the closest minnow trap (e.g., all salamanders captured between 37.5m and 62.5m were assigned the fish index score for the trap at 50m). We elected to focus on unique individuals captured because recapture rates were low (< 10% of all individuals were captured more than once) and certain individuals exhibited “trap happy” behavior (Reinhardt & Hrodey, 2019). In the first year of surveys, we also placed traps in the upstream reaches to verify that fish were absent. We removed upstream traps in subsequent years to minimize disturbance.

Quantifying stream drying

To quantify the risk of a salamander experiencing stream drying, we used a salamander’s initial capture position as a proxy for watershed area, which declines with distance from the mainstem (Cochrane et al., 2024b). As watershed area declines, the likelihood that a salamander will experience intermittent flow or stream drying increases (Galster, 2007). From 2023 onwards, we also took weekly measurements of the wetted width of the streams every 10m to account for localized variation in hydrology resulting from variation in substrate and flow conditions (Hauer & Lamberti, 2006). We assigned both mean and

minimum wetted width data to individual salamanders based on the measurement site nearest to the salamander's capture position.

Quantifying conspecific density

To estimate the spatial variation in density of *G. porphyriticus*, we used R package marked (Laake et al., 2013) to estimate abundance using a series of Jolly-Seber models for open populations (Appendix S1: Table S1; Jolly, 1965; Seber, 1965). To estimate density, we first sorted salamanders into bins based on their initial capture positions. Each bin encompassed 25m of continuous stream channel length, for a total of 40 bins per stream. We estimated the average density of salamanders within a bin by multiplying the estimated abundance in a stream (from the model output) by the proportion of unique individuals captured in that bin across all years. For example, if the model estimated mean abundance as 100 salamanders in a stream, and approximately 5% of marked individuals were captured in a given bin, we estimated that the average density of salamanders in that bin was 5 individuals per 25m. Data from telemetry surveys were excluded from these model calculations because unmarked salamanders were not captured in those surveys. If our hypotheses were correct, we would expect that both conspecific densities and yearly apparent survival probabilities would be lower in the furthest upstream or downstream reaches of the study streams (i.e., where fish/floods or drying were most prevalent). Therefore, we also used these same models to compare conspecific density and apparent survival in the uppermost and lowermost 10% of each stream to the interiors of each stream.

Statistical analysis

We used an exploratory logistic regression analysis to estimate the effect sizes of factors influencing dispersal traits (i.e., propensity and directionality) in *G. porphyriticus* (Tredennick et al., 2021). A series of generalized linear models (Appendix S1: Table S2) was constructed to estimate the likelihood of a salamander dispersing based on hypothesized relationships with explanatory variables (Appendix S1: Table S3). We tested for correlations among explanatory variables before running models. In cases where correlation was detected ($r > 0.7$), we removed the variable deemed less likely to influence the response variable. We ran analyses separately on larval and adult salamanders due to predicted differences in how the two stages would respond to risks (e.g., larvae are smaller and at greater risk of predation; Bruce 1972) but did not test for other interactive effects. Numeric explanatory variables were scaled to standardize model outputs. For analyses of dispersal propensity, our response variable was a binary indicator of whether a recaptured individual remained within its original home range (0) or dispersed (1). To test factors shaping directionality, we removed all non-dispersers from the dataset and reran the same models using a disperser's directionality as the response variable: 0 for downstream dispersal, 1 for upstream dispersal.

Final model selection was based on Akaike's Information Criterion, corrected for small sample sizes (AIC_c), and Akaike weights (AIC_w) using the R package MuMin (Akaike, 1973; Bartoń, 2010). Candidate

models, including the null model (no explanatory variables), were ranked by AIC_c, with the smallest AIC_c value and highest Akaike weight indicating the top model (Akaike, 1973). All candidates within $\Delta AIC < 2$ were considered viable models. In cases where the null model was one of the viable models, we interpreted that as a lack of support for any of the models (Burnham & Anderson, 2004).

RESULTS

Based on the 4m threshold for dispersal, 414 of the 1375 recaptured individuals dispersed (31%), including 217 of 540 recaptured adults (40%) and 197 of 835 recaptured larvae (24%). Dispersal propensity was consistent across streams: 32%, 29%, and 30% of all recaptured individuals dispersed in Bear, Paradise, and Zigzag Brooks, respectively. Downstream dispersal was more common than upstream dispersal ($X^2 = 29$, $df = 1$, $p = 6.4 * 10^{-8}$). Maximum distance of downstream dispersal was 881m and maximum distance of upstream dispersal was 1248m (Fig. 2). However, only 23 individuals moved more than 200m in either direction, and dispersal distance was not strongly related to dispersal direction ($t = 1.48$, $df = 197.9$, $p = 0.14$). We found that pooled dispersal distance followed a leptokurtic distribution with many individuals dispersing short distances (i.e., between 5m and 10m outside of their current home range), few individuals dispersing extremely long distances (i.e., > 200m), and a mean dispersal distance (62m) over three times greater than the median dispersal distance (18m). In 2022, we conducted telemetry surveys in the reaches between the upper and lower study reaches of each stream. Only one marked individual was detected over the entire field season, suggesting that emigration to those intervening reaches did not strongly bias our analyses.

Brook trout were only detected in downstream reaches, and no other species of fish was captured. A total of 376 unique *S. fontinalis* were captured during the four years of sampling: 75 in Bear Brook, 115 in Paradise Brook, and 186 in Zigzag Brook. Fish index scores ranged from 0 to 0.76 individuals per meter of stream channel length (Appendix S1: Figure S2). Fish generally remained in the same area of the stream for the entire summer: only 3 individuals were recaptured more than 25m from their initial capture position.

Conspecific density

Local (i.e., within 25m bins) *G. porphyriticus* density varied greatly within streams (Appendix S1: Figure S3), but average estimated total abundances were relatively similar among streams (Appendix S1: Table S4). Estimates of capture probability and yearly apparent survival were similar to those described in prior studies (Addis & Lowe, 2020; Appendix S1: Table S4). Mean yearly abundance in Bear Brook was 851 individuals (SE: 36). Based on this estimate, conspecific densities ranged from 0 to 49 salamanders per 25m bin. Mean yearly abundance in Paradise Brook was 809 individuals (SE: 27). Based on this estimate, conspecific densities ranged from 0 to 36 salamanders per 25m bin. Mean yearly abundance in Zigzag Brook was 715 individuals (SE: 76). Based on this estimate, conspecific densities ranged from 0 to 46 salamanders per 25m bin. We also found that both conspecific densities ($t = 3.71$, $df = 490$, $p = 2.29 * 10^{-4}$) and yearly apparent survival probabilities (Appendix S1: Table S5) were lower in the uppermost and

lowermost ends of each stream compared to the interiors of each stream and lower in downstream reaches than upstream reaches (Appendix S1: Table S6)

Dispersal propensity and directionality

None of our explanatory variables were strongly associated with variation in dispersal propensity of larvae or adults. For larvae, the null model was within ΔAIC < 2 of the top models, indicating a lack of strong support for any of the candidate models (Table 1a). For adults, the top model was the null model, indicating a lack of support for any of the candidate models (Table 1b). Contrary to our expectations, none of our explanatory variables were strongly associated with variation in larval dispersal directionality (Table 1c). The null model was within ΔAIC < 2 of the top model, indicating a lack of strong support for any of the candidate models. However, adult dispersal directionality was associated with several of our explanatory variables (Table 1d). Initial capture position was included in all viable models, and the top overall model included initial capture position as the sole predictor of dispersal directionality (AIC_w = 0.36). Specifically, adult salamanders in upstream reaches (i.e., those with a smaller watershed area) were more likely to move downstream, whereas salamanders in downstream reaches (i.e., those where fish were present) were more likely to disperse upstream, consistent with our initial expectations (Fig. 3b). Among other viable models, only conspecific density and overall distance moved were included. Adults dispersed further than larvae on average, although the relationship was weak (median dispersal distance 21m vs 15m; Mann-Whitney U Test; U = 23530, p = 0.07). The difference between upstream movement distances of adults and larvae was pronounced (median dispersal distance 19m vs 9m; U = 3415; p = 0.003), but we found no evidence for a difference in downstream dispersal distances (23m vs 19m; U = 8744; p = 0.70).

Table 1
Model selection for logistic regression models assessing variation in dispersal propensity (a, b) and directionality (c, d) of *Gyrinophilus porphyriticus* larvae and adults in Bear, Paradise, and Zigzag Brooks using Akaike's Information Criterion

(a) Larval propensity	**ΔAIC_c**	**AIC_w**
Propensity~ Initial Position	0.00	0.26
Propensity~ NULL	0.25	0.23
Propensity~ Stream + Initial Position	0.63	0.19
Propensity~ Initial Position + Fish Index	1.64	0.11
(b) Larval directionality	ΔAIC_c	AIC_w
Directionality~ Fish Index + Wetted Width	0.00	0.24
Directionality~ NULL	0.31	0.21
Directionality~ Fish Index	0.59	0.18
Directionality~ Conspecific Density	0.80	0.16
(c) Adult propensity	ΔAIC_c	AIC_w
Propensity~ NULL	0.00	0.57
Propensity~ Initial Position	1.94	0.22
Propensity~ Conspecific Density	1.94	0.22
(d) Adult directionality	ΔAIC_c	AIC_w
Directionality~ Initial Position	0.00	0.36
Directionality~ Initial Position + Distance Moved	0.02	0.35
Directionality~ Initial Position + Conspecific Density	1.75	0.15
Directionality~ NULL	2.74	0.04

Notes: Capture-mark-recapture data were collected from 2012–2025. The top three candidate models (within $\Delta AIC_c < 2$), along with the null model, are listed here. The full list of tested models can be found in Appendix S1: Table S2. Explanatory variable definitions, as well as the reasoning for their inclusion in tested models, can be found in Appendix S1: Table S3.

DISCUSSION

In this study, we show evidence of context-dependent dispersal directionality in a headwater stream salamander. In three study streams, adult salamanders in downstream reaches were more likely to disperse upstream, and adult salamanders in upstream reaches were more likely to disperse downstream, consistent with our initial expectations. Consequently, *G. porphyriticus* densities were lower

in the uppermost and lowermost ends of streams, where context-dependent directionality was most pronounced. Upstream reaches are prone to drying, increasing the risk of desiccation for *G. porphyriticus* (Feder, 1983). Downstream dispersal from these reaches therefore reduces the likelihood of the individual experiencing stream drying (Cochrane et al., 2024b). Meanwhile, downstream reaches contain a predator of *G. porphyriticus* and are more prone to flooding, and both of these risks reduce salamander survival (Resetarits, 1995; Galster, 2007; Cochrane et al., 2024a). While we did not find a strong direct relationship between fish density and dispersal directionality, this may be due to the difference in spatial resolution of sampling. Fish were sampled at 25m increments, whereas salamanders were sampled at 1m increments, potentially obscuring the relationship between fish density and salamander behavior. Still, salamander survival was lower in reaches where fish were present compared to reaches where fish were absent (Appendix S1: Table S6). Together, context-dependent changes in directionality likely maximize the probability of survival (and therefore fitness) for the dispersing individual (Kim & Choi, 2020). Consistent with this hypothesis, we found that yearly apparent survival probabilities in the uppermost and lowermost ends of each stream were lower than yearly apparent survival probabilities in the intervening channels (Appendix S1: Table S5).

Our results suggest that it is critical not to underestimate the sensitivity of dispersal behavior to the local balance of risk factors. If we had pooled individuals within streams, disregarding their spatial positions, we would have found evidence of a strong downstream bias in dispersal, driven largely by the elevated abundance of salamanders in the upstream reaches. However, our results instead suggest that individuals are responding to local environmental variation along streams such that an individual's dispersal directionality is contingent on its position in space. Consequently, the dispersal behavior of downstream individuals differed predictably from the dispersal behavior of upstream individuals. Broadly speaking, studies that fail to account for context-dependent dispersal directionality risk underestimating intraspecific (and intrapopulation) variation in dispersal behavior. For example, studies aiming to predict rates of dispersal among discrete patches (or subpopulations) on the landscape that base these predictions on the average directionality of individuals across all patches, failing to account for patch-level variation in directionality, may make incorrect conclusions about patch-specific rates of immigration and emigration (Poethke & Hovestadt, 2002). Similarly, we posit that supposedly random directionality in many systems may in fact be the result of yet-unidentified context-dependent directionality in multi-dimensional space.

We did not find evidence for context-dependent directionality in larval salamanders. Differences in dispersal ability may account for this result. Adults rely on cutaneous respiration and can leave the stream for short periods of time, which allows them to disperse upstream along the channel, avoiding the energetic cost of moving against the flowing water, and to disperse between isolated pools when channels begin to dry (Baguette and Van Dyck, 2007). In contrast, larvae have gills and can only disperse within the channel (Bruce, 1972), which may impose energetic and physical constraints that dampen behavioral variation in directionality (Baguette & Van Dyck, 2007). Consistent with this hypothesis, we found that median downstream dispersal distance was relatively similar between life history stages (21m for adults, 15m for larvae), but median upstream dispersal distance for adults (19m) was more

than twice the median upstream dispersal distance for larvae (9m). It is also possible, however, that larvae either preferentially disperse downstream or simply lack the variation in dispersal behavior that we observed in adults.

We also did not find evidence of a relationship between dispersal propensity and any of our explanatory variables. 40% of adult salamanders and 24% of larval salamanders dispersed during the study, regardless of environmental conditions. Additionally, despite high environmental heterogeneity within and among the study streams, a similar proportion of individuals in each stream dispersed (32%, 29%, and 30% in Bear, Paradise, and Zigzag Brooks, respectively). If dispersal propensity were indeed influenced by environmental heterogeneity, we would expect to see higher dispersal propensity in relatively poor-quality habitat and lower dispersal propensity in relatively high-quality habitat. The lack of evidence for such relationships – along with the consistency of dispersal frequencies across streams – suggests that dispersal propensity may be an intrinsic trait of salamanders, rather than an environmentally-dependent behavior (Addis and Lowe 2020).

Investigating dispersal distance was not a primary goal of this study, but those data – which we needed to distinguish dispersers from non-dispersers – do provide additional insight on dispersal behavior. Despite the extreme variability in dispersal distance (Fig. 2), we did not see a relationship between dispersal distance and dispersal direction (t = 1.48, df = 197.9, p = 0.14). We interpret these results to mean that dispersal distance, regardless of direction, is a result of a deliberate action. In particular, these results show that downstream dispersal is not simply a consequence of downstream drift in the flowing water (Müller, 1982).

Our results could have been influenced by animals moving out of the study reaches. For example, a salamander at the upper end of one of the upstream study reaches that dispersed upstream would be impossible to recapture, making it appear as though all successful dispersers in that area dispersed downstream. Also, individuals could have dispersed into the space between our study reaches, biasing our results similarly. However, given the relatively short dispersal distances of most individuals (Fig. 2), our failure to detect more than one individual in the spaces between our study reaches during a total of 18 telemetry surveys in 2022, and the physical barrier presented by the weirs that set the upper limits of the upstream study reaches, we do not believe that emigration strongly biased our results. We also assumed that individual capture probabilities did not vary through space. Given the consistent search effort of capture-mark-recapture surveys (i.e., flipping one rock per meter), we recognize that individuals in more rock-dense areas of the stream (i.e., those with more cover objects present in a given meter of stream channel length) may have been less likely to be captured than individuals in areas with lower rock density (Williams & Berkson, 2004). Our telemetry surveys, however, were not subject to this bias because those surveys used radio detection to check for salamanders under all possible cover objects between bankfull edges. The observed relationships between spatial position and dispersal directionality were consistent both before and after incorporating these telemetry data, suggesting that spatial variation in capture probabilities was not a substantial source of bias. Lastly, we recognize that we do not know the mechanisms that allow for such fine-scale variation in dispersal behavior along streams

(Fig. 3). However, localized inbreeding along these streams could allow some genetically based variation in dispersal behavior to persist, even in the absence of external cues (Lowe et al., 2024).

The possibility of context-dependent dispersal directionality is rarely accounted for or considered in most models of animal movement. Yet, failure to account for non-random dispersal, directional or otherwise, reduces the accuracy of model predictions and may result in suboptimal management decisions. For example, assessing context-dependent directionality may be particularly important for correctly predicting range shifts for threatened or invasive species where geographic variation in risk is known to control the likelihood of successful dispersal (Pepper et al., 2019). If detected, context-dependent directionality would allow managers to focus intervention on areas where individuals are more likely to disperse towards, improving dispersal success in threatened species or reducing dispersal success in invasives (Richardson et al., 2015). Notably, we detected context-dependent directionality in an organism with a low perceptual range (Olden et al., 2004; Pittman et al., 2014) and limited dispersal ability, suggesting that this phenomenon may be more common in species that are better equipped to detect and respond to the risk landscape (Pe'er & Kramer-Schadt, 2008). We hope that context-dependent directionality can be a useful concept for modeling animal movement and suggest that future research investigate the factors necessary for the evolution and persistence of context-dependent directionality.

Abbreviations

AIC
Akaike's information criterion
AIC_w
Akaike weights
ΔAIC
Difference in AIC values
SE
Standard error
df
Degrees of freedom

Declarations

Consent to publication

Not applicable

Data availability statement

Data and code can be found on GitHub at https://github.com/Elyons1313/Context-dependent-directionality-in-a-headwater-stream-salamander and will be uploaded to the Hubbard Brook

Environmental Data Initiative Repository (https://hubbardbrook.org/data-catalog/) upon preliminary acceptance.

Conflict of interest statement

The authors declare no conflicts of interest.

Funding

This research was funded by the U.S. National Science Foundation (DEB-1114804, DEB-1050459, DEB-1655653, IOS-2520169) and is a contribution of the Hubbard Brook Ecosystem Study. Hubbard Brook is part of the LTER network, which is supported by the U.S. National Science Foundation. Hubbard Brook Experimental Forest is operated and maintained by the U.S. Department of Agriculture, Forest Service, Northern Research Station.

Author contributions

EL and WL designed the methodology. EL led the data analysis and writing of the manuscript with feedback provided by WL. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgments

The authors thank all those who reviewed this manuscript for their helpful feedback. We thank D. Heinz, B. Schuster, C. Benson, T. Michael, and C. Ackerman for their assistance in the field. This research was conducted under Montana State Institutional Care and Use Protocol #067-16WLDBS-121616.

References

1. Addis BR, Lowe WH. Long-term survival probability, not current habitat quality, predicts dispersal distance in a stream salamander. Ecology. 2020;101(4).
2. Akaike H. Maximum likelihood identification of Gaussian autoregressive moving average models. Biometrika. 1973;60(2):255–65.
3. Alberts SC, Altmann J. Balancing costs and opportunities: dispersal in male baboons. Am Nat Univ Chic Press. 1995;145(2):279–306.
4. Armsworth PR, Roughgarden JE. The impact of directed versus random movement on population dynamics and biodiversity patterns. Am Nat. 2005;165(4):449–65.
5. Baguette M, Van Dyck H. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. Landsc Ecol. 2007;22(8):1117–29.
6. Bartoń K, Mumin. Multi-Model Inference. 2010. P. 1.48.11. Available from: https://CRAN.R-project.org/package=mumin

7. Bayer MO, Lowe WH. Top-down effects of salamanders on macroinvertebrates in fishless headwater streams. Herpetologica Herpetologists' Leag. 2021;77(2):111–20.
8. Bilton DT, Freeland JR, Okamura B. Dispersal in freshwater invertebrates. Annu Rev Ecol Syst. 2001;32(1):159–81.
9. Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado M, Gibbs M, et al. Costs of dispersal. Biol Rev. 2012;87(2):290–312.
10. Bormann F, Likens G. Pattern and process in a forested landscape. New-York Springer-Verl; 1979.
11. Bowler DE, Benton TG. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol Rev. 2005;80(2):205–25.
12. Bruce RC. Variation in the life cycle of the salamander *Gyrinophilus porphyriticus.* Herpetologica. JSTOR. 1972;28:230–45.
13. Burnham KP, Anderson DR. Multimodel Inference: Understanding AIC and BIC in model selection. Sociol. Methods Res. 2004;33(2):261–304.
14. Cayuela H, Schmidt BR, Weinbach A, Besnard A, Joly P. Multiple density-dependent processes shape the dynamics of a spatially structured amphibian population. Vander Wal E, editor. J. Anim. Ecol. 2019;88(1):164–77.
15. Cochrane MM, Addis BR, Lowe WH. Stage-specific demographic effects of hydrologic variation in a stream salamander. Am. Nat. 2024a May 1;203(5):E175–87.
16. Cochrane MM, Addis BR, Swartz LK, Lowe WH. Individual growth rates and size at metamorphosis increase with watershed area in a stream salamander. Ecology. 2024b Feb;105(2):e4217.
17. Cochrane MM, Lowe WH. Headwater-stream salamander movements and home-range size increased under drought. Freshw. Sci. 2025 June 1;44(2):159–69.
18. Feder ME. Integrating the ecology and physiology of plethodontid salamanders. Herpetologica [Herpetologists' Leag Allen Press]. 1983;39(3):291–310.
19. Galster JC. Natural and anthropogenic influences on the scaling of discharge with drainage area for multiple watersheds. Geosphere. 2007;3(4):260.
20. Gardiner T, Hill J. Directional dispersal patterns of Chorthippus parallelus (Orthoptera: Acrididae) in patches of grazed pastures. J Orthoptera Res. 2004 June;13(1):135–41.
21. Gomi T, Sidle RC, Richardson JS. Understanding processes and downstream linkages of headwater systems. Bioscience. 2002;52(10):905.
22. Hauer FR, Lamberti GA. Methods in stream ecology. Elsevier; 2006.
23. Heyer R, Donnelly MA, Foster M, Mcdiarmid R. Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution; 2014.
24. Jolly GM. Biometrika. 1965 June;52(1/2):225. Explicit Estimates from Capture-Recapture Data with Both Death and Immigration-Stochastic Model.
25. Kim K, Choi W. Local dynamics and coexistence of predator–prey model with directional dispersal of predator. Math Biosci Eng. 2020;17(6):6737–55.

26. Klarevas-Irby JA, Wikelski M, Farine DR. Efficient movement strategies mitigate the energetic cost of dispersal. Ecol Lett. 2021 July;24(7):1432–42.
27. Koenig WD, Van Vuren D, Hooge PN. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends Ecol Evol. 1996;11(12):514–7.
28. Laake JL, Johnson DS, Conn PB, Isaac N. Marked: an R package for maximum likelihood and Markov Chain Monte Carlo analysis of capture-recapture data. Methods Ecol Evol. 2013;4(9).
29. Liu R, Shuai J, Wu J, Zhu H. Modeling Spatial Spread of West Nile Virus and Impact of Directional Dispersal of Birds. 2003.
30. Lowe WH, Addis BR, Cochrane MM. Outbreeding reduces survival during metamorphosis in a headwater stream salamander. Mol Ecol. 2024 June;33(12):e17375.
31. Malish MC, Gao S, Kopp D, Hong Y, Allen DC, Neeson T. Small increases in stream drying can dramatically reduce ecosystem connectivity. Ecosphere. 2023;14(3):e4450.
32. Mcelroy B, delonay A, Jacobson R. Optimum swimming pathways of fish spawning migrations in rivers. Ecology. 2012;93(1):29–34.
33. Mcguire KJ, Torgersen CE, Likens GE, Buso DC, Lowe WH, Bailey SW. Network analysis reveals multiscale controls on streamwater chemistry. Proc. Natl. Acad. Sci. 2014;111(19):7030–5.
34. Müller K. The colonization cycle of freshwater insects. Oecologia. 1982;52(2):202–7.
35. Munro JL. The mode of operation of Antillean fish traps and the relationships between ingress, escapement, catch and soak. ICES J. Mar. Sci. 1974 June 1;35(3):337–50.
36. Olden JD, Schooley RL, Monroe JB, Poff NL. Context-dependent perceptual ranges and their relevance to animal movements in landscapes. J Anim Ecol. 2004;73(6):1190–4.
37. Pe'er G, Kramer-Schadt S. Incorporating the perceptual range of animals into connectivity models. Ecol Model. 2008;213(1):73–85.
38. Pepper N, Gerardo-Giorda L, Montomoli F. Meta-modeling on detailed geography for accurate prediction of invasive alien species dispersal. Sci Rep. 2019;9(1):16237.
39. Pittman SE, Osbourn MS, Semlitsch RD. Movement ecology of amphibians: A missing component for understanding population declines. Biol Conserv. 2014;169:44–53.
40. Poethke HJ, Hovestadt T. Evolution of density–and patch–size–dependent dispersal rates. Proc. R. Soc. Lond. B Biol. Sci. 2002;269(1491):637–45.
41. Pusey A, Wolf M. Inbreeding avoidance in animals. Trends Ecol Evol Elsevier Curr Trends. 1996;11(5):201–6.
42. R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. 2022. Available from: https://www.R-project.org/
43. Reinhardt UG, Hrodey PJ. Trap happiness and catch bias in sea lamprey traps. Fishes 2019 June 12;4(2):34.
44. Resetarits WJ. Competitive asymmetry and coexistence in size-structured populations of brook trout and spring salamanders. Oikos. 1995 June;73(2):188.

45. Richardson KM, Doerr V, Ebrahimi M, Lovegrove TG, Parker KA. Considering dispersal in reintroduction and restoration planning. Adv. Reintroduction Biol. Aust. N. Z. Fauna. Australia: Csiro Publishing Clayton; 2015. pp. 59–72.
46. Rogers HS, Beckman NG, Hartig F, Johnson JS, Pufal G, Shea K et al. The total dispersal kernel: a review and future directions. Aslan C, editor. Aob PLANTS. 2019 Sept 1;11(5):plz042.
47. Seber GAF. A Note on the Multiple-Recapture Census. Biometrika. 1965 June;52(1/2):249.
48. Tredennick AT, Hooker G, Ellner SP, Adler PB. A practical guide to selecting models for exploration, inference, and prediction in ecology. Ecol Wiley Online Libr. 2021;102(6):e03336.
49. Turchin P. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Massachusets, Estados Unidos: Sinauer Associates; 1998.
50. Vucetich JA, Peterson RO, Schaefer CL. The effect of prey and predator densities on wolf predation. Ecology. 2002;83(11):3003–13.
51. Warren DR, Likens GE, Buso DC, Kraft CE. Status and distribution of fish in an acid-impacted watershed of the northeastern united states (Hubbard Brook, NH). Northeast Nat 2008 Sept;15(3):375–90.
52. Waser PM. Does competition drive dispersal? Ecology. 1985;66(4):1170–5.
53. Williams AK, Berkson J. Reducing False Absences in Survey Data: Detection Probabilities of Red-Backed Salamanders. Russell, editor. J. Wildl. Manag. 2004;68(2):418–28.

Figures

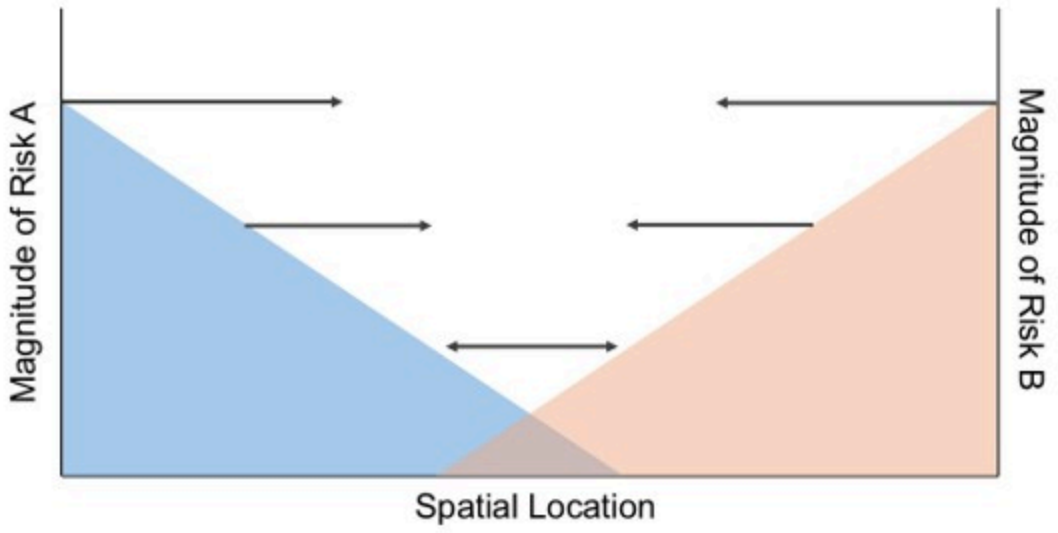


Figure 1

Conceptual figure illustrating how organisms may respond to the presence of multiple risk factors as a function of their spatial location. The y-axis indicates the magnitude of a given risk factor at a location – x-axis. Arrows indicate the hypothesized directionality of dispersal, with longer arrows indicating stronger effects. Organisms subject to the influence of both factors may respond differently than organisms exposed to either factor by itself.

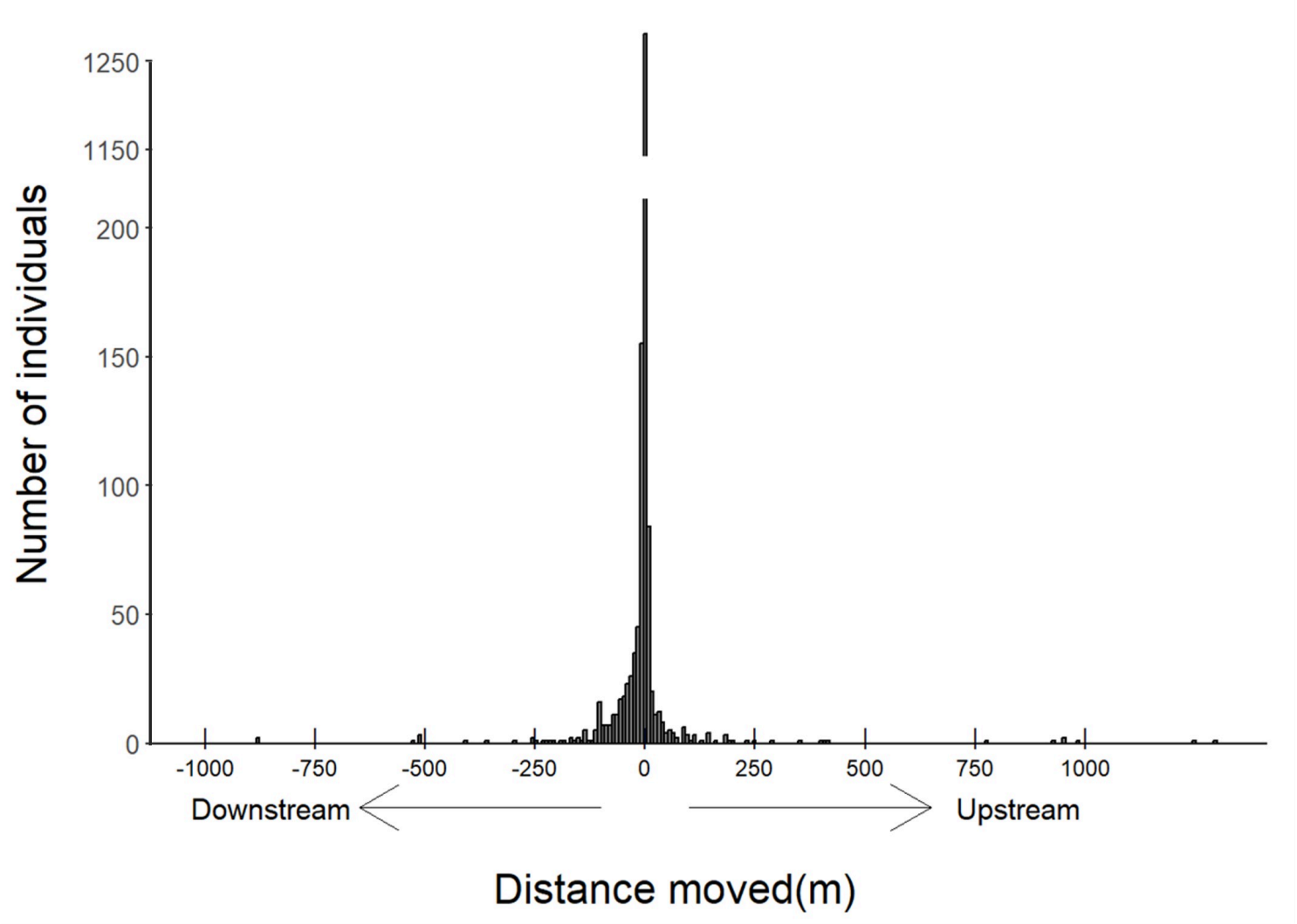


Figure 2

Histogram showing the total distance moved by all recaptured *Gyrinophilus porphyriticus* salamanders from three streams in the Hubbard Brook Experimental Forest (New Hampshire, USA). Individuals that moved 4m or less (i.e., non-dispersers) are represented by the center bar. Negative values indicate downstream movements, positive values indicate upstream movements. Each bar represents a total of 8m of movement distance to fit all non-dispersers in a single group (i.e., a movement distance of 0 ± 4m). The gap in the center bar indicates a break in the y-axis that was necessary to accommodate the large number of non-dispersers.

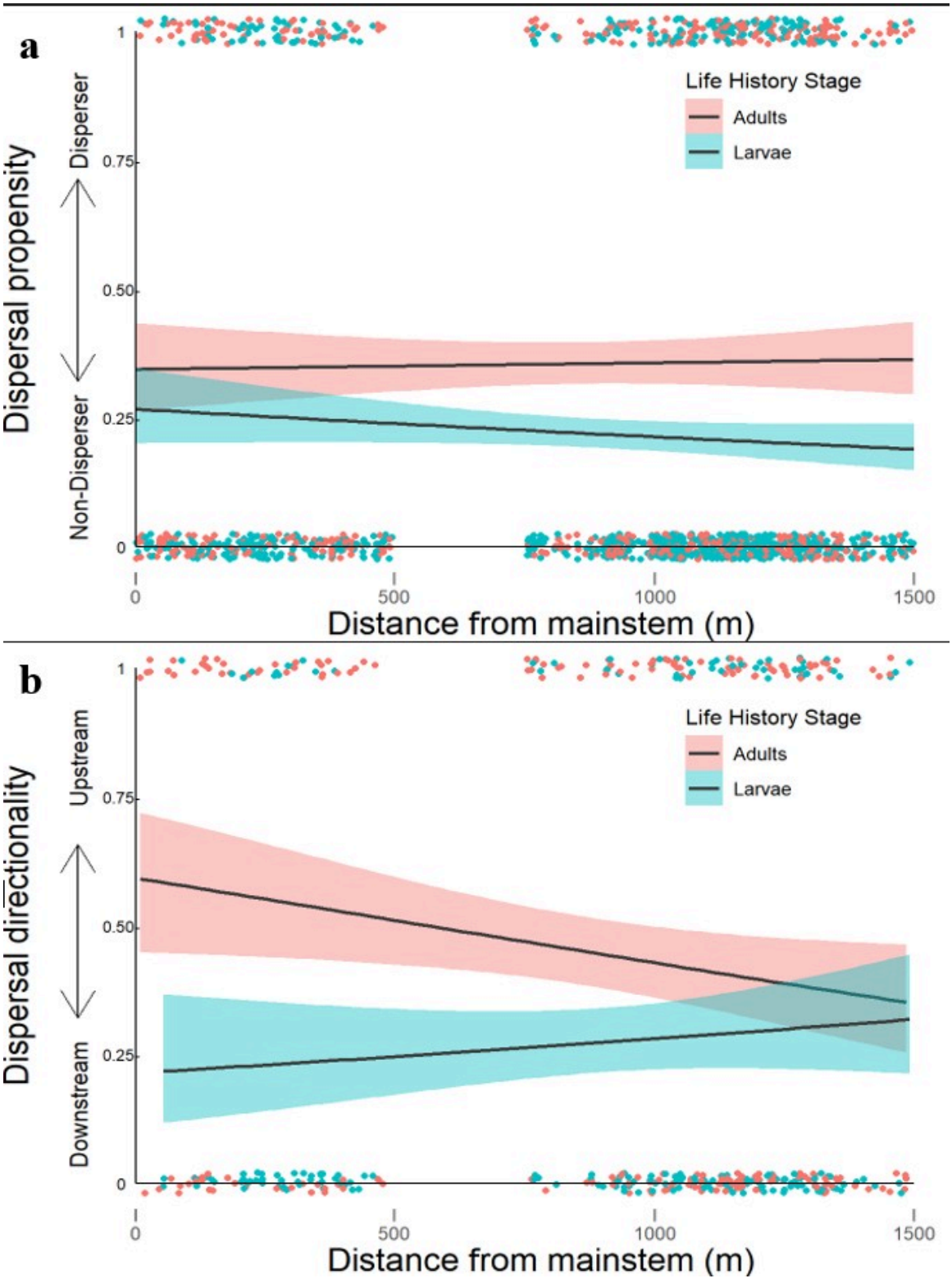


Figure 3

Adults have a higher dispersal propensity than larvae, but dispersal propensity is not related to capture position (a). Adults are more likely to disperse upstream in downstream reaches, and more likely to disperse downstream in upstream reaches, but larval dispersal directionality was not strongly dependent on capture position (b). For both plots, the solid black lines indicate the slope of the logistic regression on the relationship between the initial capture position (in terms of distance from the mainstem) and the

response variable. Bands indicate 95% confidence intervals. All salamanders were captured between 2012-2025 using capture-mark-recapture methods in three streams in the Hubbard Brook Experimental Forest.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- AppendixS1.pdf