

Multiple-Predator Effects and Functional Redundancy of Pond Predators

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ABSTRACT.—Functional redundancy occurs when different predator species have similar effects on the diversity, abundance, and composition of a prey community. When multiple predators coexist, their interactions can alter prey survival and ultimately diversity through emergent multiple-predator effects (MPEs). MPEs can be exacerbated by differences in predator behavior; however, little is known about the magnitude of MPEs when predators compete for the same prey or have similar behavioral traits. To understand functional redundancy and the interactions of multiple predators in similar niches, as well as their impacts on the composition of a prey community, we conducted two experiments using two ambystomatid salamander predators (*Ambystoma opacum* and *Ambystoma annulatum*). We exposed a suite of tadpole prey (*Anaxyrus americanus*, *Rana sphenocephala*, *Rana sylvatica*, *Pseudacris feriarum*, and *Pseudacris crucifer*) to different experimental food webs in a mesocosm experiment, and a single prey species (*R. sphenocephala*) in microcosm experiment with substitutive and additive designs to test for MPEs. We found no evidence for functional redundancy between the two predators: *A. annulatum* selectively preyed on competitively dominant prey species (*A. americanus*) and did not alter community diversity. *Ambystoma opacum* decreased prey diversity relative to the control because of natural phenological mismatch with *A. americanus*. Interactions between the two predators (e.g., predator inference) were lacking, indicating that predation risk from each predator was independent for the one prey species we tested. A better understanding of community and ecosystem-level effects by *A. annulatum* can inform future conservation efforts and management decisions regarding this endemic species.

Functional redundancy occurs when different predator species have similar effects on the diversity, abundance, and composition of a prey community (Lawton and Brown, 1993). The concept of redundancy has a long history in ecology (Rosenfeld, 2002; Loreau, 2004), having been investigated in many ecosystems, including oceanic (e.g., Baker et al., 2004; Nyström, 2006), freshwater (e.g., Morin, 1995; Chalcraft and Resetarits, 2003a), and terrestrial systems (e.g., Thibault et al., 2010). For example, evidence provided from coral reef ecosystems indicates that species can be grouped into functional groups based on their ecological role in reef resilience (i.e., zooxanthellae, reef-building corals, and herbivores; Nyström, 2006). Co-occurring species of symbiotic zooxanthellae were able to fill the same niche as a species that had been eliminated by a bleaching event, functionally replacing the lost species (Baker et al., 2004; Nyström, 2006). However, there is conflicting evidence for functional redundancy across taxa, with some studies showing a lack of redundancy between species (Kurzava and Morin, 1998; Chalcraft and Resetarits, 2003a) and others showing equivalence for some variables (Morin, 1995; Chalcraft and Resetarits, 2003b; Baker et al., 2004; Nyström, 2006). Identifying functional redundancy between predator species is particularly important because it could explain equivalent predatory effects being exerted on an ecosystem in areas where predator composition differs, or multiple predators are present. For example, when predators exhibit a mosaic distribution or when predators have differing densities across a landscape, there is more potential for novel predator interactions (Kurzava and Morin, 1998; McCoy et al., 2009). Thus, identifying redundancy could improve the predictive power of ecological models and further our understanding of biodiversity.

In communities with high predator diversity, complex predator–predator interactions may ensue. Such situations

increase the potential for multiple predators to interact via cooperation, intraguild predation, or competition that shifts predator function, especially when the predators differ in niche position (Sih et al., 1998; McCoy et al., 2012). In some cases, predator–predator interactions can lead to emergent multiple predator effects (MPEs) when the effects of multiple predators cannot be accurately predicted based on the effects of each predator alone, ultimately reshaping prey communities in nonlinear ways (Soluk and Collins, 1988; Vance-Chalcraft and Soluk, 2005; McCoy et al., 2012). These effects are usually quantified experimentally by rearing prey alone, with a single predator, or with two predators together. Risk enhancement occurs when prey survival is reduced more in the presence of multiple predators than would be expected based on individual predator species' foraging rates. For example, risk enhancement was found with mayflies in streams as stonefly predators flushed them out of rock refuges, exposing them to fish predators (Soluk and Collins, 1988; Soluk, 1993). Alternatively, risk reduction for prey can occur when interference among predators reduces prey mortality rates (Vance-Chalcraft and Soluk, 2005). For example, the predatory ability of eastern newts (*Notophthalmus viridescens*), an intermediate predator, was strongly affected by the presence of another strong predator, lesser siren (*Siren intermedia*) via direct consumption of both adult and larval newts (Fauth and Resetarits, 1991). This is interesting because if competitively dominant prey perceive one predator as a "riskier" threat relative to another predator, community diversity may not shift as expected (Davenport and Chalcraft, 2013). However, because of a shared food resource, predators in these studies occupied different trophic positions and exhibited intraguild predation, with one predator species preying upon the other. To our knowledge, few studies have considered how MPEs could affect the ability of ecologically similar predators to alter prey diversity, or to serve functionally redundant roles.

Pond food webs can be complex, encompassing interactions across trophic levels according to what species are present in a

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given area (Cortwright and Nelson, 1990). In particular, these communities contain numerous apex and intermediate predators. For example, previous studies have identified both eastern newts and larval marbled salamanders (*Ambystoma opacum*) as keystone species (Morin, 1981, 1995; Chalcraft and Resetarits, 2003b) because they enhance local tadpole diversity by consuming competitively dominant prey species (i.e., *Anaxyrus* spp. or *Scaphiopus* spp. tadpoles), suggesting that these predators may be functionally equivalent (Morin, 1995). When both species were present, however, *Ambystoma opacum* had reduced growth, indicating potential interactions between predators that led to risk reduction in anuran prey. However, MPES and the impacts of functional redundancy on prey diversity with similar predator species is less known, providing a fruitful area of research to develop.

To explore the relationship between functional redundancy and MPES and the effects of these interactions on prey diversity, we performed mesocosm experiments on two different prey communities (hereafter, multiple prey and single prey) using the larval stages of two ecologically similar sympatric salamander species, *A. opacum* and the ringed salamander (*Ambystoma annulatum*). In the multiple-prey experiment, we tested overall community response to the predators with five prey species. Because of similarities in life history and limited documentation of antagonistic interactions at the larval stage for these species (Ousterhout et al., 2015), we expected functional redundancy between the two intermediate-level predators on prey response variables, and equivalent MPES. As well, because of the predicted functional redundancy between the two predator species, we expected that intraspecific and interspecific MPES would be equivalent in magnitude in both experiments.

MATERIALS AND METHODS

Focal Species.—Ambystomatid salamanders are pond-breeding species, all of which have aquatic larvae that serve as top or intermediate predators in pond communities (Morin, 1983, 1995; Relyea and Yurewicz, 2002; Anderson and Whiteman, 2015). *Ambystoma annulatum* are endemic to the Ozark highlands and Ouachita Mountains of Missouri, Arkansas, and Oklahoma (Petranka, 1998), and are a species of conservation concern across their distribution. *Ambystoma opacum*, however, are a common and wide-ranging species found across eastern North America, with populations as far west as Texas and as far north as New Hampshire (Petranka, 1998).

Although most species in the genus breed in the spring, both *A. annulatum* and *A. opacum* breed in the fall (Petranka, 1998). Fall breeding requires larvae to overwinter, permitting these two species to serve as important predators on aquatic amphibian communities that develop in the spring because of their phenology-induced size advantage (Cortwright and Nelson, 1990; Urban, 2007; Anderson and Semlitsch, 2014). Most work on *A. annulatum* has focused more on their impacts on a congeneric spring-breeding species, the spotted salamander (*Ambystoma maculatum*), rather than their effects on overall prey diversity and abundance in pond communities (Anderson and Semlitsch, 2014, 2016; Anderson et al., 2017). Larval *A. opacum* are also known to be voracious predators in aquatic food webs (Stenhouse et al., 1983; Cortwright and Nelson, 1990; Urban, 2007, 2010). Both species can co-occur where their ranges overlap and often breed in the same ponds; however, ponds with only one species are not uncommon (Ousterhout et al., 2015).

Multiple Prey Experiment.—To assess functional redundancy and the predatory abilities of *Ambystoma* larvae, we conducted a 3-mo-long mesocosm experiment with five prey species. Briefly, we filled each of 16 1,100-L plastic mesocosms (1.83 m diameter \times 0.6 m high, Behlen Country Farm and Ranch Equipment®) with tap water and rested them for 1 wk before adding a water conditioner (AmQuel by Kordon®) to eliminate chloramine from the water supply. We inoculated each mesocosm with two 500-mL samples of local pond water to establish a zooplankton and periphyton community as well as adding 1.5 kg of dry leaf litter to serve as substrate (primarily *Quercus* spp.; Anderson and Whiteman, 2015). We left all mesocosms open to allow natural deposition of additional prey items (Anderson and Semlitsch, 2014; Anderson and Whiteman, 2015) and drilled 5-mm holes into the lips to allow for drainage of excess rainwater. All predatory invertebrates that were observed in mesocosms were too small to interfere with our experiment (larval *Gyrinidae* spp. and *Dytiscidae* spp. \leq 1.5 cm in total length) and were removed daily.

We collected larvae of both predator species and most anuran prey in March 2016. We collected all *A. annulatum* larvae from three ponds at Fort Leonard Wood (hereafter, FLW) in Pulaski County, Missouri and all *A. opacum* larvae from three wetlands in Jackson County, Illinois. We acquired tadpoles either by collecting multiple partial egg masses (*Anaxyrus americanus*: 5 masses, *Pseudacris feriarum*: 10 masses, *Rana sylvatica*: 10 masses, and *Rana sphenoccephala*: 6 masses) or amplexant pairs of adults that then laid eggs in captivity (*Pseudacris crucifer*: 10 pairs) from ponds in Bollinger, Cape Girardeau, Wayne, and Scott counties of Missouri. We collected all organisms via dip net, hand capture, or metal minnow trap and transported them to an experimental facility at Southeast Missouri State University (SEMO) that had large windows, resulting in natural 12 : 12 light : dark cycle. Air temperature was constant throughout holding at 19–21°C. We held egg masses individually in plastic containers (30 \times 15 \times 11.5 cm) filled to a standard volume and changed the water every other day until hatching. Upon hatching, we counted tadpoles from each egg mass equally for each mesocosm and added them to the mesocosms.

We randomly assigned all organisms to one of four different experimental food webs: (1) Control with only prey, (2) six *A. opacum* with prey, (3) six *A. annulatum* with prey, and (4) three *A. opacum* and three *A. annulatum* with prey (hereafter “mixed”). We replicated each food web 4 times for 16 total mesocosms arranged in 4 experimental blocks (1 replicate per block). We stocked each mesocosm with the same number of an assortment of tadpole prey that co-occur in natural ponds. Previous studies have used 150–650 larval amphibian prey in each mesocosm (Fauth and Resetarits, 1991; Fauth, 1999; Chalcraft and Resetarits, 2003a). Thus, we used a total of 540 tadpoles per mesocosm for this experiment, according to availability: 100 American toads (*Anaxyrus americanus*), 160 southern leopard frogs (*Rana sphenoccephala*), 140 wood frogs (*Rana sylvatica*), 15 upland chorus frogs (*Pseudacris feriarum*), and 125 spring peepers (*Pseudacris crucifer*; Morin, 1983; Wilbur, 1997; Alford, 1999). We size-matched predators before adding them to mesocosms; all predators in a single mesocosm were \pm 0.07 g (*A. annulatum*: mean = 0.64 g, range = 0.37–1.14; *A. opacum*: mean = 0.82 g, range = 0.51–1.10). We apportioned individuals across all treatments and blocks such that each block and treatment had roughly equivalent body size ranges of predators, and to reduce the variance in total biomass across predator treatments; refer to Table S1 for raw predator size data.

We used densities of tadpole prey as well as salamander predators that fall within naturally occurring conditions and we held total predator density constant with a substitutive design (Morin, 1983; Petranka, 1989; Scott, 1990; Ousterhout and Semlitsch, 2015; Semlitsch et al., 2015).

We added *R. sphenocéphala*, *R. sylvatica*, *P. feriarum*, and *P. crucifer* tadpoles to mesocosms on 24 March 2016 and salamander predators on 26 March 2016. We added *A. americanus* tadpoles on 27 April 2016. This species often breeds later than the other prey species; thus, the addition of *A. americanus* tadpoles at a later date follows natural phenological progression. We monitored and maintained the mesocosms until metamorphosis was completed by all species, or the majority of remaining organisms had halted development in preparation for overwintering as larvae (approximately 70 d, *R. sphenocéphala* only). We defined metamorphosis as forelimb emergence for tadpoles or gill absorption for salamanders. We measured size at metamorphosis in terms of mass upon complete reabsorption of the tail or gills in the lab (Semlitsch et al., 1988). We handled and housed all animals in accordance with Institutional Animal Care and Use Committee (IACUC) policies.

Single Prey Experiment.—To test for functional redundancy and MPEs of *A. annulatum* and *A. opacum* on one of our prey species further, we conducted a 2-d experiment from 21–23 April 2015 on a covered outdoor patio attached to a greenhouse. We collected multiple masses of *R. sphenocéphala* eggs from a roadside ditch at FLW on 22 March 2015. We transported the eggs back to the lab, where we stored them in plastic containers filled with 10 L of water, and changed the water every few days. Eggs hatched on approximately 5 April 2015. We collected larval salamander predators from several ponds at FLW on 20 April 2015 and housed them in individual containers for 24 h to ensure viability and to standardize hunger levels. We filled plastic containers (32 × 9 × 11 cm) with 3 L of tap water and let stand for 4 d prior to the start of the experiment to allow chlorine to evaporate. We set up containers on two tables outside that received natural light but were underneath a shade cloth suspended above the tables, which limited direct sunlight. We also added three pieces of window screen to each container that we glued into an irregular shape as refuge (Drake et al., 2014). We lined the outside walls of each container with paper to limit disturbance and visual cues but left the top open to conduct observations.

We had 5 predator treatments (outlined below) crossed with 2 prey densities (10 or 20 tadpoles). We had two blocks (the two tables), with three replicates per block randomly assigned to containers for a total of six replicates per treatment. Our predator treatments employed both substitutive and additive designs (Griffen, 2006; Soomdat et al., 2014) as follows: (1) one *A. annulatum* with tadpoles, (2) one *A. opacum* with tadpoles, (3) one *A. annulatum* and one *A. opacum* with tadpoles, (4) two *A. annulatum* with tadpoles, and (5) two *A. opacum* with tadpoles.

Larval salamander body size often impacts predation rates on amphibian prey (Maret and Collins, 1996; Urban, 2007; Anderson et al., 2020). Therefore, we haphazardly selected individuals matched for size in treatments that contained two larvae to minimize size bias in interactions in the same manner as for the multiple-prey experiment (*A. annulatum*: mean = 8.95 mm, range = 6.55–11.70; *A. opacum*: mean = 8.73 mm, range = 6.49–12.20). We photographed predators at the end of the experiment to measure head width and snout–vent length (SVL) using ImageJ 1.5 (Schneider et al., 2012). We started the experiment at 2000 h on 21 April 2015. We recorded how many

prey were alive after a 48-h period on 23 April 2015. We handled and housed all animals in accordance with IACUC policies.

Data Analysis.—We analyzed the multiple-prey experiment using the program R 3.3.2 to assess the predatory effects of salamanders on each experimental food web (R Core Team, 2019). We performed a MANOVA (“MANOVA” function in base R) on mass at metamorphosis and larval period for each prey species, using predator treatment as the predictor. We used survival as a covariate to control for the effect of prey species density on these response variables. If the MANOVA was significant, we then examined univariate ANOVAs. We also performed an ANOVA for diversity. Survival for salamander larvae and tadpoles is defined as the sum of (1) the number of individuals that underwent metamorphosis, and (2) the number of larvae that survive to the experiment’s end date, reported as a proportion of initial input. We used generalized linear mixed models with binomial errors to analyze survival, with treatment and block as predictors and an individual level random effect to account for overdispersion in the data (Warton and Hui, 2011). If no individuals survived from any replicate of given treatment, that treatment was removed from the analysis because it would create complete separation in the data. Likewise, if no individuals underwent metamorphosis, we removed that treatment from larval period and mass analyses (*R. sphenocéphala*). Larval period was unknown for salamanders as they were collected as already hatched larvae. However, anuran tadpoles were collected as eggs; larval period was defined as the number of days from the date of addition to the mesocosm to date of total tail absorption. All ANOVAs used the Tukey multiple comparison of means with 95% family-wise confidence levels to assess treatment differences. Finally, Simpson’s diversity index (hereafter, diversity) was calculated for anuran prey for each tank, providing a measure of species evenness in each treatment (R package “vegan”). Block effects were not significant ($P > 0.05$) for all responses except for diversity and *P. crucifer* survival, which were significant. Thus, block was retained for all statistical models. We determined the coefficient of determination for mass, larval period and diversity models. For the survival models, we determined the variance explained by the fixed effects using the *r.squaredGLMM* function in the ‘MuMIn’ package. Following the experiment, we euthanized all surviving metamorphs and larvae and placed specimens in the Natural History Museum at the author’s institution.

For the single-prey experiment, we again used a generalized linear mixed model with predator treatment, prey density, predator size (mean head width), and block as predictors. We averaged head width across the two individuals when present. We started with fitting a three-way interaction of predator treatment, predator size, and prey density, and sequentially dropped nonsignificant interactions terms, but always retained the manipulated variables (prey density and predator treatment). We again determined the variance explained by the fixed effects using the *r.squaredGLMM* function in the ‘MuMIn’ package.

To determine whether *A. annulatum* and *A. opacum* exhibited MPEs in both the multiple-prey and single-prey experiments, we replicated the analysis of Soomdat et al. (2014) to assess our expected values of prey survival with the different combinations of predators based on the multiplicative risk model (MRM, Soluk, 1993; Sih et al., 1998; Vance-Chalcraft and Soluk, 2005) and compare them to the observed survival data. In the single-prey experiment, we calculated the expected survival for *R. sphenocéphala* in the additive design (*A. annulatum* + *A. opacum*)

as follows:

$$E_{A,O}=(P_A \times P_O)/P_C,$$

where $E_{A,O}$ is the expected proportional survival with both predator species, P_A is the average survival with one *A. annulatum*, P_O is the average survival with one *A. opacum*, and P_C is the survival in a predator-free control. We did not have a control treatment with no predators, but assumed background prey mortality was equal across treatments. For the substitutive design, we calculated the expected survival as

$$E_{A,A}=(P_{A,A} \times P_{O,O})^{0.5},$$

where $P_{A,A}$ and $P_{O,O}$ are the average survival with two *A. annulatum* and two *A. opacum* respectively. Similar to Soomdat et al. (2014), we also calculated the expected proportional survival when *R. sphenoccephala* was preyed upon by pairs of conspecifics, where $E_{A,A} = (P_A \times P_A)/P_C$ for *A. annulatum* (*A. opacum* not shown). We calculated the expected survival separately for each prey density. For the multiple-prey experiment, we could not compute the expected survival for all anuran prey as some had survival rates of zero, which resulted in expected survival of zero based on the MRM. Therefore, we focused only on *R. sphenoccephala*, which we could compare across both experiments. We used the substitutive design of the MRM above, but included the survival in the control food web. For each experiment, we determined whether MPEs occurred by comparing whether the 95% confidence intervals for the observed effects included the expected value; if the expected value was outside this range, we inferred MPEs to have occurred (Soomdat et al., 2014).

RESULTS

Multiple-Prey Experiment.—*Anaxyrus americanus* survival was highest in the *A. opacum* food web (69.5%) and the control food web (43.8%), differing significantly from both the mixed food web (7.8%) and the *A. annulatum* food web (0.0%, $\chi^2 = 41.889$, $P < 0.001$, $R^2 = 0.47$; Fig. 1a, Table S2). *Pseudacris crucifer* emerged from all experimental food webs, but survival was low overall (<11%); survival was higher in the *A. annulatum* food web (10.4%) than in any other food web ($\chi^2 = 22.175$, $P < 0.001$, $R^2 = 0.21$; Fig. 1b, Table S2). *Rana sphenoccephala* survival was significantly higher in the *A. annulatum* food web (5.7%) than in the *A. opacum* food web (0.2%), and was higher in the control food web (20.3%) than in any other food web ($\chi^2 = 30.624$, $P < 0.001$, $R^2 = 0.57$; Fig. 1c, Table S2). This indicates that *A. opacum* selectively preyed upon *R. sphenoccephala* as compared to the differential predation displayed by *A. annulatum*. *Rana sylvatica* did not emerge from any food webs and *P. feriarum* survived only in the control food web. Therefore, we did not conduct a formal analysis for either species. Total anuran survival was highest in control and *A. opacum* food webs (16.1% and 13.5%, respectively) and lowest in *A. annulatum* and mixed food webs (4.1% and 2.3%, respectively; Fig. 2).

There was no significant difference in larval period of any anuran among food webs with surviving individuals (Table S3, S4, Fig. S1). *Anaxyrus americanus* and *R. sphenoccephala* mass at metamorphosis was not significantly different among food webs with surviving individuals. However, *P. crucifer* emerged from mixed food webs larger than from control food webs ($F_{3,9} = 5.316$, $P = 0.022$, $R^2 = 0.41$; Tables S5, S6, Fig. S2), indicating

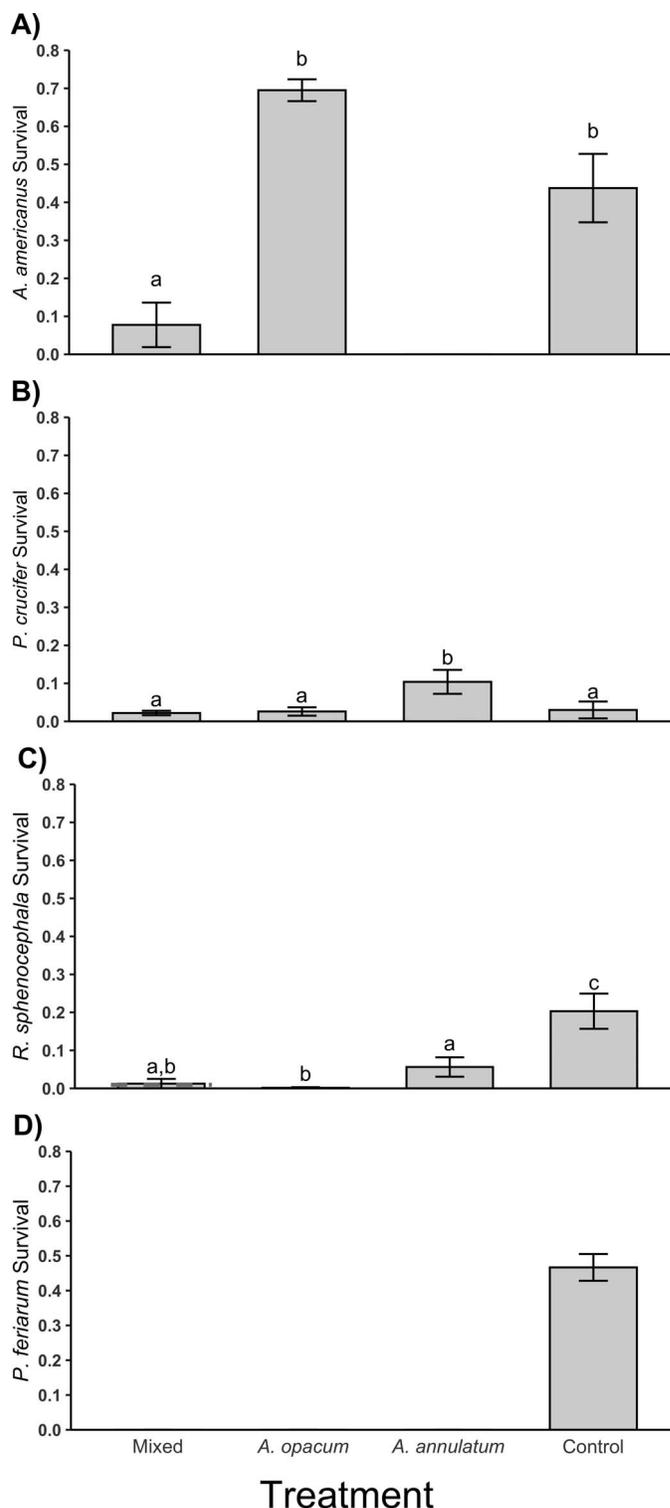


FIG. 1. Mean proportional survivorship of (a) *Anaxyrus americanus*, (b) *Pseudacris crucifer*, and (c) *Rana sphenoccephala* across predator treatments in the multiple-prey experiment. Lower-case letters above bars identify pairs of means that are significantly different. Red lines indicated expected survival values based on the additive design of the MRM. Values shown are treatment means \pm 1 SE. $n = 4$ in all cases.

that a thinning effect may have occurred when both predators were present.

Predator food web had significant effects on anuran diversity ($F_{3,9} = 8.620$, $P = 0.005$, $R^2 = 0.66$). Food webs with six *A.*

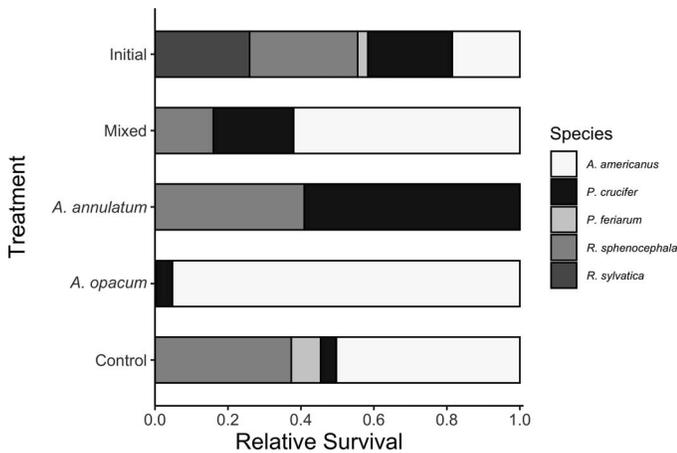


FIG. 2. Proportion of total tadpoles surviving in the multiple-prey experiment is shown by total bar height. Species composition of surviving individuals is broken down by food web.

opacum had lower anuran diversity than control food webs ($P = 0.003$; Fig. 3). Additionally, there were marginal statistical differences in diversity measures between *A. annulatum* and *A. opacum* food webs, with the *A. annulatum* food web diversity being higher, as well as between mixed and control food webs, with the mixed food web being lower ($P = 0.054$ and $P = 0.096$, respectively; Fig. 3, Table S7).

Predator food web had no significant effect on survival for *A. annulatum* ($\chi^2 = 0.112$, $P = 0.738$, $R^2 = 0.16$) or *A. opacum* ($\chi^2 = 0.107$, $P = 0.744$, $R^2 = 0.006$). Survival was on average higher for *A. opacum* than *A. annulatum*, regardless of food web ($\chi^2 = 5.042$, $P = 0.02$; Fig. S3). On average, *A. annulatum* emerged from experimental food webs 29.4% larger than *A. opacum*. *Ambystoma annulatum* averaged 2.044 g at metamorphosis, and *A. opacum* emerged at 1.444 g (Table S8, Fig. S4). Additionally, *A. opacum* in our experiment emerged from food webs earlier and over a shorter period of time than *A. annulatum*; *A. opacum* metamorphs emerged between 22 April and 5 May, and *A. annulatum* metamorphs emerged between 29 April and 22 May.

Observed survival of *R. sphenoccephala* in the mixed food web (1.3%) did not vary from the expected value (0.9%); that is, the expected value was within the 95% confidence interval (CI) of the observed survival data (Fig. 1). Summary statistics of analysis are presented in the supplementary materials.

Single Prey Experiment.—Survival of *R. sphenoccephala* varied with density ($\chi^2 = 11.318$, $P < 0.001$), predator treatment ($\chi^2 = 52.341$, $P < 0.001$), predator size ($\chi^2 = 17.982$, $P < 0.001$) and block ($\chi^2 = 7.817$, $P = 0.005$), but no interactions among any variables were significant. These factors combined explained a large percentage of the variation in the data ($R^2 = 0.41$). Observed survival was greater in the high-density treatment averaged over predator treatments, and when predators were smaller (Fig. 4a,b). Averaged over density treatments, survival was highest with one *A. opacum*, and lowest with two *A. annulatum* and one *A. annulatum* + one *A. opacum*. Survival was greater with one *A. annulatum* as compared with two, but was not different between one and two *A. opacum*. Survival was also greater with two *A. opacum* compared to one *A. opacum* + one *A. annulatum* and two *A. annulatum* (Fig. 4c). See Table S9 for all pairwise differences.

Observed survival of *R. sphenoccephala* was not different from expected survival with one *A. annulatum* + one *A. opacum*, using either the additive or substitutive versions of the MRM for both low (additive expected: 15.0%; substitutive expected: 14.7%)

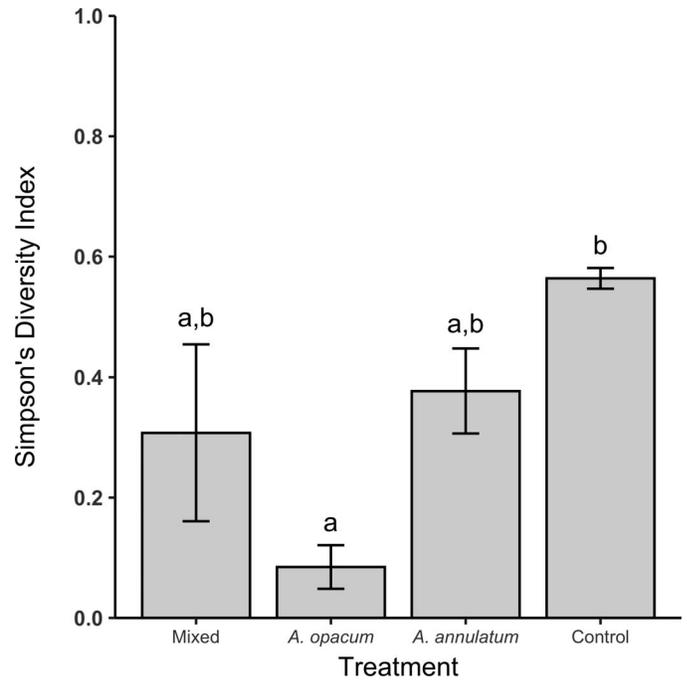


FIG. 3. Mean species diversity among predator treatments as represented by the Simpson's diversity index in the multiple prey experiment. Lower-case letters above bars identify pairs of means that are significantly different. $n = 4$ in all cases.

and high densities (additive expected: 40.7%; substitutive expected: 21.2%; Fig. 4); the 95% CI of survival in all cases included the expected values. Similarly, the expected values of the additive MRM for intraspecific pairs (i.e., comparisons of one versus two *A. annulatum*) were also within the 95% CI of the observed data (*A. annulatum* low: 4.0%; *A. annulatum* high: 33.1%; *A. opacum* low: 56.3%; *A. opacum* high: 50.1%; Fig. 4).

DISCUSSION

Complex communities with a diversity of predators and prey present the opportunity for a myriad of interactions, with some species having functionally redundant roles. However, predator–predator interactions may reinforce or weaken the effects of predators on prey. Our results indicate that *A. annulatum* is an important predator to consider in local pond communities, and has the potential to have a large impact. Moreover, in the multiple-prey experiment the effects of *A. annulatum* and *A. opacum* on prey community were remarkably different, dismissing the possibility for functional redundancy. Additionally, and perhaps more interestingly, *A. opacum* significantly reduced diversity as compared to the control food web, whereas *A. annulatum* did not, further supporting the lack of redundancy (Fig. 3). Our results also suggest no significant effects of predators on one another, contrasting with previous work with larval salamanders in this system (Walls and Jaeger, 1987; Walls, 1995; Brunkow and Collins, 1998).

The mechanism of our documented differences in predator effects is likely greater temporal overlap of prey with *A. annulatum*, which occurred because of natural phenology during the year our multiple-prey experiment was conducted. Phenology can play a major role in shaping community structure and interactions in a pond, and can vary significantly on a season-to-season basis (Anderson et al., 2019; Rudolf, 2019). With a minimum of 7 d of additional pond occupancy, *A. annulatum*

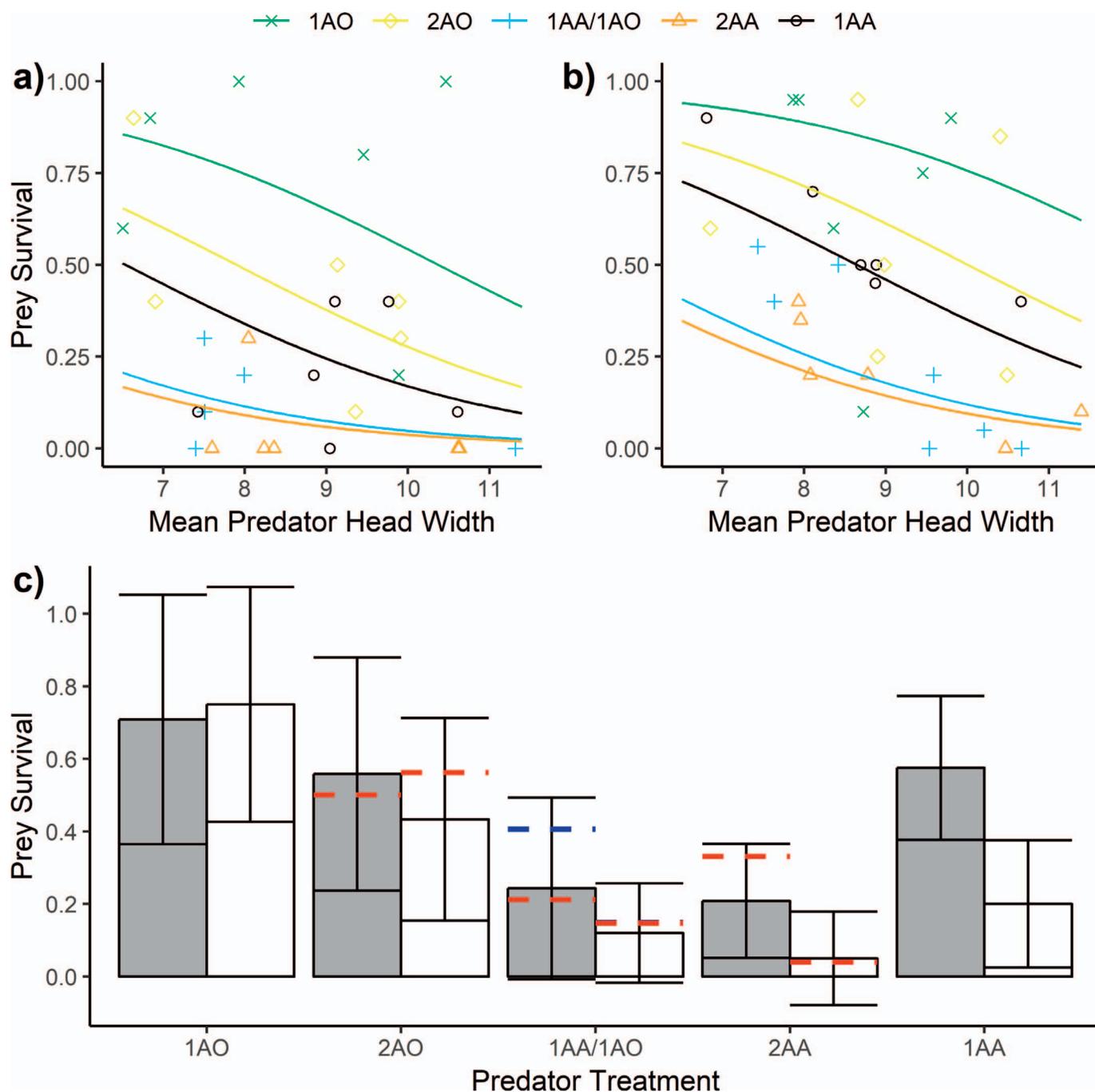


FIG. 4. Prey (*Rana sphenocephala*) survival from the single-prey experiment. Survival is a function of predator treatment (different colors and shapes) and mean predator head width (mm) in low-density (a) and high-density (b) treatments. AO = *Ambystoma opacum* and AA = *A. annulatum*. (c) Shows observed mean survival (\pm 95% CI) based on predator treatment and prey density (gray bars = high density, white bars = low density), compared with expected survival (dashed horizontal lines) for pairs of con- and heterospecifics. Red horizontal lines indicated expected values based on the additive design, whereas the blue lines indicate the substitution design of the multiplicative risk model.

had greater opportunity to prey on tadpoles, in particular the competitively dominant prey species (*A. americanus*), which were added to mesocosms at a later date than the other prey. Seventeen salamanders across all treatments (all *A. opacum*) emerged on or before the date of *A. americanus* addition and the 12 remaining surviving *A. opacum* emerged in the 8 d following *A. americanus* addition. Because *A. opacum* metamorphosed earlier than *A. annulatum*, it had a shorter overlap with *A. americanus*. This allowed *A. americanus* to survive in *A. opacum* food webs (now without predators) while still being consumed

in *A. annulatum* food webs, although prey preference, discussed below, may also play a role. Differences in timing of metamorphosis between these species have been consistent across other experiments (Anderson, unpubl. data), suggesting this life history difference may be characteristic, though evidence from natural ponds is needed. Phenological mismatches have been linked with strong impacts in predator-prey studies (Alford, 1989; Lawler and Morin, 1993; Anderson and Semlitsch, 2014) and are important to consider for future studies.

Contrary to our hypotheses, we found that *A. opacum* and *A. annulatum* did not exhibit redundant roles as predators. This matches the findings of several other tests of functional redundancy, where predator species were not replaceable (Kurzava and Morin, 1998; Chalcraft and Resetarits, 2003b; Resetarits and Chalcraft, 2007). In our case, both species served as strong predators in our experimental ecosystems, with several prey taxa exhibiting low survival values consistent with other studies (Wilbur, 1987; Fauth and Resetarits, 1991). However, the resulting anuran prey community was different; *A. annulatum* consumed more *A. americanus* tadpoles and *A. opacum* consumed more *R. sphenoccephala* tadpoles. In years with greater temporal overlap among *A. opacum* and late spring-breeding anurans, it is possible that *A. opacum* would consume *A. americanus* tadpoles as well, but this interaction is likely dictated by year-to-year variation in breeding phenology. The presence of *A. annulatum* in a mesocosm did not result in statistically increased diversity as compared to *A. opacum*, but there is reasonable evidence for a biological effect; diversity in food webs containing *A. annulatum* was more than double that of diversity in food webs containing only *A. opacum*. Our mixed food web treatment in the multiple-prey experiment did not differ significantly from either single-species treatment for any of the response variables; however, it appears that the temporal mismatch exhibited by *A. opacum* was enough to increase diversity in mixed treatments marginally, with more *A. americanus* surviving. As well, predators in this study were matched for size within each mesocosm. In a natural system, size variation may result in even more striking nonredundancy because of competition or aggression between predators.

Several other mechanisms could also explain the effects of *A. annulatum* in our multiple-prey experiment, although natural phenology in our study system made it difficult to test species-specific effects. First, it is possible that selective predation upon *A. americanus* by *A. annulatum* produced the differences in prey community composition, but we lack definitive evidence of dietary preferences. To our knowledge, there are no studies that have documented the dietary preferences of either *A. opacum* or *A. annulatum*. Regardless of cause, consumption of the stronger competitor (*A. americanus*) allowed less competitive prey species like *P. crucifer* and *R. sphenoccephala* to survive until metamorphosis. Second, both *A. annulatum* and *A. opacum* overlap in geographic range and often co-occur in a single pond (Peterman et al., 2014). Interspecific competition could reduce the effectiveness of *A. opacum* as a predator, though we saw no evidence of risk reduction (i.e., interference) in either the multiple-prey or single-prey experiment, at least for the one prey species we tested. Finally, range overlap of these two predators could result in higher larval salamander densities than would be documented if only one species was present, which would not occur in other portions of *A. opacum*'s range. Larval density of ambystomatids affects larval traits via intra- and interspecific competition (Stenhouse et al., 1983; Stenhouse, 1985) and can have significant negative effects on size at metamorphosis and survival in *A. opacum* (Scott, 1990). Therefore, interspecific competition may complicate the interaction between these two species when they overlap.

Multiple predator effects have been documented under numerous contexts, including prey density, habitat complexity, and predator body size. In the single-prey experiment, we found that prey density did not influence MPEs and risk enhancement/reduction. This result was somewhat surprising given larval ambystomatids are thought to be highly aggressive,

although behavioral aggression is poorly studied in *A. annulatum* (Walls and Jaeger, 1987; Brunkow and Collins, 1998; Brodman, 2004). This could have occurred because of one predator overwhelmingly influencing mortality, and the second predator contributing only a minor effect (Sih et al., 1998); if this occurred in our experiment, the more effective predator was likely *A. annulatum*, given its significantly higher impact on survival compared to *A. opacum* when either alone or in conspecific pairs (Fig. 4). Intra- and interspecific MPEs were equivalent in our single-prey experiment, indicating that there is potential for functional redundancy between these species when only one prey species is present; however, this scenario is unlikely in natural environments and has limited biological relevance. We also found that tadpole survival varied with predator size, a known result caused by larvae being gape-limited predators; large larvae are not as limited by gape size as their smaller counterparts, and are therefore more effective at consuming prey over a longer period of time (Urban, 2007; Anderson et al., 2016). Additionally, as *A. annulatum* and *A. opacum* share habitats and have similar life history traits, there is potential for niche partitioning and aggression via behavioral differences.

Interestingly, our experiment showed no significant difference in diversity between *A. annulatum* and control food webs, but did indicate a significant difference between *A. opacum* and control food webs (Fig. 3). At the same time, tadpole survival in control food webs was higher and on average, tadpoles emerged smaller, and took longer to emerge (Figs. 1, S1, S2). We hypothesize that a thinning effect occurred in food webs containing *A. annulatum* that reduced the total number of surviving larval anurans, lessening the strength of interspecific competition among surviving prey (Van Buskirk and Yurewicz, 1998; Davenport and Chalcraft, 2012; Anderson and Semlitsch, 2014). Individuals that emerged from *A. annulatum* treatments were larger and emerged earlier than individuals in the control food webs, both of which are variables linked to increased reproductive success in amphibians (Berven and Gill, 1983; Smith, 1987; Semlitsch et al., 1988). Additionally, by inflicting greater mortality upon competitively dominant prey species (*A. americanus*), *A. annulatum* relieved competitive pressure on weaker anuran species and affected overall diversity. Prey item choice by predators can directly and indirectly affect interspecific competition between tadpoles and has drastic effects on ecosystem structure (Morin, 1983, 1995). In short, predator presence thinned larval anuran populations enough to result in lower overall anuran survival, but greater potential fitness for survivors.

Our results indicate the importance of understanding how different predator species may play vital roles in shaping local ecosystem structure. Identifying additional situations of functional redundancy as well as varied prey survival via MPEs will aid in future management decisions. The consequences of MPEs are often context dependent and in some systems may alter biodiversity in an unpredicted manner, though this was not the case for our experiment. Further research should prioritize and elucidate how MPEs can predict the outcomes of range-restricted species. Understanding the conditions under which predators can be redundant also has important conservation implications. If a greater per-capita effect is observed for our focal species (*A. annulatum*) on a local scale, there is great potential for other endemic species to do the same. Identifying specific traits or indicators of interacting variability are pivotal to enhancing the likelihood of maintaining biodiversity. In the

future, a better understanding of geographical variation and ecosystem-level function can initiate management decisions to protect endemic species and preserve biodiversity.

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SUPPLEMENTARY DATA

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