

# Can natural selection maintain long-distance dispersal? Insight from a stream salamander system

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**Abstract** Dispersal distributions are often characterized by many individuals that stay close to their origin and large variation in the distances moved by those that leave. This variation in dispersal distance can strongly influence demographic, ecological, and evolutionary processes. However, a lack of data on the fitness and phenotype of individual dispersers has impeded research on the role of natural selection in maintaining variation in dispersal distance. Six years of spatially explicit capture-mark-recapture data showed that survival increased with dispersal distance in the stream salamander *Gyrinophilus porphyriticus*. To understand the evolutionary implications of this fitness response, we tested whether variation in dispersal distance has a phenotypic basis. We used photographs of marked individuals to measure head, trunk, and leg morphology. We then tested whether dispersal distances over the six-year study period were predicted by these traits. Dispersal distance was significantly related to leg morphology: individuals with relatively long forelimbs and short hindlimbs dispersed the farthest. These results support the hypothesis that positive fitness consequences maintain phenotypes enabling long-distance dispersal. More broadly, they suggest that natural selection can promote variation in dispersal distance and associated phenotypes, offering an alternative to the view that dispersal distance is driven by stochastic or landscape-specific mechanisms.

**Keywords** Dispersal · Fitness · Morphology · Phenotype · Selection · Spatial dynamics

## Introduction

Dispersal is a fundamental process in population biology, ecology, and evolution (Wright 1951; Hastings 1977; Clobert et al. 2001). Broadly defined as permanent movement away from an origin, dispersal in most animals and plants is characterized by many individuals

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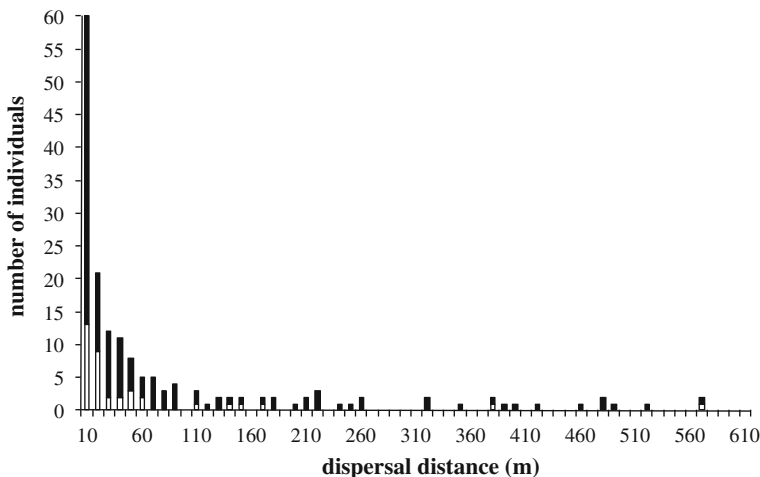
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that stay close to their origin and large variation in the distances moved by those that leave (Dobzhansky and Wright 1943; Mayr 1963; Endler 1977). This produces leptokurtic dispersal distributions, with high peaks around a distance of 0 (the “stayers”), and long tails encompassing the variation in dispersal distance (e.g., Fig. 1; Turchin 1998; Skalski and Gilliam 2003; Petrovskii and Morozov 2009). The high frequency of stayers is generally attributed to the energetic cost and risks of dispersal, but we have much less understanding of what causes the remaining, and often significant, variation in dispersal distances (Johnson and Gaines 1990; Nathan 2005; Ronce 2007).

Darwin saw that variation in dispersal distance played a key role in range expansion (Darwin 1859), and recent theory and models show that long-distance dispersal can contribute disproportionately to population persistence (Tittler et al. 2006; Van Houtan et al. 2007), range shifts (Higgins and Richardson 1999; Simmons and Thomas 2004), and invasions (Suarez et al. 2001; Caswell et al. 2003). However, low detectability and small post-dispersal sample sizes have impeded research on how dispersal distance affects individual fitness and phenotypic evolution (Koenig et al. 1996; Nathan 2005). Consequently, we have been unable to assess the role of natural selection in maintaining long-distance dispersal in wild populations, and instead attribute variation in dispersal distance to extrinsic factors (Carlquist 1981; Levin et al. 2003; Ronce 2007).

We hypothesized that long-distance dispersal is maintained by an increase in the upper limit of settlement site quality with dispersal range. As dispersal range increases, so does the number of potential settlement sites. The diversity of site conditions and the upper limit of site quality should also increase with dispersal range, assuming that conditions in empty sites (i.e., those available for settlement) are randomly distributed and, for the purpose of generality, ignoring structural characteristics of specific landscapes (Pulliam and Danielson 1991; Morris 1992; Koenig 1999). This should cause fitness measures to increase with dispersal distance and maintain phenotypes that allow long-distance dispersal. If fitness measures do not increase with dispersal distance, or if dispersal distance is unrelated to



**Fig. 1** Dispersal distribution of *Gyrinophilus porphyriticus* in Merrill Brook, a first-order stream in northern New Hampshire, USA. Data are from individuals recaptured between 1999 and 2004 that dispersed  $\geq 3$  m from their initial location ( $n = 169$ ). Mark-recapture surveys were conducted each June, July, and August. Labels on the x-axis give the upper bound of each bin. Open portions of the columns are individuals that were photographed for the analysis of morphological predictors of dispersal distance ( $n = 37$ )

phenotype, it would support the alternative hypothesis that variation in dispersal distance results from stochastic or landscape-specific mechanisms (Carlquist 1981; Tufto et al. 1997; Morales 2002).

Ronce (2007) identifies three stages of dispersal: (1) the discrete response of moving away from an origin (“emigration”), (2) the vagrant stage, and (3) settling. From studies of dimorphisms between dispersive and non-dispersive individuals, we know that selection mediates the discrete emigration response (e.g., Sorensen 1978; Harrison 1980; Friedenberg 2003; Duckworth and Badyaev 2007). Studies have also shown that phenotype can predict dispersal distance during the vagrant stage. These include Fraser et al.’s (2001) examination of behavioral syndromes in the Trinidad killifish (*Rivulus hartii*) and Phillips et al.’s (2006) study of leg length in cane toads (*Bufo marinus*). But, to our knowledge, in no system do we have information on both the phenotypic basis and fitness consequences of dispersal distance (i.e., effects on survival or reproduction). This information is crucial if we hope to understand whether natural selection has a role in maintaining the large variation in dispersal distances observed in natural populations (e.g., Fig. 1; Endler 1977; Clobert et al. 2001; Dytham 2009).

In a previous study, survival probability was shown to increase with dispersal distance in the stream salamander *Gyrinophilus porphyriticus* (Lowe 2010). That analysis was based on 6 years of spatially explicit capture-mark-recapture data; dispersal distance was total distance moved during the six-year period, and survival probability was estimated using Cormack-Jolly-Seber models with dispersal distance as an individual covariate (White and Burnham 1999; Pollock 2002). *G. porphyriticus* is long-lived and annual recruitment is low (Lowe 2003), suggesting that survival is the major determinant of lifetime fitness (Roff 2002; Clark and Martin 2007).

Here we build on these results, taking advantage of the same data set to test the hypothesis that positive effects of dispersal distance on fitness maintain phenotypes enabling long-distance dispersal. We used digital photographs of *G. porphyriticus* individuals marked in the first year of the study to measure morphological traits hypothesized to affect dispersal ability. We then used multiple regression analysis to test whether dispersal distances over the next 6 years were predicted by these morphological traits. Our analysis shows that dispersal distance has a phenotypic basis in *G. porphyriticus*: individuals with relatively long forelimbs and short hindlimbs dispersed the farthest. In combination with our previous findings, these results link individual fitness and phenotype to dispersal distance, suggesting that selection can maintain long-distance dispersal in natural populations.

## Materials and methods

### Study species and site

*Gyrinophilus porphyriticus* belongs to the family Plethodontidae, the lungless salamanders. This species is found in small, cool, well-oxygenated streams along the Appalachian uplift, from central Alabama to southern Quebec (Petranka 1998). The larval period is estimated to be 3–5 years (Bruce 1980). During the day, larvae and adults are found in interstitial spaces among the larger substrate particles of the streambed. In the northern Appalachians, larval size range is 26–80 mm snout-vent length (SVL), adults can reach 120 mm SVL, and both stages feed primarily on invertebrates (Greene et al. 2008).

The study site was Merrill Brook, a fishless, first-order stream in Dartmouth College's Second College Grant, located in northern New Hampshire, USA. Merrill Brook flows into the fourth-order Dead Diamond River; a wetland at the confluence serves as a barrier to brook trout (*Salvelinus fontinalis*) that might enter Merrill Brook from the larger river. Sampling occurred throughout a 1-km long section of Merrill Brook that started at the confluence with the outflow wetland and ended 1,000 m upstream of that point, encompassing the perennial portion of the stream.

Undisturbed headwater streams in New Hampshire have low conductivity (12.0–15.0  $\mu\text{S cm}^{-1}$ ), slight acidity (pH of 5.0–6.0), high dissolved oxygen content (80–90% saturation), and moderate mid-day temperatures in the summer (13.0–17.0°C) (Likens and Bormann 1995). Sampling throughout Merrill Brook matched these data. Other salamanders encountered in Merrill Brook were *Eurycea bislineata* and *Desmognathus fuscus* (both Plethodontidae).

### Survey methods

Surveys of Merrill Brook were conducted in June, July and August of 1999–2004, resulting in a total of 18 surveys (6 years  $\times$  3 surveys/year). A cover-controlled, active search sampling method was used (Heyer et al. 1994). Moving upstream, the surveyor turned cobble-sized rocks (64–256 mm in diameter) within the channel and along the edge; surveys continued until 1,200 rocks had been turned. The even distribution of cobble allowed for a constant effort of just over one rock per meter of stream length, so surveys provided spatially explicit information on individual salamanders encountered throughout the stream. An aquarium dip-net was used to capture salamanders, including those flushed by the current.

All unmarked *G. porphyriticus* larvae and adults encountered were individually marked by subcutaneous injection of fluorescent elastomer (Northwest Marine Technologies, Shaw Island, Washington, USA). Retention of these marks is high throughout the life of the animals (Grant 2008). The longitudinal position (distance from the confluence, m) and length (SVL, mm) of all individuals encountered were recorded. Salamanders were distributed randomly along Merrill Brook (Lowe 2009). All surveys were conducted by the lead author to eliminate among-observer sampling variation.

### Quantifying dispersal distance

This study system has two properties that are critical to overcoming detection-related obstacles to research on dispersal distance (Koenig et al. 1996; Nathan 2001). First, the relative mobility of *G. porphyriticus* is low, so surveys can detect dispersal events that are long-distance and rare relative to the majority of movements (Fig. 1; Lowe 2003, 2009). Second, *G. porphyriticus* is constrained to linear stream corridors; larvae are restricted to the stream channel, and although adults can move short distances into riparian forests at night (<3 m from the stream, on average), they return to the stream during the day (Greene et al. 2008). The probability of detecting marked animals declines with movement distance in two-dimensional landscapes (Koenig et al. 1996), but when movement is along linear habitats like stream corridors and sampling is consistent throughout the available habitat (e.g., from bank to bank), detection probability is not affected by movement distance (Pollock et al. 2002).

We used data from recaptured animals to quantify individual variation in dispersal distance. Dispersal distance was the total distance moved (m along the stream) over the six-year study period. In Merrill Brook and 15 streams where shorter mark-recapture

studies were conducted (1–2 years), there were no differences in movement distributions related to size (SVL), life history stage (larva v. adult), or sex (Lowe 2003; Lowe et al. 2006). Further, there was no within-year variation in movement distributions associated with stream flow (Lowe 2003; Lowe et al. 2006). These findings allowed us to pool movement data across sizes, life-history stages, sexes, and time. Relative to the major ecological and morphological differences between life history stages in other amphibians, larvae and adults of *G. porphyriticus* are very similar (Petranka 1998), which may explain the similarity of movement patterns in the two stages (Lowe 2003).

Of the animals recaptured more than once over the 6 years ( $n = 109$ ), only one moved from a capture location and subsequently returned to that location (Lowe 2009). This suggests that the majority of movements were discrete, unidirectional dispersal events, not migratory movements (Semlitsch 2008). In these animals, number of captures was proportional to time. However, there was no relationship between number of captures and dispersal distance (Lowe 2010), suggesting that movement is not Brownian. Earlier analyses suggested that individual home ranges were approximately  $3 \text{ m}^2$  (i.e., 3 m in stream length, given that the mean width of Merrill Brook is approximately 1 m; Lowe 2003). Therefore, salamanders that dispersed  $<3 \text{ m}$  from their initial locations were not included in the analysis of morphological predictors of dispersal distance, under the assumption that individuals could have been anywhere in their home range when initially marked. However, these animals were used in analyses of the discrete emigration response, and ontogenetic and sexual effects on morphology and dispersal (described below).

Among animals that moved  $\geq 3 \text{ m}$  from their initial locations and were recaptured more than once, total distance moved over the six-year study period (our index of dispersal distance) was strongly correlated with net movement from the initial capture location (an alternative index of dispersal distance; Turchin 1998) ( $r = 0.55$ ,  $n = 31$ ,  $P < 0.01$ ), further confirming that most movements were unidirectional dispersal events. In the full data set, there was no relationship between the number of times an individual was recaptured and dispersal distance ( $r_s = 0.11$ ,  $n = 221$ ,  $P > 0.10$ ; Lowe 2010), which justified combining movement data from individuals recaptured once with data from individuals recaptured multiple times.

### Morphological measurements

In 1999, the first year of the long-term capture-mark-recapture study, photographs of all animals were taken at first capture, when animals were marked. Animals were placed on a level, lighted stage. The camera was held 20 cm above the animal, which allowed us to capture the entire dorsal surface of the animal in the photograph, along with a ruler. The ruler was a length reference in each photograph for converting morphological measurements to mm. These photographs were used to collect measurements of the head, trunk, and legs—three body elements predicted to affect dispersal ability, either by affecting locomotory performance in the stream channel or in adjacent terrestrial habitat.

We expected undulatory swimming performance and overall hydrodynamics to be influenced by the shape of the head and trunk (Gray 1968; D'Aout and Aerts 1999; Triantafyllou et al. 2000). We defined the trunk as the area from the posterior insertion point of the forelimbs to the anterior insertion point of the hind limbs (Brandon 1966; Carroll et al. 1999). Head and trunk shape were quantified with measurements of maximum length and width from the dorsal view (e.g., Adams and Beachy 2001). Tail shape is also likely to influence swimming performance, but most individuals were missing the posterior end of the tail, which may have been lost in interactions with predators (Brodie et al. 1979). Therefore, we were unable to collect consistent measurements of tail morphology.

We expected leg length to be a key determinant of walking performance, both on the stream bed and in the terrestrial environment (Bennett et al. 1989; Azizi and Horton 2004). To quantify leg length, we measured the lengths of the humerus and femur, as represented by the distance from the posterior insertion point of the limb to the first joint (Gallant and Teather 2001; St-Amour et al. 2010). Limb elongation is common in terrestrial salamanders that rely primarily on walking for locomotion (Duellman and Trueb 1986; Petranka 1998).

### Morphological analyses

To quantify morphological variation in the head, trunk, and legs, we generated size-adjusted shape variables using principal component analysis (PCA). Specifically, we extracted three principal components from each of three covariance matrices representing the three body elements: head, trunk, and legs. Each covariance matrix was comprised of log-transformed SVL and the two measurements specific to that body element (head [max. length and width], trunk [max. length and width], and legs [humerus length and femur length]). The first principal components (PC1) were expected to represent generalized size because SVL was positively correlated with all morphological measurements. The second and third principal components (PC2 and PC3) were expected to be size-adjusted morphological characters (Bookstein 1989; Jungers et al. 1995; Adams and Beachy 2001).

We first tested whether morphology predicted the discrete emigration response (i.e., stay v. leave; Ronce 2007). For this analysis, we categorized all salamanders for which we had photographs as either “non-dispersers” (dispersal distance <3 m) or “dispersers” (dispersal distance  $\geq 3$  m). We then used logistic regression to test whether this categorical response variable was related to any of the size-adjusted variables describing head, trunk, and leg morphology (PC2 and PC3). For the main analysis, we tested whether morphology predicted dispersal distance in “dispersers”. We used stepwise multiple regression analysis, with  $P$  to enter and remove variables of 0.10 (Kleinbaum et al. 1998), to identify the most predictive model of dispersal distance (log-transformed) from the set of size-adjusted variables describing head, trunk, and leg morphology (PC2 and PC3). Because predictor variables were selected based on a priori hypotheses of how morphology affects dispersal ability, and because there were few predictor variables in this analysis, family-wise error rate was assumed to be low (Finos et al. 2010).

Both analyses correct for the expected positive correlation between all morphological measures based on variation in overall body size, thus ensuring that morphological predictors were not confounded with variation in body size. Because the morphological predictors were size-adjusted principal components, we did not expect multicollinearity to be a problem in these analyses (Graham 2003). To confirm that there was no ontogenetic effect on emigration or dispersal distance, we tested for relationships between body size (SVL, log-transformed) and these two response variables using logistic regression and Pearson product-moment correlation analysis, respectively.

To further confirm that our analyses were not confounded by ontogenetic effects on dispersal distance or morphology, we combined “non-dispersers” and “dispersers” and used analysis of variance (ANOVA) to test for differences between larvae and adults in dispersal distance and size-adjusted morphological variables. Additionally, the sex of 57 recaptured individuals was identified in the field using the characteristics described in Noble (1954). Of these known-sex animals, 35 were also photographed ( $n = 15$  males, 20 females), which allowed us to test for differences between the sexes in dispersal distance and size-adjusted morphological variables.

## Results

### Survey results

Over the six-year study period, 972 *G. porphyriticus* individuals were marked and 221 individuals were recaptured. Of the recaptured individuals, 84 were first captured as larvae and 137 were first captured as adults. There were 169 individuals that dispersed  $\geq 3$  m from their initial location (Fig. 1), with a maximum dispersal distance of 565 m.

Of the individuals photographed in 1999, 57 were recaptured in the next 6 years. Dispersal distances of 20 of these individuals were  $< 3$  m, leaving 37 individuals for the analysis of morphological predictors of dispersal distance. Within this subset, dispersal distances were distributed throughout the range observed in the full data set (Fig. 1). Of these 37 animals, 15 were initially captured as larvae and the rest were initially captured as adults. Snout-vent lengths were 30–102 mm.

### Principal component analyses

Head length, head width, and SVL were positively correlated ( $r = 0.92$ – $0.97$ ), and head PC1 was positively weighted by all three variables (Table 1). Head PC2 was negatively weighted by head length and positively weighted by head width. Head PC3 was positively weighted by head length and negatively weighted by head width.

**Table 1** Percent of the total variance explained and factor loadings (eigenvectors) for principal components derived from morphological measurements of the head, trunk, and legs of *G. porphyriticus* individuals recaptured during a 6-year mark-recapture study

Body element	Variance explained (%)	Eigenvectors		
		Snout-vent length	Head length	Head width
<b>Head</b>				
PC1	96	0.54	0.59	0.60
PC2	3	0.50	−0.80	0.34
PC3	1	0.68	0.11	−0.72
<b>Trunk</b>				
		Snout-vent length	Trunk length	Trunk width
PC1	97	0.51	0.66	0.55
PC2	2	0.29	−0.74	0.61
PC3	1	0.81	−0.15	−0.57
<b>Legs</b>				
		Snout-vent length	Humerus length	Femur length
PC1	80	0.47	0.74	0.48
PC2	13	0.09	−0.58	0.80
PC3	7	0.88	−0.34	−0.34

All measurements were in mm, converted from photographs taken at initial capture

Trunk length, trunk width, and SVL were positively correlated ( $r = 0.95\text{--}0.96$ ), and trunk PC1 was positively weighted by all three variables (Table 1). Trunk PC2 was negatively weighted by trunk length and positively weighted by trunk width. Trunk PC3 was negatively weighted by trunk length and width.

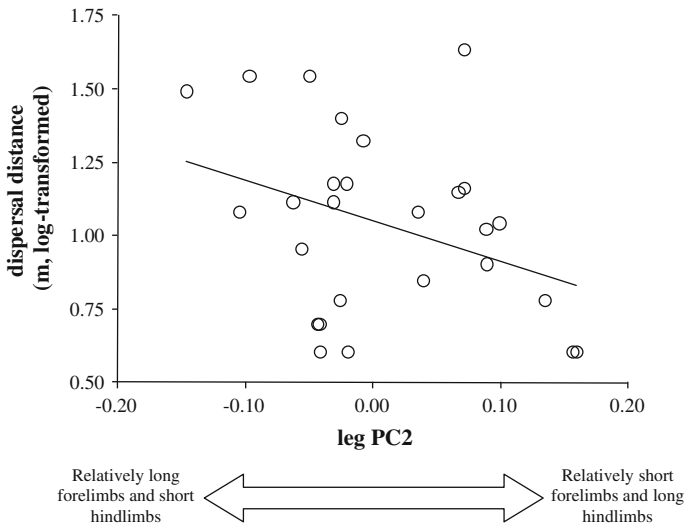
Humerus length, femur length, and SVL were positively correlated ( $r = 0.64\text{--}0.74$ ), and leg PC1 was positively weighted by all three variables (Table 1). Leg PC2 was negatively weighted by humerus length and positively weighted by femur length. Leg PC3 was negatively weighted by humerus length and femur length.

### Predictors of emigration

For the analysis of the discrete emigration response, 20 individuals were categorized as “non-dispersers” based on dispersal distances  $<3$  m and the remaining 37 individuals were categorized as “dispersers”. Emigration was unrelated to salamander morphology, as represented by PC2 and PC3 of head, trunk, and leg measurements ( $\chi^2 < 0.97$ ,  $n = 57$ ,  $P > 0.32$ ). Emigration was also unrelated to body size, whether represented by SVL or by PC1 of head, trunk, and leg measurements ( $\chi^2 < 0.26$ ,  $n = 57$ ,  $P > 0.61$ ).

### Predictors of dispersal distance

Stepwise multiple regression analysis resulted in a model of *G. porphyriticus* dispersal distance that included only leg PC2 as a significant predictor ( $F_{1,35} = 5.36$ ,  $r^2 = 0.133$ ,  $P = 0.026$ ; Table 1). Dispersal distance was negatively related to leg PC2, indicating that individuals with relatively long forelimbs and short hindlimbs dispersed the farthest (Fig. 2). Of the six principal components entered as candidate predictors, only trunk PC3



**Fig. 2** The relationship between size-adjusted leg morphology, represented by the second principal component of snout-vent length, humerus length, and femur length (leg PC2), and dispersal distance of 37 *Gyrinophilus porphyriticus* individuals in Merrill Brook. Leg PC2 was negatively weighted by humerus length and positively weighted by femur length (Table 1). Therefore, this relationship indicates that individuals with relatively long forelimbs and short hindlimbs dispersed the farthest



and head PC3 were significantly correlated ( $r = 0.41$ ,  $n = 37$ ,  $P = 0.01$ ). Significance levels for all other pairwise correlations were  $>0.10$ .

There was no relationship between body size (SVL) and dispersal distance ( $r = -0.05$ ,  $n = 37$ ,  $P = 0.75$ ). This was also true when we used PC1 of head, trunk, and leg measurements to represent body size ( $r = -0.03$  to  $-0.04$ ,  $n = 37$ ,  $P = 0.77$ – $0.86$ ), and is consistent with previous analyses showing no ontogenetic variation in dispersal (Lowe 2003).

When “non-dispersers” and “dispersers” were combined, ANOVAs showed no differences between larvae and adults in dispersal distance and size-adjusted morphological variables ( $F_{1,55} < 1.66$ ,  $P > 0.20$ ), and no differences between males and females in these traits ( $F_{1,33} < 2.88$ ,  $P > 0.09$ ). The only exception was trunk PC3, which was greater in adults than larvae ( $F_{1,55} = 7.26$ ,  $P = 0.01$ ), but unrelated to emigration response and dispersal distance. Results were the same when we restricted these analyses to animals that moved  $>3$  m from their initial locations (i.e., “dispersers”).

## Discussion

This study provides novel insight on the phenotypic and evolutionary basis of long-distance dispersal. Leg morphology predicted total dispersal distance over a six-year period in *G. porphyriticus*: the greater the length of the forelimbs relative to the hindlimbs, the greater the dispersal distance (Fig. 2). During the same period, survival probability—likely the major determinant of lifetime fitness in *G. porphyriticus*—increased with dispersal distance (Lowe 2010). In an a posteriori analysis, we tested for an effect of leg morphology on survival of the photographed animals using estimates of monthly survival probability from the capture-mark-recapture model in Lowe (2010). Individual survival probability decreased with leg PC2 ( $F_{1,35} = 4.81$ ,  $r^2 = 0.12$ ,  $P = 0.03$ ), further supporting the interconnection of leg morphology, dispersal distance, and fitness. In combination, these results support the hypothesis that positive fitness effects maintain phenotypes enabling long-distance dispersal in *G. porphyriticus*.

Phenotypic dimorphisms can produce leptokurtic dispersal distributions (e.g., Fig. 1), where the high peaks around a distance of 0 are comprised of “stayers” and the large tails result from a subpopulation of “movers” (Skalski and Gilliam 2003; Petrovskii and Morozov 2009). Similarly, populations in which individuals shift between two, discrete behavioral modes (e.g., “encamped” v. “exploratory”) will exhibit cumulative dispersal distributions with high peaks of individuals observed during “encamped” periods, and tails comprised of individuals observed during “exploratory” periods (Morales et al. 2004; Fryxell et al. 2008). However, these models of phenotypic variation do not account for the continuous variation in dispersal distances observed in natural populations, which is generally attributed to extrinsic, system-specific factors acting on movers (e.g., wind, water, habitat boundaries; Carlquist 1981; Morales 2002; Nathan 2006).

Extrinsic factors undoubtedly explain part of the variation in dispersal distances in most populations. Our results suggest that another part of that variation may be explained by continuous, phenotypic variation and underlying fitness relationships. In the Introduction we describe a hypothesis for positive effects of dispersal distance on individual fitness that may underlie these intrinsic drivers—an increase in the upper limit of settlement site quality with dispersal distance. The generality of this hypothesis comes from the assumption that conditions determining the quality of empty sites are randomly distributed, but the conditions determining site quality are expected to be species-specific. For *G. porphyriticus* in

Merrill Brook, where predatory fish are absent, these conditions may include availability of flow refugia (Baumgartner et al. 1999; Lowe et al. 2004), abundance of invertebrate prey (Burton 1976; Greene et al. 2008), or abundance of terrestrial predators (Brodie et al. 1979). Based on growth rates of *G. porphyriticus* individuals, quality of occupied sites appears to be randomly distributed in Merrill Brook (Lowe 2010), but we cannot test this assumption for empty sites without knowing the specific determinants of site quality.

It is possible that dispersal distance, fitness measures, and phenotype in *G. porphyriticus* are not linked by the proposed, adaptive mechanism. For example, if individuals with relatively long hindlimbs are more likely to leave the stream through terrestrial habitat (e.g., Grant et al. 2010), we might observe the same relationships between leg PC2 and dispersal distance (Fig. 2), and between leg PC2 and Cormack-Jolly-Seber estimates of survival, which confound mortality with permanent emigration (White and Burnham 1999; Lowe 2010). Extensive terrestrial dispersal would be surprising in light of what we know about the natural history, morphology, and behavior of *G. porphyriticus* (Brandon 1966; Petranka 1998; Greene et al. 2008), but is possible. Also, Merrill Brook is close to the northern edge of the geographic range of *G. porphyriticus*, raising the possibility that dispersal-related phenotypes are maintained in part by spatial sorting—where traits enhancing dispersal rate accumulate at expanding range edges, and assortative mating between fast-dispersing individuals at the range edge results in an evolutionary increase in dispersal rates in successive generation (Shine et al. 2011).

Within Merrill Brook, morphology was unrelated to emigration, although leg morphology is important in determining the fitness consequences of that emigration response (Fig. 2; Lowe 2010). Unlike species with highly-specialized dispersal morphotypes (Sorensen 1978; Harrison 1980), leg morphology in *G. porphyriticus* also influences non-dispersal activities, such as foraging, refuge use, and escape behavior. This may reduce the likelihood of strong morphological divergence between dispersers and non-dispersers (Endler 1986; Futuyma 2005). More generally, these results support a model of dispersal with at least two, discrete levels of control (Ronce 2007): (1) the regulation of emigration, and (2) the regulation of dispersal distance once emigration has occurred. Greater effort to differentiate these stages, both conceptually and empirically, will help in resolving feedbacks between proximal drivers of dispersal and ultimate effects on demographic and evolutionary processes (Clobert et al. 2001; Ronce 2007; Lowe and Allendorf 2010). It is also important to acknowledge that individuals in the “non-disperser” category may have dispersed after the six-year sampling period, increasing morphological variation in that category. Especially in long-lived species like *G. porphyriticus*, the effect of sampling duration on discrete response variables can be significant (Zar 1984).

The combination of long forelimbs and short hindlimbs (Fig. 2) may be indicative of a locomotory tradeoff, where improvements in walking performance must entail minimal cost in swimming performance (Rose and Lauder 1996; Orzack and Sober 2001). Adults of *G. porphyriticus* are highly aquatic and retain many morphological traits of larvae that increase swimming performance, such as laterally-compressed tails, flattened heads, and elongated bodies (Brandon 1966; Azizi 2005). In terrestrial salamanders, elongated limbs support the body above the ground during walking (Duellman and Trueb 1986; Petranka 1998), but long hindlimbs increase drag in the mid-body during undulatory swimming (Gray 1968; Gillis 1996). Elongation of only the forelimbs may allow individuals to walk on the stream bed and on land with greater efficiency, but without significantly compromising swimming performance and hydrodynamics.

Dispersal can be costly in terms of energetic investment and mortality risk (Johnson and Gaines 1990; Morris 1992; Stamps et al. 2005; Taylor and Buckling 2010), yet data on how

these costs change with distance are extremely rare (but see Johnson et al. 2009). Resolving this cost-distance relationship is a key to understanding why long-distance dispersal remains rare in our study population (Fig. 1; Lowe 2010). If costs increase with distance to offset post-dispersal benefits, then the frequency of long-distance dispersal and associated phenotypes should decrease (Rousset and Gandon 2002). If costs are small relative to post-dispersal benefits, or unrelated to distance, then the frequency of long-distance dispersers should increase. Costs are not high enough to eliminate long-distance dispersal and associated phenotypes in our study population. However, long-distance dispersal is rare, as in other species (Darwin 1859; Nathan 2001), suggesting that selection is frequency-dependent (Kimura 1955; Endler 1986; Doebeli and Ispolatov 2010). Additionally, variation in *G. porphyriticus* leg morphology was greater than in head or trunk morphology (Table 1). Maintenance of this non-ontogenetic morphological variation is consistent with frequency-dependent selection (Lewontin 1974; Futuyma 2005).

To fully understand how natural selection maintains long-distance dispersal in *G. porphyriticus*, we will need to know the plasticity and heritability of leg morphology (Endler 1986). This will require further investigation with common-garden experiments (Bonte et al. 2008), sibship assignment (Bernatchez and Duchesne 2000), and parent-offspring heritability analyses (Freeman and Herron 2001). Our capture-mark-recapture data do, however, provide indirect evidence that leg morphology is not environmentally dependent. Size-corrected mass is an accurate index of body condition and local habitat quality in *G. porphyriticus* (Green 2001; Lowe 2003, 2009). In a posteriori analysis, we found no relationship between initial size-corrected mass and leg PC2 of photographed animals ( $r = -0.06$ ,  $n = 37$ ,  $P = 0.74$ ). Dispersal distance and related fitness measures were also unrelated to initial size-corrected mass (Lowe 2010), reducing the likelihood that dispersal distance and associated phenotypes are determined by the pre-dispersal environment (Ims and Hjermann 2001; Benard and McCauley 2008; Clobert et al. 2009).

Along with the positive fitness consequences shown previously (Lowe 2010), evidence that dispersal distance has a phenotypic basis in *G. porphyriticus* suggests that evolutionary mechanisms do play a role in maintaining long-distance dispersal (Fig. 1). Specifically, our results show that there are predictable fitness benefits of long-distance dispersal, and that individuals have specific morphological traits that allow for long-distance dispersal. Although further analyses are needed, these results support the hypothesis that natural selection for phenotypes enabling long-distance dispersal may, in part, explain the prevalence of “fat-tailed” dispersal distributions in diverse species (Endler 1977; Johnson and Gaines 1990; Skalski and Gilliam 2003). This offers an alternative to the view that long-distance dispersal is driven exclusively by stochastic or landscape-specific mechanisms (Carlquist 1981; Tufto et al. 1997; Morales 2002), and reinforces the importance of empirical studies of the causes and consequences of dispersal in natural populations (Nathan 2001; Ronce 2007; Lowe and Allendorf 2010).

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