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Matching habitat choice and plasticity contribute to phenotype–environment covariation in a stream salamander

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Abstract. Populations optimize the match of phenotype to environment by localized natural selection, adaptive phenotypic plasticity, and habitat choice. Habitat choice may also be achieved by several mechanisms, including matching habitat choice, where individuals distribute themselves based on self-assessment of the phenotype–environment match. Matching habitat choice is a relatively untested concept, but one that could advance our understanding of the interplay of movement ecology and intraspecific phenotypic variation. Morphology of the salamander *Gyrinophilus porphyriticus* differs in riffles and pools, the dominant habitats in headwater streams where this species occurs. Specifically, individuals found in riffles have shorter limbs than those found in pools. Here, we used 4 yr of spatially explicit capture–mark–recapture data from three streams to test the contributions of phenotypic plasticity and matching habitat choice to this phenotype–environment covariation. We quantified morphological variation in *G. porphyriticus* with size-corrected principal component (PC) scores and assessed phenotype–environment match based on the difference between habitats in these PC scores. We found that both phenotypic plasticity and matching habitat choice contribute to phenotype–environment covariation in *G. porphyriticus*. The phenotypes of individuals that switched habitats (i.e., riffle→pool, pool→riffle) changed to become better matched to the recipient habitat, indicating a plastic response to local habitat conditions. Consistent with matching habitat choice, individuals were also more likely to switch habitats if their initial phenotype was a better match to the alternative habitat, independent of subsequent changes in morphology due to plasticity. Realized performance, survival adjusted for the likelihood of remaining in each habitat, was higher in individuals with phenotypes matched to each habitat than in those with mismatched phenotypes, but performance was generally lower in riffles than pools, suggesting that other factors influence the use of riffles. Our results underscore the value of considering how matching habitat choice interacts with other mechanisms that allow organisms to maximize performance when faced with environmental heterogeneity. More broadly, our study shows that it is important to account for movement in any study of the causes or consequences of intraspecific trait variation, a challenge that may require novel research approaches and experimental designs.

Key words: amphibian; capture–mark–recapture; ecomorphology; matching habitat choice; movement ecology; phenotypic plasticity; survival.

Introduction

Intraspecific phenotypic variation, whether occurring within or across generations, allows populations to respond to environmental variation (Endler 1986, Agrawal 2001, Edelaar et al. 2017). Spatial patterns of phenotype–environment covariation, in particular, may result from several different mechanisms that optimize individual and population performance (Moran 1992, Morris 2003, West-Eberhard 2003). Edelaar et al. (2008) identify three primary mechanisms that allow this phenotype–environment matching to occur: localized natural selection, adaptive phenotypic plasticity, and habitat choice. Habitat choice itself may be achieved by several mechanisms (Akcali and Porter 2017), including matching habitat choice (Ravigne et al. 2004, Edelaar et al. 2008), where individuals distribute themselves based on self-assessment of functional performance, independent of previous experience (i.e., imprinting; Davis 2008) or genetic background (Jaenike and Holt 1991).

Matching habitat choice is an exciting concept that could expand our understanding of the interplay of movement and phenotypic variation, and the ecological implications of that interplay. Matching habitat choice is a particular form of phenotype-dependent movement that leads to the spatial aggregation of like phenotypes,

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thus offering insight on the fundamental causes of movement and dispersal (Edelaar and Bolnick 2012, Lowe and McPeek 2014). Matching habitat choice may also have important ecological consequences through effects of locally dominant phenotypes on intraspecific interactions (Svanback and Bolnick 2007), species coexistence (Hausch et al. 2018), and food web structure (Gibert and DeLong 2017). It is likely that matching habitat choice has contributed to patterns of phenotype–environment covariation, and associated ecological effects. previously ascribed to localized selection or plasticity, but has gone undocumented due to the novelty of the concept and general lack of movement analysis in study designs. There are, in fact, few empirical studies of matching habitat choice (Karpestam et al. 2012) and none testing how matching habitat choice interacts with phenotypic plasticity or localized natural selection to affect phenotype–environment covariation (Sultan and Spencer 2002, Scheiner et al. 2012, Edelaar et al. 2017).

Streams are heterogeneous environments by many biotic and abiotic criteria (Vannote et al. 1980, Downes et al. 1995, McGuire et al. 2014), but perhaps most obviously and importantly in channel gradient and water flow conditions (Montgomery and Buffington 1997). Gradient and flow are commonly used to delineate stream habitats (e.g., pools, runs, riffles, cascades; Frissell et al. 1986, Gordon et al. 1992, Hawkins et al. 1993), and these conditions are known to affect many biological processes (Bisson et al. 1988, Iwata 2007, Travis et al. 2014). The spatial dimensions of flow-delineated habitats are highly variable, but generally scale with the size of streams (e.g., as a function of discharge, bank-full width, stream order) such that habitats may differ between meters of channel length in headwaters, and at larger scales (10–100 m) in mainstem streams and rivers (Frissell et al. 1986). This environmental heterogeneity and associated patterns of phenotypic variation in stream organisms (Langerhans 2008, Senay et al. 2015, Jacobson et al. 2017) suggest that streams may be useful study systems for testing mechanisms that produce phenotype–environment covariation.

Here our goal was to assess mechanisms contributing to phenotype–environment covariation in a stream salamander system. Morphology of our study species, *Gyrinophilus porphyriticus*, differs between riffles and pools, the two dominant habitats in the headwater study streams (Lowe et al. 2018). Specifically, unbiased principal component analysis of head, trunk, and leg morphology showed that larvae and post-metamorphic adults have shorter limbs in riffles and longer limbs in pools. Riffles are defined by high velocity, turbulent flows and high channel gradients; pools are defined by low velocity, circulating flows and low channel gradients (modified from Montgomery and Buffington 1997). Shorter limbs likely reduce drag in riffles (Delvolve et al. 1997, Bennett et al. 2001), whereas longer limbs may facilitate underwater walking in pools (Ashley-Ross and Bechtel 2004, Pontzer 2007). An experimental analysis of swimming performance supported this interpretation of the drag costs of longer limbs (B. R. Addis and W. H. Lowe, *unpublished data*). However, until now we have not examined the mechanism(s) producing phenotype–environment covariation, or the ultimate effects of morphological variation on salamander performance in the two habitats.

We hypothesized that adaptive phenotypic plasticity or matching habitat choice produce phenotype–environment covariation in our study system. From capture–mark–recapture studies lasting up to 6 yr, we know that many *G. porphyriticus* individuals stay at their initial capture locations, but movements of more than 450 m along stream channels also occur (Lowe 2003). Therefore, based on the fine spatial scale of habitat variation in these headwater systems (<10 m), both phenotypic plasticity and matching habitat choice are potential mechanisms underlying phenotype–environment covariation. We had no a priori reason to expect one mechanism to be more likely than the other because both entail tradeoffs likely to apply in dynamic stream environments (Edelaar et al. 2017). For example, matching habitat choice allows for rapid and direct matching of phenotype to environment via movement, but these movements may be costly (Lima 2002, Shepard et al. 2013). Likewise, phenotypic plasticity does not require movement, but it does require time for morphological changes to occur, and for individuals to experience the benefits of those changes (Padilla and Adolph 1996, Miner et al. 2005). We also had no reason to expect that phenotypic plasticity and matching habitat choice would not to act together, other than a lack of evidence from other systems. We did not expect localized natural selection or genetically based preferences to contribute to phenotype–environment covariation because of high gene flow between habitats, but we recognize that this does not necessarily preclude genetic effects (Bolnick et al. 2009, Richardson et al. 2014, Fitzpatrick et al. 2015).

With 4 yr of spatially explicit capture–mark–recapture data from three study streams, we first characterized phenotypic variation within and between habitats in greater detail than in previous analyses (i.e., Lowe et al. 2018), providing loadings for all morphological variables used in principal component analysis of phenotypic variation, and frequency distributions of morphotypes in the two habitats. We then assessed the contributions of phenotypic plasticity and matching habitat choice by taking advantage of individuals that moved from one habitat to the other (i.e., riffle→pool, pool→riffle) or remained in the same habitat during the study (i.e., riffle→riffle, pool→pool). Because we quantified phenotypes at each capture event, we were able to assess phenotypic plasticity by testing whether the phenotypes of individuals that switched habitats changed to match the mean phenotype of the alternative, recipient habitat. To assess matching habitat choice, we tested whether initial phenotype predicted the probability of individuals subsequently settling in riffles or pools. This analysis

was based only on phenotypes at the first capture event, so was unbiased by any effects of phenotypic plasticity, allowing us to distinguish between the two possible mechanisms underlying phenotype–environment covariation. The capture–mark–recapture models used to test for matching habitat choice also estimate survival probabilities, which, in combination with movement probabilities, provide insight on the realized performance of phenotype–environment combinations (i.e., based on survival and likelihood of remaining in the focal habitat; Pollock 2002, Lebreton et al. 2009).

Methods

Study species and site

Gyrinophilus porphyriticus belongs to the family Plethodontidae, the lungless salamanders, and is found in small, cool, well-oxygenated streams along the Appalachian uplift in the eastern United States (Petranka 1998). Larvae are exclusively aquatic; adults are mainly aquatic but can forage terrestrially at night (Greene et al. 2008). During the day, larvae and adults are found in interstitial spaces among the larger substrate particles of the streambed. In the northern Appalachians, larvae range in size from 26 to 80 mm snout-to-vent length (SVL) and adults can reach 120 mm SVL (Lowe 2003). The larval period lasts 3–5 yr (Bruce 1980) and adults can live to be 14 yr (W. H. Lowe, *unpublished data*). Sexing *G. porphyriticus* in the field is difficult, but in an earlier study (Lowe and McPeek 2012) we sexed 35 individuals (15 males, 20 females) in a population in northern New Hampshire and found no differences in the morphology or movement patterns of females and males. Past studies have also shown than movements by *G. porphyriticus* larvae and adults are upstream biased (e.g., Lowe 2003), so we did not expect passive downstream drift to be the primary mechanism of movement between habitats.

This research took place in three hydrologically independent first-order streams in the Hubbard Brook Experimental Forest (HBEF), central New Hampshire, USA (43°56′ N, 71°45′ W): Bear Brook, Paradise Brook, and Zigzag Brook. All three streams flow into the mainstem of Hubbard Brook, a tributary of the Pemigewasset River. Typical of headwater streams in New Hampshire, the study streams have low conductivity (12.0–15.0 μS), 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). The dominant tree species in forests surrounding these streams were *Acer saccharum*, *Fagus grandifolia*, *Betula alleghaniensis*, *Picea rubens*, *Abies balsamea*, *B. papyrifera*.

Field surveys

Capture–mark–recapture (CMR) surveys were conducted mid-June through mid-September of 2012–2015. We surveyed 500 m long reaches in each stream, which began 750–1,000 m above the confluence with Hubbard Brook. Predatory brook trout (*Salvelinus fontinalis*) occur in the downstream sections of the study streams, but not in the upstream study reaches (Lowe et al. 2018). Each stream was surveyed nine times in each field season, for a total of 36 surveys per stream over the 4-yr study period. We conducted three surveys of each stream during three two-week periods distributed evenly throughout the field season. In each survey, a constant search effort was maintained by turning one cover object per meter of stream length. Salamanders were individually marked with visible implant elastomer (Northwest Marine Technologies, Washington, USA; Grant 2008), then returned to the same location where they were found (i.e., cover object and meter of stream).

All *G. porphyriticus* individuals were photographed to quantify body morphology. Animals were placed on a level stage with the camera approximately 20 cm above the stage, which allowed us to photograph the entire dorsal surface of the animal, along with a ruler. The ruler was used to calibrate morphological measurements in mm. We used these photographs to measure head, trunk, and leg morphology, as well as SVL, the standard measure of body size in amphibians (Heyer et al. 1994). We also recorded the habitat (riffle, pool) where each salamander was captured, based on flow and gradient conditions 0.5 m upstream and downstream of a salamander's location (see *Introduction* for habitat criteria).

Quantifying morphological variation

To quantify variation in *G. porphyriticus* body morphology, we extracted principal components from trait covariance matrices comprised of log-transformed SVL, head length and width, trunk length and width, humerus length and femur length. We expected the first principal component (PC1) to represent generalized body size because SVL would be positively correlated with all morphological measurements. We used the second principal component (PC2) in analyses of phenotypic plasticity and matching habitat choice because it accounts for the greatest proportion of the remaining morphological variation, after removing variation associated with body size (Bookstein 1989, Jungers et al. 1995, Adams and Beachy 2001). We included head, trunk, and limb measurements in our analysis based on the expectation that any of these traits could differ between riffles and pools, and because we had no a priori expectation of which traits would be most important (Lowe et al. 2018). Principal component analysis allowed us to quantify overall morphological variation in an unbiased way consistent with this scientific process, rather than, for example, using only size-corrected limb measurements, which could give the false impression that differences in limb morphology were predicted a priori.

We used mixed model ANOVAs, implemented in JMP version 9.0 (SAS Institute, Cary, North Carolina, USA),

to quantify phenotype–environment covariation in our three study reaches. Specifically, we tested for variation in PC1 and PC2 morphology scores as a function of habitat (riffle, pool), life history stage (larva, adult), and the habitat × life history stage interaction. Stream (Bear, Paradise, Zigzag) was included as a random effect in these ANOVA models. These analyses included only data from initial captures of individuals. From PCA loadings in previous analyses, we expected morphology PC2 scores to be lower in riffles than in pools, indicating that individuals in riffles had relatively shorter limb lengths than individuals in pools. Our predictions for phenotypic plasticity and matching habitat choice are based on this expected difference in PC2 scores (i.e., limb length in riffles < limb length in pools). We included life history stage in ANOVAs to assess ontogenetic effects on phenotype–environment covariation. Similarly, we analyzed variation in morphology PC1 scores to ensure that habitat-specific differences in morphology were not confounded with differences in body size.

Testing for phenotypic plasticity

If phenotypic plasticity contributes to phenotype–environment covariation, we predicted that the phenotypes of individuals that switched habitats would change to become more similar to the mean phenotype in the alternative habitat. Specifically, we predicted that morphology PC2 scores of individuals that moved from riffles to pools would become more positive ($PC2_{final} - PC2_{initial} > 0$), and morphology PC2 scores of individuals that moved from pools to riffles would become more negative ($PC2_{final} - PC2_{initial} < 0$). We expected individuals that remained in the same habitat to show no significant change in phenotype ($PC2_{final} - PC2_{initial} = 0$). Phenotypic plasticity may have contributed to matching in these individuals, but that response would have occurred (or started) before our study began, reducing the magnitude of phenotype change during the study. We used one-tailed t tests to assess our directional predictions for individuals that switched habitats, and two-tailed t tests for our predictions that change in PC2 scores would not differ from 0 in individuals that remained in the same habitat (Zar 1996). Because an individual could remain in the same habitat by staying in the same location or by moving to the same habitat at a different location, we also tested whether the amount of phenotypic change differed in these two groups.

Testing for matching habitat choice

We used multistate CMR models implemented in Program MARK (Cooch and White 2017) to assess the contribution of matching habitat choice to phenotype–environment covariation (White and Burnham 1999, Lebreton et al. 2009). With this approach, we were able to test whether the initial phenotype of individuals influenced their probability of settling in riffle or pool habitat. If matching habitat choice is a mechanism producing phenotype–environment covariation, we predicted that individuals would move to (or remain in) the habitat corresponding to their initial phenotype. Specifically, for individuals initially captured in riffles, higher morphology PC2 scores should lead to higher probabilities of moving into pools, as opposed to remaining in riffles. For individuals initially captured in pools, lower morphology PC2 scores should lead to higher probabilities of moving into riffles, as opposed to remaining in pools. Again, because this analysis was based on initial phenotypes (i.e., at the first capture event), and not influenced by phenotypic changes after the first capture, it was independent of our analysis phenotypic plasticity. With these CMR models, we were also able to assess whether the pattern of phenotype–environment covariation reflects differences in individual performance within each habitat (Edelaar et al. 2017).

Multistate CMR models estimated monthly recapture (p) and survival (S) probabilities in riffles (rf) and pools (pl), and transition probabilities between habitats ($\psi^{rf\to pl}$, $\psi^{pl\to rf}$). Survival probability represents the probability that an animal alive at time t in one state (i.e., habitat) will be alive at time $t + 1$, independent of state 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. 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 $t + 1$. Likewise, one minus the transition probability is the conditional probability that an animal in one state at time t will be in the same state at $t + 1$ (e.g., $1-\psi^{pl\to rf} = \psi^{pl\to pl}$). Estimates of S^{rf}, S^{pl}, $\psi^{rf\to pl}$, and $\psi^{pl\to rf}$ were used to calculate monthly survival/transition probabilities ($\Phi^{rf\to rf}$, $\Phi^{pl\to pl}$, $\Phi^{rf\to pl}$, $\Phi^{pl\to rf}$), representing the probability of an animal surviving from t to $t + 1$ and either moving to the other habitat (e.g., $\Phi^{rf\to pl} = S^{rf}\psi^{rf\to pl}$) or remaining in the same habitat (e.g., $\Phi^{rf\to rf} = S^{rf}[1-\psi^{rf\to pl}]$). We considered $\Phi^{rf\to rf}$ and $\Phi^{pl\to pl}$ to represent realized performance of individuals (and associated phenotypes) because they incorporate survival and the likelihood of remaining in each habitat (Williams et al. 2002).

For this analysis, we collapsed the three surveys in each two-week survey session into a single observation for each month of the field season (e.g., mid-June to mid-July, etc.), resulting in a total of 12 sampling occasions over the 4-yr study period. Relative to models including all 36 surveys, this increased the accuracy and precision of parameter estimates (e.g., Grant et al. 2010). For individuals captured more than once during a two-week survey session, we used only data from the first capture (e.g., morphology, habitat). Previous CMR analyses did not support the inclusion of stream-specific survival probabilities (Lowe et al. 2018); therefore, after confirming that this remained true using data from only the upstream reaches, we pooled data across the three

study streams for subsequent analyses. Estimates of survival probability confound mortality with permanent emigration. We do not believe that emigration strongly biased our analyses because the weirs above our study reaches likely prevented most upstream emigration, only two individuals were detected moving between downstream and upstream reaches, and overland emigration is unlikely considering the highly aquatic habits and morphology of *G. porphyriticus*. We have also shown significant genetic divergence among streams and between downstream and upstream reaches along streams (Lowe et al. 2006), further indicating that rates of immigration and emigration are low.

We first used model selection to determine a parsimonious structure of recapture probabilities, while retaining consistent structure in survival and transition probabilities (Lebreton et al. 1992, Grant et al. 2010). We modeled recapture probabilities as constant or variable by life history stage (larva, adult), time (month), and stage × time. Life history stages were represented as attribute groups in Program MARK (Cooch and White 2017). We used the most parsimonious structure for recapture probabilities to then assess variation in survival and transition probabilities by stage, time, and stage × time. First, we held transition probabilities constant to identify the most parsimonious structure for survival, then used the resulting parameterization to identify the best model structure for transition probabilities. These candidate model sets were justified by variation in discharge and other environmental conditions that could cause recapture, survival, and transition probabilities to vary over time, and by the morphological, behavioral, and ecological differences between *G. porphyriticus* larvae and adults (Petranka 1998, Bailey et al. 2004).

We used the best-fitting model from these initial rankings to test for effects of morphological phenotype on habitat-specific survival and transition probabilities. Specifically, we built a set of candidate models that included morphology PC2 as an individual covariate on survival and transition probabilities, then tested whether model likelihood increased when survival and transition probabilities were functions of individual morphology (Pollock 2002). Program MARK can reconstitute parameter estimates across the observed range of individual covariates, allowing the visualization of functional relationships between, for example, PC2 scores and transition probabilities. We included morphology PC2 as an individual covariate on recapture probabilities to ensure that any apparent effects of morphology on survival or transition probabilities were not caused by variation in detection.

For each step in these analyses, we used Akaike's information criterion, or AIC (Akaike 1973), to select the most parsimonious model structure from candidate model sets. Models were ranked by second-order AIC differences (ΔAIC_c; Burnham and Anderson 2002). Relative likelihood of each model in a candidate set was then estimated with AIC_c weights (Buckland et al. 1997). When rankings of the top models were ambiguous (i.e., $\Delta AIC_c < 2.0$; Burnham and Anderson 2002), we used 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 equal support for both models, in which case the model with fewer parameters is more parsimonious (Cooch and White 2017). Prior to model selection, we used Program U-CARE (Choquet et al. 2009) to perform goodness-of-fit tests on the saturated multistate model. None of the five lack-of-fit tests performed on the saturated model with program U-CARE were significant, indicating that the multistate framework was appropriate for the data set.

Results

Field surveys

Over the 4-yr study period, we marked 530 *G. porphyriticus* individuals in the upstream reach of Bear Brook (387 larvae, 143 adults), 521 individuals in Paradise Brook (405 larvae, 116 adults), and 420 individuals in Zigzag Brook (300 larvae, 120 adults). One individual in Bear Brook and one individual in Zigzag Brook moved from the upstream study reaches to downstream reaches (see Lowe et al. 2018), suggesting that emigration did not influence our results. Fig. 1 shows the distribution of riffle and pool habitat in the three study reaches, based on habitat classifications at individual capture locations. Frequencies of riffle and pool habitat were, respectively, 0.46 and 0.54 in Bear Brook, 0.35 and 0.65 in Paradise Brook, and 0.36 and 0.64 in Zigzag Brook.

Morphological variation

As expected, morphology PC1 had high, positive loadings for all morphological measurements and accounted for the highest percentage of overall morphological variation (89.54%; Appendix S1: Table S1). Morphology PC2 accounted for 4.73% of overall morphological variation, and this variation was independent of variation in body size (PC1). Loadings for the seven morphological variables indicate that PC2 scores predominantly reflected variation in limb lengths, where relative limb lengths increased with PC2 score (Appendix S1: Table S1).

The ANOVA of morphology PC1 showed no significant effects of habitat or the habitat × life history stage interaction (Table 1), indicating that body sizes of larvae and adults did not differ significantly between habitats. There was a significant effect of life history stage on morphology PC1 due to the difference in body size between larvae and adults. Consistent with PC1 loadings, ANOVA results were similar when we used SVL as the dependent variable, with a significant effect of life history stage only (Appendix S1: Table S2). The ANOVA of morphology PC2 showed significant effects of habitat

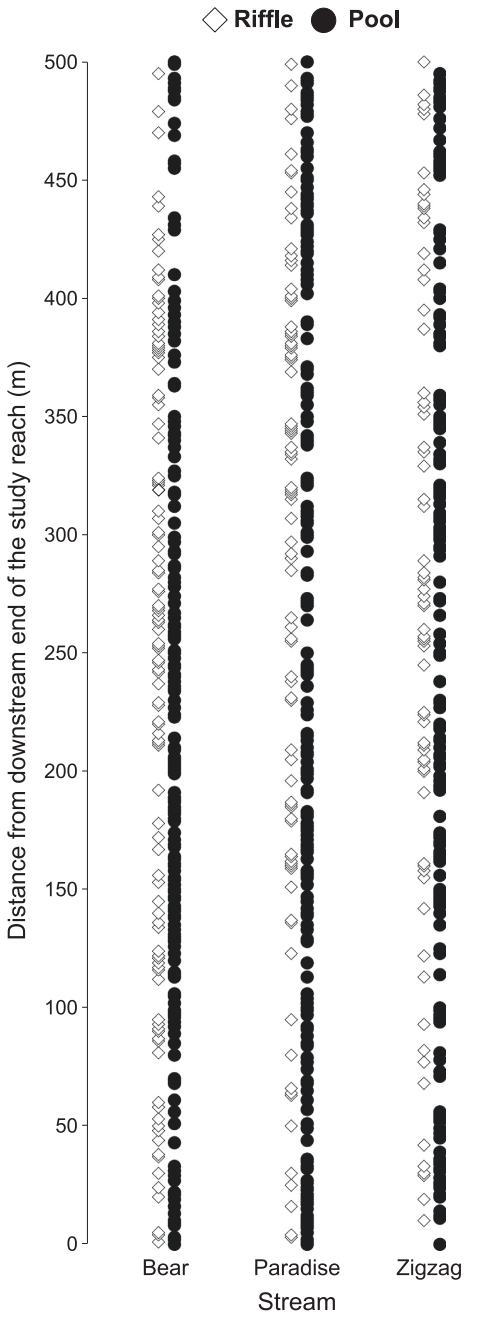

FIG. 1. Distribution of habitat types along 500-m study reaches in three streams in the Hubbard Brook Watershed, New Hampshire, USA. Habitat type was classified within channel sections extending 0.5 m downstream and upstream of salamander capture locations (distance from the downstream end of the study reach, m). Therefore, locations where salamanders were never encountered over the 4-yr study lack habitat classifications.

and life history stage, but no significant habitat × life history stage interaction (Table 1). Larvae and adults had lower morphology PC2 scores in riffles and higher scores in pools (Fig. 2), indicating that limb lengths were relatively shorter in riffles and longer in pools. ANOVA results were similar when we used size-corrected humerus and femur lengths – the variables with the highest loadings in morphology PC2 – as the dependent variables, with significant effects of habitat and life history stage, but no significant interaction (Appendix S1: Table S2). Because stream was included as a random effect in ANOVA models, these patterns of variation apply across streams. These patterns did not change when stream was included as a fixed effect.

There was considerable variation in PC2 scores within each habitat, but the trend toward lower (i.e., more negative) PC2 scores in riffles and higher (i.e., more positive) PC2 scores in pools is apparent in the raw frequency distributions (Fig. 2a). The difference in mean morphology PC2 scores between riffles and pools (Fig. 2b) represents differences in humerus and femur lengths of 3%, and ≤ 1% in the remaining morphological traits. Larvae also had lower morphology PC2 scores than adults (mean ± SE; larvae, −0.04 ± 0.02, adults, 0.18 ± 0.02), indicating ontogenetic changes in morphology. However, the lack of a significant habitat × life history stage interaction in the PC2 ANOVA, along with results of the PC1 ANOVA, shows that phenotype–environment covariation was not significantly confounded with this ontogenetic variation in morphology. On average, adults were about 60% larger than larvae (SVL 80.41 mm ± 0.55 vs. 50.6 mm ± 0.33, respectively).

Phenotypic plasticity

Of individuals that were recaptured (N = 342), 63 remained in riffles, 122 remained in pools, 79 moved from riffles to pools, and 78 moved from pools to riffles. Changes in the morphology of these individuals indicate that phenotypic plasticity contributed to phenotype–environment covariation in *G. porphyriticus* (Fig. 3). Mean change in morphology PC2 scores of individuals that moved from riffles to pools (0.2 ± 0.09) was significantly > 0 (t = 2.11, df = 78, $P_{\text{one-tailed}}$ = 0.02); mean change in PC2 scores of individuals that moved from pools to riffles (−0.15 ± 0.08) was significantly < 0 (t = −1.92, df = 77, $P_{\text{one-tailed}}$ = 0.03). Thus, in both cases, morphological phenotypes of individuals that switched habitats changed in the direction predicted by the distribution of PC2 scores in the recipient habitat (Fig. 2). Mean changes in morphology PC2 scores of individuals that remained in the same habitat were not significantly different from 0 (riffle→riffle, −0.09 ± 0.1, t = −0.93, df = 62, $P_{\text{two-tailed}}$ = 0.36; pool→pool, 0.03 ± 0.06, t = 0.48, df = 121, $P_{\text{two-tailed}}$ = 0.64), indicating no significant directional change in the phenotypes of these individuals during the study. This pattern was consistent when we used only individuals that moved to the same habitat at a different location (N^{rf} = 55, N^{pl} = 75; $P_{\text{two-tailed}}$ = 0.23–0.77), indicating that movement alone did not influence patterns of phenotypic change.

TABLE 1. ANOVA of *Gyrinophilus porphyriticus* body morphology by habitat (riffle, pool), life history stage (larva, adult), and the habitat × life history stage interaction.

Source	df	MS	*F*	*P*
Morphology PC1				
Habitat	1	0.78	0.26	0.61
Life history stage	1	4,483.38	1,493.22	<0.0001
Habitat × Life history stage	1	2.25	0.75	0.39
Error	1,465	3.00		
Morphology PC2				
Habitat	1	3.51	15.12	0.0001
Life history stage	1	14.42	62.10	<0.0001
Habitat × Life history stage	1	0.34	1.48	0.22
Error	1,465	0.23		

Notes: Stream (Bear, Paradise, Zigzag) was included as a random effect in the ANOVA models. The first principal component, morphology PC1, represents variation in overall body size. Morphology PC2 is a size-adjusted morphological character (Appendix S1: Table S1).

Matching habitat choice

In our base multi-state model, recapture probabilities (p^{rf}, p^{pl}) varied by life history stage and time, whereas survival probabilities (S^{rf}, S^{pl}) and transition probabilities ($\psi^{rf\rightarrow pl}$, $\psi^{pl\rightarrow rf}$) were constant by stage and time (Appendix S1: Table S3). The ranking of recapture probability models was unambiguous, with $\Delta AIC_c > 10$ for the top two models. Support for the top two survival probability models was similar ($\Delta AIC_c < 2.0$; Burnham and Anderson 2002), but the likelihood ratio test was not significant ($X^2 = 2.3$, $P = 0.13$), indicating that the model with fewer parameters was more parsimonious (i.e., without variation in survival in pools [S^{pl}] by life history stage). Likewise, support for the top three transition probability models was similar, but pairwise likelihood ratio tests were not significant ($X^2 < 1.3$, $P > 0.25$), indicating that the model with fewer parameters was most parsimonious (i.e., without variation in transition probabilities [$\psi^{rf\rightarrow pl}$, $\psi^{pl\rightarrow rf}$] by life history stage).

When we tested for effects of phenotypic variation on parameters in this base model, the top model included morphology PC2 as an individual covariate for recapture, survival, and transition probabilities (Table 2). This top model was well supported based on ΔAIC_c (i.e., > 2.0; Burnham and Anderson 2002). According to this model, the probability that an individual initially captured in a riffle moved to a pool ($\psi^{rf\rightarrow pl}$) increased with increasing morphology PC2 score, from a minimum of 0.18 to a maximum of 0.99. As a reference, an individual with the mean morphology PC2 score in pools (0.06; Fig. 2) was 5% more likely to move from a riffle into a pool than an individual with the mean morphology PC2 score in riffles (−0.05). The probability that an individual initially captured in a pool moved to a riffle ($\psi^{pl\rightarrow rf}$) increased with decreasing morphology PC2 score (Fig. 4), from a minimum of 0.01 to a maximum of 0.49. An individual with the mean morphology PC2 score in riffles was 20% more likely to move from a pool into a riffle than an individual with the mean morphology PC2 score in pools.

Joint survival/transition probabilities suggest that individuals remaining in riffles experienced lower realized performance – based on both survival and retention – than individuals remaining in pools, even when phenotype was well matched to the habitat (Fig. 5). This is most apparent in $\Phi^{rf\rightarrow rf}$ values at low PC2 scores and in $\Phi^{pl\rightarrow pl}$ values at high PC2 scores, where contributions of transition probabilities to the alternative habitat (Fig. 4) are low. These Φ values also show that realized performance within each habitat was highest for individuals with phenotypes well matched to that habitat.

DISCUSSION

We found that adaptive phenotypic plasticity and matching habitat choice contribute to phenotype–environment covariation in our system. The morphological phenotypes of *G. porphyriticus* individuals that switched between habitats, in either direction, changed to become better matched to the recipient habitat, indicating phenotypic plasticity in response to the different environmental conditions in riffles and pools. Additionally, we found that probabilities of switching habitats were dependent on individual phenotypes (Fig. 4). Specifically, *G. porphyriticus* individuals were more likely to switch habitats if their initial phenotype was a better match to the alternative habitat, supporting matching habitat choice (Ravigne et al. 2004, Edelaar et al. 2008). In both analyses, we based our assessment of habitat match/mismatch on the overall difference of morphology PC2 scores in riffles and pools (Fig. 2). This approach was supported by monthly survival/transition probabilities (Fig. 5), which indicate that phenotype–environment covariation is consistent with differences in the realized performance of phenotypes in the two habitats.

Our results are direct evidence of the importance of phenotype-dependent movement. Theory and empirical studies of diverse taxa (e.g., plants, invertebrates, vertebrates) have shown that dispersing individuals may not be a random subset of the population, but different from

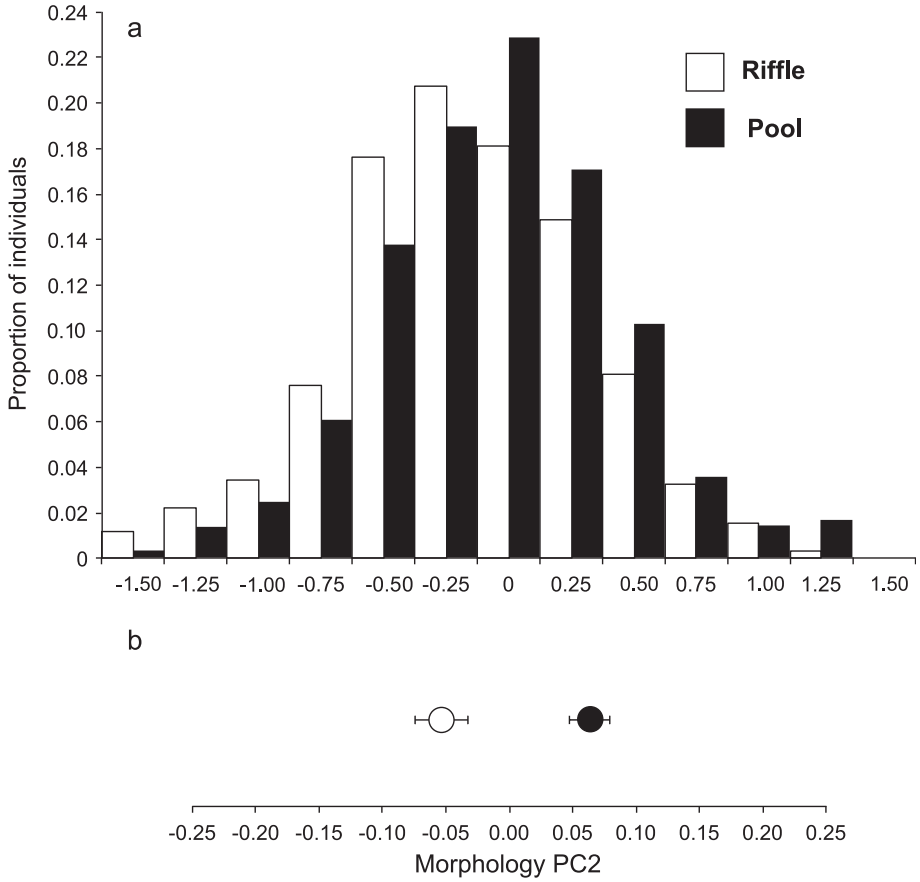

FIG. 2. (a) Frequency distributions and (b) means (±SE) of size-adjusted morphological characters (morphology PC2 scores) of *Gyrinophilus porphyriticus* individuals in riffle and pool habitats. Morphology PC2 primarily reflects variation in limb lengths (Appendix S1: Table S1); relative limb lengths increase with morphology PC2 score. Individuals are from three streams in the Hubbard Brook Watershed, New Hampshire, USA, and from 4 yr of capture–mark–recapture sampling (2012–2015). Note the difference in scale of the *x*-axes showing the overall range of variation in morphology (panel a) and the difference in means (panel b).

non-dispersers in phenotypic traits, both plastic (Imbert and Ronce 2001, Bonte et al. 2008) and genetically based (Duckworth and Kruuk 2009, Cote et al. 2010). These studies, along with the matching habitat choice literature, show that phenotype-dependent movement can have very different ecological and evolutionary effects from random movement (Edelaar and Bolnick 2012, Lowe and McPeek 2014, Canestrelli et al. 2016). In a previous study, we found that forelimb morphology predicts dispersal distance in *G. porphyriticus*: individuals with relatively long forelimbs dispersed the farthest (Lowe and McPeek 2012). Our finding that a similar trait predicts short distance movements between habitats (Fig. 4) suggests that ecological and evolutionary effects of these phenotype-dependent movements extend across spatial scales, including potential effects on interspecific interactions (Storfer 1999), population dynamics (Clobert et al. 2009), and genetic divergence (Shine et al. 2011).

Our results also underscore the importance of considering how matching habitat choice, and phenotype-dependent movement more generally, interacts with other mechanisms to produce phenotype–environment covariation (Edelaar et al. 2017). Ecological effects of phenotypic plasticity are well documented, including effects on species interactions (Relyea 2001, Benard 2004) and demography (Caswell 1983, Black and Dodson 1990). Controlled experiments are commonly used to isolate the environmental stimuli of phenotypic plasticity and document its effects. However, this approach precludes matching habitat choice by preventing movement of individuals among sites (i.e., experimental units) that vary in stimuli, and may therefore underestimate phenotypic variation and its ecological effects if plasticity and matching habitat choice act together under natural conditions. Rates of phenotype–environment matching at the population level (i.e., across individuals distributed among heterogeneous sites) should be higher when matching habitat choice and phenotypic plasticity act together; consequently, the ecological effects of phenotypic change (e.g., on survival, strength of competition, predation rate) should be more

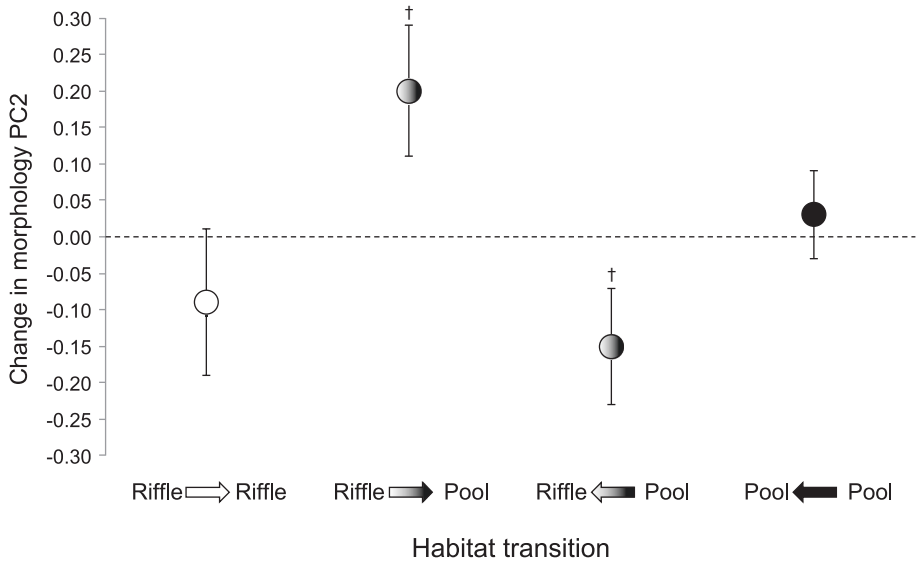

FIG. 3. Change in morphology PC2 scores for *Gyrinophilus porphyriticus* individuals recaptured during the 4-yr study ($N = 342$; mean ± SE) as a function of habitat where initially captured and habitat where last recaptured. Morphology PC2 primarily reflects variation in limb lengths (Appendix S1: Table S1); relative limb lengths increase with morphology PC2 score. In the *x*-axis labels, arrows point from initial habitat to final habitat. Means that are significantly different from 0 ($P \leq 0.03$) are indicated with daggers (†).

immediate and stronger when integrated over time. Additionally, the combined effects of matching habitat choice and phenotypic plasticity should increase phenotypic divergence among sites that differ in environmental stimuli (Jacob et al. 2015, Nicolaus and Edelaar 2018) and influence any processes sensitive to the rate of phenotypic response (Harvell 1990, Padilla and Adolph 1996, DeWitt et al. 1998).

Evidence for both adaptive phenotypic plasticity and matching habitat choice in *G. porphyriticus* implies strong selection for phenotype–environment matching, but against reliance on a single mechanism of matching. Both phenotypic plasticity and matching habitat choice have fitness costs and benefits that may explain this result. Morphological plasticity requires reorganization of an individual's body plan, which, though remarkably fast in some animals, should generally require more time than the active movements underlying matching habitat choice. We might, therefore, expect matching habitat choice to evolve in conjunction with phenotypic plasticity in systems where the rate of matching strongly affects fitness. Similarly, morphological plasticity may be costly in highly dynamic and heterogeneous environments, where the time required for morphological change reduces an individual's responsiveness in the face of temporal or spatial variation in habitat conditions (Padilla and Adolph 1996, Miner et al. 2005). This cost may apply in headwater systems, which are spatially heterogeneous (Fig. 1) and exposed to extreme discharge events that reorganize the streambed (Bormann and Likens 1979, Bilby and Likens 1980), requiring *G. porphyriticus* individuals to track changes in the distribution of habitats. Our finding that

TABLE 2. Multistate capture–mark–recapture (CMR) models assessing the effects of morphological phenotype (phen) on monthly survival (S) and transition (ψ) probabilities of *Gyrinophilus porphyriticus* individuals in riffle (rf) and pool (pl) habitats.

Model	AIC_c	ΔAIC_c	AIC_c weight	K
$S^{rf}_{(phen)}, S^{pl}_{(phen)}, p^{rf}_{(stage \times time, phen)}, p^{pl}_{(stage \times time, phen)}, \psi^{rf\to pl}_{(phen)}, \psi^{pl\to rf}_{(phen)}$	3,833.51	0.00	0.66	56
$S^{rf}_{(\bullet)}, S^{pl}_{(\bullet)}, p^{rf}_{(stage \times time, phen)}, p^{pl}_{(stage \times time, phen)}, \psi^{rf\to pl}_{(phen)}, \psi^{pl\to rf}_{(phen)}$	3,835.62	2.12	0.23	54
$S^{rf}_{(phen)}, S^{pl}_{(phen)}, p^{rf}_{(stage \times time, phen)}, p^{pl}_{(stage \times time, phen)}, \psi^{rf\to pl}_{(\bullet)}, \psi^{pl\to rf}_{(\bullet)}$	3,836.93	3.43	0.12	54
$S^{rf}_{(\bullet)}, S^{pl}_{(\bullet)}, p^{rf}_{(stage \times time, phen)}, p^{pl}_{(stage \times time, phen)}, \psi^{rf\to pl}_{(\bullet)}, \psi^{pl\to rf}_{(\bullet)}$	3,872.85	39.34	0.00	52
$S^{rf}_{(\bullet)}, S^{pl}_{(\bullet)}, p^{rf}_{(stage \times time)}, p^{pl}_{(stage \times time)}, \psi^{rf\to pl}_{(\bullet)}, \psi^{pl\to rf}_{(\bullet)}$	3,913.97	80.46	0.00	48

Notes: CMR data were collected over 4 yr (2012–2015) in three streams in the Hubbard Brook Watershed, New Hampshire, USA. Phenotypes were modeled as individual covariates on survival and transition probabilities, and represented by morphology PC2 scores (Fig. 2). Phenotypes were also included as individual covariates on monthly recapture probabilities (p) to ensure that any apparent effects on survival or transition probabilities were not caused by variation in detection. All models incorporating phenotypic variation fit the data better than the base model ($S^{rf}_{(\bullet)}, S^{pl}_{(\bullet)}, p^{rf}_{(stage \times time)}, p^{pl}_{(stage \times time)}, \psi^{rf\to pl}_{(\bullet)}, \psi^{pl\to rf}_{(\bullet)}$; Appendix S1: Table S3), which is also included in this candidate set. Parameterization for S, p, and ψ is in parentheses; $_\bullet$ indicates constant by life history stage (larva, adult), time (month), and phenotype. AIC_c is the Akaike information criterion corrected for sample size; AIC_c is the change in ΔAIC_c attributed to that model.

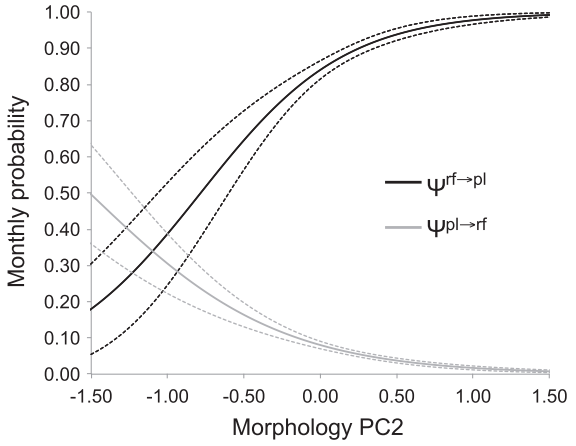

FIG. 4. Relationships between *Gyrinophilus porphyriticus* phenotype (morphology PC2 score) and monthly transition probabilities (Ψ) between riffle (rf) and pool (pl) habitats. Morphology PC2 primarily reflects variation in limb lengths (Appendix S1: Table S1); relative limb lengths increase with morphology PC2 score. Transition probability estimates are from a multistate capture–mark–recapture model (Table 2) using 4 yr of data from three streams in the Hubbard Brook Watershed, New Hampshire, USA.

ontogeny (i.e., life history stage, body size) was unrelated to morphology within habitats (Table 1, Appendix S1: Table S2) further suggests that gradual morphological responses, those that occur over the lifetime of an individual, are not favored in this system.

Matching habitat choice has advantages over phenotypic plasticity in responsiveness, but also costs that may explain why it is not the sole mechanisms of phenotype–environment matching in *G. porphyriticus*. In particular, matching habitat choice relies on active movements that may increase predation risk, energetic demands, and physiological stress (Lima 2002, Shepard et al. 2013). The mean distance moved (m along the stream channel, mean ± SE) of *G. porphyriticus* individuals that switched habitats was 23.64 ± 4.05 m, and a posteriori analysis showed no relationship between movement direction (upstream vs. downstream) and habitat transitions (riffle→pool, pool→riffle; $\chi^2 = 0.02$, df = 1, $P = 0.88$), indicating that these transitions were achieved by active movement rather than by passive drift (Stoneburner 1978, Fonseca 1999). The magnitude of movement-associated costs will vary among systems, and with the scale of matching habitat choice movements (Rothermel and Semlitsch 2002, Bonte et al. 2012). Nevertheless, abundant evidence for the costs of movement suggests that selection for matching habitat choice as a matching strategy will be constrained in most systems. Likewise, the absence of movement-associated costs is a clear benefit of phenotypic plasticity as a mechanism of phenotype–environment matching. Brook trout (*Salvelinus fontinalis*) occur in reaches downstream of those where this study was conducted (Warren et al. 2008) and are known predators and competitors of *G. porphyriticus* (Resetarits 1991, 1995). A future study might test whether trout limit matching habitat choice in *G. porphyriticus* by imposing movement-associated costs that are absent in upstream, fishless reaches (e.g., Cote et al. 2013).

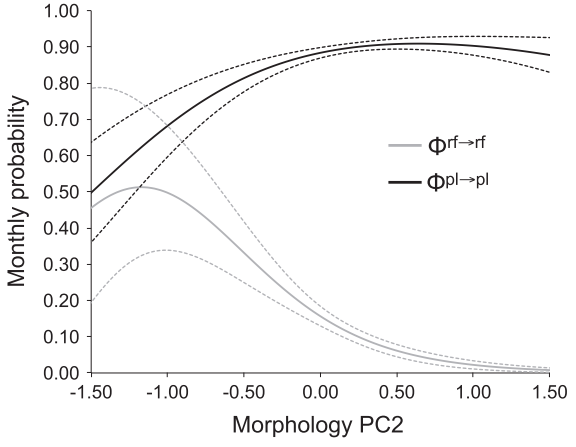

FIG. 5. Relationships between *Gyrinophilus porphyriticus* phenotype (morphology PC2 score) and monthly survival/transition probabilities (Φ) for individuals that stayed in the same habitat (riffle [rf], pool [pl]). Morphology PC2 primarily reflects variation in limb lengths (Appendix S1: Table S1); relative limb lengths increase with morphology PC2 score. Survival/transition probabilities are based on habitat-specific estimates of monthly survival (*S*) and transition (Ψ) probabilities from a multistate capture–mark–recapture model (Table 2) using 4 yr of data from three streams in the Hubbard Brook Watershed, New Hampshire, USA.

Stream plethodontids are an important model system in community ecology (Hairston 1987, Rissler et al. 2004, Bruce 2011), but the ecological effects of phenotypic plasticity have been understudied, particularly relative to other amphibians (Relyea 2001, Van Buskirk 2009). Likewise, the phenotypes of stream fishes are known to differ among flow-delineated habitats (Langerhans 2008, Senay et al. 2015, Jacobson et al. 2017), but this is the first evidence in a stream amphibian. These observations suggest that our results may be useful as a foundation for future research at the intersection of community ecology and ecomorphology in plethodontid salamanders. For example, how does the degree of phenotype–environment match (Fig. 2) affect species interactions in riffles and pools, such as coexistence with prey and predators (Svanback and Eklov 2003, Langerhans 2009)? Or, given that *G. porphyriticus* and other plethodontids can leave the stream to forage, how does the difference in limb morphology in riffles and pools influence use of the terrestrial environment and interactions with terrestrial species (Grover and Wilbur 2002, Greene et al. 2008)?

It is important to acknowledge several limitations of this study. First, although our preliminary data suggest that drag costs in riffles and pools are the proximate cause of differences in limb morphology (Fig. 2; B. R. Addis and W. H. Lowe, *unpublished data*), we have not tested this interpretation experimentally (Imre et al. 2002, Bolnick et al. 2009, Jacobson et al. 2017). Therefore, it is possible that other abiotic or biotic conditions

influence morphological divergence, including substrate size (Montgomery and Buffington 1997), prey distribution (Brown and Brussock 1991), or dissolved oxygen (Matthews and Berg 1997). A second unresolved question is why individuals use riffles given that realized performance in riffles is lower than in pools, even for individuals with low PC2 scores (Fig. 5). Use of riffles may reflect habitat-specific trade-offs in fitness components where, for example, survival is higher in pools but reproductive potential is higher in riffles. It is also possible that riffles are simply a lower quality habitat that individuals are forced to use due to intraspecific competition in pools, and that individuals with riffle phenotypes are also the weakest competitors and, consequently, more likely to move from pools into riffles (Rodenhouse et al. 1997, Loehle 2012).

This study validates matching habitat choice as a mechanism of phenotype–environment matching, even under complex and dynamic natural conditions (Edelaar et al. 2017, Nicolaus and Edelaar 2018). More broadly, our results show how crucial it is to account for movement in ecological and evolutionary research. Even with the surge in "movement ecology" theory and data in the last decades (Holyoak et al. 2005, Nathan et al. 2008, Clobert et al. 2012), it is striking to consider the significant and unexpected ways animal and plant movements have been shown to affect species interactions (Kovach et al. 2014), trait divergence (Bolnick and Stutz 2017), and demography (Williams et al. 2016). Our results reinforce the fundamental message of this growing body of research, that ecological and evolutionary responses are often inextricable from natural patterns of animal and plant movement, thus calling for broader and more explicit analyses of the effects of movement in both field and experimental studies.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2661/suppinfo

Data Availability

Data are available from the Environmental Data Initiative: https://doi.org/10.6073/pasta/4e55208c2beb68dbdcef5d78e2102897