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Long-term survival probability, not current habitat quality, predicts dispersal distance in a stream salamander

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Abstract. Dispersal evolves as an adaptive mechanism to optimize individual fitness across the landscape. Specifically, dispersal represents a mechanism to escape fitness costs resulting from changes in environmental conditions. Decades of empirical work suggest that individuals use local habitat cues to make movement decisions, but theory predicts that dispersal can also evolve as a fixed trait, independent of local conditions, in environments characterized by a history of stochastic spatiotemporal variation. Until now, however, both conditional and fixed models of dispersal evolution have primarily been evaluated using emigration data (stay vs. leave), and not dispersal distances: a more comprehensive measure of dispersal. Our goal was to test whether conditional or fixed models of dispersal evolution predict variation in dispersal distance in the stream salamander *Gyrinophilus porphyriticus.* We quantified variation in habitat conditions using measures of salamander performance from 4 yr of spatially explicit, capture–mark–recapture (CMR) data across three headwater streams in the Hubbard Brook Experimental Forest in central New Hampshire, USA. We used body condition as an index of local habitat quality that individuals may use to make dispersal decisions, and survival probability estimated from multistate CMR models as an index of mortality risk resulting from the long-term history of environmental variation. We found that dispersal distances increased with declining survival probability, indicating that salamanders disperse further in risky environments. Dispersal distances were unrelated to spatial variation in body condition, suggesting that salamanders do not base dispersal distance decisions on local habitat quality. Our study provides the first empirical support for fixed models of dispersal evolution, which predict that dispersal evolves in response to a history of spatiotemporal environmental variation, rather than as a conditional response to current habitat conditions. More broadly, this study underscores the value of assessing alternative scales of environmental variation to gain a more complete and balanced understanding of dispersal evolution.

Key words: amphibian; body condition; capture–mark–recapture methods; conditional dispersal; dispersal distance; environmental variation.

INTRODUCTION

Dispersal is expected to evolve as an adaptive mechanism to optimize individual fitness across the landscape (Bowler and Benton 2005). Dispersal incurs energy costs, opportunity costs, and mortality risk (reviewed in Bonte et al. 2012); thus, individuals should only disperse if the fitness gains of settling in a new environment exceed the fitness costs of moving or remaining philopatric. Decades of theory and empirical work have settled on three main sources of fitness costs that lead to dispersal evolution: kin competition (Hamilton and May 1977, Ronce et al. 2000, Poethke et al. 2007), inbreeding (Bengtsson 1978, Waser et al. 1986, Guillaume and Perrin 2006), and environmental variation (Johnson and Gaines 1990, McPeek and Holt 1992). While there is evidence that active dispersers base emigration decisions (i.e., stay vs. leave) on perceived costs associated with these factors (e.g., O'Riain et al. 1996, Bonte et al. 2008, Cote and Clobert 2010), it is less well understood how and whether the same factors influence dispersal distances.

Across taxa, most individuals in natural populations do not disperse, and dispersal distances vary substantially among those that do, with few individuals dispersing long distances (Mayr 1963, Endler 1977, Johnson and Gaines 1990). Research on the causes of variation in dispersal distances is challenging because it is difficult to obtain direct dispersal data in the field (Koenig et al. 1996, Nathan 2001). As a result, most dispersal research focuses on dispersal propensity, or the discrete emigration response. Dispersal distance, however, also encompasses stages of transience and settlement, and thereby provides a more complete picture of the dispersal process (Ronce 2007, Clobert et al. 2009). Furthermore,

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long-distance dispersal is predicted to contribute disproportionately to range shifts in response to climate change (Higgins and Richardson 1999, Phillips et al. 2008) and persistence in fragmented habitats (Muller-Landau et al. 2003, Bohrer et al. 2005), so understanding the drivers of variation in dispersal distance is important from an applied perspective.

Generally, environmental variation is expected to have a stronger effect on dispersal distances than kin competition and inbreeding (Bowler and Benton 2005, Duputié and Massol 2013). Short-distance movements are likely to alleviate fitness costs associated with kin competition and inbreeding because kin tend to be clumped around the natal site (Greenwood 1980, Waser and Jones 1983, Lawson Handley and Perrin 2007). Environmental variation, however, can occur across multiple spatial scales, from the microhabitat (Wilson 1998, Jimenez et al. 2015) to the landscape (Johnson et al. 1997, Clark and Clark 2000), as well as over multiple temporal scales (Tielbörger and Kadmon 2000, Anderson and Cribble 2006). It is, therefore, reasonable to expect that different scales of environmental variation favor different dispersal distances, although this possibility has yet to be evaluated empirically. Indeed, theory predicts that short- and long-distance dispersal evolve according to different properties of the landscape (Bonte et al. 2010), suggesting that focusing on environmental variation is key to understanding variation in dispersal distances in natural populations.

Two basic, conceptual models of dispersal responses to environmental variation have emerged in the literature: conditional and fixed dispersal strategies. Under conditional strategies, dispersal decisions are based on the individual's ability to perceive and act on information about local conditions, and dispersal is, fundamentally, a plastic response to current environmental variation (Clobert et al. 2009). For example, studies of dispersal propensity have shown that active dispersers are capable of initiating emigration in response to increased intraspecific competition for resources (Herzig 1995, Aars and Ims 2000, De Meester and Bonte 2010), the presence of predators or parasites (McCauley and Rowe 2010, Suhonen et al. 2010), and low food availability (Lurz et al. 1997, Kennedy and Ward 2003). However, because most studies do not track the fate of dispersers, we have little understanding of whether and how these conditional emigration responses, or the underlying stimuli themselves, relate to ultimate dispersal distances.

Under fixed strategies, dispersal is an evolved response to long-term patterns of environmental variability at large spatial scales (i.e., across multiple potential settlement sites), rather than a conditional response to the local environment. Specifically, dispersal is predicted to evolve when habitat quality varies stochastically across potential settlement sites, both temporally and spatially (Kuno 1981, Levin et al. 1984, McPeek and Holt 1992). Because these stochastic changes in habitat quality cannot be anticipated, fixed dispersal represents a bet-hedging mechanism that ultimately maximizes the long-term geometric mean fitness of dispersers (Kuno 1981, Metz et al. 1983, Armsworth and Roughgarden 2005, McPeek 2017). Direct, empirical support for fixed dispersal is limited, but indirect support can be found in systems where the development of locomotor structures are necessary for dispersal, such as wing-dimorphic insects (Harrison 1980, Denno et al. 1996). Generally, these phenotypic constraints prevent individuals from basing dispersal decisions on immediate, local habitat conditions (Hendrickx et al. 2013) and, instead, the ability to disperse is a response to a long-term pattern of stochastic environmental variation. Similar to conditional dispersal, however, fixed dispersal has predominantly been studied in terms of propensity (stay vs. leave), leaving a gap in our understanding of whether and how long-term patterns of environmental variation influence dispersal distance.

Explicitly testing for effects of current and long-term patterns of environmental variation on dispersal distances will help to resolve the prevalence of conditional vs. fixed dispersal strategies. Conditional dispersal has more empirical support in the literature than fixed dispersal, leading researchers to speculate that it is more evolutionarily advantageous and ubiquitous in nature (Bowler and Benton 2005, Bonte et al. 2008, Clobert et al. 2009). The weight of support for conditional strategies may be, in part, an artifact of the feasibility of quantifying dispersal propensity and local environmental conditions, but it is also possible that dispersal distance is governed by conditional strategies, particularly if settlement decisions are based on local conditions (Stamps 2001, Banks and Lindenmayer 2014). Alternatively, dispersal propensity and distance may be governed by different strategies. For example, assuming that settlement sites are randomly distributed, the number of these sites will increase with distance moved, making it costly and potentially unrealistic for individuals to gather the information needed to optimize conditional strategies (Delgado et al. 2014). If so, we would expect dispersal distances to be regulated by the long-term patterns of environmental variation that favor fixed dispersal strategies (Kuno 1981, Levin et al. 1984, McPeek and Holt 1992).

We used four years of spatially explicit, capture–mark–recapture data from three headwater streams to test whether current or long-term patterns of environmental variation, matching conditional vs. fixed models of the evolution of dispersal, respectively, predict variation in dispersal distances in the salamander *Gyrinophilus porphyriticus.* For our test of conditional dispersal, we used spatial variation in salamander body condition as an index of current environmental variation. Body condition, commonly measured as size-corrected mass, reflects the nutritional state of the animal, where high-condition individuals are considered to have higher foraging success and competitive ability (Jakob et al. 1996, Johnson 2007). In *G. porphyriticus*, body condition increases with gut content biomass (W. H. Lowe, *unpublished data*) and is positively correlated with reproduction (Lowe 2003), suggesting that body condition reflects local prey resources, which contribute to reproductive potential (Croll et al. 2006, Ward et al. 2009). Therefore, body condition provides an index of local habitat quality over short timescales. Under a conditional strategy, dispersal decisions are based on sampling habitat, creating the expectation that dispersal distances should be correlated with the spatial distribution of suitable habitat. Low spatial variation in body condition should cause dispersal distances to increase by increasing the distance individuals must move to encounter higher quality habitat than their starting location (Palmer and Strathmann 1981, Levin et al. 1984, Lowe 2009). When spatial variation in habitat quality, and thus body condition, is high, individuals need not move long distances to encounter higher quality habitat, and dispersal distances should decrease (Bonte et al. 2010).

For our test of fixed dispersal, we used reach- or stream-scale survival probability as an index of long-term patterns of environmental variation, and specifically mortality risk resulting from that variation (Stacey and Taper 1992, Lande 1993, Nicoll et al. 1993). In stream reaches characterized by low survival, the risk of dispersing to an alternative site is low relative to the risk of remaining at an initial site, and we expected dispersal distances to increase under these conditions (McPeek and Holt 1992, Boudjemadi et al. 1999). In contrast, when survival is high, the risk of dispersing relative to that of remaining at an initial site should increase, causing dispersal distances to decrease (Delgado et al. 2011). We estimated survival probabilities from capture histories of hundreds of individuals (White and Burnham 1999); therefore, these estimates integrate the long-term effects of environmental variation across individuals in the population, which are predicted to govern fixed dispersal strategies (Kuno 1981, Levin et al. 1984, McPeek and Holt 1992).

METHODS

Study species and sites

Gyrinophilus porphyriticus is a lungless salamander that lives in small, cool, well-oxygenated streams along the Appalachian uplift in the eastern United States (Petranka 1988). Larvae are exclusively aquatic (Bruce 1980) and adults are mainly aquatic but can forage terrestrially at night (Degraaf and Rudis 1990, Deban and Marks 2002). During the day, larvae and adults are found in interstitial spaces among the larger rocks (i.e., cobble) in the stream bed (Bruce 2003). The larval period lasts 3–5 yr (Bruce 1980) and adults can live to be 14 yr (W. H. Lowe, *unpublished data*). Previous work has shown that both larval and adult *G. porphyriticus* disperse (Lowe 2003, Lowe et al. 2006), so both life stages were the focus of this study. This species is suited for dispersal studies because movements are generally constrained to linear stream corridors, so detection probability is less affected by movement distance, overcoming a major empirical hurdle (Koenig et al. 1996). Additionally, the relative mobility of *G. porphyriticus* is low, so surveys can detect a wide range of dispersal distances, including rare long-distance dispersal events.

This work was conducted in three hydrologically independent first-order streams (Bear, Paradise, Zigzag) in the Hubbard Brook Experimental Forest, located in the White Mountains of central New Hampshire (43°56′ N,

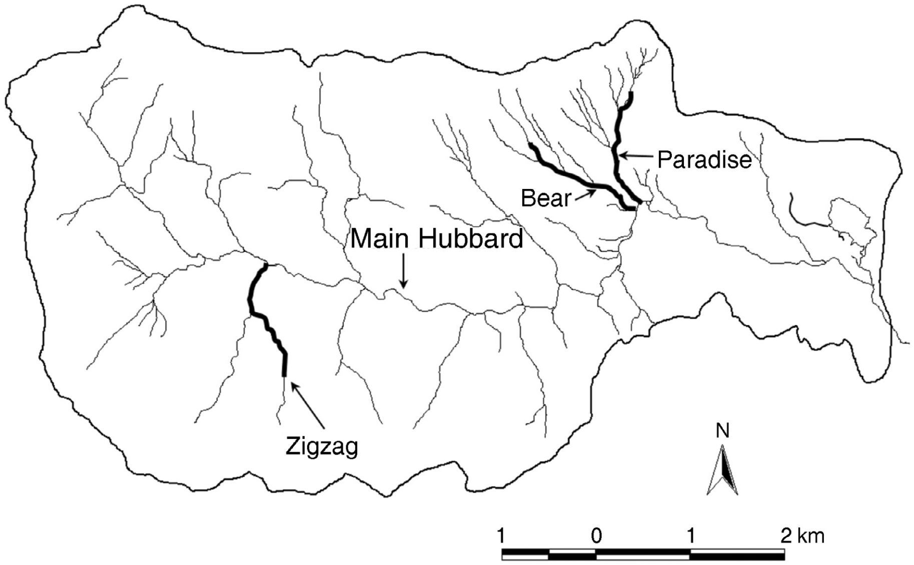

FIG. 1. Map of the three study streams in the Hubbard Brook Experimental Forest in central New Hampshire, USA. Bear, Paradise, and Zigzag Brooks are hydrologically independent and flow into Hubbard Brook.

71°45′ W; Fig. 1). These streams differ in environmental conditions, including aspect, daily discharge, and drainage slope (Lowe et al. 2006, McGuire et al. 2014). Brook trout (*Salvelinus fontinalis*) occur in the mainstem of Hubbard Brook and downstream reaches of the study streams (Warren et al. 2008, Lowe et al. 2018). Brook trout prey on and reduce growth rates of *G. porphyriticus* (Resetarits 1995), thus they may represent an important aspect of the environment that influences dispersal through effects on *G. porphyriticus* survival and body condition.

Capture–mark–recapture survey methods

Capture–mark–recapture surveys were conducted in June–September of 2012–2015. To test for differences in survival and body condition related to fish presence, or other longitudinal changes in stream environments (Vannote et al. 1980), we divided each stream into two 500-m reaches (downstream and upstream reaches). Downstream reaches began at the confluence with Hubbard Brook. Upstream reaches ended at weirs where long-term stream data are collected, and above which sampling is restricted (Bormann and Likens 1979). Distances between downstream and upstream reaches, measured along stream channels, were 400 m in Bear Brook, 250 m in Paradise Brook, and 500 m in Zigzag Brook. Our surveys were based on a robust design framework consisting of three primary sampling sessions per summer, with three secondary sampling sessions within each primary session (Pollock 1982). Each reach was surveyed nine times throughout each summer, for a total of 36 surveys per reach over the 4-yr study period. A constant search effort was maintained by turning one cover object per meter of stream to locate salamanders; thus, surveys provided spatially explicit information about the capture locations of individual salamanders. Salamanders were uniquely marked with visible implant elastomer (Northwest Marine Technology, Inc., Anacortes, Washington, USA). We did not mark larval salamanders that measured <3 cm snout–vent in order to avoid injury. Snout–vent lengths and masses were recorded for all captured individuals.

Quantifying long-term environmental variation

We first quantified long-term environmental variation for our test of fixed dispersal, then used those results to structure our analysis of current environmental variation for our test of conditional dispersal. Survival probability over the 4-yr study period served as our measure of long-term environmental variation. Because the three study streams are hydrologically independent, differ in many environmental conditions, and are genetically differentiated (Lowe et al. 2006), we expected a priori that the determinants of survival would differ among streams and, therefore, modeled each stream separately (Lowe et al. 2006, McGuire et al. 2014). We used multistate CMR models to estimate monthly survival (S) and recapture (p) probabilities of *G. porphyriticus* larvae and adults, and transition probabilities from the larval to adult stage ($\psi^{\text{larva}\rightarrow\text{adult}}$). These models were implemented in Program MARK (White and Burnham 1999, Lebreton et al. 2009). Although we originally designed our sampling to fit a robust design framework, we collapsed all secondary survey sessions to a single observation within each primary session to fit the traditional multistate framework and increase the accuracy and precision of parameters of interest (e.g., Grant et al. 2010). This resulted in a total of 12 sampling occasions over the 4-yr study period.

In multistate models, survival probability represents the probability that an animal alive at time t in one state (i.e., life-history stage) will be alive at time $t + 1$, independent of state at $t + 1$. Survival probability confounds mortality and permanent emigration in multistate models. However, we believe permanent emigration is minimal in our study streams because weirs above the upstream reaches likely act as a barrier to dispersal, and *G. porphyriticus* have not been previously detected in the mainstem of Hubbard Brook (W. H. Lowe, *unpublished data*), suggesting that downstream emigration is unlikely. Additionally, extensive overland dispersal is impossible for the strictly aquatic larvae of *G. porphyriticus* and likely rare for adults given their highly aquatic habits (Petranka 1988, Greene et al. 2008). With two states, the transition probability is the conditional probability that an animal in one state at time t will be in the other state at $t + 1$, given that the animal is alive at $t + 1$. Recapture probability is the probability that a marked animal at risk of capture at time t is captured at t, conditional on being alive and available for recapture.

First, we determined the best models for recapture probabilities (p^{larva}, p^{adult}) and transitions from the larval to adult stage ($\psi^{\text{larva}\rightarrow\text{adult}}$) simultaneously, holding apparent survival constant (Lebreton et al. 2009, Grant et al. 2010). Recapture and transition probabilities were modeled as constant, variable by time (month), and variable by stream reach (downstream, upstream). This candidate model set was justified by temporal variation in stream flow (Likens and Buso 2006) and spatial variation in fish occurrence (Warren et al. 2008) that could alter salamander behavior in such a way as to affect recapture probabilities. Temporal variation in $\psi^{\text{larva}\rightarrow\text{adult}}$ has been observed in a different stream outside of the Hubbard Brook watershed (Lowe 2012), and we hypothesized that $\psi^{\text{larva}\rightarrow\text{adult}}$ could vary as a function of fish occurrence in downstream and upstream reaches because brook trout do not prey on adults (Resetarits 1991, Benard 2004). We fixed $\psi^{\text{adult}\rightarrow\text{larva}}$ to 0 because this transition is biologically impossible. Stream reaches were represented as attribute groups in Program MARK (Cooch and White 2007).

Using the top models for recapture and transition probabilities, we modeled survival as constant, variable over time, and variable by stream reach. This allowed us to test the spatial scale over which survival varied within each stream (i.e., whether survival differed between upstream, fishless reaches and downstream reaches with fish). By objectively identifying the scale of survival variation, we were able to define relevant "stream units" for subsequent analyses. Importantly, this modeling approach allowed us to estimate survival independently for larvae and adults, and thereby test whether the spatial scale of survival also differs between life-history stages.

Model selection was based on Akaike's information criterion (AIC; Akaike 1973) and models were ranked by second-order AIC (AIC_c) differences (ΔAIC_c; Burnham and Anderson 2002). The relative likelihood of each model in the candidate set was estimated with AIC_c weights (Buckland et al. 1997). Goodness-of-fit for the saturated multistate model was assessed using the program U-CARE (Choquet et al. 2009) and by estimating the variance inflation factor ($\hat{c}$) between the top model and the saturated model. It is generally accepted that model fit is adequate if $\hat{c} < 3$ (Lebreton et al. 1992).

Quantifying current environmental variation

To quantify current environmental variation for our test of conditional dispersal, we measured spatial variation in body condition at occupied sites within each stream unit identified by survival analyses. We used the coefficient of variation (CV) as an index of variability in body condition because it is a unitless measure of relative variability that can be compared across samples (i.e., stream units) with different means (Abdi 2010). Coefficients of variation are intended for measurements on a ratio scale (i.e., all positive values) so we added 1 to all condition measurements prior to calculations to meet this criterion. We calculated the CV of body condition within each year of the study for each stream unit. Because each salamander was associated with a specific position along the stream, this approach captured spatial variation in body condition. We then calculated the mean of yearly CVs to obtain a single estimate of variation in body condition per stream unit. Consequently, these means reflect spatial variation in body condition within streams and changes in the amount of this variation over the 4 yr of the study. Body condition was calculated as residuals from ordinary least squares linear regression of log-transformed snout–vent length (SVL) and mass measurements. This approach was justified by the lack of correlation between log SVL and residuals from these regressions ($r < 0.0001$; Green 2001). Regressions were conducted separately for each stream, and for larvae and adults within each stream, matching our approach for survival estimation. Calculating condition separately for the two life-history stages was further justified by the potential for ontogenetic variation in length-mass relationships unrelated to habitat quality. To identify the time scale over which body condition varies and confirm its utility as an index of short-term environmental variation, we tested whether body condition measurements collected in the same year (i.e., summer field season), and between years, were correlated in recaptured individuals. However, we only included body condition measurements from initial captures in our calculations of the CV to avoid pseudoreplication.

Quantifying dispersal distance

We quantified dispersal distances in recaptured individuals as the net distance moved (meters along the stream) over the 4-yr study period (i.e., the distance between initial and last capture locations; Turchin 1998). To quantify variability in dispersal distance among stream units, we calculated the interquartile range (IQR) of dispersal distances because it reflects the relative dispersion of the data, but is robust to outliers (Hubert and Vandervieren 2008). Home ranges in *G. porphyriticus* are approximately 3 m^2 (Lowe 2003), which roughly translates to 3 m in stream length. In previous analyses, we considered dispersal to be movements >3 m to distinguish dispersal from daily movements within the home range (i.e., foraging, refuge use, searching for mates; Burgess et al. 2016). Because the majority of *G. porphyriticus* do not disperse (Lowe 2003, Lowe 2009), the IQR of distances within stream units reflects both non-dispersal and dispersal movements, as lower quantiles ranged from 0 to 1 m. However, we believe the IQR is the most accurate representation of the spread of dispersal distances in our stream units because it is not biased by few individuals that move far distances relative to the majority.

Statistical analyses

To test for effects of alternative scales of environmental variation on *G. porphyriticus* dispersal distances, we identified the best model of dispersal distance IQR from a set of univariate and multivariate linear regression models using AIC model selection. Candidate univariate models included spatial variation in body condition or monthly apparent survival probability, reflecting conditional vs. fixed models of dispersal evolution, respectively. The multiple regression model included spatial variation in body condition and monthly apparent survival probability, to address the possibility that dispersal distance may be predicted by both current and long-term patterns of environmental variation simultaneously.

We tested for covariation in spatial variation in body condition and survival probability to ensure that these two metrics captured different aspects of environmental variation (i.e., current vs. long-term; Graham 2003). We also tested whether model likelihood increased when body condition was added as an individual covariate in survival models (Pollock 2002). If model likelihood increases when survival is a function of body condition, it would suggest that survival at the scale of the stream units may be confounded with variation in condition within the stream units. Therefore, this analysis represents an additional test of the independence of our two metrics of environmental variation.

RESULTS

Capture–mark–recapture surveys

Over the 4-yr study period, we marked 662, 635, and 384 larval *G. porphyriticus* in Bear, Paradise, and Zigzag Brooks, respectively. We marked 268, 241, and 169 adult *G. porphyriticus* in Bear, Paradise, and Zigzag Brooks, respectively. More individuals were marked in upstream reaches than downstream reaches in all three streams. Ratios of the number of upstream to downstream individuals were 1.34:1 in Bear Brook, 1.48:1 in Paradise Brook, and 3.13:1 in Zigzag Brook.

Long-term environmental variation: survival probability

Parameterization of the top models for recapture and transition probabilities differed among streams (Table 1). For Paradise and Zigzag Brooks, the difference in AIC_c (ΔAIC_c) between the top two models of p and $\psi^{larva\rightarrow adult}$ was <2, indicating that both models have approximately equal support (Table 1; Burnham and Anderson 2002). However, both the top- and second-ranked models of p and $\psi^{larva\rightarrow adult}$ yielded the same parameterization for survival, justifying retaining the top model of p and $\psi^{larva\rightarrow adult}$ for these streams. The difference in AIC_c between the top- and second-ranked models was >2 for Bear Brook, indicating considerable support for the top model (Table 1).

In the top models, monthly apparent survival of larvae and adults was either constant over time and reach or variable by reach, but never variable by time alone (Table 2). The difference in AIC_c (ΔAIC_c) between the top and second-ranked survival models was >2 in Bear and Zigzag Brooks, indicating considerable support for the top models. The difference in AIC between the top and second-ranked model for Paradise Brook was <2. The 95% confidence intervals on adult survival estimates for the downstream and upstream reach broadly overlapped (downstream, 0.90–0.96; upstream, 0.91–0.97), which increased our confidence that the top model, with no variation in adult survival between reaches, was the most accurate and conservative. None of the lack-of-fit tests performed on the saturated model with the program U-CARE were significant, indicating that the multistate framework was appropriate for the data set (Choquet et al. 2009). Estimates of median $\hat{c}$ were 1.03, 1.04, and 1.33 for Bear, Paradise, and Zigzag Brooks, respectively, further indicating adequate model fit (Lebreton et al. 1992).

Overall, these analyses showed that the spatial scale of variation in survival differed among our study streams. Survival differed between downstream and upstream reaches for adults in Bear Brook and for larvae in Paradise Brook (Tables 2, 3). In contrast, survival was constant between reaches for larvae in Bear and Zigzag Brooks, and for adults in Paradise and Zigzag Brooks (Tables 2, 3). We considered the possibility that detecting between-reach differences in survival was contingent on sample size, as highly parameterized models are not supported when data are thin. Our sample size was highest for larvae in Bear Brook (n = 662), yet model ranking did not support a difference in larval survival between reaches. In contrast, model ranking supported a difference in adult survival between reaches in Bear Brook, which had much smaller sample sizes (downstream, n = 123; upstream, n = 145). Additionally, when we forced multistate models to estimate survival for upstream and downstream reaches separately, confidence intervals broadly overlapped in cases where model

TABLE 1. Multistate capture–mark–recapture (CMR) models of monthly larval and adult recapture probabilities (p^{larva}, p^{adult}) and larva–adult transition probability ($\psi^{larva\text{-}adult}$) for *Gyrinophilus porphyriticus* in Bear, Paradise, and Zigzag Brooks.

Model	AIC_c	ΔAIC_c	AIC_c wt	K
Bear				
$S^{larva}(.)$, $S^{adult}(.)$, $p^{larva}(reach)$, $p^{adult}(time)$, $\psi^{larva\text{-}adult}(reach)$	2,106.53	0	0.74	17
$S^{larva}(.)$, $S^{adult}(.)$, $p^{larva}(reach)$, $p^{adult}(time)$, $\psi^{larva\text{-}adult}(.)$	2,108.77	2.24	0.24	16
$S^{larva}(.)$, $S^{adult}(.)$, $p^{larva}(.)$, $p^{adult}(time)$, $\psi^{larva\text{-}adult}(.)$	2,114.67	8.14	0.01	15
Paradise				
$S^{larva}(.)$, $S^{adult}(.)$, $p^{larva}(time)$, $p^{adult}(time)$, $\psi^{larva\text{-}adult}(.)$	1,876.64	0	0.63	25
$S^{larva}(.)$, $S^{adult}(.)$, $p^{larva}(time)$, $p^{adult}(time)$, $\psi^{larva\text{-}adult}(reach)$	1,877.88	1.23	0.34	26
$S^{larva}(.)$, $S^{adult}(.)$, $p^{larva}(time)$, $p^{adult}(time)$, $\psi^{larva\text{-}adult}(time)$	1,883.92	7.28	0.02	35
Zigzag				
$S^{larva}(.)$, $S^{adult}(.)$, $p^{larva}(reach)$, $p^{adult}(reach)$, $\psi^{larva\text{-}adult}(.)$	927.17	0	0.31	7
$S^{larva}(.)$, $S^{adult}(.)$, $p^{larva}(reach)$, $p^{adult}(.)$, $\psi^{larva\text{-}adult}(reach)$	927.77	0.60	0.23	7
$S^{larva}(.)$, $S^{adult}(.)$, $p^{larva}(reach)$, $p^{adult}(reach)$, $\psi^{larva\text{-}adult}(reach)$	927.77	0.60	0.23	8

Notes: Larval and adult survival probabilities (S^{larva}, S^{adult}) were held constant for this analysis. Here, we only show the top three models for each stream. Second-order Akaike's information criterion values (AIC_c), AIC_c differences(ΔAIC_c), AIC_c weights (AIC_c wt), and number of estimable parameters (K) are provided for all models. Parameterization for S, p, and ψ is in parentheses; a period indicates constant by stream reach and time.

Table 2. Multistate capture–mark–recapture (CMR) models assessing variation in monthly survival probabilities of *Gyrinophilus porphyriticus* larvae and adults (S^{larva}, S^{adult}) in Bear, Paradise, and Zigzag Brooks.

Model	AIC$_c$	ΔAIC$_c$	AIC$_c$ wt	*K*
Bear				
$S^{\text{larva}}(.)$, $S^{\text{adult}}(\text{reach})$, $p^{\text{larva}}(\text{reach})$, $p^{\text{adult}}(\text{time})$, $\psi^{\text{larva-adult}}(\text{reach})$	2,098.06	0	0.72	18
$S^{\text{larva}}(\text{reach})$, $S^{\text{adult}}(\text{reach})$, $p^{\text{larva}}(\text{reach})$, $p^{\text{adult}}(\text{time})$, $\psi^{\text{larva-adult}}(\text{reach})$	2,100.13	2.07	0.25	19
$S^{\text{larva}}(\text{time})$, $S^{\text{adult}}(\text{reach})$, $p^{\text{larva}}(\text{reach})$, $p^{\text{adult}}(\text{time})$, $\psi^{\text{larva-adult}}(\text{reach})$	2,104.67	6.61	0.03	28
Paradise				
$S^{\text{larva}}(\text{reach})$, $S^{\text{adult}}(.)$, $p^{\text{larva}}(\text{time})$, $p^{\text{adult}}(\text{time})$, $\psi^{\text{larva-adult}}(.)$	1,869.65	0	0.70	26
$S^{\text{larva}}(\text{reach})$, $S^{\text{adult}}(\text{reach})$, $p^{\text{larva}}(\text{time})$, $p^{\text{adult}}(\text{time})$, $\psi^{\text{larva-adult}}(.)$	1,871.57	1.92	0.27	27
$S^{\text{larva}}(.)$, $S^{\text{adult}}(.)$, $p^{\text{larva}}(\text{time})$, $p^{\text{adult}}(\text{time})$, $\psi^{\text{larva-adult}}(.)$	1,876.64	6.99	0.02	25
Zigzag				
$S^{\text{larva}}(.)$, $S^{\text{adult}}(.)$, $p^{\text{larva}}(\text{reach})$, $p^{\text{adult}}(\text{reach})$, $\psi^{\text{larva-adult}}(.)$	927.17	0	0.59	7
$S^{\text{larva}}(.)$, $S^{\text{adult}}(\text{reach})$, $p^{\text{larva}}(\text{reach})$, $p^{\text{adult}}(\text{reach})$, $\psi^{\text{larva-adult}}(.)$	929.21	2.04	0.21	8
$S^{\text{larva}}(\text{time})$, $S^{\text{adult}}(.)$, $p^{\text{larva}}(\text{reach})$, $p^{\text{adult}}(\text{reach})$, $\psi^{\text{larva-adult}}(.)$	929.9	2.74	0.15	17

Notes: Recapture probabilities (p^{larva}, p^{adult}) and larva–adult transition probability ($\psi^{\text{larva-adult}}$) were parameterized based on results in Table 1. Only the three top models for each stream are shown. Second-order Akaike's information criterion values (AIC$_c$), AIC$_c$ differences (ΔAIC$_c$), AIC$_c$ weights (AIC$_c$ wt), and number of estimable parameters (*K*) are provided for all models. Parameterization for *S*, *p*, and ψ is in parentheses; a period indicates constant by stream reach and time.

Table 3. Interquartile ranges of dispersal distances, survival probabilities, and body condition coefficients of variation for each of the eight stream units identified by capture–mark–recapture survival analyses (see Table 2).

Stream	Stage	Reach	Interquartile range of distance	Survival probability†	Body condition (CV)	Range of annual body condition CVs
Bear	larva	combined	4.5	0.96 (0.006)	8.11	5.96–10.23
Bear	adult	downstream	10.0	0.88 (0.023)	5.15	3.85–6.75
Bear	adult	upstream	3.0	0.95 (0.013)	6.64	4.97–10.32
Paradise	larva	downstream	7.0	0.91 (0.013)	7.56	6.07–9.15
Paradise	larva	upstream	4.0	0.95 (0.007)	7.52	6.84–9.04
Paradise	adult	combined	8.0	0.94 (0.012)	7.33	5.63–8.55
Zigzag	larva	combined	2.0	0.96 (0.010)	7.83	6.28–10.28
Zigzag	adult	combined	7.5	0.91 (0.019)	7.15	5.04–8.86

† Values are means with SE in parentheses.

ranking supported a single estimate of survival. Thus, we have confidence that our modeling approach accurately and objectively identified the spatial scales over which survival differed in our study streams. This approach yielded eight independent estimates of monthly survival across stages, reaches, and streams, ranging from 0.88 to 0.96 (Table 3). Larval and adult survival estimates were not correlated ($r = -0.40$, $P = 0.51$), confirming independence of this metric across life-history stages. We refer to the spatial scale pertaining to each of the eight survival estimates as a "stream unit" because, in some cases, there were multiple survival estimates per stream.

Current environmental variation: body condition

Means of annual CV of body condition, our index of current environmental variation within each of the eight stream units, ranged from 5.15 to 8.11 (Table 3). Across the 4 yr of the study, ranges of annual CV values within each stream unit were 2.91–5.36 indicating temporal, as well as spatial, variation in body condition. In each stream, mean annual CV values were higher for larvae (range 7.52–8.11) than adults (range 5.15–7.33), and were not correlated across life-history stages ($r = -0.78$, $P = 0.12$). In recaptured individuals, body condition measurements taken within the same summer season were correlated ($r = 0.35$, $P < 0.001$, $n = 372$), but body condition measurements taken in consecutive summer seasons were uncorrelated ($r = 0.05$, $P = 0.56$, $n = 128$), indicating that this index reflects environmental variation on the timescale of 1 yr.

Dispersal distance

Of the 2,359 *G. porphyriticus* individuals captured in surveys, 464 individuals were recaptured. Maximum dispersal distances of recaptured individuals in the eight stream units ranged from 81 to 481 m (Fig. 2). There was a strong correlation between the total distance moved over the study period and net movement from the initial capture location in individuals that were recaptured more than once ($n = 169$, $r = 0.78$, $P < 0.001$), indicating that most dispersal movements

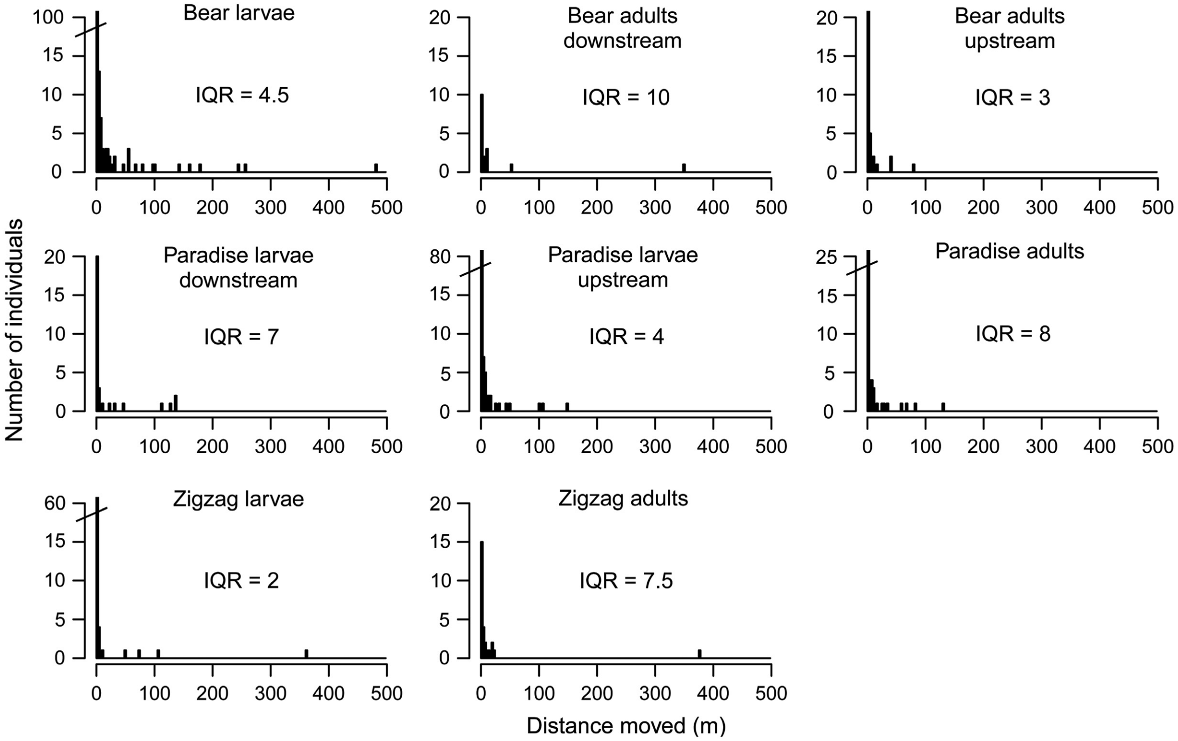

FIG. 2. Dispersal distances of *Gyrinophilus porphyriticus* larvae and adults in stream units defined from capture–mark–recapture analyses. Data are from Bear, Paradise, and Zigzag Brooks in the Hubbard Brook Experimental Forest. "Stream units" are the spatial scale over which survival differed in each of the three study streams. The interquartile range (IQR) of dispersal distances are indicated in the center of each plot. Hatches indicate a break in the *y*-axis to accommodate large numbers of individuals that dispersed < 3 m. Data are binned in 3-m increments.

are unidirectional and permanent. The interquartile range of dispersal distances, our dependent variable for testing relationships with indices of environmental variation, ranged from 2 to 10 m across the eight stream units identified by survival analyses (Fig. 2). There was no correlation between stream unit sample sizes and dispersal distance IQR ($r = -0.48$, $P = 0.22$), and dispersal distance IQR was not correlated across life-history stages ($r = 0.05$, $P = 0.94$), indicating that this metric was not biased by variation in sample size or life-history stage, respectively.

Effects of current and long-term environmental variation on dispersal distance

The best model of dispersal distance included monthly apparent survival probability alone and received 15 times more support than the second-ranked model, which included spatial variation in body condition (Table 4). The model including both monthly apparent survival and spatial variation in body condition received less support than the univariate models (Table 4). Consistent with a priori predictions, dispersal distance was negatively related to survival ($\beta = -78.09$, SE = 23.27, $t = -3.36$, $P = 0.02$, $r^2 = 0.59$; Fig. 3). This regression accounts for variation in the precision of survival estimates by weighting each estimate by the inverse standard error. The relationship between spatial variation in body condition and dispersal distance was not significant ($\beta = -1.76$, SE = 0.99, $t = -1.78$, $P = 0.13$, $r^2 = 0.24$; Fig. 4).

Monthly apparent survival was, somewhat surprisingly, positively correlated with spatial variation in body condition ($r = 0.77$, $P = 0.03$), but overwhelming support for the model with survival alone (Table 4) indicates

TABLE 4. Models of dispersal distance in *Gyrinophilus porphyriticus* larvae and adults in Bear, Paradise, and Zigzag Brooks.

Model	AIC$_c$	ΔAIC$_c$	AIC$_c$ wt	*K*	Adjusted R^2
Survival	40.16	0	0.93	3	0.59
Spatial bodycond	45.73	5.56	0.06	3	0.26
Survival + spatial bodycond	49.13	8.97	0.01	4	0.53

Notes: Second-order Akaike's information criterion values (AIC$_c$), AIC$_c$ differences (ΔAIC$_c$), AIC$_c$ weights (AIC$_c$ wt), and number of estimable parameters (*K*) are provided for all models. Independent variables, calculated from capture–mark–recapture data from 2012 to 2015, include monthly survival (survival) and spatial variation in body condition (spatial bodycond). Response variables were the interquartile range of dispersal distances in stream units defined by survival analyses.

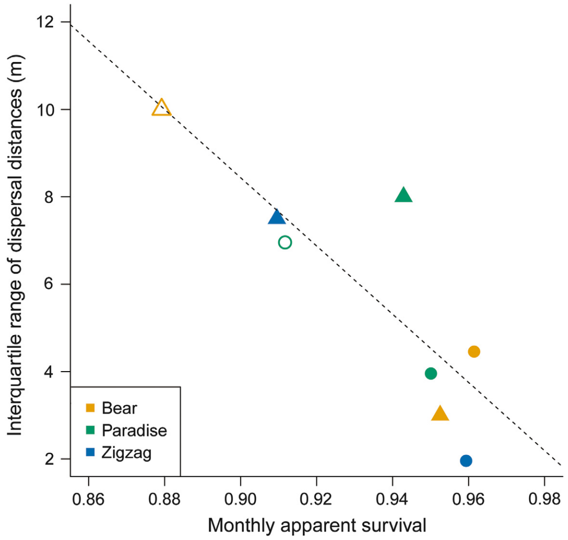

FIG. 3. The relationship between monthly apparent survival and interquartile ranges of dispersal distance in *Gyrinophilus porphyriticus*. Data are from Bear, Paradise, and Zigzag Brooks in the Hubbard Brook Experimental Forest. Each point corresponds to stream units defined from capture–mark–recapture analyses. Colors correspond to the three study streams. Triangles represent adult *G. porphyriticus* and circles represent larval *G. porphyriticus*. When survival analyses distinguished between upstream and downstream reaches, open shapes represent downstream reaches and filled shapes represent upstream reaches. The best-fit linear regression line is plotted ($\beta = -78.09$, SE = 23.27, $t = -3.36$, $P = 0.015$, $r^2 = 0.59$).

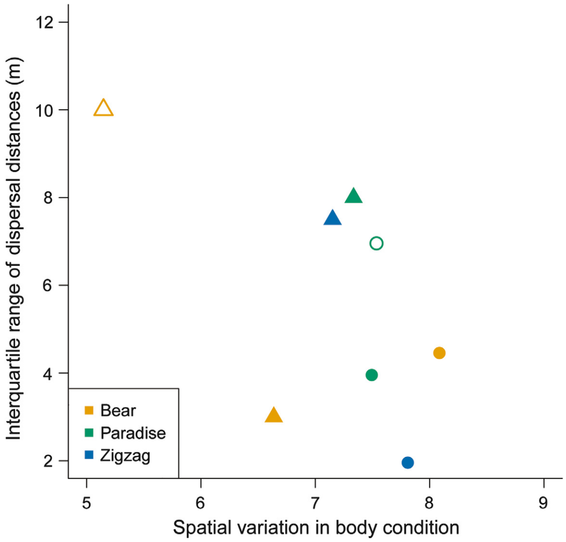

FIG. 4. The relationship between spatial variation in body condition and interquartile ranges of dispersal distance in *Gyrinophilus porphyriticus*. Data are from Bear, Paradise, and Zigzag Brooks in the Hubbard Brook Experimental Forest. Each point corresponds to stream units defined from capture–mark–recapture analyses. Colors correspond to the three study streams. Triangles represent adult *G. porphyriticus*, and circles represent larval *G. porphyriticus*. When survival analyses distinguished between upstream and downstream reaches, open shapes represent downstream reaches and filled shapes represent upstream reaches.

that survival probability was the best predictor of variation in dispersal distances. Further, model likelihood did not increase when body condition was added as an individual covariate in the best-fitting survival models (Appendix S1:Table S1), suggesting that variation in body condition within stream units did not cause survival probabilities to differ among stream units, and that these two metrics reflect different aspects of environmental variation.

DISCUSSION

Theory has long predicted that dispersal can evolve as a fixed trait, independent of local conditions, in environments characterized by a history of stochastic spatiotemporal variation (Kuno 1981, Levin et al. 1984, McPeek and Holt 1992). Yet, empirical work has predominantly supported conditional dispersal, where individuals use local habitat cues to make dispersal decisions (Bowler and Benton 2005, Bonte et al. 2008, Clobert et al. 2009). We show that dispersal distances in a species of stream salamander increased in environments characterized by low survival probability, a long-term and large-scale measure of habitat quality. Dispersal distance was unrelated to spatial variation in body condition, our measure of current, local habitat quality. These results suggest that salamanders do not base dispersal decisions on cues related to habitat quality in their immediate vicinity, but instead that increased dispersal distances are an evolved response to risky environments.

Our finding that dispersal distances increased as survival declined (Fig. 3) supports the hypothesis that habitats characterized by low survival are risky from an individual's perspective, causing the relative risk of long-distance dispersal to decrease and the relative benefit to increase. This interpretation aligns with models predicting that dispersal evolves as a bet-hedging strategy in stochastically varying environments (Kuno 1981, Metz et al. 1983, Armsworth and Roughgarden 2005), rather than models where dispersal is conditional on individual perceptions of local habitat quality (Clobert et al. 2009). More specifically, our results suggest that long-distance dispersal in our study streams represents a response to a historical pattern of environmental stochasticity resulting in low survival, consistent with fixed models of dispersal evolution (Gadgil 1971, Kuno 1981, Levin et al. 1984, McPeek and Holt 1992).

Capture–mark–recapture model ranking supports our assumption that survival probabilities reflect long-term variation in habitat quality because models where survival varied over time received little support (Table 2). Nevertheless, our ability to quantify long-term environmental variability was limited by the length of our study, 4 yr, and we acknowledge that long-lived salamanders could base dispersal decisions on environmental variation over longer timescales. Estimating survival probabilities over longer timescales would, therefore, help confirm the utility of this metric as an index of long-term variation in habitat quality, and we continue surveying these streams for that purpose. We do know, however, that survival probabilities reflect longer-term environmental variability than body condition, which varied between years.

Also consistent with fixed dispersal models (Levin et al. 1984), the spatial scale over which we estimated survival was large (500 or 1,000 m of stream length), much larger than typical dispersal movements of *G. porphyriticus* (Fig. 2) and encompassing many potential settlement sites. These sites varied in quality, as indicated by spatial variation in body condition within stream units, creating the potential for fitness benefits of dispersal, even within stream units characterized by low survival. Further, because most individuals in our data set did not move far (70% moved < 4 m), it is unlikely that these survival estimates are confounded by the fitness consequences of dispersal (e.g., higher mortality of dispersing individuals than non-dispersers).

Dispersal distances could be affected by landscape structure, either directly or in combination with long-term survival probabilities. For example, if survival increases with habitat availability, individuals in low survival stream units would be forced to move farther distances to find suitable habitat than individuals in stream units with higher survival. To evaluate this possibility, we conducted post hoc analyses to test for correlations between habitat availability, survival, and dispersal distances. We quantified spatial variation in suitable sites using the Morisita dispersion index (Morisita 1959), and tested for aggregation of salamanders into 10 m sub-reaches within each stream unit. Values > 1.0 indicate increasing aggregation into these sub-reaches, thereby indicating a decrease in the availability of suitable habitat as there is no known benefit of aggregation in *G. porphyriticus*. We found evidence of aggregation in all stream units (Morisita values ranged from 1.23 to 1.79), but Morisita values were not correlated with survival ($r = 0.07$, $P = 0.86$) or with the IQR of dispersal distances ($r = -0.24$, $P = 0.56$). This indicates that the relationship between survival and dispersal distances in our stream units was not confounded by variation in habitat availability.

We did not detect a relationship between current, local habitat quality, measured with individual body condition, and dispersal distances (Fig. 4), suggesting that salamanders do not base dispersal distances on habitat sampling during periods of transience. This result may reflect constraints on habitat sampling as dispersal distance increases. Assuming that suitable habitat is randomly distributed, the number of potential settlement sites increases with dispersal distance (Morris 1992, Koenig 1999). For long-distance dispersal, it becomes unrealistic for individuals to sample all (or even a modest percentage of) potential sites (Delgado et al. 2014). Additionally, more time spent sampling likely increases the costs of dispersal by increasing risk of mortality, increasing energy expenditure, or reducing time available for other activities such as mating or foraging (Bonte et al. 2012). Dispersing without sampling habitat may, therefore, be favored for longer movements because it reduces costs by minimizing the number of steps needed to achieve a certain distance (Zollner and Lima 1999, Barton et al. 2009). Rather than reflecting constraints on habitat sampling, it is also possible that salamanders base dispersal decisions on an aspect of habitat quality not reflected by body condition. Future work to identify proximate sources of variation in body condition, as well as other determinants of local habitat quality, will allow us to more thoroughly evaluate the prevalence of conditional dispersal in *G. porphyriticus*.

The lack of relationship between current, local habitat quality, and dispersal distances underscores the value of treating dispersal propensity and dispersal distance as functionally distinct. There is a large body of work linking dispersal propensity to fine-scale fluctuations in habitat quality, leading researchers to predict that factors increasing dispersal propensity should also increase dispersal distance, yet few studies have tested this prediction (Hovestadt et al. 2001, Rousset and Gandon 2002, Duputié and Massol 2013). To explore this possibility, we tested post hoc for a relationship between dispersal propensity and both survival probability and spatial variation in body condition. Home ranges in *G. porphyriticus* are approximately 3 m^2 (Lowe 2003), so we calculated dispersal propensity as the proportion of individuals that moved >4 m to be sure that dispersal movements were distinct from daily movements within the home range (Burgess et al. 2016). We found no relationship between survival probability and dispersal propensity ($\beta = -1.57$, SE = 1.15, $t = -1.37$, $P = 0.22$), or between spatial variation in body condition and dispersal propensity ($\beta = -0.03$, SE = 0.03, $t = -1.12$, $P = 0.30$). These results caution against using dispersal propensity as a proxy for dispersal distance, and, perhaps more importantly, suggest that dispersal propensity and distance evolve independently (Bonte et al. 2010, Duputié and Massol 2013, Burgess et al. 2016).

Our modeling results clearly indicate that large-scale, long-term variation in survival better predicts dispersal distances than current, local variation in habitat quality (Table 4). We did, however, find an unexpected positive correlation between spatial variation in body condition and survival probability, indicating a possible mechanistic link between these two variables. We know of no studies reporting a causal relationship between variability in body condition and survival, although positive relationships between mean body condition and survival have been reported (Schmutz and Ely 1999, Vitz and Rodewald 2011, Boulanger et al. 2013). Importantly, post hoc analyses showed no correlation between mean body condition and survival probability across our eight stream units ($r = -0.22$, $P = 0.60$), and spatial variation in body condition and mean body condition also were not correlated ($r = -0.34$, $P = 0.41$). Further, including body condition as an individual covariate in survival models did not improve model fit (Appendix S1: Table S1), indicating that variation in body condition within stream units did not cause survival probabilities to differ among stream units. Instead, our results suggest that habitat heterogeneity itself positively affects *G. porphyriticus* survival (Kindvall 1996, Piha et al. 2007), such as by providing access to different conditions for optimal foraging vs. predator avoidance (Sih 1982, Gilliam and Fraser 1987, Creel et al. 2005), although the mechanism underlying this relationship clearly requires further investigation.

We used indices of individual performance (survival, body condition) as proxies for environmental differences among our study sites because performance consequences ultimately drive adaptive evolution (Arnold 1983). Further, a rich body of work links habitat quality to body condition (e.g., Bearhop et al. 2004, Burton et al. 2006, Maceda-Veiga et al. 2014) and survival (e.g., Paradis 1995, Kindvall 1996, Carvell et al. 2017). However, a drawback of our approach is that it does not reveal proximate drivers of salamander dispersal. It is difficult to generate a priori hypotheses for the proximate variables affecting dispersal, or survival, in this system because we know that the study streams are highly heterogeneous by many biotic and abiotic measures, and across multiple scales (Schwarz et al. 2003, Likens and Buso 2006, McGuire et al. 2014). Our finding that survival of *G. porphyriticus* larvae was not consistently lower in the downstream reaches with brook trout underscores this challenge (Fig. 3). Variation in survival between downstream and upstream reaches may be a function of several interrelated factors that differ along the stream continuum, in addition to brook trout occurrence, such as discharge, substrate embeddedness and its effects on refuge availability, and invertebrate prey composition (Vannote et al. 1980, Hubert and Kozel 1993, Lowe and Bolger 2002).

This study represents the first empirical support for models predicting that dispersal evolves as a fixed strategy in risky environments. Further efforts to characterize long-term and large-scale patterns of environmental variation, and to quantify dispersal distances, rather than emigration propensity, may reveal previously unrecognized contributions of fixed dispersal strategies in other systems (Levin et al. 1984, McPeek and Holt 1992). These relationships may be more likely in species that are not constrained to linear habitats like streams, where potential habitat available for sampling increases exponentially with dispersal distance, making conditional strategies even more impractical and costly for long-distance dispersers (Bocedi et al. 2012, Bonte et al. 2012, Delgado et al. 2014). Finally, our results suggest that dispersal distances will be greater in populations that have evolved in high-risk environments. Quantifying long-term environmental variation and resulting risk landscapes may, therefore, be useful for predicting dispersal distances and associated population and range dynamics under future environmental change (Higgins and Richardson 1999, Bohrer et al. 2005, Phillips et al. 2008).

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