Functional Responses of Larval Marbled Salamanders (*Ambystoma opacum*) and Adult Lesser Sirens (*Siren intermedia*) on Anuran Tadpole Prey

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Predation can have strong effects on the structure of pond-breeding amphibian communities. Many factors can influence the outcome of predator–prey interactions, including differences in densities, identities, and body sizes of both predator and prey. These different mediating factors can impart synergistic impacts on predation rates, though distinguishing such interactions among multiple factors are underexplored. We examined whether different body sizes of two predators, larval Marbled Salamanders (*Ambystoma opacum*) and adult Lesser Sirens (*Siren intermedia*), varied in their ability to forage on larval anurans across a range of prey densities. We specifically tested whether attack rates and handling times, the two main parameters of functional response models, varied across three size classes in both predator species. We found that larval Marbled Salamanders exhibited a Type II (saturating) functional response and that larger individuals had higher attack rates and shorter handling times, resulting in greater prey mortality at higher prey densities with larger predators. In contrast, Lesser Sirens were largely ineffective predators despite being an order of magnitude larger in body size than Marbled Salamanders; tadpole mortality was largely unrelated to their own density. Predator body size was a significant predictor of prey mortality for both predator species. Overall, our study shows that species identity could be as important as predator body size when predicting the outcomes of predator–prey interactions.

T HE outcome of predator–prey interactions is often mediated by numerous factors, including densities of either the predator or prey (Holling, 1959; Stier et al., 2013), food web complexity (Walls and Williams, 2001; Davenport and Chalcraft, 2012), species identity (Chalcraft and Resetarits, 2003a; Anderson et al., 2016a), or variability in predator–prey body size ratios (Woodward and Hildrew, 2002; Brose et al., 2006). Because prey survival can vary concurrently with many of these and other mediating factors (e.g., Anderson and Semlitsch, 2016; Uiterwaal et al., 2017), it is important to evaluate how synergistic impacts can affect predator–prey dynamics. Disentangling these context-dependent interactions can ultimately help determine which factors best predict community structure and variability in the outcomes of species interactions (Agrawal et al., 2007).

The relative sizes of predators and species identity are particularly important in predator–prey dynamics. For instance, the greater the difference in body size ratios between predators and prey can alter predator foraging rates (e.g., greater efficiency of larger predators over smaller prey), influence handling times (e.g., larger predators having reduced gut limitations or shorter search efforts because of greater vagility), or otherwise alter prey susceptibility (Emmerson and Raffaelli, 2004; Kalinkat et al., 2013; Uiterwaal et al., 2017), leading to changes in the stability of food webs (Woodward and Hildrew, 2002). Changes in predator–prey dynamics based on body size differences are especially relevant for gape-limited predators, where consumption can only occur if prey do not exceed the gape of the predator (Persson et al., 1996). When comparing across predator species, however, differences in body size alone may not be sufficient to determine predator effects: similarly-sized individuals of different predator species could have asymmetric interaction strengths with prey species, leading to complex community outcomes from these two factors.

Because of the commonality of this potential scenario, understanding functional redundancy (Chalcraft and Resetarits, 2003a; Resetarits and Chalcraft, 2007) among both predator species and size classes is an important but underexplored aspect of predator–prey dynamics.

Predator–prey interactions have been well studied in larval stages of pond-breeding amphibians and identified as a dominant process for both population and community dynamics (Wellborn et al., 1996; Wilbur, 1997). Several predator species have been shown to have a disproportionate impact in structuring these communities, including fishes, aeshnid dragonflies, and obligately aquatic salamanders (e.g., adult Red-Spotted newts; Morin, 1983; Hecnar and M'Closkey, 1996; Semlitsch et al., 2015). Many of these predaceous taxa also have size-structured populations, resulting in differential threats to prey, depending on encounter rates with each species and size class (Wilbur, 1988). However, despite the importance of this relationship, simultaneous comparisons across predator size classes and species and their effects on amphibian prey are infrequent.

Despite our knowledge of predator–prey dynamics in pond ecosystems, predator functional response curves are still poorly understood. Studies that manipulate a predator foraging across a range of prey densities have rarely been performed in these assemblages (Travis et al., 1985; Vonesh and Bolker, 2005; Hossie and Murray, 2010; McCoy et al., 2011; Anderson, 2016), but would be expected to vary across the different axes of mediating factors outlined above. The few studies that have examined predator functional response curves typically have used amphibians as prey (cited above), rather than the predator (but see Ranta and Nuutinen, 1985; Anderson et al., 2016a; Thorp et al., 2018). Previous studies with larval ambystomatids have focused on only two size classes (Anderson et al., 2016a), which, while useful for predictive models, is less informative about natural size-

structured populations that typically exemplify salamander assemblages (Ziemba and Collins, 1999; Anderson et al., 2016b; Mott and Sparling, 2016). Furthermore, how ambystomatids forage on anuran tadpoles, relative to congeners (Anderson et al., 2016a), across a range of densities is also unknown, which may result in different outcomes due to varied responses of each group to predation threats (Relyea, 2007). Such studies are needed to better connect natural dynamics to ecological theory, which ultimately will lead to better predictive models of population and community dynamics.

In this study, we evaluated whether three different size classes of two predator species, Lesser Sirens (*Siren intermedia*) and larval Marbled Salamanders (*Ambystoma opacum*), varied in their functional response curve shape, as well as attack rate and handling time parameter estimates. We tested these predators' foraging abilities on tadpoles of commonly co-occurring anurans: Lesser Sirens were exposed to tadpoles of the Southern Leopard Frog (*Rana sphenocephala*) and Marbled Salamanders to tadpoles of the Upland Chorus Frog (*Pseudacris feriarum*). Based on previous studies (Anderson et al., 2016a), we expected both species to forage with a Type II functional response, and for larger size classes of each species to have higher attack rates and shorter handling times. We also expected Lesser Sirens to have higher attack rates and shorter handling times than Marbled Salamanders, due to their greater relative body size.

MATERIALS AND METHODS

Study system.—Lesser Sirens, Marbled Salamanders, Southern Leopard Frogs, and Upland Chorus Frogs are widely distributed species across the southeastern US. Being obligately paedomorphic, Lesser Sirens only occur in permanent wetlands, whereas Marbled Salamanders and both frog species occupy wetlands across a gradient of water permanency. Both Lesser Sirens and larval Marbled Salamanders are top predators in permanent wetlands (Fauth and Resetarits, 1991), in some cases filling keystone roles (Morin, 1995). To our knowledge, data exist on foraging of Marbled Salamanders, but there is nothing known on Lesser Siren foraging ecology. Tadpoles of both frog species can be a common prey species of Marbled Salamanders and Lesser Sirens (Fauth and Resetarits, 1991; Chalcraft and Resetarits, 2003a; Hampton, 2009).

Experimental set-up.—This experiment occurred at Southeast Missouri State University (SEMO) in March 2018. We filled 60 plastic containers (30 × 15 × 11.5 cm) with homogenized local pond water to a standardized volume (approximately 250 mL). Pond water provided natural periphyton for tadpole consumption during experiments. The containers were placed inside a room within an experimental facility at SEMO that had large windows, resulting in natural 12:12 light:dark cycle. Air temperature was constant throughout the experiment at approximately 21°C. No cover was provided for predators or prey, which could amplify foraging rates and reduce handling times relative to interactions in natural ponds as predators would have unimpeded access to prey.

We collected Southern Leopard Frog egg masses from Cape Girardeau County on 27 February 2018 and Upland Chorus Frog egg masses from Scott County, Missouri on 6 March

Table 1. Mean and standard deviation (SD) in body mass (in grams) and snout–vent length (SVL, in cm) of each size class of Marbled Salamander and Lesser Siren predators. SVL was not measured for Marbled Salamanders.

Species	Size	Mean mass	Mass SD	Mean SVL	SVL SD
Marbled Salamander	Large	0.59	0.09		
	Medium	0.26	0.02		
	Small	0.13	0.02		
Lesser Siren	Large	62.85	25.51	21.84	2.36
	Medium	23.63	9.42	16.12	1.63
	Small	13.49	1.49	13.43	0.52

2018 and brought them back to the experimental facility at SEMO upon collection. We used two different prey species because we could not obtain enough eggs of either one by themselves. Southern Leopard Frog eggs hatched on 4 March 2018, and Upland Chorus Frog eggs hatched on 11 March 2018. We used Lesser Sirens collected from local wetlands near SEMO between 2 March 2018 and 8 March 2018, which were part of ongoing mark–recapture efforts (Davenport, unpubl. data). Larval Marbled Salamanders were collected from a variety of locations (Ohio, North Carolina, and Mississippi) across eastern USA between 2–26 February 2018 for other unrelated projects (Davenport, unpubl. data). Since predators were captured over the course of a few days, we likely had variability in time since last meal in nature. Therefore, we housed all predators individually for at least 12 hours to standardize hunger levels.

We used five tadpole prey densities (5, 10, 20, 40, or 80 tadpoles per container; Gosner stage 23–25), with two replicates per density. We crossed these prey densities across three predator size classes for each of our predator species. We sorted each predator species into the three size classes and weighed them (in grams, Table 1). We also measured SVL of Lesser Sirens, but were unable to for Marbled Salamanders due to their smaller size. We were unable to size match Marbled Salamanders from the different locations, resulting in geographic bias across treatments: 9/10 individuals in the small size class were from North Carolina and 1/10 from Mississippi, all individuals in the medium size class were from Ohio, and the large class had 7/10 individuals from Mississippi and 3/10 from North Carolina. Thus, we acknowledge that our study cannot entirely differentiate size from potential local adaptation in foraging rates across its range for this predator. Functional response trials commenced on 8 March 2018 for Lesser Sirens and 20 March 2018 for Marbled Salamanders, and the number of remaining tadpoles was recorded after 24 hrs.

Analysis.—We first distinguished between Type II (saturating) and Type III (sigmoidal) functional response curves by examining whether initial prey abundance was a predictor of the response, proportion of prey surviving, using generalized linear models with binomial errors (Juliano, 2001). We fit these models separately for each size class to determine size-specific functional response patterns. Each model contained linear and quadratic terms of prey abundance. For all size classes of Marbled Salamanders and the small size class of Lesser Sirens, the linear term was significant and negative, indicating a Type II functional response. We therefore fit Type II functional response curves for all Marbled Salaman-
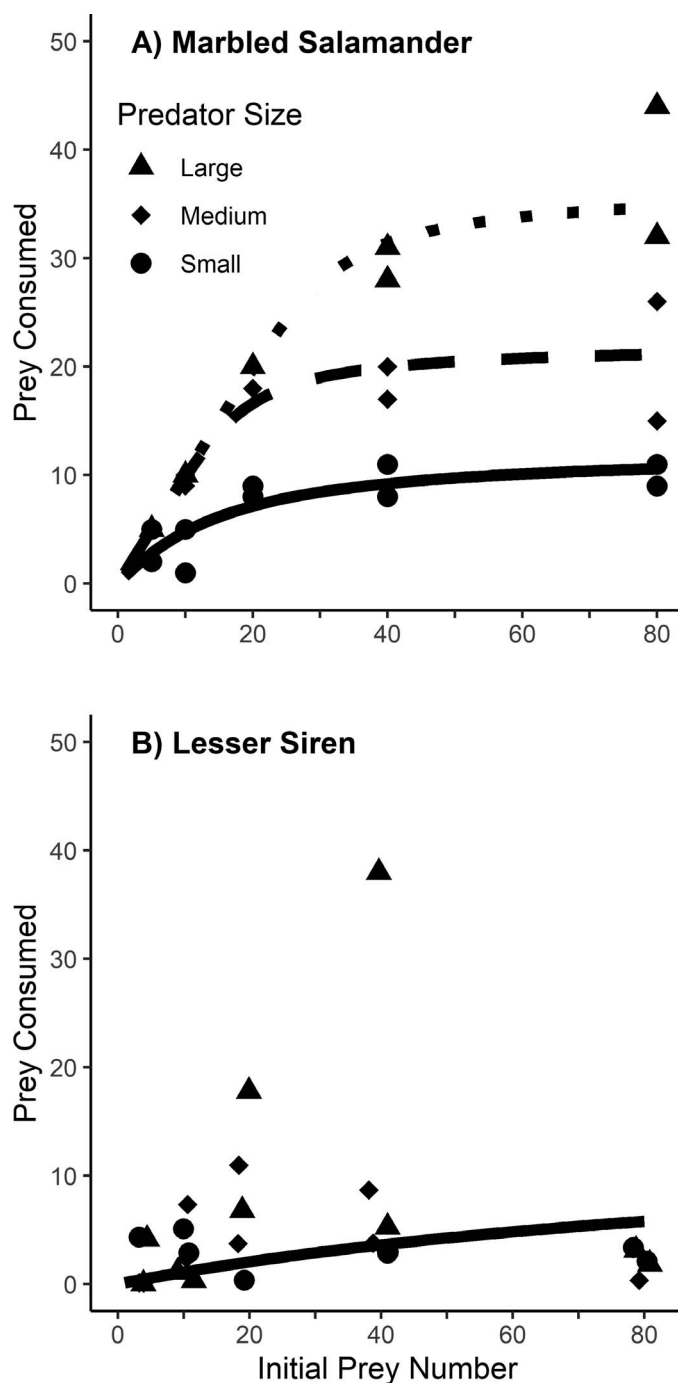
Fig. 1. Functional response curves of Marbled Salamanders (A) and Lesser Sirens (B). Different shapes are empirical data points, coded by predator size class. Points are adjusted horizontally to minimize overlap. Lines are predicted values based on Type II functional response curves, fit with the Roger's random predator equation. No lines are shown for medium and large Lesser Sirens due to inadequate model fit.

der and small Lesser Siren treatments using the 'mle2' function in the 'bbmle' package in R (Bolker, 2008). We used the Roger's random predator equation version of the Type II functional response to account for prey depletion during the study (Juliano, 2001). We fit models for each size class and species separately to estimate attack rate and handling time parameters. We determined differences among size classes by comparing overlap in 95% confidence intervals of parameters.

For medium and large Lesser Sirens, initial prey density was statistically unrelated to proportion preyed upon (see Results), indicating prey mortality rates may be unrelated to their density. Because the typical functional response shapes did not adequately fit the data, we performed an exploratory analysis of prey density with number killed using generalized additive models (GAM), which assess smoothed nonlinear relationships between continuous variables without having to specify a functional form of the model. Such an approach was used to understand whether there were patterns of prey survival and density not revealed through other analyses.

To further understand how variation in predator body size explained prey survival, we fit a single Type II functional response model to the data for all size classes of Marbled Salamanders combined, and extracted the residuals from the model. We then compared whether linear, quadratic, or cubic models of scaled Marbled Salamander size best explained the residuals, i.e., the variation in prey consumption, using AICc (Burnham and Anderson, 2002) and the coefficient of determination (R^2). Given we could not identify a functional response for Lesser Sirens, we did not perform this analysis for this predator. Instead, we analyzed percent prey survival as a function of their scaled mass using a generalized linear model with quasibinomial errors. We initially included linear, quadratic, and cubic terms of Lesser Siren size, dropping higher order polynomials if they were not significant.

RESULTS

Marbled Salamanders.—There was clear separation in functional response curves for the three size classes of Marbled Salamanders, with larger size classes having greater estimated attack rates and shorter estimated handling times compared with smaller size classes (Fig. 1A, Table 2). Using overlap in 95% confidence intervals as our threshold of significant differences among size classes, comparisons among all three handling time estimates were different. However, attack rates of the largest size class had a wide CI range, encompassing the two smaller size classes. The small and medium size classes were different in attack rates, with smaller individuals having lower attack rate estimates (Table 2). A quadratic model of body mass best explained the residuals of a functional response model encompassing data from all size classes of Marbled Salamanders (ΔAICc from quadratic to cubic model: 1.8; $R^2 = 0.71$; Fig. 2), indicating body size explained much of the variation in foraging rates.

Lesser Sirens.—Visually, foraging rates exhibited a quadratic pattern with initial prey numbers, with mortality peaking at intermediate densities before declining to be extremely low at the highest densities, a pattern that does not match any standard functional response curve (Fig. 1B). This pattern was especially pronounced for medium and large Lesser Sirens. However, both the generalized linear models noted above and GAM models revealed that initial prey density was a poor predictor of prey mortality for each size class (all $P > 0.05$). Nonetheless, for small Lesser Sirens, the Type II model converged and revealed that both attack rates and handling times were significantly different from 0 (Table 2). The attack rate was lower than all of the size classes of Marbled Salamanders, while the handling time estimate was greater than the medium and large size classes. A quadratic

Table 2. Functional response parameter estimates for attack rates (a) and handling times (h), standard errors, *P*-values and 95% confidence intervals for different size classes of Marbled Salamanders and Lesser Sirens. Medium and large Lesser Sirens are not shown due to poor model fit.

Species	Size	Parameter	Estimate	SE	P	2.50%	97.50%
Marbled Salamander	Small	a	0.022	0.008	0.007	0.006	0.038
		h	3.928	0.852	0.000	2.259	5.598
	Medium	a	0.150	0.047	0.002	0.057	0.242
		h	2.174	0.203	0.000	1.776	2.572
	Large	a	0.222	0.119	0.063	−0.012	0.456
		h	1.309	0.135	0.000	1.045	1.573
Lesser Siren	Small	a	0.003	0.001	0.001	0.001	0.004
		h	3.406	0.000	0.000	3.406	3.406

regression model of Lesser Siren body size best predicted percent survival (linear term: $P = 0.03$; quadratic term: $P = 0.06$), with highest predicted survival occurring for tadpoles with either small or large Lesser Sirens (Fig. 3).

DISCUSSION

A multitude of factors influence whether individual predators are successful at capturing and consuming prey. Differentiating the relative importance of these diverse factors can help build a comprehensive framework for understanding the forces structuring ecological communities. In this study, we found strong size- and species-specific differences between predators in their ability to consume prey. Marbled Salamanders and Lesser Sirens varied in their ability to consume tadpoles, but only in the former species was there an interpretable and consistent pattern across body sizes—larger salamander larvae had higher foraging rates and showed reduced satiation at higher prey densities. In contrast, Lesser Sirens were largely ineffective predators, despite being an order of magnitude larger in body size than Marbled Salamander larvae (Fig. 1). These contrasting abilities of two very different salamander predators exemplify the complexity of understanding natural pond food webs, as interaction

strengths among links can vary in myriad ways depending on the context.

Larger Marbled Salamanders were more effective at consuming tadpoles at higher prey densities than smaller size classes, consistent with previous results of foraging abilities in this species (Anderson et al., 2016a). This can be explained largely by differences in gape limitation and gut capacity: larger larvae can more easily capture and consume prey because of reduced limitation on gape constraints, and at higher prey densities were less likely to be satiated because of larger gut capacity. Body size also explained a substantial fraction of the residual variation in the functional response curve analysis, further indicating the importance of predator body size in its foraging abilities. Our results on foraging ability are interesting because previous work posited that the ability of larval Marbled Salamanders to serve as keystone predators in pond communities was likely manifested by a gape constraint (Chalcraft and Resetarits, 2003b). Based on our findings, variability in Marbled Salamander size may ultimately control the likelihood of changes in larval anuran diversity in local ponds. Previous work of ours supports this idea, where Marbled Salamanders of a similar body size to the larger individuals in this study were not found to be keystone predators for structuring an anuran assemblage (Stemp et al., unpubl. data). The gape limitation of larval Marbled
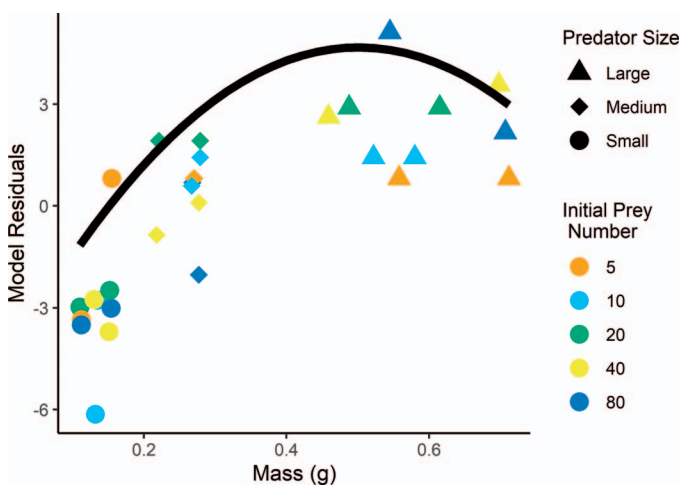

Fig. 2. Variability in foraging rates explained by body size for Marbled Salamanders. Points represent the residuals of a Type II functional response curve fit to data from all size classes as a function of body mass. The solid black line indicates predicted values based on a quadratic linear model of residuals and Marbled Salamander body size.
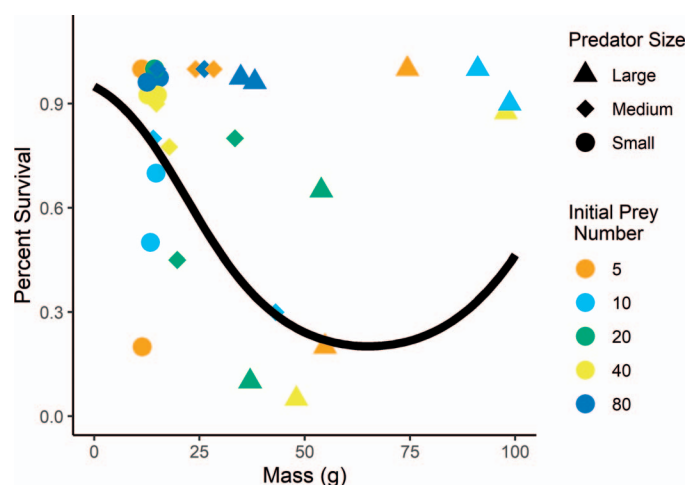

Fig. 3. Variability in prey survival explained by body size for Lesser Sirens. Points are percent survival of Southern Leopard Frog tadpoles as a function of Lesser Siren body mass. The solid black line shows the predicted values of percent survival with a quadratic model of body size.

Salamanders has also been implicated as a mechanism driving riskier foraging behavior in prey, where individuals forage more in the presence of gape-limited predators to grow into size refuges and minimize predation risk (Urban, 2007). Further research should investigate the effects of different size classes of larval Marbled Salamanders on tadpole foraging behavior and community diversity.

Lesser Sirens were ineffective foragers at the highest prey densities, regardless of their body size. This result was surprising given that predator–prey interaction strengths often scale positively with body size ratios (Emmerson and Raffaelli, 2004). Additionally, Lesser Sirens were several orders of magnitude larger than larval Marbled Salamanders (>13 g vs. <0.6 g, respectively), but they always ate less than 4% of the tadpoles offered at the highest density and in two cases ate zero; in contrast, Marbled Salamanders ate between ~11–55% of the offered tadpoles at the highest density. One possibility explaining this result is that at our highest prey density, Lesser Sirens suffered from confusion effects (McClure et al., 2009), resulting in poor foraging rates. Contributing to this hypothesis, Western Lesser Sirens (*Siren intermedia nettingi*) are known to have poor eyesight and instead rely on chemical cues to consume prey (Martin et al., 2013). Lesser Sirens also appear to show a parabolic relationship between body size and percent survival: intermediate-sized individuals showed the greatest foraging abilities, at least for prey at lower densities (Fig. 3). It is not immediately clear why this would be the case, since all size classes would be sufficiently large to consume the tadpoles. One potential reason could be that Lesser Sirens are thought to be filter feeders sifting through pond bottoms and aquatic vegetation for prey items (Altig, 1967). While we have witnessed Lesser Sirens actively foraging in tanks for prey items, we did not provide any substrate for filter feeding, which possibly could have affected foraging rates (Davenport, unpubl. data). Alternatively, the experimental container-to-body size ratio could have impacted their ability to forage naturally, especially when prey densities were higher. Related to this idea, when Lesser Sirens were larger, their foraging movements may have initiated a fright response in the tadpoles that would have made them harder to capture.

Predation is one of the integral processes that contributes to pond diversity and community dynamics (Wellborn et al., 1996; Wilbur, 1997). Identifying how different factors mediate predator–prey dynamics is therefore critical to accurately predict diversity in these ecosystems. Our study shows that in a given wetland, prey species may face substantial variability in predation risk, depending on the size and species of predators they encounter. Assessment of interaction strengths, here measured as attack rates and handling times, across a range of conditions between different pairs of predators and prey can help build predictive frameworks for understanding which species interact most strongly and what modifies those relationships in these communities.

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