

## ORIGINAL ARTICLE

# Macrogeographic variation of a pond predator's top-down effects in a common garden environment

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Email: kmstemp@ncsu.edu**Abstract**

Geographic variation in species behavior and life history has been well documented in biology. Species with wide geographic distributions (i.e., across a continent) but small home ranges (i.e.,  $<1 \text{ km}^2$ ) likely experience wide variability in abiotic environments across the entirety of their range, possibly exhibiting strong local adaptation. Understanding variation across a large geographic scale is especially important when considering species that have strong ecological importance, such as keystone species. Yet, few studies have compared the potential cascading ecological effects of a predator with a keystone role in at least part of its range. To understand how keystone ability in pond food webs can vary across a large geographic range, we conducted an artificial pond experiment with a known keystone predator in at least part of its range, the marbled salamander (*Ambystoma opacum*). To do so, we collected size-matched salamander larvae from three geographically distant populations ( $>650 \text{ km}$  apart) in Ohio, Mississippi, and North Carolina and placed them in mesocosms with a suite of spring breeding amphibian prey species. We observed differential survival of some prey species leading to differences in spring-breeding amphibian diversity among the three predator populations, indicating that keystone predation may vary at a geographic scale. Prey diversity was lowest with predators from northern (Ohio) populations of salamanders. Further understanding of large-scale variability in ecologically important predators and the potential effects of translocating wide-ranging ambystomatid species is needed to direct future conservation efforts and preserve biodiversity.

**KEYWORDS**

amphibian, diversity, geographic, intraspecific variation, keystone

## 1 | INTRODUCTION

Keystone predators have strong top-down effects on prey community composition even at relatively low densities, and can reverse the order of competitive hierarchy in prey communities, increasing overall community diversity (Mills, Soulé, & Doak, 1993; Morin, 1981; Paine,

1969). Intraspecific variation in the ability to function as a keystone predator is thought to shift across the geographic distribution of a species (Navarrete & Menge, 1996; Paine, Castillo, & Cancino, 1985; Paine, 1980). Indeed, intraspecific variation in keystone ability has been observed in marine ecosystems (Paine et al., 1985; Paine, 1980), freshwater ecosystems (Fauth, 1999a;

Kurzava & Morin, 1994), and North American grassland ecosystems (Amarasekare, 2008; Cully et al., 2010; Kotliar, Miller, Reading, & Clark, 2006). Intraspecific variation in keystone roles is often context dependent and the presence of other intermediate or top-level predators can affect outcomes (Amarasekare, 2008; Davenport & Chalcraft, 2013; Des Roches et al., 2018; Fauth & Resetarits, 1991). As well, local adaptation in foraging abilities to certain prey items (Bassar et al., 2010; Richardson & Urban, 2013) could also alter their ability to act as keystone species. Additionally, keystone predators in one population can be outcompeted and replaced by novel predators in nearby communities, even across small geographic extents (Fauth, 1999a). Therefore, understanding geographic patterns in intraspecific variation is especially important when considering species of ecological importance (i.e., keystone predators).

Scale is an important factor to consider in understanding geographic variation in ecology. Microgeographic (i.e., within a metapopulation) variation and adaptation, or the lack thereof, has recently been studied in a variety of ecological systems, with an emphasis in freshwater ecosystems (Davenport & Lowe, 2018; Richardson, Urban, Bolnick, & Skelly, 2014; Richardson & Urban, 2013). However, large-scale differences between populations of the same species are much less studied (i.e., populations across a species' range), and may be even more important for understanding widespread geographic trends in species interactions (Chamberlain, Bronstein, & Rudgers, 2014; Early & Keith, 2019; Travis, 1996). For example, when predatory starfish were removed from experimental plots in Washington State, Chile and New Zealand, populations in Chile responded by rapidly reverting to their natural unaltered state while the other populations created a more modified size-structured prey community (Paine et al., 1985). Thus, there is the potential for distinct ecological communities to develop and variability in the stability of interactions across large scales, depending on the ability of predators to act as keystones. Yet, in some situations, life history traits (larval dispersal capabilities or genetic predisposition for adult body size) result in homogeneous population level response, even at large scales (Kurzava & Morin, 1994; Navarrete & Manzur, 2008; Pennings & Silliman, 2005). With previous research on this topic providing such varied results, further investigation into geographic variation in keystone ability is warranted.

In freshwater ponds, several species have been identified as keystone predators, including the eastern newt (*Notophthalmus viridescens*), mole salamander (*Ambystoma talpoideum*) and marbled salamander (*A. opacum*) (Chalcraft & Resetarits, 2003; Fauth, 1999a; Kurzava & Morin, 1994; Morin, 1981, 1995; Wilbur, 1997). These

predatory salamanders selectively consumed competitively dominant prey species (i.e., *Anaxyrus* spp. or *Scaphiopus* spp. tadpoles), relieving competitive pressure on weaker competitors (i.e., *Pseudacris* sp. tadpoles), and ultimately increasing diversity (Morin, 1981; Wilbur, 1997). There is some evidence for geographic variation in keystone ability in these taxa, though such effects were either attributed to body size variation (Kurzava & Morin, 1994) or differences in relative abundance (Fauth, 1999a) between predator populations. We do not know of any studies confirming population-level differences in keystone ability when those two factors are held constant. Therefore, more mechanistic tests that control for variation in such traits would allow a stronger understanding of how populations may intrinsically vary in their ability to act as keystone predators.

To better understand how keystone ability can vary across a large-scale geographic range and to identify unique keystone populations, we conducted a common garden experiment with mesocosms that exposed larval *A. opacum* from three geographically distant populations (>500 km apart) to a suite of common prey species. We purposefully controlled for predator body size and density to investigate the effect of predator source population on predator keystone ability. We anticipated that size-matched predators from all populations would have identical effects on prey community composition and would generally enhance prey diversity relative to predator-free controls.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system

Marbled salamanders (*Ambystoma opacum*) are a common and wide-ranging species found across eastern North America, with known populations as far west as Texas and north to New Hampshire (Petranka, 1998). Like many amphibians, these salamanders have complex life cycles with predacious aquatic larvae and terrestrial adults (Lannoo, 2005; Wilbur, 1997). However, unlike most other ambystomatid salamanders, courtship and breeding in *A. opacum* occurs on land in the fall and eggs are deposited in dry or nearly dry depressions (Lannoo, 2005). Larvae then overwinter in ponds, resulting in individuals that are larger in body size than many spring-breeding species, thus allowing them to serve as an important predator in aquatic amphibian communities (Anderson, Linares, Dodson, & Semlitsch, 2016; Davenport & Chalcraft, 2012; Morin, 1995; Urban, 2007; Wilbur, 1997). When prey communities are diverse, these predators can cause shifts in the competitive hierarchies of prey species, in some cases even reversing the outcome of competitive dominance (Morin, 1981, 1983).

## 2.2 | Experimental design

We conducted a mesocosm experiment at Southeast Missouri State University (SEMO) from October 2017 to June 2018. We set up an experimental array of mesocosms (modified 1,000 L cattle tanks) to replicate natural ponds using established methods, which are briefly described here (Semlitsch & Boone, 2009). We filled mesocosms in early October 2017 with tap water, and added 150 ml of water conditioner (AmQuel by Kordon) to remove chlorine and chloramine. We added 1.5 kg of leaf litter to provide a nutrient base and several 500 ml inoculations of local pond water containing zooplankton to establish a prey base for larval salamanders. Mesocosms were left open, but colonization of the mesocosms by predatory insects was rare due to the experiment occurring primarily over the winter months.

We collected 16 larval *A. opacum* from each of three different populations across their range (Figure S1). Larvae were collected from one natural wetland complex in Hinds County, Mississippi (32°16'55"N 90°21'06"W), one complex in Hamilton County, Ohio (39°17'57"N 84°42'14"W), and two complexes in Wake County, North Carolina (35°49'15"N 78°21'06"W) between February 22, 2018 and February 26, 2018. Larvae were immediately transported in coolers back to SEMO after capture, where they were placed in individual holding containers. Salamanders were size matched both within and between populations (mean = 0.251 g, range 0.171–0.409 g) with all *A. opacum* in a single mesocosm within  $\pm 0.24$  g of one another (Table S1). All salamander predators were added to mesocosms on March 2, 2018. Our experimental food webs all contained amphibian prey and were as follows: (a) four *A. opacum* from North Carolina (NC), (b) four *A. opacum* from Ohio (OH), (c) four *A. opacum* from Mississippi (MS) and (d) predator-free control. We replicated each predator population four times and the predator-free control three times for 15 total mesocosms arranged in four experimental blocks (one replicate per block).

We collected all amphibian prey as egg masses from Scott, Cape Girardeau and Wayne Counties, Missouri during March and April 2018. All prey species were collected from communities within *A. opacum*'s range, but where *A. opacum* was not detected during 3 years of surveys (Davenport, unpublished data), to reduce local adaptation of prey to predator cues. After egg masses hatched, all mesocosms received tadpole prey (based on availability) of four different species of anurans, with the timing of additions matching the natural phenological patterns in Missouri. We added 200 southern leopard frogs (*Rana sphenoccephala*) on March 5, 200 chorus frogs (*Pseudacris feriarum*) on March 11, 37 American toads (*Anaxyrus*

*americanus*) on April 7, and 200 Cope's gray treefrogs (*Hyla chrysoscelis*) on 9 May. We also added 45 hatchling *Ambystoma* larvae on 3 April, which included a mix of spotted salamanders (*A. maculatum*) and small-mouthed salamanders (*A. texanum*). We refer to these as *Ambystoma* hereafter in all results. Each mesocosm received a total of 682 prey items across the duration of the experiment, and all prey densities fall within the range of naturally occurring values, and are similar to values used in previous experimental studies (Alford, 1999; Chalcraft & Resetarits, 2003; Dananay & Benard, 2018; Fauth & Resetarits, 1991; Ousterhout, Anderson, Drake, Peterman, & Semlitsch, 2015; Pintar & Resetarits, 2018).

Tanks were monitored daily for individuals undergoing metamorphosis. Metamorphosis was defined as reabsorption of external gills for salamanders and emergence of a forelimb for anurans. All emerging prey were placed in holding containers in the laboratory until full gill/tail reabsorption, after which snout-vent length (hereafter termed "SVL") and mass measurements were taken. We recorded the day on which individuals were measured to calculate larval period length. We terminated the experiment on 25 June, at which point the tanks were drained through a dipnet and the leaf litter thoroughly searched to recover any remaining individuals. Following the experiment, all surviving metamorphs and larvae were euthanized and specimens were placed in the SEMO Natural History Museum.

## 2.3 | Analysis

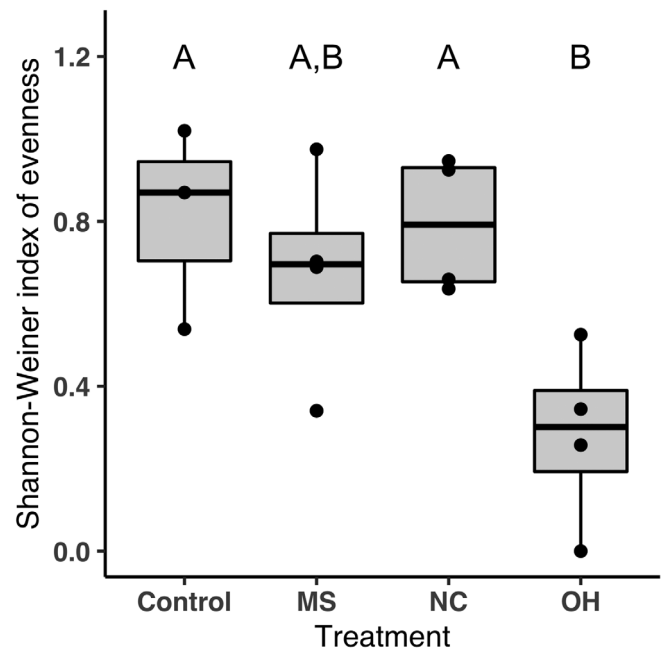
We used the program R 3.3.3 to assess the top-down effects of larval salamander source population on each experimental food web (R Core Team 2019). To test for variation in species evenness among populations, we first calculated the Shannon–Weiner index of evenness and Simpson's diversity index for each tank (included all five surviving amphibian species) using the R package "vegan" (Chalcraft & Resetarits, 2003; Oksanen et al., 2009). We then analyzed amphibian prey diversity using analysis of variance (ANOVA) with predator population as the predictor, using the ANOVA function the "car" package (Fox & Weisberg, 2019). To examine the effects of predator population on prey responses, we performed a MANCOVA ("MANOVA" function in base R) on larval period length, SVL, and mass at metamorphosis for these species, using predator population as the predictor. We used survival as a covariate to control for the effect of prey species density on these response variables. Larval period was defined as date of addition to the mesocosm to date of total tail reabsorption. All predictors were first log-transformed to better conform to the multivariate

normal distributional assumption of a MANCOVA. If the MANCOVA was significant, we then examined univariate ANCOVAs. We analyzed prey survival separately because we used a different model structure: generalized linear mixed models with binomial errors, predator population as the fixed effect, and an individual-level random effect to account for overdispersion (Warton & Hui, 2011). Survival for prey salamander larvae and tadpoles is defined as the sum of the (a) number of individuals that underwent metamorphosis, and (b) number of larvae that survived to the experiment's end date, as a proportion of initial input. It is assumed that tadpoles surviving to the end of the experiment would have reached size refugia from predators and would have emerged, given more time, or overwintered as larvae (*R. sphenoccephala*). Survival for *A. americanus* and *H. chrysoscelis* was too low to perform meaningful tests of their responses, therefore prey response models were only conducted for *R. sphenoccephala*, *P. feriarum*, and *Ambystoma*. We also analyzed *A. opacum* survival, date of emergence, and size at metamorphosis, using similar model structures as above for the prey. The MANOVA for predator response was not significant, but we conducted univariate analyses to further examine potential variation. Larval period length was unknown for *A. opacum* as they were collected as already hatched larvae, however, date of emergence was defined as date of addition to the mesocosm to date of total tail reabsorption in the lab. For all models, we used the Tukey multiple comparison of means with 95% family wise confidence levels to assess experimental food web differences, using the “emmeans” package (Lenth, 2020).

### 3 | RESULTS

#### 3.1 | Prey response

Prey diversity, as measured by Shannon–Wiener evenness, was highest in predator-free control and NC food webs, and lowest in the OH food web ( $F_{3,11} = 4.628$ ,  $p = .025$ , Figure 1, Table S2). The prey diversity results from Simpson's diversity index were the same ( $F_{3,11} = 4.811$ ,  $p = .022$ ). Pairwise comparisons can be found in Table S3 for all surviving prey. Total prey survival was highest in the predator-free control food web, as compared to any other food webs ( $\chi^2 = 72.10$ ,  $p < .001$ ; Figure 2). There was no significant food web effect for *Ambystoma* survival ( $\chi^2 = 5.74$ ,  $p = .13$ ; Figure 3a). *Rana sphenoccephala* survival was significantly lower in all food webs than the predator-free control food web ( $\chi^2 = 26.34$ ,  $p < .001$ , Figure 3b). The OH food web was also different from the NC and MS food webs; indeed, only two *R. sphenoccephala* survived in the OH food web. *Pseudacris*

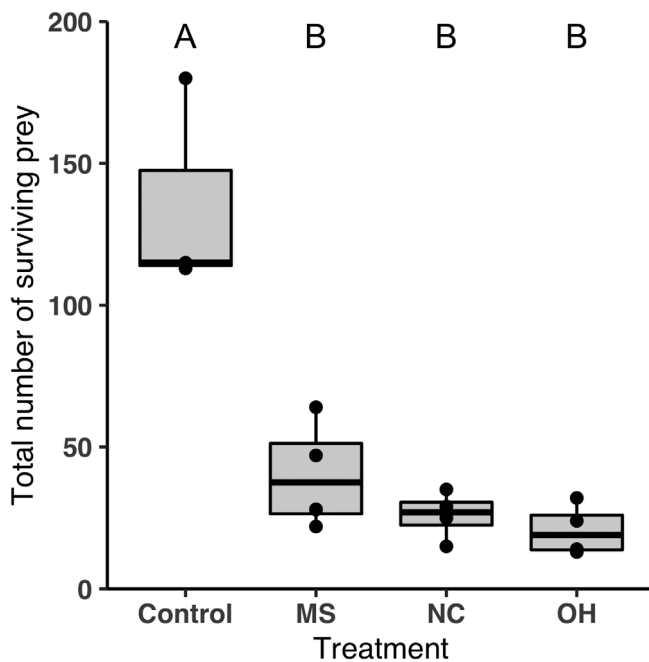


**FIGURE 1** Community diversity of five amphibian prey in a mesocosm experiment on the effects of population source of predatory *Ambystoma opacum* salamanders, as represented by the Shannon–Wiener Index of Evenness. Source populations represented are: MS, Mississippi, NC, North Carolina and OH, Ohio. Circles represent actual data points. Capital letters above boxes identify pairs of means that are significantly different.  $n = 4$  in all cases except for the control, where  $n = 3$

*feriarum* survival was significantly lower in all food webs relative to the predator-free control food web ( $\chi^2 = 16.52$ ,  $p < .001$ ; Figure 3c). Only three individuals of *A. americanus* survived from one of the predator-free control replicates, while only two replicates (one OH and one MS) had surviving *H. chrysoscelis* (Figure 3d,e). Relative abundance of surviving prey varied across food webs; the prey community in OH food webs was only 2.4% *R. sphenoccephala*, 30.1% *H. versicolor* and 66.3% *Ambystoma*. In NC food webs, the prey community was 26.9% *R. sphenoccephala*, 9.6% *P. feriarum* and 63.5% *Ambystoma*. MS food webs were comprised of 48.4% *R. sphenoccephala*, 15.5% *H. versicolor* and 26.7% *Ambystoma*. Finally, control food webs were 50.2% *R. sphenoccephala*, 35.8% *P. feriarum* and 13.2% *Ambystoma* (Figure 4). The MANCOVA on larval period length, SVL and mass was not significant for *R. sphenoccephala*, *Ambystoma* or *P. feriarum*, so we did not evaluate univariate ANCOVAs (Figures S2–S4).

#### 3.2 | Predator response

*Ambystoma opacum* survival was not related to source population ( $\chi^2 = 0.098$ ,  $p = .952$ , Table S3). Additionally,

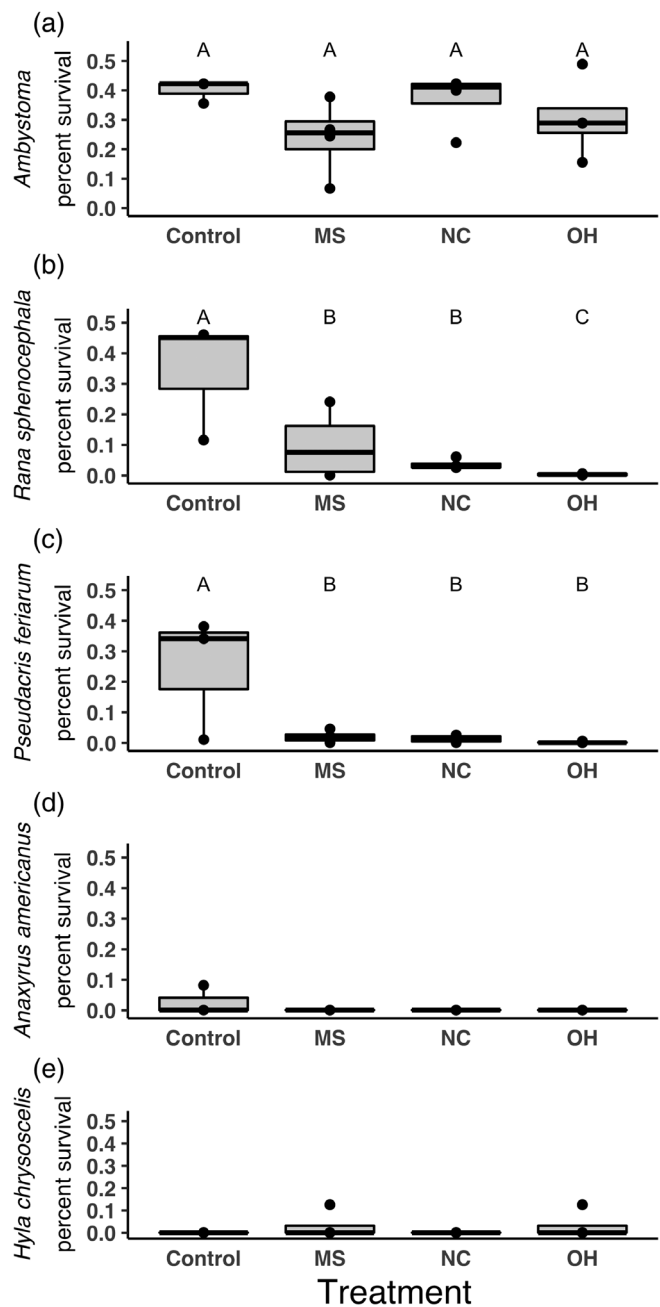


**FIGURE 2** Total number of surviving prey that emerged from each of four experimental food webs in a mesocosm experiment evaluating predator source population. Source populations represented are: MS, Mississippi; NC, North Carolina; OH, Ohio. Circles represent actual data points. Capital letters above boxes identify pairs of means that are significantly different.  $n = 4$  in all cases except for the control, where  $n = 3$

the MANOVA on initial predator mass, mass at metamorphosis and date of emergence were not significant, nor were significant in the univariate ANOVAs (Tables S4 and S5).

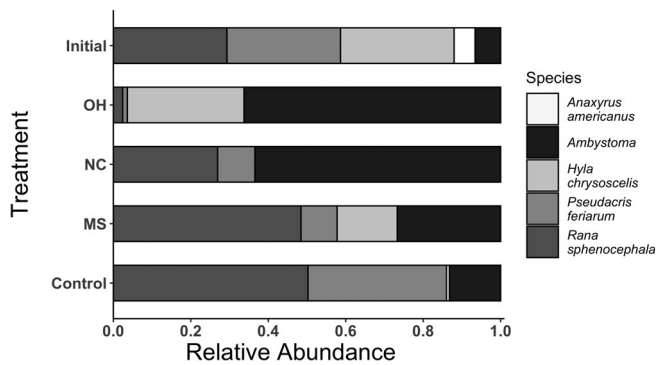
#### 4 | DISCUSSION

Geographic variation in predation ability may play an important role in determining local community composition, especially in aquatic ecosystems. We detected differences in top-down predator effects across a large geographic scale on prey diversity and prey composition (Figures 1 and 2). No predator populations demonstrated effects consistent with keystone predation, with prey diversity being equivalent to or less than the predator-free control food web in all cases (Figure 1). For example, prey survival was generally low in the presence of a predator: of five prey taxa, only three (*R. sphenoccephala*, *Ambystoma* and *P. feriarum*) produced enough surviving individuals to analyze for individual traits (Figure 3). *Anaxyrus americanus* only produced three metamorphs from a single predator-free control replicate, and *H.*



**FIGURE 3** Mean percent survivorship of (a) *Ambystoma*, (b) *Anaxyrus americanus*, (c) *Hyla chrysoscelis*, (d) *Pseudacris feriarum* and (e) *Rana sphenoccephala* across predator treatments in a study evaluating predatory *Ambystoma opacum* source population. Source populations represented are: MS, Mississippi; NC, North Carolina; OH, Ohio. Circles represent actual data points. Capital letters above boxes identify pairs of means that are significantly different.  $n = 4$  in all cases except for the control, where  $n = 3$

*chrysoscelis* produced metamorphs in only two food webs (one OH and one MS) where predator survival was low. All prey items in this experiment were added in order of



**FIGURE 4** Relative survival of each of five amphibian prey species by food web. Each food web represents replicate mesocosms with predators from different source populations and a common amphibian prey community. Source populations represented are: MS, Mississippi; NC, North Carolina; OH, Ohio. The top bar indicates initial prey densities at the start of the experiment, and each species is represented by a grayscale tone

natural phenological progression; thus, when these late-breeding, competitively inferior species were added to the experiment, they were likely perceived as prey for larger intermediate predators like *Ambystoma*.

We detected differences in prey diversity across predator populations, namely that diversity was lowest in our northern predator population (OH). This result occurred after controlling for predator size and density, variables that influenced prey responses in previous studies (Fauth, 1999a; Kurzava & Morin, 1994), while allowing all populations to experience the same environmental conditions. Furthermore, even in food webs where diversity measures were similar (the predator-free control, MS and NC food webs), the resulting relative abundance of surviving prey was dramatically different and prey community composition was altered. For example, relative *Ambystoma* abundance was higher for the NC and OH food webs compared to the predator-free control and MS food webs, and *R. sphenoccephala* comprised nearly half of MS and predator-free control food webs, but only 2.4% of OH food webs. Our findings reinforce the importance of context-dependent interactions between potential keystone predators and their prey.

We propose several reasons for the differential effects observed in our experiment. First, variation in predator traits (e.g., behavior, foraging efficiency or physiology) across spatial scales may be responsible for the variation in prey survival and diversity. For example, foraging rates of larval spotted salamanders (*A. maculatum*), an intermediate consumer, have been shown to vary substantially on a large spatial scale, with northern populations

showing a greater response to predation risk when foraging while populations ~200 km further south were more affected by intraspecific density (Urban & Richardson, 2015). Thus, it is reasonable to speculate that variation in predator behavior (i.e., foraging rate or aggression) across the large geographic scale we examined could have resulted in significant variation in prey diversity. Second, local adaptation to abiotic factors may have an effect on keystone function. We conducted this experiment in southeastern Missouri (37.31° N), centrally located between our three experimental populations: MS (32.28° N), NC (35.82° N) and OH (39.30° N). Some species show negative latitudinal clines in critical thermal maxima, for example, lower critical thermal maxima at more northern localities, indicating their physiology is linked to climate (Gatz, 1973). Therefore, populations from more northern latitudes (i.e., OH) that were displaced to our study site may be more efficient predators in a more temperate environment than at their source location. As well, populations from more southern latitudes (MS and NC) may have been less effective predators in the cold winter conditions at our study site relative to their natal ponds. Finally, there is also the potential for variation in natural community composition and diversity to impact keystone predators across spatial gradients (Amarasekare, 2008). Variation in prey density (i.e., at the edge of their range) or local patterns of sympatry at each site could influence the way a predator interacts with that species, potentially leading to species-specific consumption (Stenhouse, 1985). Selective predation has been documented in some populations of *A. opacum* (Morin 1995). While all prey could be found with *A. opacum*, variation in competitive abilities of prey species could also modify the impact of predators. As *A. opacum* were collected as larvae in our study, we acknowledge the possibility that individuals may have encountered prey items prior to collection. However, larvae from most populations were collected before spring-breeding anurans were active and we did not detect any anuran species at any of our collection sites. It is worth noting that some dragonflies (*Libellulidae*) colonized mesocosms in mid-June during the last weeks of the experiment. It is also highly unlikely that the dragonflies unduly influenced amphibian survival because colonization occurred after most salamanders and anurans had already metamorphosed and individual dragonflies were too small to consume any remaining amphibian prey.

Overall, we found that predator populations differed in their effects on a common prey assemblage, but surprisingly we found no keystone effect of *A. opacum*. The specific mechanism for our documented variation in prey diversity remains unknown. Life history traits are known to vary across a species' range, especially in organisms with wide geographic distribution (Kurzava & Morin,

1994; Laurila, Lindgren, & Laugen, 2008; Morrison & Hero, 2003). However, we did not detect differences in survival, size at metamorphosis or date of emergence in any of the predator populations we examined. Future research should focus on variation in predator behavior across a large geographic scale, as well as variation in the predatory ability of wide-ranging populations of a single species. Abiotic factors and species' tolerance to environmental changes could also be the driving force in changing keystone predator abilities, making studies of large-scale geographic variation vital to understanding variation in population- and community-level processes. As the future of climatic stability becomes less certain, changes to species interactions will only become more difficult to identify and predict on a large scale (Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010; Yang & Rudolf, 2010). Further research into the factors that cause changes in community composition, especially in regard to ecologically important species like keystones, is important for determining prey community composition and ecological function, and will aid in promoting and preserving biodiversity in a constantly changing world (Gilman et al., 2010).

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#### CONFLICT OF INTEREST

The authors declare no conflict of interest.

#### AUTHOR CONTRIBUTIONS

**Kenzi M. Stemp, Jon M. Davenport** and **Thomas L. Anderson**: Formulated the ideas, and designed the methodology. **Kenzi M. Stemp** and **Jon M. Davenport** performed the experiment. **Kenzi M. Stemp** and **Thomas L. Anderson**: Performed the analyses. **Kenzi M. Stemp, Jon M. Davenport** and **Thomas L. Anderson**: Wrote the paper.

#### DATA AVAILABILITY STATEMENT

Upon acceptance, the raw data in this manuscript will be made available via a data repository (e.g., Dryad, figshare etc.) of the author's choice.

#### REFERENCES

- Alford, R. A. (1999). Ecology: Resource use, competition, and predation. In R. W. McDiarmid & R. Altig (Eds.), *Tadpoles: The biology of anuran larvae* (pp. 240–278). Chicago, IL: The University of Chicago Press.
- Amarasekare, P. (2008). Spatial dynamics of a keystone predator. *Journal of Animal Ecology*, 77, 1306–1315. <https://doi.org/10.1111/j.1365-2656.2007.0>
- Anderson, T. L., Linares, C., Dodson, K. N., & Semlitsch, R. D. (2016). Variability in functional response curves among larval salamanders: Comparisons across species and size classes. *Canadian Journal of Zoology*, 94, 23–30.
- Bassar, R. D., Marshall, M. C., López-Sepulcre, A., Zandonà, E., Auer, S. K., Travis, J., ... Reznick, D. N. (2010). Local adaptation in Trinidadian guppies alters ecosystem processes. *Proceedings of the National Academy of Sciences of the United States of America*, 107(8), 3616–3621. <https://doi.org/10.1073/pnas.0908023107>
- Chalcraft, D. R., & Resetarits, W. J. (2003). Predator identity and ecological impacts: Functional redundancy or functional diversity? *Ecology*, 84(9), 2407–2418.
- Chamberlain, S. A., Bronstein, J. L., & Rudgers, J. A. (2014). How context dependent are species interactions? *Ecology Letters*, 17(7), 881–890. <https://doi.org/10.1111/ele.12279>
- Cully, J. F., Collinge, S. K., van Nimwegen, R. E., Ray, C., Johnson, W. C., Thiagarajan, B., ... Holmes, B. E. (2010). Spatial variation in keystone effects: Small mammal diversity associated with black-tailed prairie dog colonies. *Ecography*, 33, 667–677. <https://doi.org/10.1111/j.1600-0587.2009.05746.x>
- Dananay, K. L., & Benard, M. F. (2018). Artificial light at night decreases metamorphic duration and juvenile growth in a widespread amphibian. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20180367. <https://doi.org/10.1098/rspb.2018.0367>
- Davenport, J. M., & Chalcraft, D. R. (2012). Evaluating the effects of trophic complexity on a keystone predator by disassembling a partial intraguild predation food web. *Journal of Animal Ecology*, 81(1), 242–250. <https://doi.org/10.1111/j.1365-2656.2011.01906.x>
- Davenport, J. M., & Chalcraft, D. R. (2013). Nonconsumptive effects in a multiple predator system reduce the foraging efficiency of a keystone predator. *Ecology and Evolution*, 3(9), 3063–3072. <https://doi.org/10.1002/ece3.691>
- Davenport, J. M., & Lowe, W. H. (2018). Testing for microgeographic effects on the strength of interspecific competition. *Copeia*, 106(3), 501–506. <https://doi.org/10.1643/ce-18-006>
- Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., Schweitzer, J. A., & Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. *Nature Ecology & Evolution*, 2(January), 57–64. <https://doi.org/10.1038/s41559-017-0402-5>
- Early, R., & Keith, S. A. (2019). Geographically variable biotic interactions and implications for species ranges. *Global Ecology and Biogeography*, 28, 42–53. <https://doi.org/10.1111/geb.12861>

- Fauth, J. E. (1999a). Identifying potential keystone species from field data—An example from temporary ponds. *Ecology Letters*, 2, 36–43.
- Fauth, J. E., & Resetarits, W. J. (1991). Interactions between the salamander *Siren intermedia* and the keystone predator *Notophthalmus viridescens*. *Ecology*, 72(3), 827–838.
- Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd Edition). Thousand Oaks, CA: SAGE Publications. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.
- Gatz, J. A. J. (1973). Intraspecific variations in critical thermal maxima of *Ambystoma maculatum*. *Herpetologica*, 29(3), 264–268.
- Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology & Evolution*, 25(6), 325–331. <https://doi.org/10.1016/j.tree.2010.03.002>
- Kotliar, N. B., Miller, B. J., Reading, R. P., & Clark, T. W. (2006). The prairie dog as a keystone species. In J. Hoogland (Ed.), *Conservation of the black-tailed prairie dog: Saving north America's Western grasslands* (pp. 53–64). Washington, DC: Island Press.
- Kurzava, L. M., & Morin, P. J. (1994). Consequences and causes of geographic variation in the body size of a keystone predator, *Notophthalmus viridescens*. *Oecologia*, 99, 271–280.
- Lannoo, M. (2005). In M. Lannoo (Ed.), *Amphibian declines: The conservation status of United States species*, Berkeley, CA: University of California Press.
- Laurila, A., Lindggen, B., & Laugen, A. T. (2008). Antipredator defenses along a latitudinal gradient in *Rana temporaria*. *Ecology*, 89(5), 1399–1413.
- Lenth, R. (2020). emmeans: Estimated marginal means, aka least-squares means (R package version 1.4.4).
- Mills, L. S., Soulé, M. E., & Doak, D. F. (1993). The keystone-species concept in ecology and conservation. *Bioscience*, 43(4), 219–224.
- Morin, P. J. (1981). Predatory salamanders reverse the outcome of competition among three species of anuran tadpoles. *Science*, 212(4500), 1284–1286.
- Morin, P. J. (1983). Predation, competition, and the composition of larval anuran guilds. *Ecological Monographs*, 53(2), 119–138.
- Morin, P. J. (1995). Functional redundancy, non-additive interactions, and supply-side dynamics in experimental pond communities. *Ecology*, 76(1), 133–149. <https://doi.org/10.2307/1940637>
- Morrison, C., & Hero, J.-M. (2003). Geographic variation in life-history characteristics of amphibians: A review. *Journal of Animal Ecology*, 72, 270–279. <https://doi.org/10.1046/j.1365-2656.2003.00696.x>
- Navarrete, S. A., & Manzur, T. (2008). Individual- and population-level responses of a keystone predator to geographic variation in prey. *Ecology*, 89(7), 2005–2018.
- Navarrete, S. A., & Menge, B. A. (1996). Keystone predation and interaction strength: Interactive effects of predators on their main prey. *Ecological Monographs*, 66(4), 409–429.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Henry, M., & Stevens, H. (2009). *vegan: Community ecology package* (R package version 1.15-3). Retrieved from <http://cran.r-project.org/package=vegan>
- Ousterhout, B. H., Anderson, T. L., Drake, D. L., Peterman, W. E., & Semlitsch, R. D. (2015). Habitat traits and species interactions differentially affect abundance and body size in pond-breeding amphibians. *Journal of Animal Ecology*, 84(4), 914–924. <https://doi.org/10.1111/1365-2656.12344>
- Paine, R. T. (1969). A note on trophic complexity and community stability. *The American Naturalist*, 103(929), 91–93. <https://doi.org/10.1086/282586>
- Paine, R. T. (1980). Food webs: Linkage, interaction strength and community infrastructure. *The Journal of Animal Ecology*, 49(3), 666–685. <https://doi.org/10.2307/4220>
- Paine, R. T., Castillo, J. C., & Cancino, J. (1985). Perturbation and recovery patterns of starfish-dominated intertidal assemblages in Chile, New Zealand, and Washington state. *The American Naturalist*, 125(5), 679–691.
- Pennings, S. C., & Silliman, B. R. (2005). Linking biogeography and community ecology: Latitudinal variation in plant-herbivore interaction strength. *Ecology*, 86(9), 2310–2319. <https://doi.org/10.1890/04-1022>
- Petranka, J. W. (1998). *Salamanders of the United States and Canada*, Washington, DC: Smithsonian Institution Press.
- Pintar, M. R., & Resetarits, W. J. (2018). Variation in pond hydroperiod affects larval growth in southern leopard frogs, *Lithobates sphenoccephalus*. *Copeia*, 106(1), 70–76. <https://doi.org/10.1643/CE-17-696>
- R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Richardson, J. L., & Urban, M. C. (2013). Strong selection barriers explain microgeographic adaptation in wild salamander populations. *Evolution*, 67(6), 1729–1740. <https://doi.org/10.1111/evo.12052>
- Richardson, J. L., Urban, M. C., Bolnick, D. I., & Skelly, D. K. (2014). Microgeographic adaptation and the spatial scale of evolution. *Trends in Ecology & Evolution*, 29(3), 165–176. <https://doi.org/10.1016/j.tree.2014.01.002>
- Semlitsch, R. D., & Boone, M. D. (2009). Aquatic mesocosms. In C. K. J. Dodd (Ed.), *Amphibian ecology and conservation: A handbook of techniques* (pp. 87–102). Oxford, England: Oxford University Press.
- Stenhouse, S. L. (1985). Interdemic variation in predation on salamander larvae. *Ecology*, 66(6), 1706–1717.
- Travis, J. (1996). The significance of geographical variation in species interactions. *The American Naturalist*, 148, S1–S8.
- Urban, M. C. (2007). Predator size and phenology shape prey survival in temporary ponds. *Oecologia*, 154, 571–580. <https://doi.org/10.1007/s00442-007-0856-2>
- Urban, M. C., & Richardson, J. L. (2015). The evolution of foraging rate across local and geographic gradients in predation risk and competition. *The American Naturalist*, 186(1), E16–E32. <https://doi.org/10.1086/681716>
- Warton, D. I., & Hui, F. K. C. (2011). The arcsine is asinine: The analysis of proportions in ecology. *Ecology*, 92, 3–10. <https://doi.org/10.1890/10-0340.1>
- Wilbur, H. M. (1997). Experimental ecology of food webs: Complex systems in temporary ponds. *Ecology*, 78(8), 2279–2302.



Yang, L. H., & Rudolf, V. H. W. (2010). Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters*, *13*(1), 1–10. <https://doi.org/10.1111/j.1461-0248.2009.01402.x>

### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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