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CAUSES OF VARIATION IN DISPERSAL DISTANCE IN THE STREAM SALAMANDER GYRINOPHILUS PORPHYRITICUS

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CAUSES OF VARIATION IN DISPERSAL DISTANCE IN THE STREAM SALAMANDER

GYRINOPHILUS PORPHYRITICUS

By

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Dissertation

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Causes of variation in dispersal distance in the stream salamander *Gyrinophilus porphyriticus*

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ABSTRACT

Dispersal is expected to evolve as an adaptive mechanism to optimize individual fitness across the landscape. While there is evidence that active dispersers base emigration decisions (i.e., stay vs. leave) on perceived costs associated with environmental variation and inbreeding, it is less well understood how and whether these same factors influence dispersal distances— a more comprehensive measure of dispersal. More generally, the challenge of quantifying dispersal in the field has resulted in a paucity of data on the fate and fitness of dispersing individuals, leaving us with little knowledge of the factors influencing individual variation in dispersal distance. In my dissertation, I use a combination of morphological, performance, demographic, and genetic data to understand the selective forces shaping variation in dispersal distances in the stream salamander *Gyrinophilus porphyriticus*.

I found that phenotypic attributes that facilitate long-distance dispersal restrict other locomotor performances. Specifically, salamanders that dispersed farther in the field had longer forelimbs, but swam at slower velocities under experimental conditions. These results suggest that salamanders disperse by walking, and that longer limbs may lower the cost of transport by increasing stride length. Longer limbs also impose more drag, potentially explaining the reduced swimming performance of long-distance dispersers. These results are novel in demonstrating a trade-off associated with variation in dispersal distance, and, more broadly, suggest that this and other trade-offs associated with continuous variation in dispersal distance may constrain dispersal evolution.

I show that large-scale, long-term environmental variation – reflected in survival probabilities of *G. porphyriticus* – better predicts dispersal distances than current, local variation in habitat quality. These results provide the first empirical support for early theory that treated dispersal as an innate, ‘fixed’ quality of individuals that evolves in response to a history of spatiotemporal environmental variability at large spatial scales. Importantly, these results challenge the current paradigm that most dispersal is conditional and based on gathering information about local habitat quality. Based on these findings, I develop a conceptual model of dispersal evolution where informed strategies explain short-distance dispersal, and fixed strategies explain long-distance dispersal.

I provide rare empirical support for the basic prediction that inbreeding risk decreases with dispersal distance. Further, I show that the degree to which dispersal functions to reduce inbreeding risk in *G. porphyriticus* is mediated by other environmental conditions influencing dispersal distance. Specifically, dispersal effectively reduced inbreeding risk in downstream reaches where dispersal distances were greater. In contrast, dispersal did not reduce inbreeding risk in upstream reaches, where dispersal distances were shorter. These results suggest that selective pressures influencing dispersal distances in *G. porphyriticus* can vary at fine spatial scales (i.e., reach-scale), with resulting consequences on inbreeding risk. Population genetic data indicated that inbreeding avoidance is likely not the primary driver of dispersal distance, but downstream and upstream reaches differ in many abiotic and biotic factors (i.e., discharge, streamwater chemistry, substrate size, prey and predator communities) that may explain differences in dispersal distances.

Collectively, my dissertation research provides empirical insight on the causes of individual variation in dispersal distance and constraints on the evolution of dispersal. My work demonstrates that data on dispersal distances are crucial for disentangling the relative importance of the many selective pressures influencing dispersal in natural populations. Previous studies have shown that long-distance dispersal is predicted to contribute disproportionately to range shifts in response to climate change and persistence in fragmented habitats. Therefore, understanding the processes promoting and constraining long-distance dispersal in natural populations may help to address several pressing applied issues.

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CHAPTER 1: Introduction and overview

Dispersal drives ecological and evolutionary processes by affecting population growth rates and gene flow (Tittler et al. 2006, Van Houtan et al. 2007). Long-distance dispersal, in particular, plays a key role in determining population and species persistence by setting the rate of range shifts and facilitating connectivity across fragmented habitat (Higgins and Richardson 1999; Bohrer et al. 2005; Phillips et al. 2008). However, the challenge of quantifying dispersal in the field has resulted in a paucity of data on the fate and fitness of dispersing individuals, leaving us with little understanding of the factors influencing individual variation in dispersal distance (Koenig et al. 1996, Nathan 2001, Lowe and McPeck 2014). Most dispersal research has instead focused on the discrete emigration response (stay vs. leave). Dispersal distances provide a more complete picture of the dispersal process because they encompass not only emigration, but also subsequent stages of transience and settlement (Ronce 2007, Clobert et al. 2009).

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. Across taxa, most individuals in natural populations do not disperse, whereas dispersal distances vary substantially among those that do, with few individuals exhibiting long-distance dispersal (Mayr 1963, Endler 1977, Johnson and Gaines 1990). The relative rarity of long-distance dispersal suggests that the costs of dispersal increase with distance, but empirical tests of this prediction remain scarce.

Decades of theory and empirical work have settled on three main sources of fitness costs that lead to the evolution of dispersal: 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, McPeck 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. Additionally, we have little understanding of the relative importance of these drivers in natural populations where dispersal may be shaped by many, potentially conflicting selective forces (Guillaume & Perrin, 2006; Perrin & Goudet, 2001; Waser, Austad, & Keane, 1986).

In my dissertation, I use a combination of morphological, performance, demographic, and genetic data to understand the selective forces shaping variation in dispersal distances in the

stream salamander *Gyrinophilus porphyriticus*. My specific research objectives were to test for locomotion-based tradeoffs associated with variation in dispersal distance, test for effects of environmental variation on dispersal distance, and evaluate the effects of dispersal distance on inbreeding risk. Last, I integrate early theory and recent empirical work to develop a new conceptual model of dispersal evolution – where dispersal strategies differ with dispersal distances.

The goal of my dissertation was to understand the processes leading to continuous variation in dispersal distances, but this naturally leads to the question of how to define long-distance dispersal. It is generally acknowledged that short-distance dispersal influences local processes (i.e., population dynamics, resource use), while long-distance dispersal affects large-scale process (i.e., range shifts, colonization dynamics; Kot et al. 1996, Hanski 1998, Nathan et al. 2003). However, ‘local’ and ‘large-scale’ must still be scaled to the movement capacities of species. Likewise, thresholds for distinguishing long-distance dispersal must be species-specific, but should be considerably higher than mean or median dispersal distances (Nathan et al. 2003). The dispersal distances I quantified in *G. porphyriticus* ranged from 0 – 881m, and the mean and median distances were 12.77m and 1m, respectively. Therefore, I am confident that I detected movements that were both long-distance and rare relative to the majority of movements by *G. porphyriticus*, but I also acknowledge that the extent to which these long-distance movements affect large-scale processes remains an open question. Because my research did not require delineating individuals as short- or long-distance dispersers, the analyses I present here are not biased by the subjectivity associated with defining long-distance dispersal.

Research objectives and findings

A distance-performance tradeoff in the phenotypic basis of dispersal

The costs of dispersal are widely believed to trade off with the benefits (e.g., reduced competition, increased reproductive success) to influence emigration decisions (Clobert et al. 2009; Bonte et al. 2012; Ronce and Clobert 2012). Differences in morphological, physiological, and behaviors traits between dispersers and residents may indicate selection for ‘dispersal phenotypes’ to reduce dispersal costs (Harrison 1980; Benard and McCauley 2008; Edelaar and Bolnick 2012), but phenotypic attributes that facilitate dispersal may also induce costs. Cost-benefit trade-offs are well documented for the discrete emigration response (Denno et al. 1989, Mole and Zera 1993), but this framework has not been applied to understand individual variation in dispersal distance. However, the rarity of long-distance dispersal highlights the need to consider the possibility that phenotypic specialization for long-distance dispersal creates costs that have gone unrecognized. Instead, variation in dispersal distance is often attributed to

extrinsic stochastic or environmental factors (Carlquist 1981, Tufto et al. 1997, Morales 2002), rather than phenotypic attributes of the individual.

In Chapter 2, I assessed locomotion-based trade-offs associated with dispersal distance. Locomotion serves many different functions, including foraging, prey capture, predator escape, and dispersal, each requiring different morphological or physiological specializations. In aquatic vertebrates, morphological specialization for sustained swimming for long-distance dispersal may create a cost through reduced maneuverability, affecting fast-starts for prey capture or predator escape (Webb 1984, Weihs 2002). I used 4 years of intensive, spatially explicit capture-mark-recapture data to test for a morphological basis of dispersal distance under natural field conditions. Next, I tested whether morphological traits related to dispersal distance in the field also influenced swimming performance in an experimental water chamber. Specifically, I addressed the following research question:

- Do phenotypic attributes associated with variation in dispersal distance constrain swimming performance?

I found that salamanders that dispersed farther in the field had longer forelimbs but swam at slower velocities under experimental conditions. The positive relationship between forelimb length and dispersal distance suggests that *G. porphyriticus* disperse primarily via walking because salamanders do not actively use their limbs for swimming (Delvolvé et al. 1997). Longer forelimbs may facilitate moving greater distances by increasing stride length, thereby lowering the cost of transport (Pontzer 2007). Post-hoc analyses showed that the longest-limbed individuals could experience up to 18% more drag than the shortest-limbed individuals, potentially explaining the reduced swimming performance of long-distance dispersers. This study is novel in demonstrating a trade-off associated with variation in dispersal distance and, specifically, that phenotypic attributes that facilitate long-distance dispersal restrict other locomotor performances. This work challenges the long-standing view that dispersal distance is extrinsically controlled by environmental factors, and underscores the importance of considering dispersal as a continuous trait that is shaped by selection.

Effects of environmental variation on dispersal distance

Dispersal represents a mechanism to escape fitness costs resulting from changes in environmental conditions (Johnson and Gaines 1990, McPeck and Holt 1992). 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). 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, fixed

dispersal is predicted to evolve when habitat quality varies stochastically across potential settlement sites, both temporally and spatially (Kuno 1981; Levin et al. 1984; McPeck and Holt 1992). Empirical support is more abundant for conditional dispersal, leading researchers to speculate that conditional strategies are more evolutionarily advantageous, and therefore, more prevalent than fixed strategies. However, because most studies do not track the fate of dispersers, we have little understanding of whether and how conditional and fixed emigration responses – or the underlying stimuli themselves – relate to ultimate dispersal distances.

In Chapter 3, I 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 dispersal evolution – predict variation in dispersal distances. For my test of conditional dispersal, I used spatial variation in salamander body condition as an index of current environmental variation. For my test of fixed dispersal, I used survival probability from multistate CMR models as an index of long-term patterns of environmental variation, and specifically mortality risk resulting from that variation (Stacey and Taper 1992, Nicoll et al. 1993, Lande 1993). I addressed the following research question:

- Are current or long-term patterns of environmental variation associated with variation in dispersal distances?

I found that dispersal distance 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, a measure of current, local habitat quality. Long-distance dispersal in my study streams, therefore, likely represents a response to a historical pattern of environmental variation resulting in low survival, consistent with fixed models of dispersal evolution (Gadgil 1971, Kuno 1981, Levin et al. 1984, McPeck and Holt 1992). This finding 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. Post-hoc analyses showed that neither current nor long-term patterns of environmental variation affected dispersal propensity, a more common measure of dispersal, underscoring the necessity of treating dispersal propensity and dispersal distance as functionally distinct processes. More broadly, this study provides the first empirical support for fixed models of dispersal evolution predicting that dispersal evolves in response to a history of spatiotemporal environmental variation, rather than individual perceptions of immediate conditions.

Dispersal distance predicts inbreeding risk

Avoiding the harmful effects of inbreeding has been identified as an important driver of dispersal evolution (Bengtsson 1978, Waser et al. 1986). Dispersal distances should strongly affect inbreeding risk because the likelihood of mating with relatives decreases with increasing distances, yet few studies have tested this basic prediction (Szulkin and Sheldon 2008). Evaluating dispersal distances in the context of the spatial scale of genetic relatedness will

provide insight on the importance of inbreeding avoidance relative to other selective pressures influencing dispersal distances. Importantly, the degree to which dispersal functions to reduce inbreeding may be mediated by other environmental conditions influencing dispersal distance, such as the presence of predators, competition for resources, and changes in habitat quality (Cronin et al. 2004, Bitume et al. 2013, Baines et al. 2014).

In Chapter 4, I evaluated whether dispersal distance predicts inbreeding risk, and whether this relationship changes under different environmental conditions. Many abiotic and biotic factors differ along streams, such as discharge, streamwater chemistry, substrate size, and the composition of prey and predator communities, creating a diverse suite of selective pressures that might influence salamander dispersal (Vannote et al. 1980, Hubert and Kozel 1993, Lowe and Bolger 2002, McGuire et al. 2014). I hypothesized that these or other environmental factors may lead to different relationships between dispersal distance and inbreeding risk in the downstream and upstream reaches of headwater streams in *G. porphyriticus*. In this chapter, I used demographic and population genetic data from 5 headwater streams used as replicates to address the following research questions:

- Do dispersal distances differ between downstream and upstream reaches?
- Does the effect of dispersal on inbreeding risk differ between downstream and upstream reaches?

I found that dispersal distances were greater in downstream reaches than upstream reaches, suggesting that selective pressures influencing dispersal differ at fine spatial scales. Inbreeding risk, measured as the proportion of individuals within 50m that were relatives, was lower for dispersers than residents in downstream reaches. In contrast, there was no difference in inbreeding risk between dispersers and residents in upstream reaches. These results demonstrate that dispersal reduces inbreeding risk and that environmentally-associated variation in dispersal distances leads to variation in the effects of dispersal in inbreeding risk. Population genetic data indicated that inbreeding depression is unlikely in our study populations, suggesting that selective pressures other than inbreeding avoidance maintain dispersal in *G. porphyriticus*. These results underscore the importance of interpreting dispersal distances in the context of spatial patterns of genetic relatedness to disentangle inbreeding avoidance from other selective pressures influencing dispersal distances.

Scale- dependent evolution of dispersal

In Chapter 5, I develop a conceptual model that can be used to explain variation in dispersal distances in natural populations. This model integrates conditional and fixed models of dispersal evolution (introduced in Chapter 3) in one scale-dependent model. Conditional and fixed dispersal models represent two very different views of dispersal evolution, hinging on differences in the perception and use of information. My argument for a scale-dependent model of dispersal evolution is based primarily on the scaling of information-gathering costs with

dispersal distance. Therefore, for clarity, here I refer to conditional strategies as ‘informed’ strategies.

Models of informed dispersal are based on individuals’ ability to perceive and assess fitness returns at the current location and in transit to a settlement site. This view is supported by accumulating empirical evidence that individuals use information about habitat quality and environmental conditions to make emigration and settlement decisions (e.g., Massot et al. 2002; Bonte et al. 2008). In contrast, early theoretical models treated dispersal as a ‘fixed’ trait, where individuals have an innate propensity to disperse that is independent of local conditions (e.g., Gadgil 1971; Roff 1975; Hastings 1983; Holt 1985; McPeck and Holt 1992). The fitness benefits of fixed dispersal strategies stem from unpredictable spatiotemporal variation in ecological conditions, and dispersal represents a bet-hedging strategy that ultimately maximized the long-term geometric mean fitness of dispersers (McPeck 2017). Empirical support for fixed dispersal, however, is still scarce, leading researchers to speculate that informed strategies are more evolutionarily advantageous and common (Bowler and Benton 2005, Bonte et al. 2008, Clobert et al. 2009).

I suggest that the prevalence of the informed strategy in empirical studies is, in part, an artifact of a focus on the discrete emigration and settlement responses associated with short-distance movements. The importance of information becomes less clear when we consider continuous variation in dispersal distance. Specifically, the dramatic increase in potential settlement sites with increasing dispersal distances make informed strategies impractical and costly at large spatial scales. I propose that informed strategies are useful for explaining the emigration and settlement decisions that govern short-distance dispersal, but fixed strategies are more likely to explain long-distance dispersal because they reduce the cost of large-scale movements. Environmental conditions are also more likely to vary unpredictably with increasing distance from an origin, further reducing the benefits of information gathering at large spatial scales.

I hope this opinion article will unify and advance research on the evolutionary forces producing variation in the frequency and distance of dispersal events in natural populations. Fixed strategies merit more attention in dispersal research, and my hypothesis that informed and fixed strategies can act simultaneously illuminates opportunities for further theoretical and applied work. For example, range shifts in response to a shifting climate window will likely require long-distance dispersal to cross large gaps of unsuitable habitat (Travis and Dytham 2012). Therefore, identifying individual- or species-level traits underlying informed or fixed strategies could help predict species persistence under ongoing environmental change.

Synthesis and significance

My dissertation research provides empirical insight on the causes of individual variation in dispersal distance and constraints on the evolution of dispersal (Burton et al. 2010, Burgess et al. 2015, Bonte and Doherty 2017). The difficulty of tracking animals in the field has resulted in an historical focus on emigration and settlement stages of dispersal, while processes affecting distance decisions during transience have received comparatively less attention (Bowler and Benton 2005). By focusing on phenotypic differentiation *among* dispersers, rather than between dispersers and residents, my research is novel in showing that phenotypic attributes that facilitate long-distance dispersal can constrain other locomotor performances. More broadly, this and other trade-offs associated with continuous variation in dispersal distance may constrain dispersal evolution. The importance of considering continuous variation in dispersal distance in dispersal research is further underscored by my results showing that patterns of environmental variation leading to increased dispersal distances do not affect dispersal propensity (i.e., the discrete emigration response). This finding cautions against using dispersal propensity as a proxy for dispersal distance, and, perhaps more importantly, suggests that dispersal propensity and distance evolve independently (Bonte et al. 2010, Duputié and Massol 2013, Burgess et al. 2015).

Data on dispersal distances are also crucial for disentangling the relative importance of the many selective pressures influencing dispersal in natural populations. The prediction that different distances are required to alleviate fitness costs associated with kin competition, inbreeding, and environmental variation – the 3 putative drivers of dispersal evolution – remains largely untested (Duputié and Massol 2013). By quantifying the spatial scale of genetic relatedness, I was able to determine that dispersal distances were great enough in downstream reaches to lower inbreeding risk, but this effect was not observed in upstream reaches where dispersal distances were shorter. These results therefore suggest that inbreeding avoidance is not the primary driver of dispersal distances in *G. porphyriticus*, and that selective pressures influencing dispersal distances differ at fine spatial scales in headwater systems. Importantly, these data provide rare empirical support for the basic prediction that inbreeding risk decreases with dispersal distance.

My research challenges the current paradigm that most dispersal is a conditional response to local environmental cues. Instead, I show that large-scale, long-term environmental variation – reflected in survival probabilities – better predicts dispersal distances than current, local variation in habitat quality. These results provide the first empirical support for early theory that treated dispersal as an innate, ‘fixed’ quality of individuals that evolves in response to stochastic, spatiotemporal variation in environmental conditions (Kuno 1981, Levin et al. 1984, McPeck and Holt 1992). I suggest fixed dispersal strategies may help to explain the evolution and maintenance of long-distance dispersal in natural populations, where the costs of information-

gathering about potential settlement sites under conditional dispersal strategies become prohibitively high. Previous work has shown that 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). Therefore, future efforts to characterize fixed dispersal and associated phenotypes in natural populations may help to address several pressing applied issues.

Dissertation format

The following chapters are formatted for publication in peer-reviewed scientific journals. I use the collective ‘we’ throughout the dissertation to reflect that each of these chapters include important contributions from many collaborators.

CHAPTER 2: A distance-performance trade-off in the phenotypic basis of dispersal

Abstract

Across taxa, individuals vary in how far they disperse, with most individuals staying close to their origin and fewer dispersing long distances. Costs associated with dispersal (e.g., energy, risk) are widely believed to trade off with benefits (e.g., reduced competition, increased reproductive success) to influence dispersal propensity. However, this framework has not been applied to understand variation in dispersal distance, which is instead generally attributed to extrinsic environmental factors. We hypothesized that variation in dispersal distances results from trade-offs associated with other aspects of locomotor performance. We tested this hypothesis in the stream salamander *Gyrinophilus porphyriticus*, and we found that salamanders that dispersed farther in the field had longer forelimbs but swam at slower velocities under experimental conditions. The reduced swimming performance of long-distance dispersers likely results from drag imposed by longer forelimbs. Longer forelimbs may facilitate moving longer distances, but the proximate costs associated with reduced swimming performance may help to explain the rarity of long-distance dispersal. The historical focus on environmental drivers of dispersal distances misses the importance of individual traits and associated trade-offs among traits affecting locomotion.

Introduction

Dispersal is a key driver of ecological and evolutionary processes by affecting population growth rates and gene flow (Tittler et al. 2006, Van Houtan et al. 2007). Across taxa, most individuals in natural populations do not disperse, whereas dispersal distances vary substantially among those that do, with few individuals exhibiting long-distance dispersal (Mayr 1963, Endler 1977, Johnson and Gaines 1990). However, most dispersal research has focused on the discrete emigration response (stay or leave), leaving us with little understanding of the factors influencing individual variation in dispersal distance. Identifying the factors that underlie variation in dispersal distance is critical because long-distance dispersal contributes disproportionately to range shifts (Higgins and Richardson 1999), invasions (Kot et al. 1996; Miller and Tenhumberg 2010; Lindström et al. 2011), and population persistence (Bohrer et al. 2005).

Dispersal incurs energy, mortality risk, and opportunity costs that are widely believed to trade off with the benefits of dispersal (e.g., reduced competition, increased reproductive success) to influence the propensity to disperse (Clobert et al. 2009; Bonte et al. 2012; Ronce and Clobert 2012). We now have evidence from multiple taxa that dispersing individuals are not a random subset of the population and, instead, differ from residents in morphological,

physiological, and behavioral traits (Harrison 1980; Benard and McCauley 2008; Edelaar and Bolnick 2012). These differences may indicate selection for ‘dispersal phenotypes’, but phenotypic attributes that facilitate dispersal may also induce costs. For example, investment in flight structures for dispersal creates a resource allocation trade-off with reproduction in many wing dimorphic insects (Denno et al. 1989, Mole and Zera 1993). However, the influence of phenotypic variation across dispersing individuals on dispersal distances is relatively unstudied due to the difficulty of directly quantifying dispersal distances in the field (Koenig et al. 1996; Nathan 2001; Lowe and McPeck 2012). The rarity of long-distance dispersal alone suggests that it is costly, and highlights the need to consider the possibility that phenotypic specialization for long-distance dispersal also creates costs that have gone unrecognized. Indeed, cost-benefit trade-offs are well documented for the discrete emigration response, but this framework has not been applied to understand individual variation in dispersal distance. Instead, variation in dispersal distance is often attributed to extrinsic stochastic or environmental factors (Carlquist 1981, Tufto et al. 1997, Morales 2002), rather than phenotypic attributes of the individual.

Locomotor performance, for example, seems a likely candidate to influence distances that individuals move, as well as potential costs of long-distance dispersal. Locomotion serves many different functions, including foraging, prey capture, predator escape, and dispersal, each requiring different morphological or physiological specializations. In aquatic vertebrates, morphological specialization to maximize stability and reduce drag comes at a cost to maneuverability (Webb 1984, Weihs 2002). These locomotor performance differences may allow sustained swimming for long-distance dispersal, but create a cost through reduced fast-starts for prey capture or predator escape. We cannot, however, assess such trade-offs using indirect, proximate indices of dispersal ability (e.g., velocity, acceleration, maneuverability) because this common approach inherently confounds dispersal with other aspects of locomotor performance (Cormont et al. 2011, Bringloe et al. 2013, Arnold et al. 2016). The lack of direct data on individual dispersal distances and their associated phenotypes under natural conditions has, until now, precluded more rigorous assessment.

We assessed locomotion-based trade-offs associated with dispersal distance in the stream salamander *Gyrinophilus porphyriticus*. Our goal was to provide novel empirical insight on whether phenotypic attributes associated with variation in dispersal distance constrain other aspects of locomotor performance. First, we used 4 years of intensive, spatially explicit capture-mark-recapture data to test for a morphological basis of dispersal distance under natural field conditions. Trunk and leg morphology are known to affect swimming and walking performance in salamanders, respectively (D’Août and Aerts 1999, Azizi and Horton 2004), leading to predictions that these traits may influence dispersal distance in *G. porphyriticus*. Next, we tested whether morphological traits related to dispersal distance in the field also influenced swimming performance in an experimental water chamber. *Gyrinophilus porphyriticus* may disperse by swimming, or, given the turbulent nature of headwater streams, may instead walk along the

stream bottom or on land (adults only) (Grover and Wilbur 2002, Greene et al. 2008). However, regardless of the mode of locomotion employed for dispersal, swimming is likely important for other ecological functions, including capture of invertebrate prey and escape from aquatic predators (Brodie et al. 1979, Petranka 1988, Resetarits 1995).

Materials and methods

Study species and site

Gyrinophilus porphyriticus belongs to the Plethodontidae, the lungless salamanders, and is found 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 cobble (Bruce 2003). The larval period lasts 3-5 years (Bruce 1980) and adults can live to be 14 years (W.H. Lowe, *unpublished data*). Previous work in this system has shown that both larval and adult *G. porphyriticus* disperse (Lowe 2003, Lowe et al. 2006b), 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, 71°45'W). These streams differ in environmental conditions, including aspect, daily discharge, and drainage slope (Lowe et al. 2006b, McGuire et al. 2014).

Capture-mark-recapture survey methods

Capture-mark-recapture surveys were conducted in June-September of 2012 – 2015. 1-kilometer sections encompassing the majority of the perennial portion of each stream were surveyed 9 times throughout each summer, for a total of 36 surveys per stream over the 4-year study period. A constant search effort was maintained by turning one cover object per meter of stream; thus, surveys provided spatially explicit information about the capture locations of individual salamanders. Previously unmarked salamanders were injected with visible implant elastomer (Northwest Marine Technologies, Washington, USA). All encountered individuals were photographed (see below) and snout-vent length (SVL) was recorded.

Quantifying dispersal distance

We quantified dispersal distances in recaptured individuals as the net distance moved (m along the stream) over the 4-year study period. Due to the rarity of long-distance dispersal, it was necessary to pool movement data across streams, sexes, life-history stages and time to achieve sufficient sample sizes to test for relationships between morphology, dispersal distance, and swimming performance. Previous surveys of *G. porphyriticus* showed no differences in movement distributions of adults v. larvae or males v. females (Lowe 2003, Lowe et al. 2006a). Additionally, movement is not influenced by intra-annual variation in stream flow (Lowe 2003, Lowe et al. 2006a), justifying pooling movement data across streams.

Home ranges in *G. porphyriticus* are approximately 3m^2 (Lowe 2003), which roughly translates to 3m in stream length. Therefore, we considered a dispersal event as any movement $> 4\text{m}$ in stream length from an initial location to ensure that dispersal movements were distinct from daily movements within the home range (Van Dyck and Baguette 2005, Burgess et al. 2015). 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 ($n = 34$, $r = 0.86$, $p < 0.001$), indicating that most dispersal movements are unidirectional (i.e., only downstream or only upstream) and permanent.

Morphological analyses

To test whether individual variation in trunk and limb morphology was associated with differences in dispersal distance, we photographed each captured individual alongside a ruler and measured trunk width, trunk length, humerus length and femur length from these digital photos. Humerus length and femur length served as proxies for fore- and hindlimb morphologies, as obtaining accurate measurements of the distal portions of the limbs from photographs was generally not possible. Because we expected all body measurements to be correlated with the overall size of the animal (SVL), we generated size-adjusted shape variables using principle components analysis (Adams and Beachy 2001, Cosentino and Droney 2016). We extracted two principal components from each of four covariance matrices representing the four body elements. Each covariance matrix included log-transformed SVL and one of the four body measurements (log-transformed). The first principal components (PC1) represented the generalized size of the salamander, and the second principal components (PC2) represented size-adjusted morphological characters.

To test for an association between morphology and dispersal distance, we performed stepwise multiple regression analysis to identify size-adjusted morphological characters (PC2s) that best predicted dispersal distance in individuals that dispersed (moved $> 4\text{m}$). Model selection was based on Akaike information criterion (AIC). Our initial model only included four

predictor variables that were based on *a priori* hypotheses of how morphology affects dispersal; therefore, we assumed low family-wise error.

Performance assays

To test for a locomotion-based trade-off with dispersal distance, we assessed burst-swimming performance in controlled experiments. We constructed an in-stream chamber (71cm long \times \times 22.5cm wide \times 25cm tall) that was placed in a pool in the stream channel in Zigzag brook so that salamanders did not experience any flow or incline during the swimming trials. The water depth in the chamber was 8 – 10cm. Previously marked individuals captured in 2014 and 2015 underwent swimming trials. Salamanders were prodded a maximum of 3 times to elicit a swim response. Using dorsal-view video, we sampled swimming trials at 60 frames per second using a GoPro Black 3+. We used a wide-view to capture the length of the swimming chamber, which created distortion that we removed before kinematic analyses. We calculated an undistortion transformation using a gridded image and X-ray of Moving Morphology (XROMM) Undistorter, and we applied the undistortion correction to each video file using the XrayProject 2.2.5 script in MATLAB (Brainerd et al. 2010). A contrasting bead attached with a rubber band on the salamander's torso served as an anatomical landmark, and this point was digitized in MATLAB using a custom script, DLTdv5 (Hedrick 2008). We used Igor Pro (v.6) to derive mean velocity (m/s) and peak acceleration (m/s^2) from digitized position data (m). These measures were obtained by averaging over a series of 11 digitized points to minimize effects of random digitizing error that were inflated by taking derivatives. This smoothing may produce different values from instantaneous measures achieved with higher frame rates or from other averaging algorithms (Walker 1998). However, the performance of all animals in this study was evaluated using the same methods, such that performance measures within this study are directly comparable. Salamanders were immediately returned to their last capture location following swimming trials. The challenge of collecting both dispersal and performance data from the same set of individuals prevented us from assessing the repeatability of swimming performance, but other studies have demonstrated high repeatability of locomotor performance in amphibians (Walton 1988, Kolok 1999).

To assess whether the same morphological variable(s) associated with dispersal distance also influenced swimming performance, we used stepwise multiple regression analysis to identify the most predictive model of each performance metric from the set of size-adjusted trunk and limb variables (PC2s). Because we were interested in whether swimming performance itself predicted dispersal distance, we used linear regression to evaluate this possibility. All statistical analyses were conducted in the program R version 3.3.1 (R Development Core Team 2016).

Results

Capture-mark-recapture surveys

We marked 2368 *G. porphyriticus* individuals over the 4-year study period in the 3 study streams. Of these, 575 individuals were recaptured, including 159 adults and 417 larvae. There was no difference in the dispersal distributions of larvae and adults (Kolmogorov-Smirnov test, $p > 0.28$). 132 individuals dispersed $> 4\text{m}$ from their initial locations. The maximum dispersal distance detected was 481m (Figure 1).

To test for locomotion-based trade-offs with dispersal distance, we needed individuals that dispersed in the field (moved $> 4\text{m}$) and had measures of swimming performance ($n = 50$). This subset included 26 adults and 24 larvae. The range of dispersal distances in this reduced dataset matched that of the full dataset, and the distributions did not differ (Kolmogorov-Smirnov test, $p = 0.95$; Figure 1).

Morphological variation

The first principal components of each of the four covariance matrices representing the four body elements were positively correlated with log-transformed SVL, confirming that PC1s represented the generalized size of salamanders ($r = 0.95 - 0.99$). The second principal components, therefore, represented size-adjusted shape variables. Second principal components were positively weighted by the body measurements; therefore, the proportional size of each body element (e.g. log trunk length / log SVL) was positively correlated with PC2 score ($r = 0.43 - 0.84$, $p < 0.001$, Figure 2) Among the PC2 values, only trunk length PC2 and trunk width PC2 were correlated ($r = 0.58$, $n = 50$, $p < 0.001$).

Morphological predictors of dispersal distance

Among dispersers ($n = 50$), the single significant morphological correlate of log-transformed dispersal distance was forelimb PC2 ($\beta = 0.36$, $\text{SE} = 0.17$, $t = 2.14$, $P = 0.037$, $r^2 = 0.07$), such that individuals with longer forelimbs dispersed farther (Figure 3). Dispersal distance was unrelated to SVL and trunk and limb PC1s ($r = 0.0-0.1$, $n = 50$, $P = 0.49-0.99$), indicating that there was no ontogenetic variation in dispersal distance.

Morphological predictors of swimming performance

Log-transformed peak velocity (mean: 0.18 m/s; range: 0.05 – 0.35 m/s) and log-transformed peak acceleration (mean: 0.76 m/s²; range: 0.25 – 1.26 m/s²) were positively correlated ($r = 0.82$, $n = 50$, $p < 0.001$); therefore, we used only peak velocity as our swimming performance metric.

Among dispersers, forelimb PC2 was the single significant morphological correlate of peak velocity ($\beta = -0.04$, $SE = 0.02$, $t = -2.06$, $p = 0.042$, $r^2 = 0.06$) such that individuals with shorter forelimbs attained the highest peak velocities (Figure 3). Peak velocity was unrelated to SVL and trunk and limb PC1s ($r = 0.06-0.15$, $n = 50$, $p = 0.31-0.68$), indicating that there was no ontogenetic variation in swimming velocity. Peak velocity was unrelated to dispersal distance ($\beta = -0.48$, $SE = 1.18$, $t = -0.41$, $p = 0.67$).

Discussion

Our study is novel in demonstrating a trade-off associated with continuous variation in dispersal distance and, specifically, that phenotypic attributes that facilitate long-distance dispersal restrict other locomotor performances. These results provide empirical insight on the causes of individual variation in dispersal distance and constraints on the evolution of dispersal (Burton et al. 2010, Burgess et al. 2015, Bonte and Dahiré 2017), and support an alternative to the historical view that dispersal distance is controlled by extrinsic environmental factors. As importantly, by integrating field and experimental data, this study shows the risk of relying on proximate measures of locomotor performance (e.g., swimming velocity) as proxies for dispersal ability (Cormont et al. 2011, Bringlee et al. 2013, Arnold et al. 2016). Our results suggest that these proximate performance measures may not only misrepresent dispersal ability, but instead reflect fundamental constraints on dispersal ability.

The positive relationship between forelimb length and dispersal distance suggests that *G. porphyriticus* individuals disperse primarily via walking – either underwater (larvae and adults) or overland (adults only) – because salamanders do not actively use their limbs for swimming (Delvolvé et al. 1997). This finding adds to a growing body of work linking limb morphology to dispersal or movement capacity (Phillips et al. 2006, Lowe and McPeck 2012, Arnold et al. 2016). Salamander limbs function in walking by generating thrust against the ground to propel the animal forward (Azizi and Horton 2004). Mechanistically, longer limbs increase stride length and allow the animal to move a greater distance per step, thereby lowering the cost of transport (Pontzer 2007). The absence of a relationship between hindlimb length and dispersal distance in our data may be a function of the reduced requirement for stability in aqueous environments, in contrast to walking on land where legs play a larger role in supporting the body (Ashley-Ross 1994).

Longer limbs increase hydrodynamic drag during swimming, which may explain why swimming velocity declined with forelimb length (Figure 3). Aquatic salamanders generally hold their limbs close to the body during swimming to reduce drag (Delvolvé et al. 1997, Bennett et al. 2001). However, we noticed that *G. porphyriticus* individuals displayed a wide range of limb postures while swimming – in some cases extending them to be nearly perpendicular to the long

axis of the body. We modelled drag as a function of forelimb length in *G. porphyriticus* and found that the longest-limbed individuals could experience up to 18% more drag than the shortest-limbed individuals (range 5.0 – 5.9 milliNewtons; see Appendix for details). This increase in drag solely due to longer forelimbs could represent a significant selective pressure on limb length in aquatic salamanders.

Our finding that the same trait was associated with both dispersal distance and swimming performance, but in opposite ways, is indicative of an adaptive trade-off. Using proximate performance measures, trade-offs between endurance and speed have been shown in other species (Bennett et al. 1989, Reidy et al. 2000), and our results may reflect a similar relationship. We did not measure endurance directly, but our results suggest that dispersal distance is determined by the reduction in transport costs of walking with increased stride length, rather than by improvements in swimming performance. Swimming speed has, however, been linked to predator escape in larval amphibians (Dayton et al. 2005), including larval salamanders (Storfer 1999), and both adult and larval *G. porphyriticus* are susceptible to predation (Brodie et al. 1979, Resetarits 1991, 1995). Therefore, it is likely that predation pressure represents a strong selective force shaping swimming performance in this system.

The lack of correlation between body size and dispersal distance is surprising because other ecological interactions change with body size in *G. porphyriticus*. For example, predation pressure from brook trout is size-dependent, with larvae being more affected than adults due to the gape limitation of brook trout (Resetarits 1995, Lowe et al. 2004). Thus, if dispersal were extrinsically controlled by environmental factors (Carlquist 1981, Tufto et al. 1997, Morales 2002), we would expect that dispersal distance might also change with body size and life-history stage. Because we did not detect these ontogenetic relationships, we interpret our findings as support for the role of natural selection in maintaining variation in dispersal phenotypes and distances, rather than dispersal distance being conditional on stage/size or environmental cues. Tests of the fitness consequences and genetic basis of the forelimb phenotype are clearly needed to definitively assess this interpretation. Furthermore, given the complexity of the dispersal process (Nathan 2001, Ronce 2007), and the scatter in our data (Figure 3), accurate predictions of dispersal distance will likely rely on models that incorporate both individual traits and extrinsic environmental factors (Bocedi et al. 2014, Henry et al. 2016).

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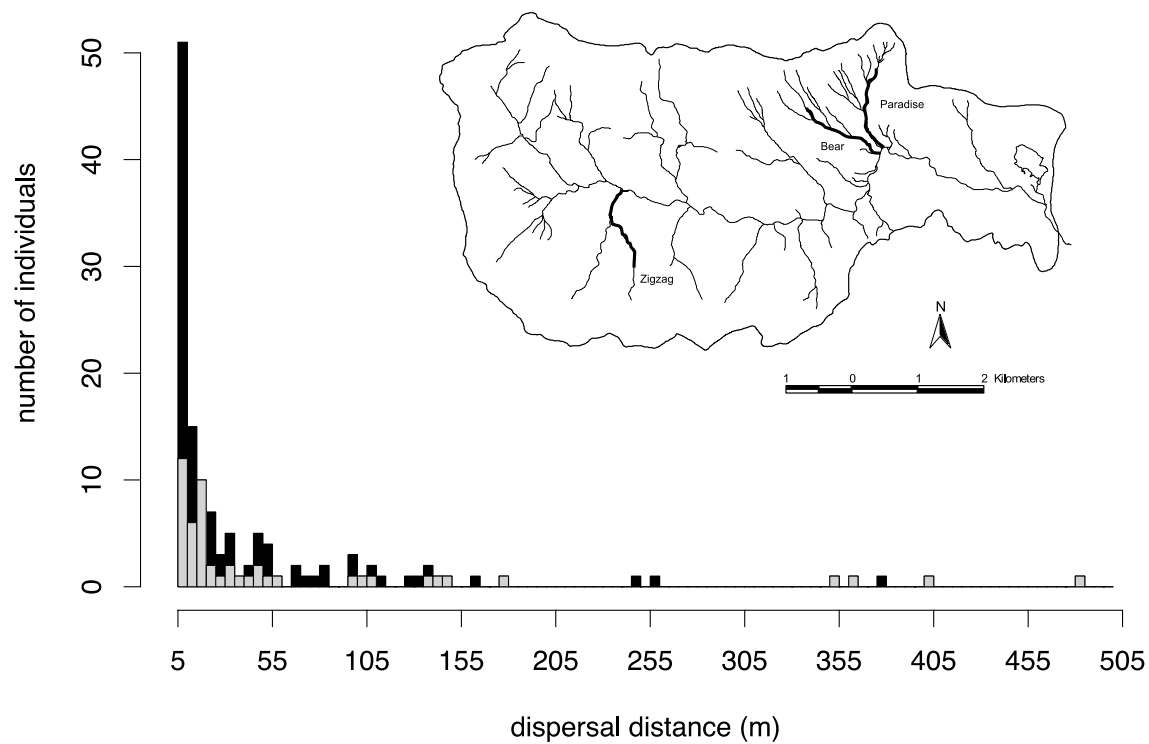


Figure 1. Dispersal distances of *Gyronophilus porphyriticus* from 3 streams in the Hubbard Brook Watershed in central New Hampshire (inset map). Distances are from individuals recaptured between 2012-2015 that dispersed > 4m from their initial location ($n = 150$). Data are binned in 4m increments. Grey portions of the columns are individuals for which both morphological and performance data were collected ($n = 50$).

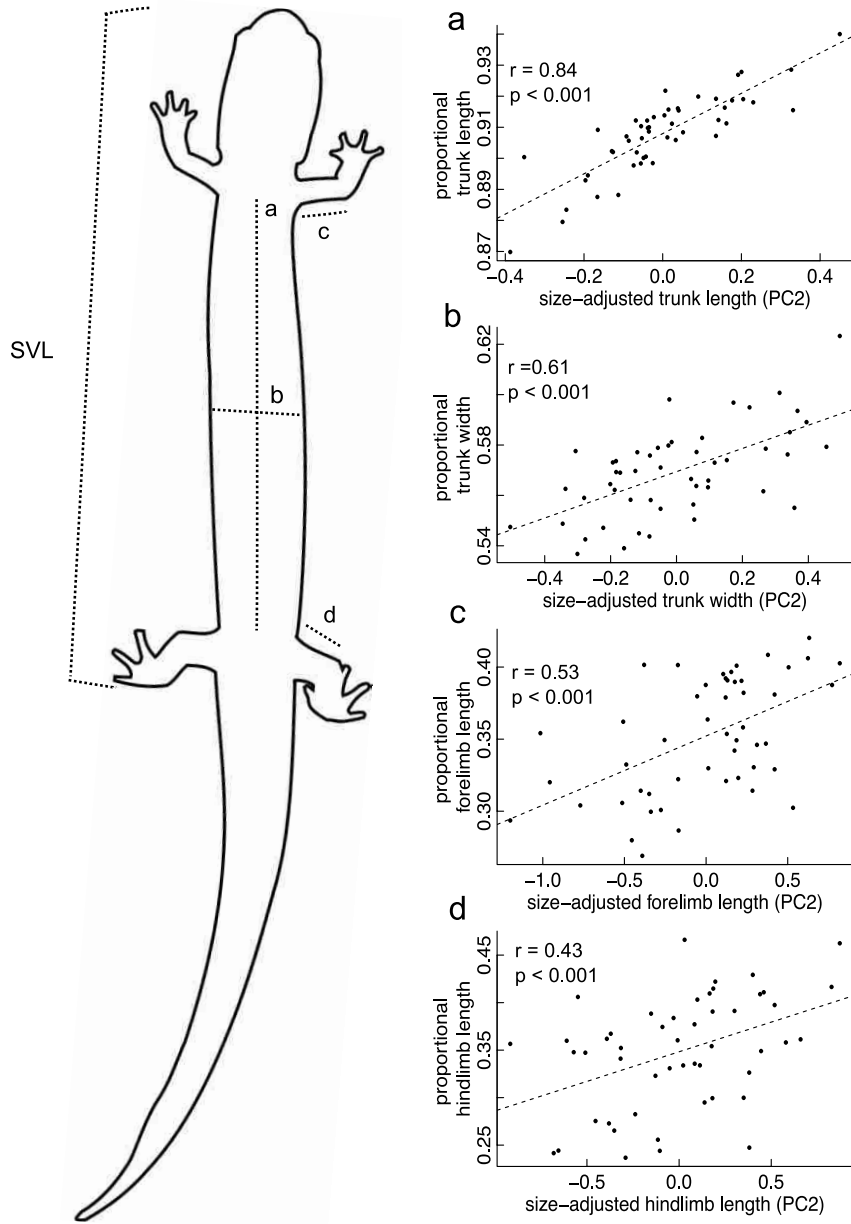


Figure 2. Correlations between size-adjusted morphological variables (PC2 scores) and proportional size of each body element (e.g. log trunk length / log snout-vent length [SVL]) for *Gyrinophilus porphyriticus* individuals in the Hubbard Brook Watershed ($n = 50$). Letters in the top left of plots correspond to the actual measurements on salamanders. PC2 scores were from principal components analyses including each body measurement and SVL. The percentage of variation accounted for by these PC2s is indicated within each plot. Lines of best fit are plotted for each correlation to show trends.

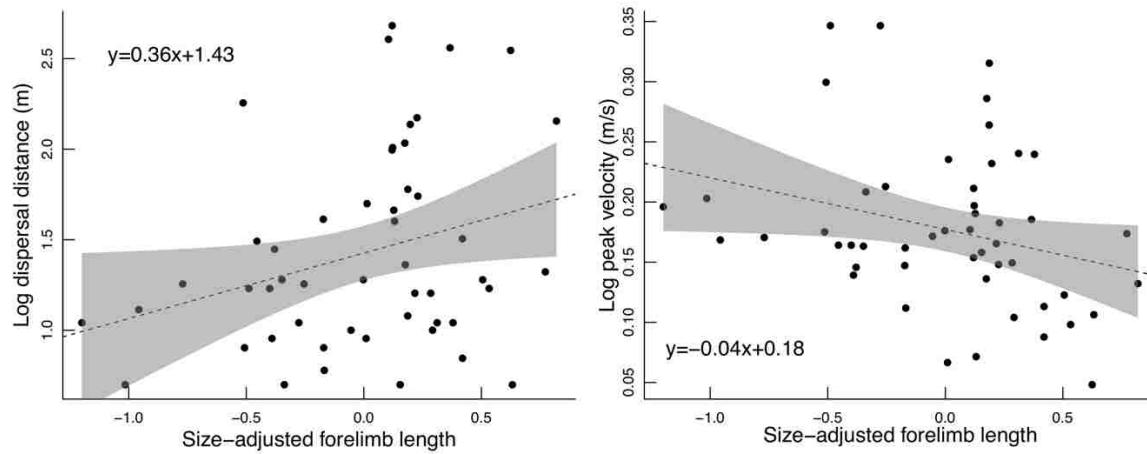


Figure 3. The relationship between sized-adjusted forelimb length (PC2) and dispersal distance (left) and swimming velocity (right) in *Gyrinophilus porphyriticus* individuals that dispersed > 4m in the Hubbard Brook Watershed ($n = 50$). Dotted linear regression lines indicate significant associations ($P < 0.05$); grey bands indicate 95% confidence intervals. Size-adjusted forelimb length is positively weighted by humerus length; therefore individuals with longer forelimbs dispersed the farthest but swam at the lowest velocities.

Appendix

Drag calculation

To explore the potential for forearm length to increase drag, we calculated the extent to which the range of forearm lengths represented in our study salamanders might increase drag according to the equation

$$F_D = \frac{1}{2} \rho v^2 C_D A$$

where F_D is the force of drag, ρ is the density of water (1000 kg m^{-3}), v is the velocity of water relative to the salamander, C_D is the coefficient of drag, and A is the cross-sectional area perpendicular to the flow. We held velocity constant at 0.29 m s^{-1} , the mean swimming velocity of salamanders in this study. The coefficient of drag for a cylinder at Reynolds numbers ranging from $10^2 - 10^5$ is one, which we considered reasonable for salamanders in headwater stream environments. For cross-sectional area, we simplified the shape of the salamander to a circle (trunk) with 2 rectangles (forelimbs) to represent the widest part of the salamander with forelimbs perpendicular to flow. The circular area was calculated from the average trunk width of the 48 dispersers (11.38mm). The rectangular area of the limbs was calculated based on an average width of 3 mm and the length varied according to the humerus length measured from each photograph (mean = 4.59mm). Thus, the only term that varied in the drag calculations was cross-sectional area, as a function of variation in forelimb length.

CHAPTER 3: Effects of environmental variation on dispersal distance in a stream salamander

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. While there is evidence that active dispersers base emigration decisions (stay vs. leave) on environmental factors related to habitat quality (e.g., conspecific density, food availability, mortality risk), it is less well understood how these factors influence dispersal distance – a more comprehensive measure of dispersal. 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, and not dispersal distances. 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 quality using measures of salamander performance from 4 years of spatially explicit, capture-mark-recapture (CMR) data across 3 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 predicting that dispersal evolves in response to a history of spatiotemporal environmental variation, rather than individual perceptions of immediate conditions. More broadly, this study underscores the value of assessing alternative scales of environmental variation to gain the most complete understanding of dispersal evolution.

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, McPeck 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, 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 (Suhonen et al. 2010, McCauley and Rowe 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; McPeck 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; McPeck 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 exponentially 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; McPeck 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 a snapshot of local habitat quality at a given time point. Under a conditional strategy, 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 survival probability as an index of long-term patterns of environmental variation, and specifically mortality risk resulting from that variation (Stacey and Taper 1992, Nicoll et al. 1993, Lande 1993). In habitats 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 (McPeck and Holt 1992, Boudjemadi et al. 1999). In contrast, when survival is high on average, 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; McPeck and Holt 1992).

Materials and 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 years (Bruce 1980) and adults can live to be 14 years (W.H. Lowe, *unpublished data*). Previous work has shown that both larval and adult *G. porphyriticus* disperse (Lowe 2003; Lowe et al. 2006a), 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, 71°45'W; Figure 1). These streams differ in environmental conditions, including aspect, daily discharge, and drainage slope (Lowe et al. 2006b; 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-meter 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 400m in Bear Brook, 250m in Paradise Brook, and 500m in Zigzag Brook. Our surveys were based on a robust design framework consisting of 3 primary sampling sessions per summer, with 3 secondary sampling sessions within each primary session (Pollock 1982). Each reach was surveyed 9 times throughout each summer, for a total of 36 surveys per reach over the 4-year study period. A constant search effort was maintained by turning one cover object per meter of stream; thus, surveys provided spatially explicit information about the capture locations of individual salamanders. Salamanders were uniquely marked with visible implant elastomer (Northwest

Marine Technologies, Washington, USA). Snout-vent lengths and weights 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-year 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. 2006b), we expected *a priori* that the determinants of survival would differ among streams and, therefore, modeled each stream separately (Lowe et al. 2006b, 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 multi-state 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-year 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 years of the study. Body condition was calculated as residuals from ordinary least squares linear regression of

log-transformed 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 avoid pseudoreplication, measurements from recaptured animals were not included in body condition calculations.

Quantifying dispersal distance

We quantified dispersal distances in recaptured individuals as the net distance moved (m along the stream) over the 4-year study period (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).

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 and 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-year 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 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_c 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 (lower reach: 0.90 – 0.96; upper reach: 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 dataset (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. In contrast, survival was constant between reaches for larvae in Bear and Zigzag Brooks, and for adults in Paradise and Zigzag Brooks. 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 (lower: $n = 123$; upper: $n = 145$). Additionally, when we forced multi-state models to estimate survival for upstream and downstream reaches separately, confidence intervals broadly overlapped in cases where model 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 8 independent estimates of monthly survival across stages, reaches, and streams, ranging from 0.88 – 0.96. 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 8 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 8 stream units, ranged from 5.15 – 8.12. Across the four years of the study, ranges of annual CV values within each stream unit were 1.93 – 5.35, 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 ($r = -0.76$, $p = 0.14$).

Dispersal distance

Of the 2,359 *G. porphyriticus* individuals captured in surveys, 464 individuals were recaptured. Maximum dispersal distances of recaptured individuals in the 8 stream units ranged from 81 - 481 m (Figure 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 ($n = 111$, $r = -0.67$, $p < 0.001$), indicating that most dispersal movements are unidirectional and permanent. The interquartile range of dispersal distances, our dependent variable for testing relationships with indices of environmental variation, ranged from 2 - 10 m across the 8 stream units identified by survival analyses (Figure 2). There was no correlation between stream unit sample sizes and dispersal distance IQR ($r = -0.48$, $p = 0.22$), indicating that this metric was not biased by variation in sample size.

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 12 times more support than the second-ranked model, which included spatial variation in body condition (Table 3). The model including both monthly apparent survival and spatial variation in body condition received less support than the univariate models (Table 3). Consistent with *a priori* predictions, dispersal distance was negatively related to survival ($\beta = -78.09$, SE =

23.27, $t = -3.36$, $p = 0.02$, $r^2 = 0.59$; Figure 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 ($\beta = -1.83$, $SE = 0.99$, $t = -1.85$, $p = 0.11$, $r^2 = 0.26$; Figure 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 3) indicates 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 (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; McPeck 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 distance in a 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 demonstrate that salamanders do not base dispersal decisions on cues related to habitat quality in their immediate vicinity, but instead indicate that increased dispersal distance is an evolved response to risky environments.

Our finding that dispersal distances increased as survival declined (Figure 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 habitat quality (Clobert et al. 2009). Long-distance dispersal in our study streams likely 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, McPeck 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). Also consistent with fixed dispersal models (Levin et al. 1984), the spatial scale over which we estimated survival was large (500 or 1000m of stream length), much larger than typical dispersal movements of *G. porphyriticus* (Figure 2) and encompassing many potential settlement sites. Further, because most individuals in our dataset did not move far (70% moved < 4m), 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).

We did not detect a relationship between current, local habitat quality – measured with individual body condition – and dispersal distance (Figure 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 mortality by minimizing the number of steps needed to achieve a certain distance (Zollner and Lima 1999, Barton et al. 2009).

The lack of relationship between current, local habitat quality and dispersal distance 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 m² (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. 2015). 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. 2015).

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 3).

Nevertheless, we did 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, however, *post-hoc* analyses showed no correlation between mean body condition and survival probability across our 8 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 (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 (Figure 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, McPeck and Holt 1992). Furthermore, 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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Table 1. Multistate capture-mark-recapture (CMR) models of monthly larval and adult recapture probabilities (p^{larva} , p^{adult}) and larva-adult transition probability ($\psi^{\text{larva-adult}}$) for *Gyrinophilus porphyriticus* (S^{larva} , S^{adult}) in Bear (a), Paradise (b), and Zigzag (c) Brooks. Larval and adult survival probabilities (S^{larva} , S^{adult}) were held constant for this analysis. Here we only show the top 3 models for each stream.

(a)				
Model	AIC _c	ΔAIC _c	AIC _c wt	K
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(\text{reach}), p^{\text{adult}}(\text{time}), \psi^{\text{larva-adult}}(\text{reach})$	2106.53	0	0.74	17
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(\text{reach}), p^{\text{adult}}(\text{time}), \psi^{\text{larva-adult}}(\cdot)$	2108.77	2.24	0.24	16
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(\cdot), p^{\text{adult}}(\text{time}), \psi^{\text{larva-adult}}(\cdot)$	2114.67	8.14	0.01	15
(b)				
Model	AIC _c	ΔAIC _c	AIC _c wt	K
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(\text{time}), p^{\text{adult}}(\text{time}), \psi^{\text{larva-adult}}(\cdot)$	1876.64	0	0.63	25
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(\text{time}), p^{\text{adult}}(\text{time}), \psi^{\text{larva-adult}}(\text{reach})$	1877.88	1.23	0.34	26
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(\text{time}), p^{\text{adult}}(\text{time}), \psi^{\text{larva-adult}}(\text{time})$	1883.92	7.28	0.02	35
(c)				
Model	AIC _c	ΔAIC _c	AIC _c wt	K
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(\text{reach}), p^{\text{adult}}(\text{reach}), \psi^{\text{larva-adult}}(\cdot)$	927.17	0	0.31	7
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(\text{reach}), p^{\text{adult}}(\cdot), \psi^{\text{larva-adult}}(\text{reach})$	927.77	0.60	0.23	7
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(\text{reach}), p^{\text{adult}}(\text{reach}), \psi^{\text{larva-adult}}(\text{reach})$	927.77	0.60	0.23	8

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. Parameterization for S, p, and ψ is in parentheses; “.” = 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 (a), Paradise (b), and Zigzag (c) Brooks. 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 3 top models for each stream are shown.

(a)				
Model	AICc	ΔAICc	AICc wt	K
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\text{reach}), p^{\text{larva}}(\text{reach}), p^{\text{adult}}(\text{time}), \psi^{\text{larva-adult}}(\text{reach})$	2098.06	0	0.72	18
$S^{\text{larva}}(\text{reach}), S^{\text{adult}}(\text{reach}), p^{\text{larva}}(\text{reach}), p^{\text{adult}}(\text{time}), \psi^{\text{larva-adult}}(\text{reach})$	2100.13	2.07	0.25	19
$S^{\text{larva}}(\text{time}), S^{\text{adult}}(\text{reach}), p^{\text{larva}}(\text{reach}), p^{\text{adult}}(\text{time}), \psi^{\text{larva-adult}}(\text{reach})$	2104.67	6.61	0.03	28
(b)				
Model	AICc	ΔAICc	AICc wt	K
$S^{\text{larva}}(\text{reach}), S^{\text{adult}}(\cdot), p^{\text{larva}}(\text{time}), p^{\text{adult}}(\text{time}), \psi^{\text{larva-adult}}(\cdot)$	1869.65	0	0.70	26
$S^{\text{larva}}(\text{reach}), S^{\text{adult}}(\text{reach}), p^{\text{larva}}(\text{time}), p^{\text{adult}}(\text{time}), \psi^{\text{larva-adult}}(\cdot)$	1871.57	1.92	0.27	27
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(\text{time}), p^{\text{adult}}(\text{time}), \psi^{\text{larva-adult}}(\cdot)$	1876.64	6.99	0.02	25
(c)				
Model	AICc	ΔAICc	AICc wt	K
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\cdot), p^{\text{larva}}(\text{reach}), p^{\text{adult}}(\text{reach}), \psi^{\text{larva-adult}}(\cdot)$	927.17	0	0.59	7
$S^{\text{larva}}(\cdot), S^{\text{adult}}(\text{reach}), p^{\text{larva}}(\text{reach}), p^{\text{adult}}(\text{reach}), \psi^{\text{larva-adult}}(\cdot)$	929.21	2.04	0.21	8
$S^{\text{larva}}(\text{time}), S^{\text{adult}}(\cdot), p^{\text{larva}}(\text{reach}), p^{\text{adult}}(\text{reach}), \psi^{\text{larva-adult}}(\cdot)$	929.9	2.74	0.15	17

Notes: Second-order Akaike's information criterion values (AICc), AICc differences (ΔAICc), AICc weights (AICc wt), and number of estimable parameters (K) are provided for all models. Parameterization for S, p, and ψ is in parentheses; "." = constant by stream reach and time.

Table 3. 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 2012-2015, 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.

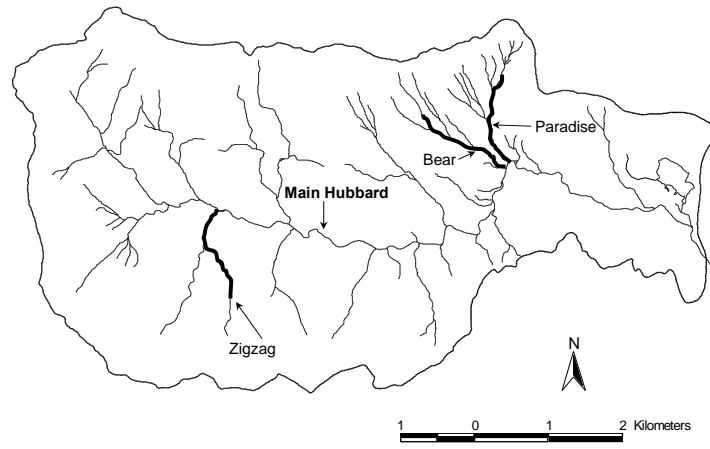


Figure 1. Map of the three study streams in the Hubbard Brook Experimental Forest in central New Hampshire, U.S.A. Bear, Paradise, and Zigzag Brooks are hydrologically independent and flow into Hubbard Brook.

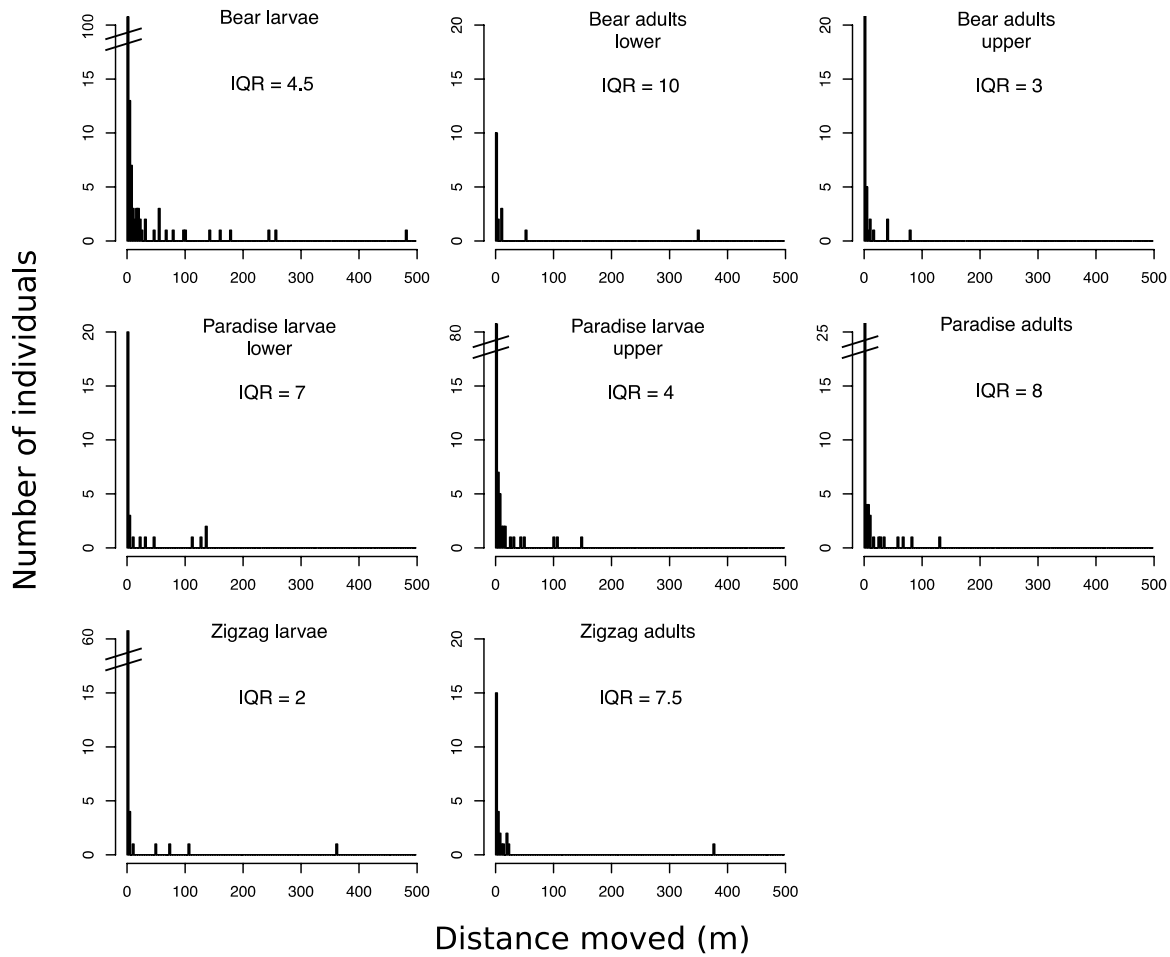


Figure 2. Dispersal distances of *Gyrinophilus porphyriticus* larvae and adults in ‘stream units’ defined from capture-mark-recapture analyses. Data are from Bear, Paradise, and Zigzag Brooks in the Hubbard Brook Experimental Forest. ‘Stream units’ are the spatial scale over which survival differed in 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 < 3m. Data are binned in 3m increments.

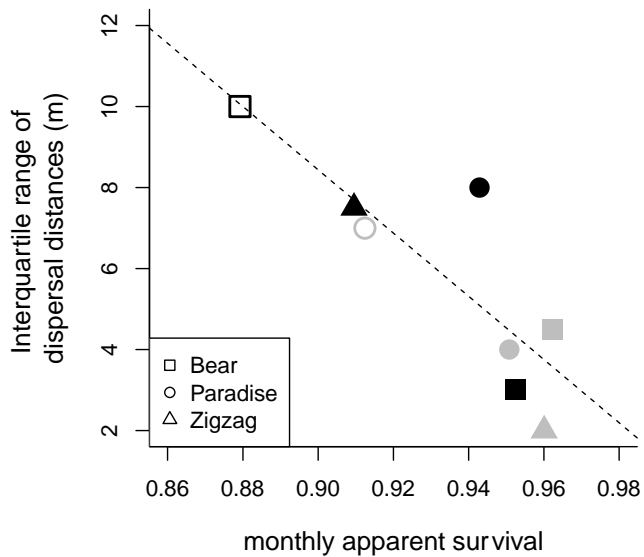


Figure 3. The relationship between monthly apparent survival and interquartile ranges of dispersal distance in *Gyrinophilus porphyriticus*. Data are from Bear, Paradise, and Zigzag Brooks in the Hubbard Brook Experimental Forest. Each point corresponds to ‘stream units’ defined from capture-mark-recapture analyses. Shapes correspond to the three study streams. Black shapes represent adult *G. porphyriticus*, and grey shapes 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 ($\beta = -78.09$, $SE = 23.27$, $t = -3.36$, $p = 0.015$, $r^2 = 0.59$).

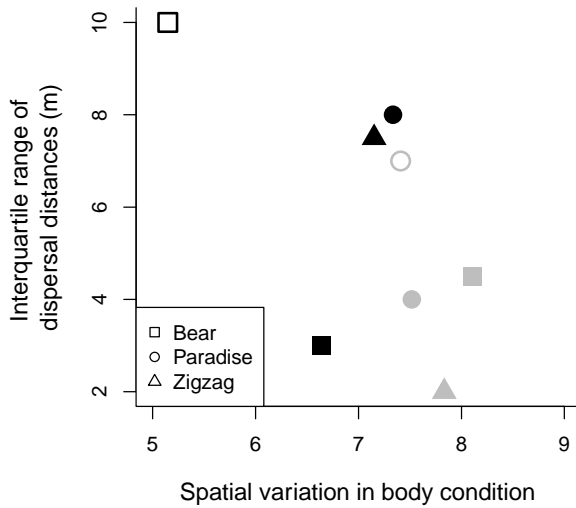


Figure 4. The relationship between spatial variation in body condition and interquartile ranges of dispersal distance in *Gyrinophilus porphyriticus*. Data are from Bear, Paradise, and Zigzag Brooks in the Hubbard Brook Experimental Forest. Each point corresponds to ‘stream units’ defined from capture-mark-recapture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

Table S1. Multistate capture-mark-recapture (CMR) models of monthly survival probabilities of *Gyrinophilus porphyriticus* larvae and adults (S^{larva} , S^{adult}), recaptures probabilities (p^{larva} , p^{adult}) and larva-adult transition probability ($\psi^{\text{larva-adult}}$) in Bear (a), Paradise (b), and Zigzag (c) Brooks with and without body condition as an individual covariate on survival.

(a)				
Model	AICc	Δ AICc	AICc wt	K
$S^{\text{larva}}(\cdot)$, $S^{\text{adult}}(\text{reach})$, $p^{\text{larva}}(\text{reach})$, $p^{\text{adult}}(\text{time})$, $\psi^{\text{larva-adult}}(\text{reach})$	2098.06	0	0.65	18
$S^{\text{larva}}(\cdot, \text{bodycond})$, $S^{\text{adult}}(\text{reach}, \text{bodycond})$, $p^{\text{larva}}(\text{reach})$, $p^{\text{adult}}(\text{time})$, $\psi^{\text{larva-adult}}(\text{reach})$	2099.31	1.25	0.35	21
(b)				
Model	AICc	Δ AICc	AICc wt	K
$S^{\text{larva}}(\text{reach})$, $S^{\text{adult}}(\cdot)$, $p^{\text{larva}}(\text{time})$, $p^{\text{adult}}(\text{time})$, $\psi^{\text{larva-adult}}(\cdot)$	1869.65	0	0.90	26
$S^{\text{larva}}(\text{reach}, \text{bodycond})$, $S^{\text{adult}}(\cdot, \text{bodycond})$, $p^{\text{larva}}(\text{time})$, $p^{\text{adult}}(\text{time})$, $\psi^{\text{larva-adult}}(\cdot)$	1874.00	4.35	0.10	29
(c)				
Model	AICc	Δ AICc	AICc wt	K
$S^{\text{larva}}(\cdot)$, $S^{\text{adult}}(\cdot)$, $p^{\text{larva}}(\text{reach})$, $p^{\text{adult}}(\text{reach})$, $\psi^{\text{larva-adult}}(\cdot)$	927.17	0	0.83	7
$S^{\text{larva}}(\cdot, \text{bodycond})$, $S^{\text{adult}}(\cdot, \text{bodycond})$, $p^{\text{larva}}(\text{reach})$, $p^{\text{adult}}(\text{reach})$, $\psi^{\text{larva-adult}}(\cdot)$	930.33	3.16	0.17	9

CHAPTER 4: Dispersal distance predicts inbreeding risk in a stream salamander

Abstract

Avoiding inbreeding is considered a key driver of dispersal evolution, and dispersal distance should be particularly important in mediating inbreeding risk because the likelihood of mating with relatives decreases with increasing dispersal distances. However, the lack of direct data on dispersal distances in most taxa has precluded empirical tests of this basic prediction. Here, we evaluated whether dispersal distance predicts inbreeding risk in the headwater stream salamander *Gyrinophilus porphyriticus*, and whether this relationship changes under different environmental conditions. Specifically, we hypothesized that variation in ecological conditions between downstream and upstream reaches, including the presence of predatory fish in downstream reaches, leads to differences in dispersal distances, resulting in reach-scale differences in the effect of dispersal on inbreeding risk. Dispersal distances were greater in downstream reaches than upstream reaches in 5 headwater streams, suggesting that selective pressures influencing dispersal in *G. porphyriticus* differ at fine spatial scales. Inbreeding risk, measured as the proportion of individuals within 50m that were relatives, was lower for dispersers than non-dispersers in downstream reaches. In contrast, there was no difference in inbreeding risk between dispersers and non-dispersers in upstream reaches. These results demonstrate that dispersal distance reduces inbreeding risk in *G. porphyriticus*, and that environmentally-associated variation in dispersal distances leads to variation in the effects of dispersal on inbreeding risk. Furthermore, these results, in addition to population genetic data, indicate that selective pressures other than inbreeding avoidance maintain dispersal in *G. porphyriticus*, and underscore the importance of explicitly addressing alternative hypotheses in dispersal research.

Introduction

Dispersal influences the genetic structure of populations by facilitating gene flow and affecting the spatial distribution of organisms (Clobert et al. 2001, Lowe and Allendorf 2010). Immigrants are also an important source of outbred mates, lowering the risk of inbreeding in small populations (Spielman and Frankham 1992, Vilà et al. 2003). Avoiding the harmful effects of inbreeding (i.e., inbreeding depression; Keller & Waller, 2002; Lynch & Walsh, 1998) has been identified as one of three main drivers of dispersal evolution (Bengtsson 1978, Waser et al. 1986), along with avoiding costs associated with kin competition (Hamilton and May 1977, Ronce et al. 2000, Poethke et al. 2007) and spatiotemporal variation in environmental conditions (Johnson and Gaines 1990, McPeck and Holt 1992). However, empirical studies of these putative drivers have been far outpaced by theory, leaving researchers with little understanding of their relative importance in natural populations where dispersal may be shaped by many, potentially

conflicting selective forces (Waser et al. 1986, Perrin and Goudet 2001, Guillaume and Perrin 2006). Understanding how dispersal is shaped by inbreeding avoidance, in particular, will become increasingly important as habitat fragmentation and climate change cause many populations to become smaller and more isolated (Haddad et al. 2015), increasing the risk of inbreeding depression and reliance on dispersal for long-term persistence.

Knowledge of the spatial structure of genetic differentiation is crucial for evaluating the role of dispersal in inbreeding avoidance because it dictates the scale of dispersal required to reduce the risk of inbreeding. Dispersal separates kin in space, and the likelihood of mating with relatives decreases with increasing dispersal distances (Szulkin and Sheldon 2008). Consequently, the minimum dispersal distance needed to reduce the risk of inbreeding depends on the spatial scale over which individuals are related (Gompper et al. 1998, Daniels and Walters 2000). Within populations, limited dispersal can create a pattern of isolation-by-distance, where individuals in close geographic proximity are more genetically similar than individuals that are farther apart (Wright 1943, Primmer et al. 2006, Broquet et al. 2006). If inbreeding avoidance is an important driver of dispersal, dispersal distances should evolve to exceed the scale of spatial clustering of relatives. Most dispersal studies, however, have focused on dispersal propensity (i.e., the decision to stay v. leave), and not dispersal distance (Bowler and Benton 2005), precluding rigorous assessment of the efficacy of dispersal for reducing inbreeding in natural populations.

Theory suggests that inbreeding depression is unlikely to explain the evolution of dispersal alone (Perrin and Goudet 2001), and we know from empirical studies that dispersal is often based on multiple cues (Bowler and Benton 2005, Bitume et al. 2013, Baines et al. 2014). Nevertheless, the prediction that dispersal should reduce an individual's spatial proximity to relatives offers a straightforward framework for testing the importance of inbreeding relative to other factors influencing dispersal. For example, Daniels and Walters (2000) found that female red cockaded woodpeckers did not disperse far enough to avoid mating with close relatives despite evidence of inbreeding depression. The authors instead posited that acquiring breeding territories was a stronger selective pressure than inbreeding avoidance, and remaining in the natal territory increased an individual's competitive advantage. More generally, this and other studies show that the degree to which dispersal functions to reduce inbreeding may be mediated by other environmental conditions influencing dispersal distance, such as the presence of predators, competition for resources, and changes in habitat quality (Cronin et al. 2004, Bitume et al. 2013, Baines et al. 2014).

Here our goal was to evaluate whether dispersal distance predicts inbreeding risk in the headwater stream salamander *Gyrinophilus porphyriticus*, and whether this relationship changes under different environmental conditions. Many abiotic and biotic factors differ along streams, such as discharge, streamwater chemistry, substrate size, and the composition of prey and

predator communities, creating a diverse suite of selective pressures that might influence salamander dispersal (Vannote et al. 1980, Hubert and Kozel 1993, Lowe and Bolger 2002, McGuire et al. 2014). We hypothesized that these environmental factors may lead to different relationships between dispersal distance and inbreeding risk in the downstream and upstream reaches of headwater streams. For example, we know that *G. porphyriticus* often co-occurs with predatory brook trout (*Salvelinus fontinalis*) in the downstream reaches of our headwater study streams, but waterfalls prevent brook trout from occupying the upstream reaches (Warren et al. 2008). If *G. porphyriticus* respond to brook trout by increasing dispersal to escape predation risk (Cronin et al. 2004, McCauley and Rowe 2010, Otsuki and Yano 2014), we would expect dispersal distances to be longer in downstream reaches compared to upstream reaches, thereby leading to comparatively lower inbreeding risk for dispersers in downstream reaches. Gradients in discharge along streams may also affect dispersal dynamics in *G. porphyriticus*. Lower base flows and more frequent drying in upstream reaches (Jensen et al. 2017) could result in longer dispersal distances as individuals track water availability, thereby leading to comparatively lower inbreeding risk for dispersers in upstream reaches than downstream reaches.

We took advantage of the natural variation in environmental conditions along 5 replicate streams in the Hubbard Brook Experimental Forest (New Hampshire, USA) to test for reach-scale differences in dispersal distances and resulting consequences for inbreeding risk in *G. porphyriticus*. Specifically, we used a combination of demographic (capture-mark-recapture) and population genetic approaches to address 3 objectives: (1) test for differences in individual dispersal distances between downstream and upstream reaches; (2) quantify spatial population genetic structure and inbreeding risk within and among the study streams; and (3) test whether the effect of dispersal on inbreeding risk varies between downstream and upstream reaches.

Materials and 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 years (Bruce 1980) and adults can live to be 14 years (W.H. Lowe, *unpublished data*). Previous work in this system has shown that both larval and adult *G. porphyriticus* disperse (Lowe 2003, Lowe et al. 2006a). Larval dispersal is restricted to linear stream corridors, but adults may be found up to 9 meters away from streams (Greene et al. 2008).

Nevertheless, extensive overland dispersal is unlikely given the highly aquatic habits of adults (Petranka 1988).

This work was conducted in 5 hydrologically independent first-order streams (Bear, Canyon, Cascade, Paradise, Zigzag) in the Hubbard Brook Experimental Forest (HBEF), located in the White Mountains of central New Hampshire (43°56'N, 71°45'W; Figure 1). All five streams flow into the mainstem of Hubbard Brook (Figure 1), a tributary of the Pemigewasset River. Brook trout (*Salvelinus fontinalis*) occur in the mainstem of Hubbard Brook and downstream reaches of Bear, Canyon, Paradise, and Zigzag Brooks, but have not been detected in Cascade Brook (Warren et al. 2008). Typical of headwater streams in New Hampshire, the study streams have low conductivity (12.0 – 15.0 μ S), slight acidity (pH of 5.0 – 6.0), high dissolved oxygen content (80 – 90% saturation), and moderate midday summer temperatures (13.0 – 17.0°C). Hydrology of HBEF streams is characterized by high spring discharge due to melting snow, and high discharge events throughout the year associated with isolated storms. Base flow conditions usually occur in August and September. The study streams are high gradient mountain headwaters with cobble, boulder, and bedrock substrate. The dominant tree species in forests surrounding these streams were *Acer saccharum*, *Fagus grandifolia*, *Betula alleghaniensis*, *Picea rubens*, *Abies balsamea*, *B. papyrifera*.

Sampling protocol

To test for reach-scale differences in the effect of dispersal on inbreeding risk, we divided each stream into two 500m reaches: downstream reaches where *G. porphyriticus* co-occur with brook trout (*Salvelinus fontinalis*), and upstream reaches without fish. Downstream reaches began at the confluence with Hubbard Brook, and upstream reaches ended at weirs where long-term stream data are collected, and above which sampling is restricted (Bormann and Likens 1979). Together, these two 500m reaches encompassed the majority of the perennial portion of each stream. Each reach was surveyed 9 times throughout the summer months (June – August), resulting in 36 total surveys from 2012 – 2015 in Bear, Paradise, and Cascade Brooks, and 27 total surveys from 2012 – 2014 in Canyon and Cascade Brooks. A constant search effort was maintained by turning one cover object per meter of stream; thus, surveys provided spatially explicit information about the capture locations of individual salamanders. Salamanders were uniquely marked with visible implant elastomer (Northwest Marine Technologies, Washington, USA). Tail clips were collected from newly captured individuals and stored in 70% ethanol for genomic analyses.

Quantifying dispersal distance

To test for differences in dispersal distance between downstream and upstream reaches, we quantified dispersal distances in recaptured individuals as the net distance moved (m along the

stream) during 2012 – 2015 in Bear, Paradise, and Zigzag, and during 2012 – 2014 in Canyon and Cascade (Turchin 1998). We considered dispersers to be individuals that moved $\geq 10\text{m}$ from their initial location over the duration of the study. Previous studies of *G. porphyriticus* used a lower cutoff of 3m to distinguish dispersers from residents because the home range size was estimated as 3m^2 (roughly 3m of stream length; Lowe and McPeck 2012). We used 10m here to ensure a clear distinction between dispersers and residents, and because we expected *a priori* that the scale over which individuals are related would be larger than the home range of an individual. Therefore, longer dispersal distances are likely needed to influence an individual's exposure to relatives. Among dispersers (i.e., individuals that moved $\geq 10\text{m}$), we tested for a difference in dispersal distance between downstream and upstream reaches using a Wilcoxon rank sum test. Because the majority of *G. porphyriticus* do not disperse (Lowe 2003, Lowe et al. 2006a, Lowe and McPeck 2012), it was necessary to pool dispersal data across streams to achieve sufficient sample sizes to test for differences in dispersal distance between stream reaches.

Genomic library preparation and sequencing

To characterize the spatial structure of genetic differentiation in *G. porphyriticus*, we prepared genomic libraries for 432 individuals across the 5 study streams. We preferentially sequenced individuals that were recaptured during the study and thus had an associated dispersal distance. This caused sample sizes to be uneven among streams, ranging from 25 – 167 individuals per stream. DNA was extracted from tissue samples using a SPRI bead protocol. Genomic DNA quality was visualized on an agarose gel and each sample was quantified using a BioTek Synergy HT Microplate reader. Libraries were prepared following the double-digest restriction-associated DNA sequencing (ddRAD-seq) method of (Peterson et al. 2012) with several modifications. Briefly, we used the restriction enzymes BspDI and SbfI to digest 300 – 1000ng of genomic DNA per individual. We then performed fragment size selection using SPRI beads prior to adapter ligation. To enable detection of PCR duplicates, we introduced a random 8 bp sequence in the P2 adapter according to the method of Schweyen et al. (2014). The use of 12 unique barcode sequences in the P1 adapter allowed us to pool 12 individuals to form a single library. Fragments in the range of 360 – 440 bp were extracted from each library using a BluePippin size selection system (Sage Science). We used 39 uniquely indexed PCR primers, enabling us to pool all individuals into a single library for sequencing following PCR. The pooled library was sequenced on 3 lanes of Illumina HiSeq 2500 (125 bp paired-end) at Hudson Alpha Institute for Biotechnology, resulting in 616,385,491 forward and reverse reads.

Quality filtering and SNP calling

Raw Illumina reads from each sequencing lane were concatenated and demultiplexed using the `process_radtags` program in STACKS version 2.1 (Catchen et al. 2011). Reads with ambiguous

barcodes (greater than 2 mismatches) were discarded from the data set. PCR clones were identified by comparing unique 8 bp oligonucleotide sequences that were ligated on to each molecule during library preparation and removed using the `clone_filter` program in `STACKS`. We used the `DDOCENT` 1.0 pipeline (Puritz et al. 2014) to remove low-quality bases (Phred quality score < 20) and construct a *de novo* assembly of putative RAD tags and call single nucleotide polymorphisms (SNPs). We required a minimum depth of 6x and a maximum of 4 mismatches to form reference contigs. Putative ddRAD loci were merged if they contained > 85% sequence similarity. `DDOCENT` uses `BWA` to map reads to reference contigs and generate alignment files, and `FREEBAYES` (Garrison and Marth 2012) to call SNPs from aligned reads of all individuals. `FREEBAYES` is a Bayesian-based variant detection program that assesses variants across all samples simultaneously, thereby allowing confident calls of genotypes with few reads. The `DDOCENT` pipeline identified 62,777 variants sites.

SNP filtering

We employed several SNP filters to remove SNPs likely to be the result of sequencing error or paralogs, the latter representing a particular challenge for salamanders with gigantic genomes due to proliferation of transposable elements (Sun et al. 2012). Briefly, we retained SNPs that were present in 70% of individuals in at least 3 of the 5 streams and had a minor allele frequency of 0.05. We required a minimum depth of coverage for each SNP of 3x per individual, but required a mean minimum site depth averaged across individuals of 10x and allowed a maximum of 300x. We removed loci with an allele balance of < 0.3 or > 0.7 in heterozygous individuals because asymmetrical allele ratios are often indicative of multicopy loci (McKinney et al. 2017). We also filtered by Hardy-Weinberg proportions, removing loci that significantly deviated from expectations in at least 3 of the 5 streams. Loci with a mean F_{IS} value of < -0.3 or > 0.3 averaged across streams were also removed. To avoid linked markers, we retained only 1 SNP per contig that was genotyped in the most individuals. To ensure that the remaining contigs were not physically linked, we calculated the r^2 statistic among contigs using `VCFTOOLS`, and removed the SNP that was genotyped in the fewest individuals per pair with $r^2 > 0.8$ in at least 3 streams. Finally, we removed 50 individuals with $\geq 30\%$ missing genotypes from the dataset. After filtering, we retained 297 SNPs (Table S1).

Assessing genetic differentiation

We used population genetic analyses to quantify the spatial structure of genetic differentiation of *G. porphyriticus*. Genetic variation within streams was calculated as observed heterozygosity (H_o) and expected heterozygosity (H_e) in `GENODIVE` version 2.0b23 (Meirmans and Tienderen 2004). Discrepancies between observed and expected heterozygosity were quantified using F_{IS} (Weir and Cockerham 1984). We tested for isolation-by-distance within streams using a simple Mantel test between pairwise matrices of Euclidean distances and pairwise genetic distances in

the ECODIST package in R (Goslee and Urban 2007). We created a Mantel correlogram to visualize isolation-by-distance patterns across different distance classes in the ECODIST R package. We used a lag of 100m and all correlograms were run for 999 permutations. We generated 95% confidence intervals with 500 iterations of 90% bootstrapping. We estimated pairwise F_{ST} between upstream and downstream reaches within each stream to test for genetic substructure within streams. Genetic variation among streams was assessed using pairwise F_{ST} . Between-reach and between-stream F_{ST} were calculated in GENODIVE and significance was assessed using 10,000 permutations.

Population size

We calculated the ratio of effective to census populations size (N_e/N) to understand the severity of inbreeding in our study streams, as the increase in homozygosity due to inbreeding is inversely proportional to effective population size. Effective population sizes (N_e) were estimated for each stream using the linkage disequilibrium method (LDNe) in NeEstimator v. 2.1 (Waples and Do 2008, Do et al. 2014). LDNe is a single-sample estimator that uses gametic disequilibria generated in small populations where there are a finite number of parents (Waples 2005). LDNe generally estimates the number of parents that contributed to the sample because disequilibria at unlinked loci decay rapidly. We assumed random mating and used a jackknife method to generate confidence intervals surrounding N_e estimates (Waples and Do 2008).

We used the POPAN formulation of the original Jolly-Seber model in Program Mark to estimate abundance (i.e., census size) of adult *G. porphyriticus* in each of the 5 study streams from our capture-mark-recapture data (White and Burnham 1999, Lebreton et al. 2009). We restricted our abundance estimation to adults because N_e estimates reflect the number of parents. Although we originally designed our sampling to fit a robust design framework, consisting of 3 primary sampling sessions per summer, with 3 secondary sampling sessions within each primary session (Pollock 1982), we collapsed all secondary survey sessions to a single observation within each primary session to increase the accuracy and precision of parameters of interest (e.g., Grant et al. 2010).

The POPAN formulation posits the existence of a hypothetical super-population (N), from which individuals enter the population (Schwarz and Arnason 1996). The probability of entering the population ($PENT$) is the probability that an animal from the super-population (N) enters the population between time t and $t+1$ and survives to time $t+1$. Survival probability (ϕ) represents the probability that marked and unmarked animals alive at time t will be alive at time $t+1$. Recapture probability (p) is the probability of capture of both marked and unmarked animals at time t , conditional on being alive and available for recapture.

We modeled ϕ , p , and *PENT* parameters as either constant or variable by time (month), for a total of 6 possible models per stream. Each model produced an estimate of the super-population (N), which represents all adult individuals that could ever enter the stream population over the study period, and which we used as our measure of adult abundance. Model selection was based on Akaike's information criterion (AIC; (Akaike 1973) and models were ranked by second-order AIC (AIC_c) differences (Δ AIC_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). When top model rankings were ambiguous (i.e., Δ AIC_c < 2.0; Burnham and Anderson 2002), we performed pairwise likelihood ratio tests (LRT) to compare model fit. A significant LRT ($P < 0.05$) indicates greater support for the model with more parameters; a non-significant LRT indicates both models are equally supported, in which case the model with fewer parameters is more parsimonious (Cooch and White 2007). Prior to model selection, we assessed goodness-of-fit for saturated models (i.e., fully time-dependent) using the program RELEASE (Cooch and White 2007).

Quantifying inbreeding risk

We quantified inbreeding risk as an individual's proximity to relatives, calculated as the proportion of individuals within 50m (i.e., in either upstream or downstream directions along the channel, amounting to 100m of stream length) that were relatives. We set this 50m cutoff *a priori* based on existing data on *G. porphyriticus* movement in a stream in northern New Hampshire (Lowe et al. 2006a). Specifically, mean dispersal distance of 287 recaptured individuals in that 6-year dataset was 47m (W.H. Lowe, *unpublished data*), suggesting that a 50m cutoff would be large enough to encompass the majority of potential mates in the Hubbard Brook streams, accounting for future movements of the focal individual and those potential mates.

We used the program RELATED (Pew et al. 2015), an R implementation of the program COANCESTRY (Wang 2011), to estimate pairwise coefficients of relatedness (r) between individuals using 297 SNPs. Seven relatedness estimators are available in COANCESTRY, including five moment estimators (Queller and Goodnight 1989, Ritland 1996, Lynch and Ritland 1999, Wang 2002, Li et al. 2014) and two likelihood methods (Wang 2007, Anderson and Weir 2007). Performance of these estimators is known to depend on many factors, including the level of relationship within the population of interest (Csilléry et al. 2006), population demographic history (Robinson et al. 2013), and number and polymorphism of genetic markers used (Blouin 2003). Simulations are therefore recommended to select the best estimator for a given dataset (Wang 2011, Taylor 2015). We used empirical allele frequencies from our study populations to simulate 100 dyads of each of the following relationship categories: parent-offspring ($r = 0.50$), full siblings ($r = 0.50$), half siblings ($r = 0.25$) and unrelated ($r = 0.0$). Estimator performance was assessed by calculating Pearson's correlation coefficient for

relatedness estimates produced by each estimator and true relatedness. The triadic likelihood method (TrioML) produced relatedness estimates that were most closely correlated with true relatedness (Pearson's $r = 0.972$) and was employed for subsequent analyses. We performed 100 bootstrap replicates over loci to calculate 95% confidence intervals for each point estimate of relatedness.

Simulations revealed some imprecision in relatedness estimates for individuals in known relationship categories (Fig S1), so we took a conservative approach and classified individuals as 'related' or 'unrelated' for subsequent analyses rather than using point estimates of relatedness coefficients. We considered related individuals to be pairs with a relatedness coefficient > 0.13 , the lower 95% confidence limit of the simulation of half-siblings with the TrioML estimator. Therefore, related pairs included parent-offspring dyads, full-siblings and half-siblings. All other individuals were considered unrelated because we did not have the power to distinguish more distant relationships from unrelated individuals (e.g., first-cousins [$r=0.125$], second-cousins [$r=0.01325$]), as the upper 95% confidence limit of unrelated individuals from simulations was 0.123.

Testing for effects of dispersal on inbreeding risk

We used a linear mixed effects (LME) model to test for effects of dispersal and stream reach on the proportion of relatives within 50m – our measure of inbreeding risk. This approach allowed us to pool data across streams by including stream as a random effect, thereby accounting for variation in relatedness among streams. We treated dispersal status (yes, no), and stream reach (downstream, upstream) as fixed effects. We included the dispersal \times reach interaction as a fixed effect to explicitly test for a difference in the effect of dispersal on inbreeding risk between downstream and upstream reaches. These analyses were conducted using the 'lme' and 'anova.lme' functions in the 'nlme' R package (Pinheiro et al. 2014). We used a 'varIdent' weighting function to correct for heteroscedasticity due to unequal variances among dispersal \times reach groups. To assess the statistical significance of the dispersal \times reach interaction, we defined significance at $p < 0.10$. Tests of interactions are often underpowered when sample sizes are small (Marshall 2007, Durand 2013), as in many ecological studies (e.g., Drake et al. 2011, Sistla et al. 2013). Given the rarity of dispersers compared to residents in *G. porphyriticus*, we anticipated small sample sizes might also interfere with our ability to detect true differences in inbreeding risk between dispersers and residents in downstream and upstream reaches. Based on the ANOVA summary of the LME model, we conducted post-hoc pairwise comparisons to identify specific differences in inbreeding risk between dispersal \times reach groups using Tukey's test in the R package 'lsmeans' (Lenth 2016). Larvae and adults were pooled for all analyses because the two life-history stages are not independent; that is, dispersal during the larval stage affects spatial proximity to relatives as an adult.

Results

Dispersal distance

We captured 2,861 salamanders across the 5 study streams during our study. Information on recapture rates and other sampling parameters are in Table 1. All but two of the recaptured individuals stayed within the same reach during the study; one individual in Bear and one individual in Zigzag moved from the upstream reach to the downstream reach. Within-reach dispersal distances in recaptured individuals ranged from 0 – 404m, and dispersal distances in dispersers (i.e., individuals that moved ≥ 10 m) were greater in downstream reaches than upstream reaches (Wilcoxon rank-sum test, $p = 0.047$; Figure 2).

Genetic differentiation

Mean expected heterozygosity was similar in the 5 study streams and ranged from 0.334 – 0.343 (Table 1). F_{IS} values were not significant for any stream ($p \geq 0.05$), but estimates were slightly positive for all streams except Cascade, indicating a deficit of heterozygotes (Table 1). Mantel tests for isolation-by-distance were significant in Bear ($r = 0.084$, $p = 0.001$) and Paradise ($r = 0.075$, $p = 0.004$; Table 1). The lack of a signal of IBD in Cascade, Canyon and Zigzag was likely due to small sample sizes (Table 1). In Bear and Paradise, Mantel correlograms indicated autocorrelation of genetic distances at < 300 m and little to no correlation at distances greater than 300m (Figure 3).

Pairwise F_{ST} values between reaches were low (0.001 – 0.008; Table 2) and only significant for Bear and Paradise, indicating weak differentiation between upstream and downstream reaches (Table 2). The lack of significant F_{ST} values between reaches in the other streams was also likely due to small sample sizes. All pairwise F_{ST} between streams were significant, ranging from 0.007 – 0.022 (Table 2). Bear and Paradise, the streams closest together on the landscape, were the least differentiated, and Cascade was the most differentiated from all other streams.

Population size

Jolly-Seber abundance models for all 5 study streams indicated that survival was constant over time, and recapture and entrance probabilities were variable over time (Table S2). The difference in AIC_c (ΔAIC_c) between the top and second-ranked models were > 2 in all streams except Canyon, indicating considerable support for the top models. Entrance probability was constant over time in the second-ranked model in Canyon. However, a likelihood ratio test between the top two models was significant ($X^2 = 10.96$, $p = 0.03$), indicating that the model with more parameters (i.e., with time-variant entrance probabilities) had the best fit. None of tests

performed in RELEASE were significant, indicating no evidence of lack-of-fit for any models. Estimates of adult abundance from the top models for each stream ranged from 587 – 899 (Table 1).

Effective population sizes estimated using LDNe ranged from 124 – 205 (Table 1). The upper 95% confidence limit for Cascade included infinity, likely due to small sample size. Effective to census population size ratios ranged from 0.163 – 0.406; however, these ratios are rough given that 95% confidence limits were sizeable for both effective and census sizes (Table 1).

Effects of dispersal on inbreeding risk

We quantified inbreeding risk as the proportion of individuals within 50m that were related ($r > 0.132$). Individuals that were not within 50m from any other individuals were excluded from subsequent analyses ($n = 7$). The number of individuals within 50m of a focal individual ranged from 1 – 30 and the proportion of these that were relatives ranged from 0 – 1; these two measures were not correlated ($r = -0.033$, $p = 0.522$). The median proportion of relatives within 50m was 0.111.

The results of the LME model and ANOVA showed a significant main effect of dispersal on the proportion of relatives within 50m ($F_{1,360} = 7.176$, $p = 0.007$), indicating that inbreeding risk was lower for dispersers than residents. However, a significant disperser \times reach interaction term ($F_{1,360} = 3.059$, $p = 0.081$) indicated that this effect was dependent on stream reach (Figure 4). Post-hoc Tukey tests showed that dispersers in downstream reaches were in proximity to fewer relatives than residents ($t = 3.080$, $p = 0.012$), but there was no difference in the proportion of relatives surrounding dispersers and residents in upstream reaches ($t = 0.899$, $p = 0.806$). The main effect of stream reach on the proportion of relatives within 50m was not significant ($F_{1,360} = 0.009$, $p = 0.926$). These results indicate that dispersal is effective for reducing inbreeding risk in downstream reaches only – where dispersal distances were greater than in upstream reaches.

Discussion

Our results show that dispersal reduces inbreeding risk in *G. porphyriticus*, and that environmentally-associated variation in dispersal distances leads to variation in the effects of dispersal on inbreeding risk. Specifically, we found that in the downstream reaches of our study streams, where dispersal distances were greater (Figure 2), dispersal significantly lowered inbreeding risk (Figure 4). This effect was not observed in upstream reaches where dispersal distances were shorter. These results indicate that selective pressures influencing dispersal distances can vary at fine spatial scales (i.e., reach-scale), with resulting consequences for

inbreeding risk. Likewise, these results show that inbreeding avoidance is not the sole evolutionary driver of dispersal distances in our study system, given that inbreeding risk has not led to increased dispersal distances in upstream reaches. More generally, our study demonstrates the importance of considering dispersal distance, rather than dispersal propensity, for determining an individual's inbreeding risk, while also underscoring the danger of ascribing variation in dispersal – whether propensity or distance – to inbreeding avoidance alone.

Our key finding that dispersal distances predict inbreeding risk was due, in part, to the spatial structure of genetic differentiation in *G. porphyriticus*. Dispersal is rare in *G. porphyriticus*, creating a pattern of isolation-by-distance along streams, where relatives are locally clustered. This pattern was statistically significant in Bear and Paradise (Figure 3), and we believe it is likely that small sample sizes prevented us from detecting IBD in the other streams (Table 1). This fine-scale clustering of relatives created conditions under which dispersal effectively lowered inbreeding risk in downstream reaches. Our data suggest that the same pattern of clustering occurred in upstream reaches: the main effect of reach was not significant in our ANOVA analyses, indicating that the proportion of relatives within 50m of a focal individual – our index of inbreeding risk – did not differ between downstream and upstream reaches. However, dispersal (based on the 10m cutoff) did not lower inbreeding risk in upstream reaches, indicating that the different effects of dispersal on inbreeding risk in downstream and upstream reaches were due to differences in dispersal distances rather than differences in spatial patterns of genetic relatedness. Without information on mate choice, we cannot know whether dispersers in downstream reaches successfully avoided inbreeding, but several studies have shown that dispersers do not discriminate between relatives and non-relatives when choosing mates (Duarte et al. 2003, Foerster et al. 2006, Hansson et al. 2007, Eikenaar et al. 2008), further underscoring the importance of dispersal distances in mitigating inbreeding risk.

Evidence of increasing genetic divergence with stream distance suggests that the majority of dispersal in *G. porphyriticus* occurs in or along stream channels. This pattern is consistent with other stream salamanders that are confined to the stream network, whereas salamanders dispersing both overland between streams and along streams tend to exhibit less genetic structure (Steele et al. 2009, Mullen et al. 2010, Miller et al. 2015). Overland dispersal is also known to increase demographic connectivity and gene flow among populations of other headwater stream organisms (Finn et al. 2006, 2007, Ponniah and Hughes 2006, Grant et al. 2010), and should, we expect, reduce the overall threat of inbreeding and the effectiveness of dispersal as an inbreeding avoidance strategy. In contrast, IBD along stream channels creates conditions where dispersal, and dispersal distance in particular, can influence individual inbreeding risk. More generally, then, the capacity of stream organisms to use overland dispersal pathways may help to predict inbreeding risk and the likelihood that specific dispersal parameters (e.g., distance, frequency, stage or sex specificity) evolve to reduce inbreeding.

Despite evidence of IBD along streams (Figure 3) and that dispersal distance predicts inbreeding risk (Figures 2 and 4), our results do not support the conclusion that inbreeding avoidance is the primary selective pressure influencing dispersal distance in *G. porphyriticus*. If this were the case, we would expect dispersal distances to be greater in upstream reaches (Figure 2), leading to reduced inbreeding risk in dispersers (Figure 4). Additionally, low F_{ST} values between streams, ranging from 0.007 – 0.022, indicate that our study streams receive approximately 16 migrants per generation assuming migration-drift equilibrium (Wright 1969). This number of migrants exceeds that which is generally needed to reduce the harmful effects of inbreeding (Wright 1951, Lowe and Allendorf 2010). Further, effective population sizes ($N_e = 124 - 205$) are likely high enough to avoid inbreeding depression (Jamieson and Allendorf 2012). Effective to census population size ratios (N_e/N) ranged from 0.16 – 0.41, within the range observed for non-threatened wild populations (Palstra and Ruzzante 2008) and higher than previously reported medians (0.11 in Frankham 1995, 0.14 in Palstra and Ruzzante 2008). It should be noted, however, that there is significant uncertainty associated with our N_e and N estimates, indicated by large confidence intervals in streams with low sample sizes (i.e., Canyon, Cascade; Table 1). It is also challenging to interpret N_e from mixed-age samples like ours; Waples et al. (2014) suggest that estimates from mixed-aged samples may be downwardly biased by as much as 30% in amphibians. This downward bias in N_e means that N_e/N ratios are also likely downwardly biased, and that these indices may overestimate the effects of inbreeding on population genetic variation.

If we rule out inbreeding avoidance as the primary driver of dispersal distance in our study system, there remain several ecological differences between downstream and upstream reaches that may explain the observed variation in dispersal distances (and associated effects on inbreeding risk). Previous research in the HBEF has shown that survival in *G. porphyriticus* is generally lower in downstream reaches (Lowe et al. 2018; Addis, Chapter 3), suggesting that increased dispersal distances in these reaches is a response to increased mortality risk. Increased mortality risk may, in turn, be a result of co-occurrence with brook trout in downstream reaches. Brook trout prey on *G. porphyriticus* larvae and reduce growth rates of larger size classes through interference competition for shared prey (Resetarits 1991, 1995, Lowe et al. 2004). Predation and competition are known to increase dispersal distances to escape predation and alleviate competition for space and resources, respectively (De Meester and Bonte 2010, Bitume et al. 2013, Otsuki and Yano 2014). However, many other factors also differ along our study streams that could lead to differential dispersal distances between downstream and upstream reaches (e.g., discharge, prey availability, refuge availability; Vannote et al. 1980, Hubert and Kozel 1993, Lowe and Bolger 2002). Finally, although inbreeding avoidance is unlikely to be the primary selective pressure influencing dispersal distances in *G. porphyriticus*, any positive fitness effects of reduced matings with relatives may help to maintain longer dispersal distances in downstream reaches (Perrin and Goudet 2001).

A strength of our study comes from using direct dispersal data, rather than inferring dispersal from genetic data. Directly measuring dispersal allowed us to test for effects of relatively short-distance movements (i.e., shorter than the spatial scale of genetic differentiation; Figure 3) on inbreeding risk. This analysis would not have been possible using indirect genetic methods that require genetic divergence among subpopulations to detect immigrants (i.e., assignment tests; Rannala and Mountain 1997, Manel et al. 2005, Hall et al. 2009). Additionally, our approach allowed us to quantify the effects of both larval and adult dispersal on inbreeding risk. Parentage analyses are commonly used to estimate dispersal distances based on the physical distance between parent-offspring dyads (Proctor et al. 2004, Cullingham et al. 2008, Waser and Hadfield 2011), but this approach precludes the possibility of adult dispersal because it assumes that offspring were born at the location where the parents were sampled (Blouin 2003). This assumption is certainly valid for species with highly philopatric adults (Dobson 1982), but dispersal by reproductive adults is also well documented (Hazell et al. 2000, Bonte et al. 2008), including in *G. porphyriticus* (Lowe 2003).

This study provides rare empirical support for the basic prediction that inbreeding risk should decrease with increasing dispersal distances. Our results also underscore the importance of interpreting dispersal distances in the context of spatial patterns of genetic relatedness to disentangle inbreeding avoidance from other selective pressures influencing dispersal distances. More broadly, this work contributes to a growing body of research showing that inbreeding, kin competition, and environmental variation – the three putative drivers of dispersal evolution – may each require different dispersal distances to reduce associated fitness costs (Bowler and Benton 2005, Duputié and Massol 2013). Likewise, we hope this work shows the value of directly quantifying dispersal distances to understand the relative importance of these selective pressures in shaping dispersal strategies in natural populations.

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Table 1. Sample sizes and genetic information for *G. porphyriticus* in 5 headwater streams in the Hubbard Brook Experimental Forest.

Stream	Total captured (down/up)	recaptured (down/up)	genotyped (down/up)	Ne (95% CI)	N _{adult} (95% CI)	Ne:N	H _e	F _{IS}	Mantel R
Bear	930 (397/533)	246 (89/157)	150 (65/85)	182 (147 - 234)	899 (649 - 1314)	0.202	0.341	0.002	0.084*
Canyon	387 (245/142)	50 (32/18)	36 (25/11)	183 (111 - 467)	451 (273 - 824)	0.406	0.334	0.017	0.036
Cascade	115 (76/39)	37 (22/15)	22 (16/6)	124 (51 - ∞)	761 (277 - 2572)	0.163	0.341	-0.017	0.140
Paradise	876 (353/523)	212 (73/139)	112 (45/67)	205 (165 - 267)	825 (645 - 1085)	0.248	0.343	0.001	0.075*
Zigzag	553 (134/419)	118 (11/107)	62 (5/57)	157 (112 - 251)	587 (407 - 905)	0.267	0.343	0.001	0.009

* p<0.05

Table 2. Pairwise F_{ST} values for *G. porphyriticus* in 5 headwater streams in the Hubbard Brook Experimental Forest. Values in the diagonal are pairwise F_{ST} between downstream and upstream reaches.

	Bear	Canyon	Cascade	Paradise	Zigzag
Bear	0.008*				
Canyon	0.015*	0.001			
Cascade	0.02*	0.017*	0.003		
Paradise	0.007*	0.014*	0.022*	0.006*	
Zigzag	0.012*	0.013*	0.022*	0.014*	0.006

* $p < 0.05$

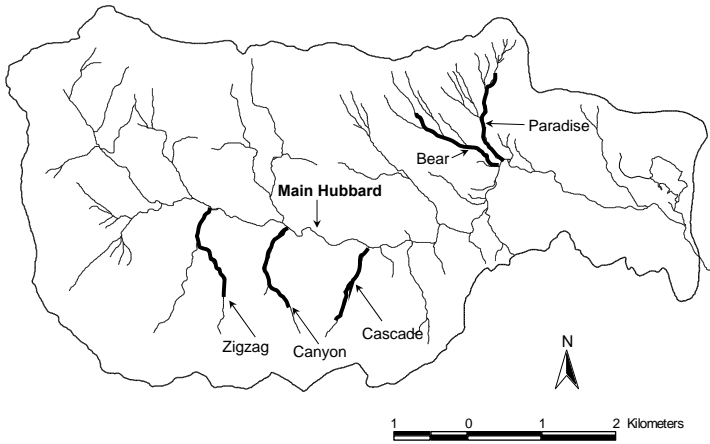


Figure 1. Map of the 5 study streams in the Hubbard Brook Experimental Forest in central New Hampshire, USA. Bear, Canyon, Cascade, Paradise, and Zigzag Brooks are hydrologically independent and flow into the Main Hubbard.

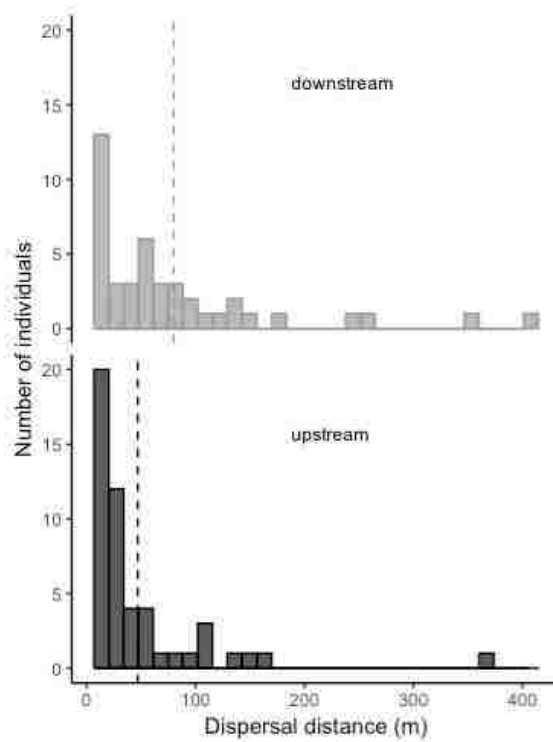


Figure 2. Distribution of dispersal distances in downstream reaches (light grey, $n = 43$) and upstream reaches (dark grey, $n = 50$) of recaptured *G. porphyriticus* in 5 streams in the Hubbard Brook Experimental Forest, USA. Only dispersers are shown – individuals that moved $\geq 10\text{m}$ from their initial location, as justified in the main text. Dotted lines indicate mean dispersal distances (downstream = 80.070m, upstream = 47.020m). Dispersal distances were significantly greater in downstream reaches than upstream reaches (Wilcoxon rank-sum test, $p = 0.047$).

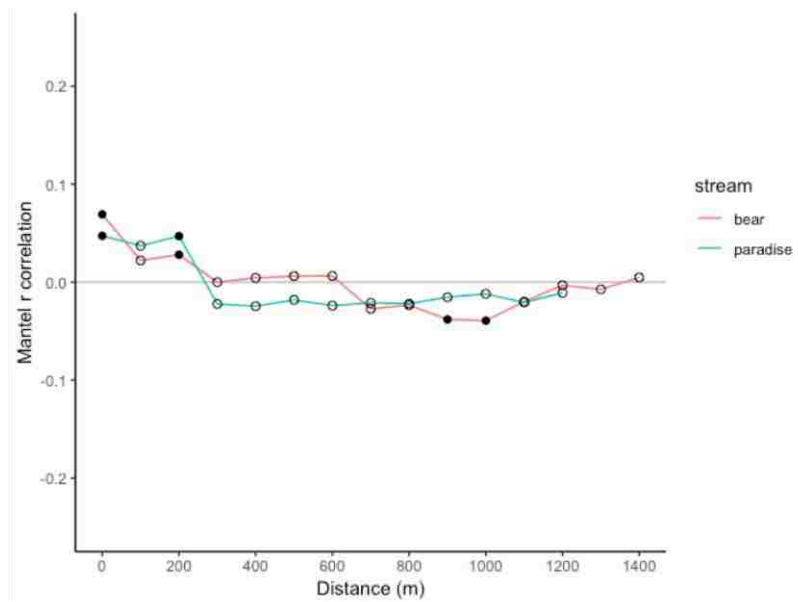


Figure 3. Mantel correlograms for *G. porphyriticus* in Bear and Paradise streams in the Hubbard Brook Experimental Forest, USA. Filled points are statistically significant and open points are not statistically significant. Each distance class is 100 m.

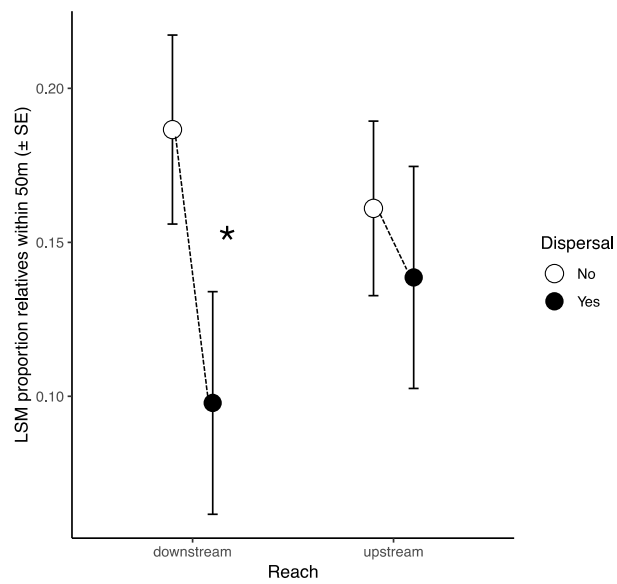


Figure 4. Results of ANOVA testing for differences in inbreeding risk (measured as the proportion of relatives within 50m) in *G. porphyriticus* dispersers and non-dispersers in downstream and upstream reaches of 5 streams in the Hubbard Brook Experimental Forest. Filled circles are dispersers (i.e., individuals that moved $\geq 10\text{m}$ from their initial location) and open circles are non-dispersers. Data are least squares means (LSM) from ANOVA. The asterisk indicates a significant difference in inbreeding risk.

Table S1. The number of variant sites retained after each filtering step for *G. porphyriticus* in the Hubbard Brook Experimental Forest.

Filter	SNP count
Raw SNP catalogue	62777
Remove individuals > 40% missing data	
Genotyped in 50% of individuals, base quality >20	31069
Minimum depth of 3 reads to call genotypes	
Genotype call rate of 70% in all pops	24214
Minor allele frequency > 0.05	11618
Allele ratio >0.3, <0.7	5251
Mean site depth >10, < 300	4141
filter by HWE (out of proportions in ≥ 3 pops)	1380
thin to 1 SNP/contig	312
remove physically linked loci ($r^2 \geq 0.8$ in ≥ 3 pops)	297

Table S2. Jolly-Seber capture-mark-recapture (CMR) models of monthly survival (ϕ), recapture (p), and entrance probabilities ($pent$) used to estimate abundance of adult *Gyrinophilus porphyriticus* in 5 study streams in the Hubbard Brook Experimental Forest. Here we only show the top 3 models for each stream.

Bear	AIC _c	Δ AIC _c	AIC _c wt	K
$\phi(\cdot), p(\text{time}), pent(\text{time})$	510.95	0	1.00	22
$\phi(\text{time}), p(\text{time}), pent(\text{time})$	525.54	14.59	0.00	30
$\phi(\text{time}), p(\text{time}), pent(\cdot)$	81470.65	80959.70	0	21
Canyon	AIC _c	Δ AIC _c	AIC _c wt	K
$\phi(\cdot), p(\text{time}), pent(\text{time})$	201.84	0	0.60	16
$\phi(\cdot), p(\text{time}), pent(\cdot)$	202.65	0.81	0.40	12
$\phi(\text{time}), p(\text{time}), pent(\text{time})$	211.66	9.82	0.00	21
Cascade	AIC _c	Δ AIC _c	AIC _c wt	K
$\phi(\cdot), p(\text{time}), pent(\text{time})$	177.29	0	0.98	16
$\phi(\text{time}), p(\text{time}), pent(\text{time})$	184.76	7.48	0.02	21
$\phi(\cdot), p(\cdot), pent(\cdot)$	38011.56	37834.27	0.00	4
Paradise	AIC _c	Δ AIC _c	AIC _c wt	K
$\phi(\cdot), p(\text{time}), pent(\text{time})$	522.53	0	1.00	22
$\phi(\text{time}), p(\text{time}), pent(\text{time})$	534.52	11.99	0.00	30
$\phi(\text{time}), p(\text{time}), pent(\cdot)$	75947.30	75424.78	0	21
Zigzag	AIC _c	Δ AIC _c	AIC _c wt	K
$\phi(\cdot), p(\text{time}), pent(\text{time})$	342.77	0	1.00	22
$\phi(\text{time}), p(\text{time}), pent(\text{time})$	361.69	18.92	0.00	30
$\phi(\cdot), p(\cdot), pent(\cdot)$	369.89	27.12	0	4

Notes: Second-order Akaike's information criterion values (AIC_c), AIC_c differences (Δ AIC_c), AIC_c weights (AIC_c wt), and number of estimable parameters (K) are provided for all models. Parameterization for ϕ , p , and $pent$ is in parentheses; “.” = constant by stream reach and time.

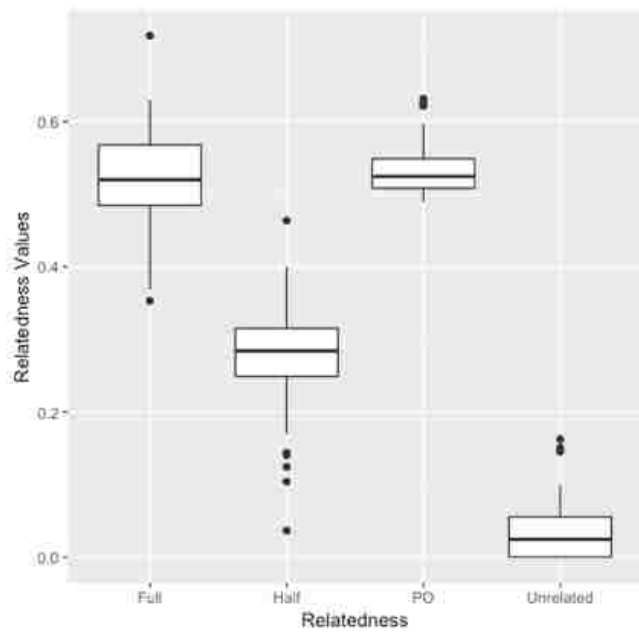


Figure S1. Relatedness coefficients estimated by TrioML in COANCESTRY for simulated dyads in 4 relationship categories (parent-offspring [$r = 0.5$], full-siblings [$r = 0.5$], half-siblings [$r = 0.25$], unrelated [$r = 0$]) using simulated genotypes based on empirical allele frequencies of 297 SNPs developed for *G. porphyriticus*.

CHAPTER 5: Evolution of dispersal is scale-dependent

Abstract

The challenge of quantifying long-distance dispersal in the field has limited our understanding of the processes leading to individual variation in dispersal distances in natural populations. Recent empirical work has shown that animals use information on habitat quality to make emigration and settlement decisions, thereby maximizing individual fitness with ‘informed dispersal’. In contrast, early dispersal theory treated dispersal as a ‘fixed’ trait, independent of local conditions. Empirical support for fixed strategies remains scarce, leading researchers to speculate that informed dispersal is more prevalent and evolutionarily advantageous. However, the costs of information acquisition at large spatial scales make informed strategies impractical for long-distance dispersal. We bring together informed and fixed models of dispersal and propose a scale-dependent model of dispersal evolution. Under our model, informed strategies explain short-distance dispersal and fixed strategies explain long-distance dispersal. We further suggest that fixed dispersal will have added adaptive significance under climate change by facilitating long-distance movements needed to track suitable habitat.

Introduction

Dispersal has long been recognized as an important process in ecology and evolution. Dispersal contributes to population growth rates (Tittler et al. 2006), facilitates gene flow and introduces adaptive alleles into populations (Swindell and Bouzat 2006, Garant et al. 2007), and allows populations to track changes in the distribution of suitable habitat (Kokko and López-Sepulcre 2006). Additionally, populations receiving immigrants are less likely to go extinct by demographic mechanisms (Brown and Kodric-Brown 1977, Hanski and Gilpin 1997) or genetic mechanisms (Spielman and Frankham 1992, Vilà et al. 2003). These effects of dispersal on population dynamics and evolutionary trajectories are often mediated by dispersal distances. For example, connectivity between geographically separated populations may be achieved only if dispersal distances are long enough to cross the intervening habitat matrix (Van Houtan et al. 2007). Long-distance dispersal, in particular, sets the rate of range shifts (Higgins and Richardson 1999) and species invasions (Kot et al. 1996), and ultimately plays a key role in determining population and species persistence (Bohrer et al. 2005).

Despite this evidence for its importance, our understanding of how long-distance dispersal is maintained in natural populations is limited by empirical and conceptual obstacles related to spatial scale. Dispersal is difficult to quantify empirically in the field, and increasingly so the greater the distance (Koenig et al. 1996, Nathan 2001). This leads to small post-dispersal

sample sizes, and a lack of related information on the fate and fitness of dispersing individuals (Lowe and McPeck 2014). This scarcity of data on the fitness consequences of dispersal impedes dispersal research generally, but poses a particular challenge in efforts to understand the causes and consequences of variation in dispersal distance – because the likelihood of recapture declines with distance (Nathan 2001, Reid et al. 2016, Cayuela et al. 2018).

Spatial scale also poses a conceptual challenge in dispersal research. We often associate dispersal with large-scale movements, but dispersal is commonly defined as movement from a natal site to a site of reproduction – with no explicit mention of spatial scale (Greenwood 1980, Duputié and Massol 2013, Burgess et al. 2015). Some reluctance to address scale in dispersal theory is expected given the species and system-specific nature of “large-scale movements”. Additionally, the distinction between short-distance and long-distance dispersal is often ambiguous (Nathan et al. 2003). It is generally acknowledged that short-distance dispersal influences local processes (i.e., population dynamics, resource use), while long-distance dispersal affects regional processes (i.e., range shifts, colonization dynamics; Kot et al. 1996, Hanski 1998, Nathan et al. 2003). However, ‘local’ and ‘regional’ must still be scaled to the movement capacities of species. Nevertheless, conceptual reckoning with scale is necessary if we hope to answer questions that are scale-dependent, such as why we see a consistent pattern of many short-distance dispersers (Janzen 1970, Hamilton and May 1977) but very few long-distance dispersers across taxa (Kot et al. 1996, Gillespie et al. 2012), and whether the proximate drivers of dispersal (e.g., behavioral, physiological, morphological traits) vary with distance (Alonso et al. 1998, Lowe and McPeck 2012).

Dispersal is a 3-part process, including stages of emigration, transience, and settlement (Ronce 2007, Clobert et al. 2009). Under a scale-free view of dispersal, it is logical to focus on emigration (stay vs. leave) and settlement (stop vs. continue), and a growing body of research emphasizes the use of information by dispersers – environmental and social – to make these discrete dispersal decisions (Bowler and Benton 2005, Clobert et al. 2009). This view of dispersal is largely consistent with the Ideal Free Distribution (IDF), where fitness declines with conspecific density and individuals apportion themselves among habitat patches to maximize individual fitness (Fretwell and Lucas 1970, Fretwell 1972). Dispersal decisions often incorporate factors other than conspecific density (e.g., Massot et al. 2002; Bonte et al. 2008; Mathieu et al. 2010). But, regardless of the cause of emigration and settlement, dispersal is the mechanism that allows individuals to maximize fitness at the landscape scale, and it relies on an ability to assess habitat – at the origin and in transit (i.e., informed dispersal; Clobert et al. 2009).

When we consider continuous variation in dispersal distance, rather than discrete emigration and settlement responses, the importance of information becomes less clear. Dispersal in most plants and animals is characterized by a majority of individuals that stay close to their natal site and significantly fewer that move far from that site (Dobzhansky and Wright 1943,

Mayr 1963, Endler 1977). This produces distance distributions with high peaks at a distance of 0 and long tails encompassing the variation in dispersal distance (i.e., leptokurtic or fat-tailed distributions; Darwin 1872; Endler 1977; Johnson and Gaines 1990). As the scale of dispersal increases, the number of potential settlement sites increases dramatically, and so does the cost of sampling those sites under an informed dispersal model (Bonte et al. 2012; Delgado et al. 2014; Figure 1). This rate of increase will depend on the movement behavior of a focal species (Schjørring 2002; Enfjäll and Leimar 2009; Bocedi et al. 2012; Figure 2), but will be highly distant-dependent (Poethke et al. 2011). Thus, although informed dispersal may be an appropriate model for variation in dispersal distances near the peaks of distance distributions, where the costs of gathering information are relatively low, it is unlikely to maintain the tails of these distributions.

We suggest that long-distance dispersal is likely an outcome of fixed dispersal strategies – those that are not contingent on assessing local habitat quality, but instead based on innate qualities of individuals. To advance empirical and theoretical research on dispersal, we propose a new, scale-explicit model of dispersal evolution where strategies differ with dispersal distance – informed strategies at short distances, fixed strategies at long distances. We first review the conceptual basis of the two dominant models of dispersal evolution – informed and fixed – to clarify the foundation and motivation for our integrated model. We then describe how these two bodies of theory can be brought together in one scale-dependent model of dispersal evolution. Finally, we show how this new model can help address a pressing challenge in applied ecology: predicting species' ability to tracking shifting habitat under climate change. Because we are primarily interested in the role of information in dispersal evolution, we do not address variation in dispersal distance in passive dispersers, where transport is achieved by an external vector (i.e., wind, transport by animals; Carlquist 1981).

Dispersal is a mechanism to maximize individual fitness

Dispersal should only be selectively advantageous if the fitness benefits of dispersing to a new habitat patch exceed the costs. Fundamentally, then, dispersal evolves as a consequence of variation in individual fitness among habitat patches (Bowler and Benton 2005). Without individual fitness variation, dispersal should not evolve because individuals do not experience a fitness advantage by moving among patches (Holt 1985, but see Hamilton and May 1977 for an exception under a scenario of kin competition). A variety of ecological conditions can contribute to fitness variation among patches (e.g., con- and heterospecific density, resource availability, patch size), but regardless of the cause, how individuals distribute themselves among habitat patches to maximize fitness forms the basis of competing views of dispersal evolution.

Informed dispersal

Models of informed dispersal are based on individuals' ability to perceive and assess fitness returns at the current location and in transit to a settlement site. This view is supported by accumulating evidence that individuals use information about habitat quality and environmental conditions to make emigration and settlement decisions (e.g., Massot et al. 2002; Bonte et al. 2008). For example, we now know that earthworm (*Aporrectodea icterica*) dispersal is triggered by unsuitable soil properties (Mathieu et al. 2010), red squirrels (*Sciurus vulgaris*) disperse when food availability is low (Lurz et al. 1997), and backswimmers (*Notonecta undulata*) disperse in response to predatory sunfish (Baines et al. 2014).

Dispersal decisions can also be based on social information, such as presence and reproductive success of conspecifics (e.g., Doligez et al. 2003; De Meester and Bonte 2010). In many insects, flight-capable wings develop in response to conspecific density thresholds. For example, crowding triggers wing development for dispersal in many species of aphids (Harrison 1980), while planthopper species living in low-density, temporary habitats develop wings to locate mates in other habitat patches (Denno et al. 1991). Vertebrates are also known to use social information in emigration and settlement decisions. Kittiwakes (*Rissa tridactyla*) use information about the reproductive success of conspecifics to evaluate their own chances of breeding successfully in a given patch (Danchin et al. 1998), and common lizards (*Lacerta vivipara*) base emigration decisions on phenotypes of incoming immigrants to gain information about habitat quality elsewhere (Cote and Clobert 2007).

In addition to the recent surge of empirical support for informed dispersal models, theory supports the role of information in the evolution and maintenance of dispersal. In particular, the ability to recognize and avoid related individuals is implicit in dispersal theory addressing kin competition (Hamilton and May 1977, Ronce et al. 2000, Poethke et al. 2007) and inbreeding avoidance (Bengtsson 1978, Waser et al. 1986, Guillaume and Perrin 2006). Kin competition is a strong driver of dispersal in the common lizard: in the presence of kin, lizards will disperse at all costs, even when cues indicate that dispersal risk is high (Cote and Clobert 2010). Dispersive naked mole rats (*Heterocephalus glaber*) are phenotypically distinct from other colony members and preferentially mated with non-colony members during mate-choice experiments, indicating that dispersal is an inbreeding avoidance mechanism in this system (O'Riain et al. 1996).

Finally, informed dispersal also aligns with habitat selection theory. In particular, the Ideal Free Distribution (IFD) posits that individuals should freely distribute themselves among habitat patches to maximize individual fitness, thereby equilibrating fitness across the landscape (Fretwell and Lucas 1970, Fretwell 1972). In the original IFD model, fitness is contingent on conspecific density: the best patches will have the fewest competitors for resources. But, like recent empirical and theoretical work on informed dispersal, the IFD is based on an underlying

hypothesis that individuals obtain and act on knowledge of the resource quality in each patch. For example, *Daphnia pulex* choose their position in a patch based on food concentrations and population densities (Larsson 1997), and little grebes (*Tachybaptus ruficollis*) only occupy low-quality ponds after high-quality ponds become overcrowded (Sebastián-González et al. 2010).

Together, this long-standing habitat selection theory and recent research on informed dispersal can explain short-distance dispersal – the majority of dispersal events – where the costs of information gathering are relatively low (Figure 1). However, it is difficult to reconcile these important bodies of work with the phenomenon of long-distance dispersal, where the costs of information gathering are prohibitive (and indeed, the original IFD assumed no dispersal costs at all; Fretwell and Lucas 1970; Fretwell 1972). While recent refinements of information-based models do allow for behavioral mitigation of these costs (Delgado et al. 2014), the problem of distance-dependent information costs has yet to be explicitly addressed in theory and empirical work on the evolution of dispersal.

Fixed dispersal

Despite the traction that the informed dispersal perspective has gained in recent years, foundational models of dispersal evolution treated dispersal as a ‘fixed’ trait, where individuals have an innate propensity to disperse that is independent of local conditions (e.g., Gadgil 1971; Roff 1975; Hastings 1983; Holt 1985; McPeck and Holt 1992). A central conclusion of these early theoretical models was that fixed dispersal should only evolve when fitness varies both spatially and temporally (Kuno 1981, Levin et al. 1984, McPeck and Holt 1992). If fitness varies temporally but not spatially, all patches experience temporal fluctuations in fitness identically, eliminating the benefits of moving among patches. If fitness varies spatially but not temporally, dispersal initially acts to balance patch abundances, but ultimately distorts abundances away from patch-specific carrying capacities (Hastings 1983, Holt 1985). This occurs because, on average, more individuals move from high-density patches (thus, high-quality) to low-density (low-quality) patches. Such distortion reduces mean individual fitness and will ultimately lead to selection against dispersal (Hastings 1983; Holt 1985, but see Pulliam (1988) for an exception under a scenario of asymmetrical competition).

The fitness benefits of fixed dispersal strategies stem from unpredictable spatiotemporal variation in ecological conditions, where the probability that a patch is above, below, or at equilibrium abundance varies randomly through time. Under these conditions, a fixed proportion of individuals dispersing among patches, independent of local conditions, acts to decrease variance in individual fitness over time by spatially averaging fitness across patches (McPeck 2017). Ultimately, this bet-hedging strategy maximizes the disperser’s long-term geometric mean fitness (Kuno 1981, Metz et al. 1983, Armsworth and Roughgarden 2005), thereby maintaining the fixed dispersal strategy in the population. Scale is not explicitly addressed in fixed models of

dispersal evolution, but in these models the fitness benefits of fixed strategies are not contingent on processes with scale-dependent costs, such as information gathering.

These fixed models have had a significant and lasting impact on dispersal research, but direct empirical support for fixed dispersal is still scarce. Indirect support is found in systems where the development of locomotor structures are necessary for dispersal, such as wing-dimorphic insects (Harrison 1980, Denno et al. 1996). In these cases, phenotypic constraints prevent individuals from basing dispersal decisions on immediate, local habitat conditions (Hendrickx et al. 2013). More generally, traits linked to dispersal that do not vary plastically in response to environmental cues are suggestive of fixed strategies, such as morphological or physiological traits that have high resource requirements and take considerable time to produce (Padilla and Adolph 1996, DeWitt et al. 1998).

Fixed dispersal has typically been modeled as having a simple genetic architecture, often controlled by one or two loci (e.g., McPeck and Holt 1992; Travis and Dytham 2002; Poethke et al. 2003). Instead, dispersal is likely a complex trait influenced by many genes of small effect (Saastamoinen et al. 2018). Heritability estimates are generally used to discern the amount of trait variation controlled by genetics, but most studies estimate heritability of dispersal proxies (i.e., putative dispersal traits, locomotive ability), and not dispersal distance or propensity explicitly (e.g., Watkins and McPeck 2006; Drangsholt et al. 2014; Mattila and Hanski 2014). Additionally, the power of such analyses is often limited by small post-dispersal sample sizes. Identifying a genetic basis for dispersal would, nevertheless, strengthen empirical support for fixed models.

Scale-dependent evolution of dispersal

Informed and fixed dispersal models represent two very different views of dispersal evolution, hinging on differences in the perception and use of information. Historically, fixed dispersal was the first to receive theoretical consideration, but the recent accumulation of empirical support for informed dispersal has led some researchers to speculate that it is more evolutionarily advantageous and, therefore, more prevalent than fixed strategies (Bowler and Benton 2005, Bonte et al. 2008, Clobert et al. 2009). We suggest that the prevalence of the informed strategy in empirical studies is, in part, an artifact of a focus on the discrete emigration and settlement responses associated with short-distance movements. But these are only two of the three steps in the dispersal process, which also includes a period of transience before settlement (Ronce 2007, Clobert et al. 2009). Shifting to focus on the transience period – and associated variation in dispersal distance – will make explicit the scale-related costs that may select for fixed strategies.

The rarity of long-distance dispersal events alone, as reflected in the leptokurtic shape of dispersal distributions (Figure 3), suggests that the costs of dispersal increase with distance. In fact, because the potential sampling area increases with distance (Figure 1), it becomes unrealistic for individuals to sample all (or even most) available patches. More time spent sampling results in increased risk of predation, higher energy expenditure, and reduced opportunity for mating (Steen 1994, Giraldeau et al. 2002, Bonte et al. 2012). Thus, while informed dispersal is likely the optimal strategy over short distances, it is very difficult to explain long-distance dispersal events based on an informed dispersal model, unless the fitness benefits of dispersal also increase dramatically with distance.

Because of the high costs of gathering information about settlement sites at large spatial scales, we hypothesize that long-distance dispersal events are more likely explained by fixed dispersal strategies (Figure 3). Specifically, we predict that the fat tails of dispersal distributions are comprised of individuals with innate dispersal propensity, and which do not gather information about settlement site quality during transience (Delgado et al. 2014). Over long distances, dispersing without gathering information on site quality is likely to result in more efficient, straight-line movements, reducing mortality during the transient stage by minimizing the number of steps needed to achieve a certain distance (Zollner and Lima 1999; Barton et al. 2009; Figure 2).

Fixed dispersal can be thought of as a cost-reducing strategy for long-distance dispersal (Figure 2), but these long-distances movements are still likely to be costly (Newton and Marquiss 1983, Forero et al. 2002). Long-distance movements should, therefore, have a high fitness payoff when successful to be maintained in populations. However, data on these fitness benefits are rare and – when available – subject to bias (Doligez and Pärt 2008). Specifically, low detectability can lead to underestimation of survival and reproductive success of long-distance dispersers relative to short-distance dispersers and residents (Greenwood et al. 1979, Pärn et al. 2009), leading to the conclusion that dispersers tend to have lower fitness than residents (e.g., Wheelwright and Mauck 1998; Pockock et al. 2005; Hoogland et al. 2006). These sampling limitations have precluded unbiased assessment of the fitness benefits of long-distance dispersal, and thus the types of movements that we suggest are likely to be fixed. There are, however, more tractable benefits of fixed dispersal at the population level. Fixed dispersal offers a mechanism for populations to overcome ‘dispersal inertia’ – a tendency for perceptive individuals to disperse less than is optimal to maximize population performance (Enfjäll and Leimar 2009, Delgado et al. 2011). As a consequence, fixed dispersal can lead to higher colonization success of new habitats and higher metapopulation connectivity (Vuilleumier and Perrin 2006).

Our argument for a scale-dependent model of dispersal evolution is based primarily on the scaling of information costs, but the scaling of environmental variation also supports our

prediction that long-distance dispersal is under fixed control. As area around an initial starting position increases (Figure 1), spatiotemporal environmental variability of potential settlement sites will increase (Wiens 1989, Legendre 1993), with the highest variability (relative to the initial position) occurring at the most distant sites (Nekola and White 1999). Thus, the conditions predicted to maintain fixed dispersal by theoretical models are themselves likely to be scale dependent, consistent with our prediction that fixed models better explain long-distance dispersal. Interestingly, Bocedi et al. (2012) recently showed that it does not pay to invest in information acquisition when the environment varies unpredictably (e.g., as distance from an initial location increase) because the cost of gathering information will not reliably be offset by the benefits. Unpredictable variation in environmental conditions can also induce time lags between the cue and dispersal decisions (i.e., stay vs. leave), which can be maladaptive (Ims and Hjermann 2001). These findings add to indirect support for the role of fixed strategies in maintaining long-distance dispersal.

Taken together, we suggest that informed dispersal is most likely to evolve when the cost of information acquisition is low and when the environment varies predictably. When these two criteria are not met, we expect fixed dispersal to prevail. By extension, we suggest that the criteria for informed dispersal are most likely to be met at small spatial scales, and so generally pertain to short-distance movements. As the scale of movement increases, it becomes more costly to gather information, and individuals are more likely to experience spatiotemporal variability in habitat quality (Wiens 1989, Legendre 1993), leading to selection for fixed dispersal. Thus, we propose that the mechanisms underlying dispersal evolution are scale-dependent, with short and long-distance dispersal evolving separately.

Dispersal and climate change

In the current era of climatic change, the survival of species will depend in part on their ability to track shifting habitat by dispersing (Kokko and López-Sepulcre 2006, Pöyry et al. 2009, Berg et al. 2010). However, many projections of future species distributions do not incorporate dispersal (Thomas et al. 2004, Thuiller et al. 2006), and the few that do generally model dispersal without individual variation in emigration and settlement responses, or in dispersal distance (Travis and Dytham 2012). Consequently, the role of information in species' ability to keep pace with climate change has received little attention, yet it is likely that the spatial arrangement of suitable habitat will strongly dictate which dispersal strategy—informed or fixed—most enhances habitat tracking.

Range shifts in response to a shifting climate window will likely require dispersing across gaps of unsuitable habitat. Species ranges often occur along an environmental gradient, with the most suitable habitat at the core of the range, and declining suitability towards the range margins

(Bridges et al. 2007). Because these marginal populations will lead climate-induced range shifts, the capacity to disperse across patches of unsuitable habitat will likely play a key role in species' ability to keep pace with climate change (Travis and Dytham 2012). Increasing habitat fragmentation may also interact with climate change to increase distances between suitable habitat patches (Travis et al. 2010, Williams et al. 2016). Consequently, long-distance dispersal will be required to colonize new habitat patches. Indeed, we have seen that long-distance dispersal, rather than short-distance dispersal, sets the rate of range expansions in theoretical models (Le Galliard et al. 2012), and Boeye et al. (2013) showed that fast rates of climate change selected for larger dispersal distances, which enhanced the ability of populations to cross gaps in unsuitable habitat.

Based on our scale-dependent model of dispersal evolution, the long-distance dispersal needed to track shifting suitable habitat will likely require fixed dispersal. To our knowledge, however, only one study has examined the role of information use and dispersal in the context of climate change. Ponchon et al. (2015) used a simulation-based approach to show that informed dispersal led to the highest level of population persistence in rapidly changing environments, whereas uninformed dispersal decreased population sizes and ultimately led to local population extinction. But Ponchon et al. (2015) did not explicitly model dispersal distance and did not include fitness costs to information acquisition. As we have previously argued, the costs of information acquisition are not negligible and likely increase with distance. This highlights a need for future research to assess how information costs influence dispersal distance evolution under different environmental scenarios.

Another important – yet under-recognized – prediction from theory is that short- and long-distance dispersal evolve according to different properties of the landscape. Bonte et al. (2010) used spatially explicit, individual-based models to show that the configuration of available habitat selects for different dispersal distances. They showed that highly autocorrelated habitat (i.e., clumped) selects for short-distance dispersal, reflecting an investment in adapting to local conditions rather than crossing gaps of unsuitable habitat, whereas spatially uncorrelated habitat (i.e., scattered) selects for long-distance dispersal. This result reinforces the hypothesis that short- and long-distance dispersal are functionally distinct and evolve separately, whether based on information costs or spatial habitat configuration.

Can we use dispersal traits to predict population persistence?

Faced with the threat of climate change, there is considerable interest in identifying individual or species-level traits that might predict vulnerability (Pöyry et al. 2009, Foden et al. 2013, Pearson et al. 2014). For species that respond to climate change primarily by shifting distributions, we suggest that individual cognitive abilities and information use may be of little relevance. Instead,

traits that enhance individuals' long distance dispersal capability may be more predictive of resilience to habitat change. Specifically, physiological or morphological traits that reduce the energy costs of dispersal are likely to be more important for the long-distance movements required to keep pace with a shifting climate window. For example, a growing body of work linking limb length to dispersal distance—with long-distance dispersers having longer limbs than short-distance dispersers (Phillips et al. 2006, Lowe and McPeck 2012, Arnold et al. 2016)—suggests a biomechanical advantage associated with limb length that may function to reduce the cost of transport over long distances (Pontzer 2007). In contrast, short-distance movements are less likely to require physiological or biomechanical specialization, but may instead require traits that enhance perception or information use, such as the ability to discriminate among habitats in order to maximize individual fitness (Edelaar et al. 2008, Karpeštam et al. 2012).

Clobert et al. (2009) advocate for estimating the contributions of genetic factors (G), environmental factors (E), and their interaction (G x E) to understand the evolution of dispersal behavior (i.e., dispersal reaction norms). Within this framework, perception-based traits underlying dispersal at local scales are likely to have a large environmental contribution and, therefore, represent plastic traits (Kingsolver and Huey 1998, Liefing and Ellers 2008). In contrast, morphological and physiological traits underlying long-distance dispersal are likely to have a larger genetic component, reinforcing the value of exploring the genetic basis of dispersal to predict species persistence under climate change. The feasibility of generating thousands of genome-wide markers has increased the likelihood of detecting genetic variants underlying phenotypic differences, but these methods have not yet been thoroughly applied to understand variation in the dispersal traits of natural populations (Saastamoinen et al. 2017).

Concluding remarks

The failure of most dispersal research to explicitly address spatial scale has resulted in a tendency to view dispersal as an information-based process. But this narrow view struggles to explain long-distance dispersal, where the costs of information gathering are prohibitive. Instead, we need to consider a model of dispersal evolution that also includes fixed dispersal, drawing on early models of dispersal evolution where dispersal was treated as an innate propensity of the individual. We hope that uniting these two bodies of dispersal theory – informed and fixed – will advance dispersal research by providing a more complete understanding of individual variation in dispersal distances. Understanding the ecological and evolutionary drivers of dispersal distances will allow us to address pressing applied questions, such as forecasting species' ability to keep pace with climate change.

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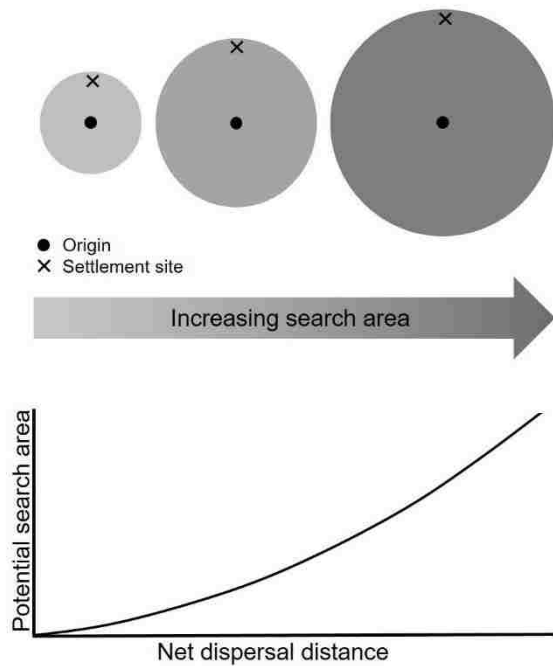


Figure 1. The effect of spatial scale on information-gathering costs. The costs of dispersal increase with distance from an origin (black dot) to a settlement site (black x). The potential search area (gray) also increases with dispersal distance, making it unrealistic for individuals to sample all potential settlement sites during large-scale movements (top panel). When dispersal is not constrained to linear corridors (i.e., stream networks, valleys), the potential search area increases exponentially with dispersal distance (bottom panel).

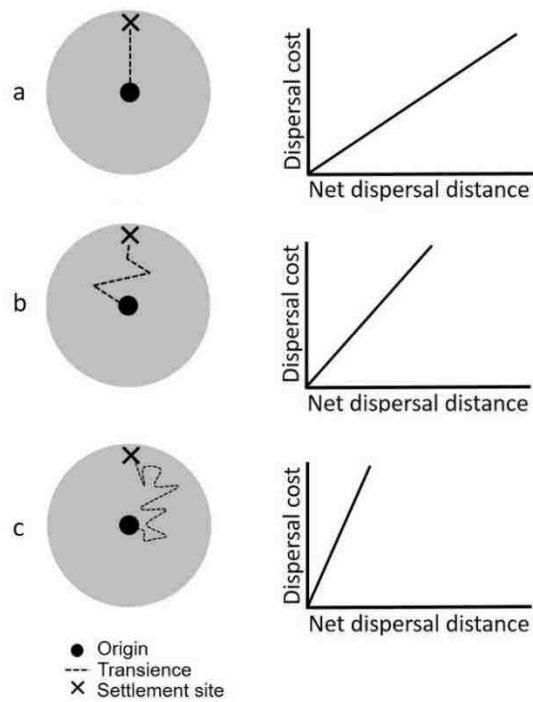


Figure 2. The effect of movement behavior on dispersal costs. Straight-line movement trajectories (a) are more efficient, thereby lowering dispersal costs by decreasing the number of steps needed to achieve a certain distance (Zollner and Lima 1999, Barton et al. 2009). In contrast, non-linear dispersal trajectories (b, c) have the effect of increasing the number of steps needed to achieve a certain distance, thereby increasing the cost of dispersal. We suggest that fixed strategies are more likely to result in straight-line trajectories, whereas informed strategies will result in non-linear trajectories. Thus, fixed dispersal represents a cost-reducing strategy for long-distance dispersal.

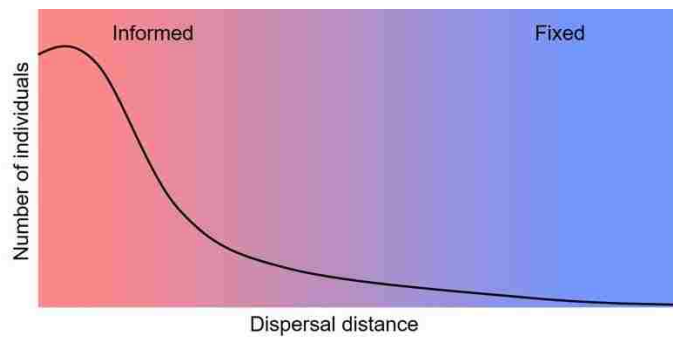


Figure 3. A scale-dependent model of dispersal evolution. The line represents a leptokurtic population dispersal distribution that is representative of most animals, with many individuals dispersing short distances and far fewer dispersing long distances. Dispersal based on information-gathering about potential settlement sites is more likely to explain short-distance movements (red hue) because the costs of habitat sampling become prohibitive at large spatial scales. Fixed dispersal, a dispersal strategy that is not based on assessing local habitat quality, is therefore more likely to explain long-distance movements (blue hue) because the fitness benefits are not contingent on processes with scale-dependent costs.

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