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Testing for Microgeographic Effects on the Strength of Interspecific Competition

Jon M. Davenport¹ and Winsor H. Lowe²

Local adaptation to an environment can vary across very fine scales—as little as a few meters in some species, kilometers in others. This divergence at microgeographic scales has been linked to dispersal ability and could be responsible for geographic variation in the strength of species interactions. For example, the spread of maladaptive traits across short distances could lead to inferior performance and local extinctions across the landscape. We utilized a model study system (headwater streams of New Hampshire) with known differences in dispersal, gene flow, and intraspecific competition to test for microgeographic variation in interspecific competition. We conducted a common garden experiment and measured survival and growth of larval Spring Salamanders from different stream reaches (fish and fishless) in response to the presence of conspecific salamanders or heterospecific Brook Trout fingerlings. We predicted that Spring Salamanders from reaches with fish would have higher competitive performance with fish than naïve salamanders from reaches without fish. No significant differences were detected in salamander survival. Overall salamander growth was negative but was not affected by reach, heterospecific competitor, or the interaction between those two factors. Based on our results, microgeographic variation does not appear to be important in determining the strength of interactions between larval Spring Salamanders and Brook Trout. Salamander dispersal between our collection reaches is possible, and high gene flow of maladaptive traits could be responsible for the overall negative growth patterns. Our research highlights the importance and complexity of testing species interactions in model systems with known microgeographic variation.

DUE to the relatively reduced dispersal ability of many amphibians, population divergence has recently been documented at microgeographic scales (Storfer et al., 1999; Lowe and McPeck, 2012). Indeed, local adaptation in amphibians can occur across scales as small as a pond basin or headwater stream drainages (Freidenburg and Skelly, 2004; Skelly, 2004; Lowe et al., 2006a, 2008, 2012). However, few studies have expanded to examine how such microgeographic adaptation affects the strength of species interactions (Fauth, 1998). In one example, stream salamanders from populations with fish displayed stronger anti-predator behaviors (decreased feeding rates and increased escape responses) than individuals from populations without fish, which translated into higher short-term survival with fish in experimental trials (Storfer and Sih, 1998; Storfer, 1999). Additionally, individuals from populations with fish that received gene flow from fishless populations exhibited weaker anti-predator responses than those from isolated populations with fish. Therefore, it appeared that greater isolation allowed for stronger adaptive response to fish predators. Stream amphibians may represent a useful model system to explore the repercussions of microgeographic variation in species interactions more broadly, particularly because the linear structure of stream networks offers more tractable gradients of isolation than terrestrial (or wetland) systems (Grant et al., 2007).

Previous work in a headwater stream system with amphibians has demonstrated that interactions (e.g., competition and predation) between Spring Salamanders (*Gyrinophilus porphyriticus*) and Brook Trout (*Salvelinus fontinalis*) can be very intense. As with Trinidadian guppies, the risk of extirpation for Spring Salamanders is lowered when barriers provide upstream refuges from Brook Trout (Resetarits, 1997). Brook Trout are restricted to lower reaches of many streams because of landscape barriers (e.g., waterfalls) and man-made culverts

(Warren et al., 2008). In those populations without trout, Spring Salamanders act as top predators in stream food webs (Beachy, 1994, 2005; Bruce, 2008). In populations with trout, the interactions are stage specific, where larval Spring Salamanders are prey for adult Brook Trout and inferior competitors to fingerling Brook Trout (Resetarits, 1991; Lowe et al., 2004).

Despite these highly asymmetric interactions between Spring Salamanders and Brook Trout, the two species still co-occur in the lower reaches of headwater streams (Resetarits, 1995; Lowe et al., 2004). Recent work has demonstrated that the morphology of dispersing Spring Salamanders differs from the morphology of non-dispersers (Lowe and McPeck, 2012) and that these differences may carry over to influence intraspecific competitive interactions. Specifically, Davenport and Lowe (2016) found that the strength of intraspecific competition varied with dispersal and gene flow between downstream and upstream reaches of headwater streams. This posits that interspecific interactions between Spring Salamanders and Brook Trout could also vary significantly along individual streams, as a function of direct exposure to Brook Trout in downstream versus upstream reaches.

Using a substitutive design, we conducted a short-term common garden experiment to test for microgeographic variation in competitive strength between larval Spring Salamanders and fingerling Brook Trout. Larval Spring Salamanders were collected from populations with and without exposure to Brook Trout separated by 200–500 meters (Fig. 1). We predicted that the origin of Spring Salamanders (from reaches with fish vs. reaches without fish) would affect performance in our experiment. Specifically, we predicted that Spring Salamanders from reaches with fish would have higher competitive performance (i.e., higher survival and growth) with fish than naïve salamanders from reaches without fish.

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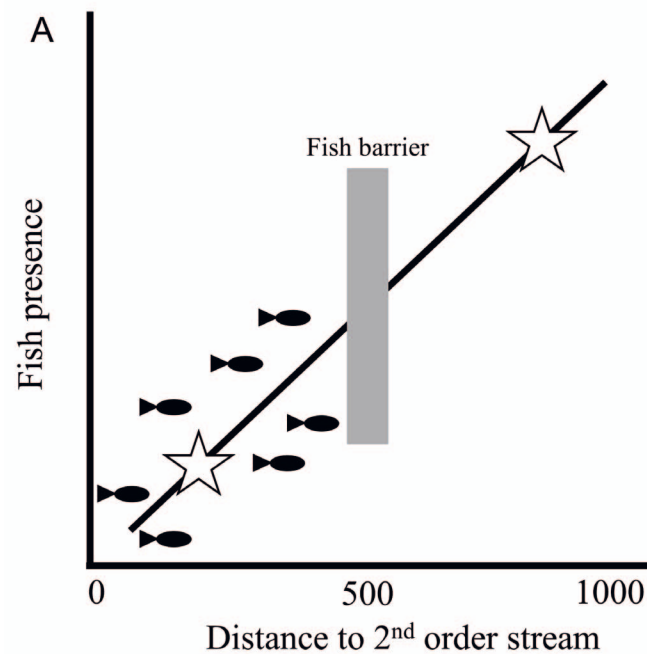


Fig. 1. (A) Stream origin sites of collected *Gyrinophilus porphyriticus* (white stars) in experiments based on distance from 2nd order Hubbard Brook and presence of Brook Trout. The gray bar illustrates a barrier for fish (e.g., waterfall or manmade culvert) at approximately 500 m from confluence with 2nd order stream that prevents fish from dispersing upstream in collection streams. (B) Picture of experimental mesocosm array on banks of Norris Brook.

MATERIALS AND METHODS

Hubbard Brook study system.—Our work was conducted in the Hubbard Brook (HB) watershed of central New Hampshire because of the wealth of information available for headwater stream communities. Hubbard Brook streams have served as a model system in ecology over the last 50 years (Holmes and Likens, 2016). Typical 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 mid-day summer temperatures (13.0–17.0°C; Likens and Buso, 2006). In addition to abiotic stream variables above, we have >10 years of population ecology (mark-recapture and genetics) data on Spring Salamanders at HB. Based on this previous research, dispersal by Spring Salamanders is strongly biased

upstream and occurs mainly along stream corridors (Lowe, 2003). Individuals of higher body condition are more likely to disperse upstream and contribute to population stability at upstream sites (Lowe et al., 2006b). Individuals dispersing the farthest also have relatively long forelimbs and short hindlimbs in comparison to non-dispersing individuals (Lowe and McPeck, 2012) and experience an increase in survival probability with dispersal distance (Lowe, 2010). Gene flow among reaches varies by stream slope with genetic distance increasing with slope between downstream and upstream sampling sites separated by 1 km (Lowe et al., 2006b, 2008, 2012). Therefore, the potential for microgeographic variation in this system has already been documented with morphological and genetic divergence between salamander populations in upstream and downstream reaches, setting the stage for our experiment.

Experimental design.—Our common garden experiment was conducted in experimental mesocosms within the HB watershed. Mesocosms were constructed from 189 L polyethylene tubs (108 cm x 62 cm x 46 cm) that were modified to allow water to flow (see Davenport and Lowe, 2016 for details). Briefly, mesocosms were situated on the bank beside Norris Brook in eight spatial blocks, with three mesocosms per block (24 total experimental units). All water was gravity fed from Norris Brook with flow being modified by ball valves emitted from vinyl tubing and was maintained at approximately 5 L/min. Substrate composition of each mesocosm was standardized with untreated playground sand topped with a single layer of gravel. Each mesocosm was then randomly assigned four cobble-sized rocks (150–340 mm in diameter) collected from the main stem of Hubbard Brook. No filters were placed in vinyl tubing to permit colonization of prey (stream invertebrates and larval salamanders of the genus *Eurycea*) from Norris Brook, and lids on top of mesocosms were opened for two weeks prior to experimental start date to allow input from falling terrestrial litter and invertebrates. Two downstream drain holes were drilled into each mesocosm to promote flow through of stream water with each drain also being covered with mesh to prevent escape. Mesocosms were constructed on 19 June 2013, and water flow from Norris Brook to the mesocosms began on 6 July 2013. After the experiment began, we secured lids on all mesocosms to prevent escape of experimental organisms.

To measure competitive performance, we deployed four different environments randomly assigned throughout the eight spatial blocks. The four treatments were: 1) one larval Spring Salamander from a fish reach vs. one larval Spring Salamander from a fishless reach, 2) one larval Spring Salamander from a fish reach vs. one Brook Trout fingerling, and 4) one larval Spring Salamander from a fishless reach vs. one Brook Trout fingerling. Each of the four treatments was replicated six times within the mesocosm array. With this substitutive design, we could evaluate how the strength of intra- and interspecific competition varied as a function of an individual's origin within a stream (fish or fishless reach) and whether salamanders were competing with a conspecific or heterospecific.

The density of individuals for the experiment was kept constant at the minimum number of individuals needed to test for competition: two individuals/m of mesocosm length. Natural salamander densities at Hubbard Brook can vary from 0.16 individuals/m to 0.46 individuals/m of stream length (Davenport and Lowe, unpubl. data). Both authors

have observed higher localized salamander densities at Hubbard Brook during periods of concentrated resources (e.g., low water flow conditions of the summer).

Field methods.—We collected larval salamanders from fish and fishless reaches (i.e., above and below known Brook Trout barriers) of two study streams (Kineo Brook and Falls Brook) within the HB watershed. Initial data indicated that trout populations only extended 100 m upstream from the confluence with the main stem of the Hubbard Brook (Lowe et al., 2006b), but subsequent surveys showed that trout persist up to 600 m from the confluence in both of these streams (Davenport, Addis, and Lowe, unpubl. data). It is also important to note that all experimental animals came from the same sampling sites used in these previous studies. In addition to salamander dispersal and survey data, we also know that aquatic conditions do not differ significantly between the downstream and upstream sampling sites of study streams (Likens and Buso, 2006).

Larval salamanders (snout–vent length [SVL] = 31–63 mm) were collected from downstream fish reaches (0–400 m from the Hubbard Brook confluence) and upstream fishless reaches (750–1000 m from the Hubbard Brook confluence) on 6–14 July 2013. Salamanders were weighed, measured, photographed, and marked before being randomly assigned to a mesocosm. Mass was used as response variable because it can be an important predictor of male reproductive success (Houck, 1988) and the outcome of interference competition (Mathis, 1991). All salamanders were uniquely marked by a dorsal subcutaneous injection of a fluorescent elastomer (Northwest Marine Technologies, Shaw Island, WA). To prevent bias, all salamanders were matched for size and then randomly assigned to mesocosms across the entire experiment. The sex of salamanders was not able to be determined for this study. All Brook Trout fingerlings (fork length 87–112 mm) were collected from pools in the main stem of Hubbard Brook with minnow traps on 6–14 July 2013. This prevented any salamanders from having prior exposure to specific trout individuals. The experiment began on 14 July 2013 and ran for 39 days. Upon termination, all large cover objects and substrate were searched in mesocosms until all experimental animals were recovered. All experimental salamanders were weighed, measured, and photographed before release back to their collection site. We also used ImageJ (Schneider et al., 2012) to verify salamander length measurements on all photographs.

Data analysis.—To determine if there were significant differences in larval salamander survival and change in growth, we analyzed data with a mixed linear effects model. We crossed salamander origin (fish or fishless reach) with competitor identity (presence of a conspecific Spring Salamander or heterospecific Brook Trout) as fixed factors and had mesocosm as a random factor to evaluate our hypotheses. We analyzed proportional change in mass, SVL, and body condition (final–initial/initial). Body condition was calculated by using the scaled mass index (Peig and Green, 2009, 2010). All statistical analyses were considered statistically significant when $P < 0.05$. All statistical analyses were conducted with SAS 9.0 software.

RESULTS

Spring Salamander survival was 96% in heterospecific treatments and 100% in conspecific treatments. Only one

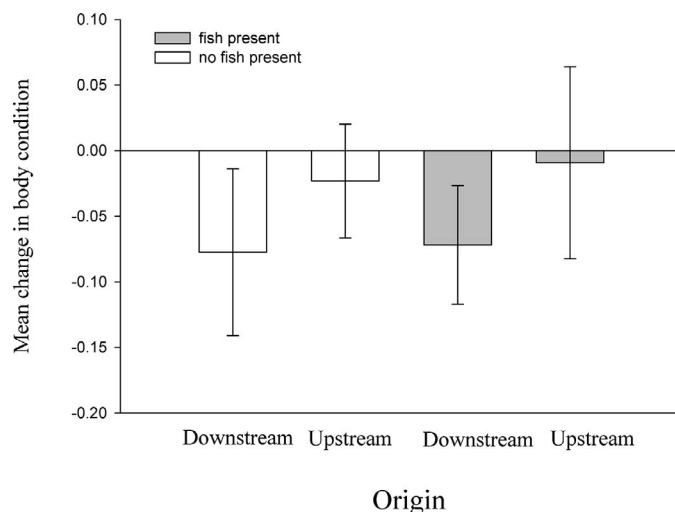


Fig. 2. Performance (measured as mean proportional change in body condition in grams) of *Gyrinophilus porphyriticus* based on reach origin and presence/absence of Brook Trout. Means are pooled across six replicates, and error bars indicate ± 1 SE.

individual from an upstream origin with a heterospecific treatment died during the experiment. That individual was excluded from all growth analyses. Proportional change in mass was not affected by salamander origin ($F_{1,19} = 0.08$, $P = 0.777$), competitor identity ($F_{1,19} = 0.01$, $P = 0.914$), or their interaction ($F_{1,19} = 0.72$, $P = 0.405$). Similarly, proportional change in SVL was not affected by salamander origin ($F_{1,19} = 1.02$, $P = 0.326$), competitor identity ($F_{1,19} = 0.01$, $P = 0.935$), or their interaction ($F_{1,19} = 1.41$, $P = 0.250$). The body condition of all salamanders changed during the experiment (Fig. 2). However, there was no significant effect on Spring Salamander body condition of salamander origin ($F_{1,19} = 1.81$, $P = 0.196$), competitor identity ($F_{1,19} = 0.01$, $P = 0.997$), or their interaction ($F_{1,19} = 0.01$, $P = 0.951$, Fig. 2). Although no statistical comparisons were made, all Brook Trout with larval salamanders gained mass during the experiment with a mean (± 1 SE) change in mass of 1.22 g (± 0.17 g).

DISCUSSION

Microgeographic variation does not appear to be important in determining the strength of interspecific competition between larval Spring Salamanders and fingerling Brook Trout. Brook Trout had a generally negative effect on Spring Salamander performance, regardless of reach origin, although these negative effects did not translate into changes in survival (Fig. 2). Our results are similar to previous research that also revealed a non-significant effect of fingerling Brook Trout on larval Spring Salamander survival but generally negative effects on salamander growth (Resetarits, 1995). This suggests that the negative effects of young Brook Trout are concentrated on growth of larval salamanders and may indirectly affect future metamorphosis timing. For example, longer larval periods and delays in maturation documented for larger plethodontids could be further extended (Bruce, 2003) similar to those observed in pond-breeding salamanders (Semlitsch et al., 1988; Scott, 1994; Searcy et al., 2014). Spring Salamanders metamorphose within 3–5 years (Bruce, 1980), and any delays in metamorphosis could carry over to affect future reproductive events (i.e., experiencing reduced odds of survival to 1st reproduction and fewer eggs per female). Alternatively, earlier ontogenetic niche shifts may

alleviate competition with Brook Trout, as salamanders can metamorphose to forage at the aquatic-terrestrial interface (Lowe et al., 2005; Greene et al., 2008).

Differences in intraspecific competitive ability previously found for Spring Salamanders do not appear to be linked to differences in interspecific competitive performance (Davenport and Lowe, 2016). Traits related to overall competitive ability should be positively associated to promote persistence of a species (i.e., increased body size and enhanced ability to acquire resources), and these associations could explain competition strength across taxa (Goldberg, 1996; Bolnick et al., 2011; Baron et al., 2015; Levine, 2016). However, the mechanism for intra- versus interspecific competitive ability for Spring Salamanders may be very different. For example, any differences in morphology or behavior that convey a competitive advantage over conspecifics may result in a disadvantage with heterospecifics (i.e., heightened aggression and larger body size).

Based on our results, it appears that persistence of Spring Salamanders with Brook Trout is not contingent on prior exposure to Brook Trout. Brook Trout are aggressive competitors and active, visual predators known to cause changes in salamander foraging behavior (Fausch and White, 1981, 1986; Resetarits, 1991, 1995; Magoulick and Wilzbach, 1998). Therefore, although increased aggression has been linked with increased competitive performance of stream salamanders in experimental settings (Southerland, 1986a, 1986b), this aggression may be outmatched by Brook Trout no matter where a Spring Salamander is from. It has been hypothesized that upstream populations of salamanders in fishless reaches may serve as sources, subsidizing downstream populations that occur with fish through downstream drift (Bruce, 1985, 1986). Under this hypothesis, downstream drift is driven by high conspecific densities in upstream reaches (Thiesmeier and Schuhmacher, 1990). In Virginia, Spring Salamander populations upstream can be up to three times greater than downstream populations, consistent with this hypothesis (Resetarits, 1991). Our results indicate the potential of downstream populations as sinks, and we are currently evaluating this hypothesis with our capture-mark-recapture data in upstream vs. downstream reaches across the HB watershed. Nonetheless, our results in combination with other published literature demonstrate that Brook Trout of any size can severely affect Spring Salamanders as predators and competitors throughout their range.

Microgeographic variation may exist in our study system but may be specific to life stage and interaction. Unlike our focus on interspecific competition, a previous work on local adaptation in stream salamanders has focused on predator-prey interactions (Storfer and Sih, 1998). Therefore, selection at the local scale could still occur, but only in response to larger Brook Trout—voracious predators of stream salamander larvae (Barr and Babbitt, 2007). Indeed, trout diets across the Hubbard Brook valley have included several species of larval salamanders, including *G. porphyriticus* (Mondelli et al., 2014). Preliminary data from another experiment suggests that there may be a stream-origin effect on anti-predator behavior of adult Spring Salamanders (Hernandez et al., unpubl. data). Resetarits (1995) found that overall activity of larvae of *G. porphyriticus* did not vary by Brook Trout presence, but the distribution of activity within a mesocosm was affected, with larval salamanders avoiding areas with Brook Trout. Future experimental work should elucidate whether anti-predator behavior is a response to local selective forces or a general response to larval predators.

Dispersal between downstream and upstream reaches within streams is possible in our system, as previous research has demonstrated long distance dispersal in Spring Salamanders (>500 m). Furthermore, the upstream bias in dispersal could be a response to negative interactions with Brook Trout in lower reaches (Lowe et al., 2006b, 2008). As a consequence, gene flow along streams may lead to a lack of microgeographic variation in competitive response to Brook Trout. Specifically, upstream gene flow may introduce maladaptive phenotypes (i.e., fish-adapted) into upstream populations and overwhelm local adaptation to fishless conditions (Storfer and Sih, 1998). We do not yet know the competitive performance of “disperser” phenotypes in this system (Lowe and McPeck, 2012; Davenport and Lowe, 2016); however, other researchers have documented morphological correlates of competitive performance in plethodontid salamanders (Adams and Rohlf, 2000; Adams, 2010). Our experimental animals were taken from two streams that differ in gene flow (Lowe et al., 2006b, 2008): while both downstream populations co-occur with fish, Kineo Brook has higher gene flow to upstream populations than Falls Brook (Lowe et al., 2008). Although our experimental design addressed this difference in gene flow, we did not find an effect of stream origin on the outcome of interspecific interactions. Future work in this system could expand to other streams that vary in gene flow to further evaluate this hypothesis.

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