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A wolf in sheep's clothing: Predatory fish have convergent consumptive effects but divergent predation-risk effects

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Abstract

Although consumptive effects of predators have long been central to ecology, predation-risk effects have emerged as major components of predator–prey interactions. Both consumptive and predation-risk effects should vary with predator functional traits (e.g., hunting mode, gape size), where consumption rates and induction of morphological and behavioral defenses correlate with prey-specific predator threat. Ambush predators, in contrast with active predators, may face selection pressure to be cryptic to avoid detection by prey. Thus, ambush predators may change prey density through consumptive effects but have reduced or absent predation-risk effects. We performed two mesocosm experiments with free-roaming and caged predators to explore post-colonization interactions of the chemically camouflaged, large-gaped, ambush predator, pirate perch (*Aphredoderus sayanus*), active, large-gaped green sunfish (*Lepomis cyanellus*), and active, small-gaped golden topminnow (*Fundulus chrysotus*), with larval gray treefrogs (*Hyla chrysoscelis*) and mole salamanders (*Ambystoma talpoideum*). We examined the consumptive and predation-risk effects of each predator on amphibian mortality, growth rates, tail morphology, and polyphenisms. Large-gaped pirate perch and green sunfish had strong, equivalent consumptive effects, but only the free-roaming active predator, green sunfish, suppressed the growth of survivors through risk-induced trait responses. Caged green sunfish induced much stronger non-consumptive mortality than pirate perch in gray treefrogs, an effect that was absent for mole salamanders; golden topminnows had intermediate effects. Tail defenses were a function of prey mortality and only manifested in free-roaming predator treatments, suggesting the necessity of predator attacks or conspecific alarm signals. Likewise, mole salamander polyphenism was unaffected by caged predators, whereas free-roaming green sunfish prevented all metamorphosis. Free-roaming golden topminnows increased the proportion of individuals remaining as larvae, and pirate perch increased the proportion of paedomorphs and metamorphs. Overall, the prey had positively correlated anti-predator responses across life stages, suggesting multicomponent

defenses. Predator effects varied with functional traits with large-gaped predators having strong consumptive effects, but active predators causing stronger risk-induced changes in growth compared to cryptic ambush predators, which provides more evidence for chemical camouflage. Our results emphasize the role of hunting mode and gape size in determining consumptive and predation-risk effects, and that predation-risk effects cannot be reliably predicted from consumptive effects.

INTRODUCTION

Predators and prey are locked in an evolutionary relationship, where selection favors adaptations and counter-adaptations that improve both predator efficacy and predator avoidance (Dawkins & Krebs, 1979). Consumptive predator effects were the dominant paradigm of predator–prey ecological theory for decades (Brooks & Dodson, 1965; Elton & Nicholson, 1942; Gotelli, 2008; Lotka, 1925; Volterra, 1926), but more recent work shows how predation-risk effects can be just as, if not more, impactful on prey populations (Boonstra, Hik, et al., 1998; Boonstra, Krebs, & Stenseth, 1998; Krebs et al., 2001; Peckarsky et al., 2008). While consumptive predator effects have obvious and immediate fitness costs for those consumed, predation-risk effects can propagate throughout a habitat and affect many prey simultaneously with potentially greater cumulative effects on populations and communities than consumptive effects (Peacor & Werner, 2001; Preisser et al., 2005). Predation-risk effects can affect fitness because they are essentially a sum of costs associated with predator tolerance ranging from physiological stress to plastic morphological and behavioral responses, that either require additional energy investments or missed resource acquisition opportunities (Brown et al., 1999; Lamanna & Martin, 2016; Lima, 1998; Peacor et al., 2013; Sih, 1980).

Predator–prey dynamics often depend upon the species identity and corresponding functional traits of the interacting predators and prey, thereby producing functionally diverse predator–prey combinations that differ in interaction strength (Chalcraft & Resetarits Jr., 2003; Schmitz, 2012). Much of the relevant literature focuses on prey and their adaptations (or lack thereof) to avoid predation, but predators are not bystanders in this evolutionary arms race and they employ a variety of strategies and counteradaptations to acquire prey (Lima, 2002). Predator functional diversity can manifest through variation in a variety of functional traits, such as body size (Rudolf, 2012), hunting mode (Preisser et al., 2007; Schmitz, 2012), metabolic rates (Brown et al., 2004; Chalcraft & Resetarits Jr., 2004), swimming and capture ability (Marras et al., 2015; Mihalitsis & Bellwood, 2019), sensory acuity (Budelmann, 1996; Veilleux & Kirk, 2014), gape size (Scharf et al., 2000), venoms (Schendel et al., 2019), and stealth (Colin et al., 2010; Corcoran & Conner, 2017). Besides instances of partial consumption, the consumptive effects inflicted by predators on individual prey typically result in death; however, predation-risk effects can vary with predator functional traits. When faced with predator diversity, a single anti-predator response is not typically sufficient, and prey may have to employ multiple anti-predator responses (Dijk et al., 2016; Pearson, 1989). For example, prey may respond differently to active foraging predators than to ambush predators (Preisser et al., 2007; Teplitsky et al., 2004; Touchon & Warkentin, 2008), thereby displaying the capacity to employ a variety of anti-predator responses (Sih et al., 1998).

A meta-analysis by Preisser et al. (2007) found that ambush predators elicit stronger predation-risk effects on prey than active predators. They hypothesized that inactive, ambush predators would only disperse cues locally, meaning their cues are more reliable indicators of immediate localized risk, whereas active predator cues may saturate an environment, rendering them as poor indicators of localized risk (Preisser et al., 2007). However, a second meta-analysis investigating different hunting modes on prey with complex life histories showed that active predators have greater predation-risk effects compared to ambush predators (Davenport et al., 2014). This seeming contradiction may resolve because ambush predators face selection pressure to be cryptic to avoid detection by prey and improve predation success (Miller et al., 2015). In this scenario, ambush predators will consume prey but have reduced or absent predation-risk effects, such as risk-induced trait responses and true non-consumptive

effects (terminology sensu Peacor et al., 2020). Active predators, on the other hand, should both consume prey and induce predation-risk effects. Thus, predator hunting mode is important for predicting the net consumptive and predation-risk effects in predator–prey interactions (Davenport et al., 2014; Preisser et al., 2007).

Fish are top predators in many freshwater habitats and have strong consumptive effects that alter community composition and species distributions (Brooks & Dodson, 1965; Wellborn et al., 1996), but fish also cause risk-induced trait responses in prey ranging from behavioral avoidance and decreased foraging activity to morphological defenses (Binckley & Resetarits Jr., 2003; Brönmark & Hansson, 2000; Chivers & Smith, 1998; Ferrari et al., 2010; Kats & Dill, 1998; Wisenden, 2000). Amphibians with complex, multistage life cycles interact with predatory fish during their larval stage and when reproducing as terrestrial adults. For example, larval treefrogs (*Hyla*) and mole salamanders (*Ambystoma*) experience high mortality when faced with fish predation (Kats et al., 1988; Resetarits Jr. et al., 2004; Resetarits Jr. & Chalcraft, 2007; Semlitsch, 1987a; Sexton & Phillips, 1986; Smith et al., 1999), but breeding females mitigate this risk by preferentially ovipositing in fishless habitats: a risk-induced trait response (Binckley & Resetarits Jr., 2002; Davenport et al., 2017; Resetarits Jr. et al., 2018; Resetarits Jr. & Wilbur, 1989). This pattern could produce a negative correlation in anti-predator responses across life stages, where the selection on anti-predator traits in one life stage reduces the selection on anti-predator traits in the other life stage (Agrawal et al., 2010; Fry, 1996). For example, if aquatic larvae lack behavioral or morphological defenses to tolerate aquatic predators and habitats also vary in predator presence, then we should expect selection pressure on breeding adults to have strong behavioral avoidance of aquatic habitats with predators (Blaustein, 1999; Resetarits Jr., 1996; Rieger et al., 2004). Conversely, if terrestrial adults do not avoid aquatic habitats with predators, then their larvae are expected to evolve behavioral or morphological traits to improve survival (Kats et al., 1988). However, recent work has shown that responses across life stages may be positively correlated and prey may utilize multicomponent anti-predator defenses (Andrade et al., 2017; Vonesh, 2005).

While many breeding amphibians show a general preference for fishless habitats, they either ignore or fail to detect pirate perch (*Aphredoderus sayanus*), a cryptic ambush predator hypothesized to employ chemical camouflage (Resetarits Jr. et al., 2022; Resetarits Jr. & Binckley, 2013). Motivated by known responses of amphibians to fish during the colonization stage (Resetarits Jr. & Binckley, 2013), we tested hypotheses regarding consumptive and predation-risk effects of varied fish predators on larval amphibians in the post-colonization stage. We conducted two predation experiments using replicated mesocosm designs and two model amphibian species: gray treefrogs (*Hyla chrysoscelis*) and mole salamanders (*Ambystoma talpoideum*), which both show risk-induced trait responses to predators (Jackson & Semlitsch, 1993; Petranka et al., 1987; Semlitsch, 1987a, 1987b; Sexton & Phillips, 1986). Prey were crossed with two levels of predator exposure, caged (predation-risk effects only) and free-roaming (consumptive and predation-risk effects) to disentangle risk-induced trait responses from thinning, selection, and risk-induced trait responses (Relyea, 2007). Predators were fish species with different hunting modes, ecology, and functional traits: green sunfish (*Lepomis cyanellus*; active, generalist, and large-gaped), pirate perch (cryptic, ambush, and large-gaped), and, for the mole salamander study only, golden topminnows (*Fundulus chrysotus*; active, surface-feeding, and small-gaped). No known small-gaped ambush predatory fishes exist in our system; thus, we could not implement a full interaction between hunting mode and gape size in our study.

Our goals were threefold: (1) to determine how variation in predator functional traits (hunting mode and gape size) drives both consumptive and predation-risk effects in prey; (2) to determine the relative contributions and interactions of consumptive effects, risk-induced trait responses, and true non-consumptive effects (i.e., predation-risk effects that affect fitness or population sizes directly; Peacor et al., 2020); and (3) to establish the efficacy of chemical camouflage in an ambush predator, pirate perch. We expected the active, large-gaped green sunfish to have the greatest consumptive effects, followed by ambushing, large-gaped pirate perch, and then active, small-gaped golden topminnows. We also expected that predation-risk effects should be a function of predator capability, such that if green sunfish have the greatest consumptive effects on prey, they should likewise have the greatest predation-risk effects on prey. However, if our ambush predator, pirate perch, is chemically camouflaged to aquatic prey, then aquatic prey should fail to properly assess true predation-risk, i.e. position along the predator imminence continuum. Therefore, prey should fail to implement predator defenses (pre-encounter defenses, post-encounter defenses, or defenses during attacks; Fanselow, 1989) and may mismatch responses to the threat of the predator.

METHODS

Study site

Our study was conducted in a field at the 318-ha University of Mississippi Field Station (UMFS) in Lafayette

County, MS (34.429° N, 89.393° W). Situated in the Northern Hilly Gulf Coastal Plain ecoregion (Chapman et al., 2004), UMFS contains over 200 ponds along with multiple small streams, wetlands, fields, and mixed forests.

Study species

Gray treefrogs are arboreal frogs native throughout eastern North America. Like most Nearctic treefrogs, they breed in ponds and ephemeral pools during the late spring and summer months and strongly avoid fish while doing so (Resetarits Jr. & Wilbur, 1989). Their herbivorous larvae are susceptible to fish predation (Kats et al., 1988), become inactive in the presence of predator chemical cues (Petranka et al., 1987), and exhibit strong density-dependent growth (Resetarits Jr. et al., 2004). Gray treefrogs have tail polyphenisms, which are risk-induced trait responses. In the presence of dragonfly naiads, an ambush predator, larval treefrog tails become colorful, elongate, and stronger to aid in predator evasion by acting as a decoy and increasing maneuverability (Blair & Wassersug, 2000; McCollum & Van Buskirk, 1996; Van Buskirk et al., 2004; Van Buskirk & McCollum, 2000b). Conversely, a neotropical treefrog, *Dendropsophus ebraccatus*, produces shallow, streamlined, achromatic tails in the presence of active foraging fish predators (Touchon & Warkentin, 2008); achromatic tails may be inconspicuous to predators, while streamlined tails may increase escape velocity (Dayton et al., 2005; Hoff & Wassersug, 2000; Van Buskirk & McCollum, 2000a). For larval gray treefrogs, Relyea (2003) considered risk-induced morphological traits as more reliable indicators of predation-risk than behavioral traits (e.g., refuge use, activity rates) because they persist late into ontogeny when behavioral defenses are abandoned (Relyea, 2003).

The mole salamander is an intermediate-sized, stout-bodied mole salamander (eponymous of the family Ambystomatidae) endemic to the southeastern United States (Shoop, 1964). They are facultatively paedomorphic, which is a polyphenism unique to salamanders species in five families (Ambystomatidae, Salamandridae, Dicamptodontidae, Hynobiidae, and Plethodontidae) (Denoël et al., 2005). In these salamanders, adults may have either a fully aquatic larval-like phenotype complete with gills (paedomorphosis) (Gould, 1977) or a terrestrial phenotype after losing larval traits (metamorphosis) (Whiteman, 1994). At UMFS, adults migrate from terrestrial hibernacula to breed in ponds from late November to early February. Aquatic larvae are predaceous and develop until late spring when individuals first start metamorphosing (Petranka, 1998). Mole salamander larvae show classic density-dependent growth patterns

(Semlitsch, 1987c). Theoretical models predict that unfavorable conditions for growth and survival in the aquatic environment should increase metamorphosis and decrease paedomorphosis (to escape poor conditions) (Werner & Gilliam, 1984; Whiteman, 1994; Wilbur & Collins, 1973). For example, the adult salamander phenotype is related to larval salamander density (more paedomorphs in low density and vice versa) (Semlitsch, 1987c), which can be directly affected by predator consumptive effects. Predators, like bluegill sunfish (*Lepomis macrochirus*), also induce predation-risk effects in mole salamanders. Bluegill decreases the occurrence of both metamorphosis and paedomorphosis, and they cause shifts in diet and reduce activity levels, thereby dramatically increasing the length of the larval period (Jackson & Semlitsch, 1993; Semlitsch, 1987a).

Our model predators consisted of three different predator species with varied hunting modes, predatory capabilities, and trophic niches: green sunfish, golden topminnows, and pirate perch. All three of these predator species have extensive range overlap with gray treefrogs and mole salamanders and co-occur naturally at UMFS. Green sunfish are voracious, generalist predators with large gapes that actively forage for prey at all depths in ponds and streams. They are one of the most widespread fishes in North America, are widely introduced to previously fishless waters both inside and outside of their native range (Lee et al., 1980a), and are one of the most abundant fish at UMFS. Green sunfish have devastating effects on amphibians (Sexton & Phillips, 1986), find gray treefrog larvae palatable (Kats et al., 1988), strongly repel adult gray treefrog oviposition (Resetarits et al., unpublished data), and their chemical cues generate strong risk-induced trait responses in larval gray treefrog behavior (Petranka et al., 1987). Golden topminnows (mole salamander experiment only) are small (Foster, 1967), gape-limited fish that are widespread in most freshwater habitats across the southeastern United States (Foster, 1967; Hubbs et al., 2008). They are active, surface-feeding fish whose diet consists primarily of small invertebrates. Hunt (1953) found that insects dominated stomach contents (~100%), but they will opportunistically consume amphibian eggs and small larvae.

Pirate perch are a unique, but common, freshwater fish that are the only member of the monotypic family Aphredoderidae and one of nine extant described species in the order Percopsiformes; their closest relatives are the amblyopsid cavefishes (Dillman et al., 2011). Adults are relatively small (Moore & Burris, 1956), but large gaped (Moore & Burris, 1956; Poly, 2004). They are nocturnal, ambush predators that occupy streams, lakes, and rivers of the eastern and central United States (Gunning & Lewis, 1955; Lee et al., 1980b; Monzyk et al., 1997; Parker & Simco, 2006; Shepherd & Huish, 1978). They feed on a wide variety of prey, including insects (up to

80% of diet; Flemer & Woolcott, 1966). Shepherd and Huish (1978) found cladocerans present in 36% of small individuals (1.0–2.9 cm) and isopods and amphipods in 20% and 8%, respectively, of intermediate-sized fish (3.0–8.9 cm). They will also opportunistically consume decapods, small fish, and amphibians (reviewed in Burr, 2020); however, their effectiveness as a predator and actual prey consumption rates are unknown, and they may feed infrequently like their closest relatives, the amblyopsid cavefishes (Dillman et al., 2011; Parker & Simco, 2006). It is hypothesized that pirate perch are chemically camouflaged toward prey as they are undetectable to colonizing insects and gray treefrogs that typically avoid predatory fishes (Binckley & Resetarits Jr., 2003; Binckley & Resetarits Jr., 2005; Resetarits Jr. et al., 2022; Resetarits Jr. & Binckley, 2013; Silberbush & Resetarits Jr., 2017).

Gray treefrog study

We constructed a square experimental array of 36, 1.8-m diameter, 1200-L cattle tanks (mesocosms; $N = 36$; Ace Roto-Mold, Hospers, IA, USA) in a mowed field at UMFS. Between 19 and 22 May 2016, each mesocosm was filled with ~1100 L of well water (depth = 0.50 m) and received randomly assigned aliquots of both dry hardwood leaf litter (2 kg) and concentrated pond inocula (1.9 L) containing algae and zooplankton from a fishless pond (number 61) at UMFS. One cylindrical mesh cage (height = 0.61 m, diameter = 0.58 m, volume = 0.16 m^3, mesh = 1.3×1.13 mm openings) was added to the center of each mesocosm (including control mesocosms). Mesocosms were fitted with a window screen lid (1.3×1.13 mm openings) that prevented colonization by other organisms and the escape of metamorphs. Mesocosms were assigned one of the following treatments: (1) free-roaming green sunfish, (2) free-roaming pirate perch, (3) caged green sunfish, (4) caged pirate perch, or (5) control. Golden topminnows were not present in this study since we hypothesized that green sunfish and pirate perch would sufficiently contrast, and this experiment preceded the mole salamander experiment (see *Mole Salamander Study* and *Results*). Free-roaming [+] predators were placed into the mesocosm outside of the cage and free to consume anuran larvae and zooplankton. Caged [−] predators were placed inside of the cage and physically prevented from interacting with anuran larvae, but free to consume invertebrates. Caged predators were not fed larval gray treefrogs. Each treatment was replicated six times ($n = 6$), except control mesocosms, which were hyper-replicated ($n = 12$). Rows (=blocks) contained one of each treatment and two controls. Green sunfish and

pirate perch were collected from pond number 144 and Bay Springs Branch, respectively, at UMFS. Fish were weighed and assigned to mesocosms on 22 May, so that all fish within a block were of similar size (green sunfish: 4.42 ± 0.12 g; pirate perch: 5.29 ± 0.39 g; mean $\pm$ SE).

From 25 to 29 May, we collected gray treefrog eggs from a separate, unrelated mesocosm array. We could not collect sufficient eggs from one night of oviposition for all mesocosms; thus, the addition of hatchlings to mesocosms was staggered so that one to two blocks were filled per day between 30 May and 3 June. Eggs were reared in the laboratory until hatching (total length < 4.5 mm), at which time they were counted into groups of 10, which were randomly assigned into groups of 200. Each group of 200 was then randomly assigned to a mesocosm within a single block and, after a 15-min acclimation period, the larvae were released into the water outside of the cage. Treefrog larvae foraged on fresh algae growth and after 19 days, metamorphs started emerging at night by climbing up the walls of mesocosms. Metamorphs were collected daily, weighed, photographed, and released into the terrestrial environment at UMFS. On 19 July 2016, a week after metamorphs stopped emerging and no larvae could be located, the experiment was terminated.

Mole salamander study

In December 2016, we constructed an experimental array of 42, 1.8-m diameter, 1200-L cattle tanks (mesocosms; $N = 42$) in a mowed field at UMFS, in the same manner and location as the previous study. Mesocosms were assigned one of the following treatments: (1) free-roaming green sunfish, (2) free-roaming pirate perch, (3) free-roaming golden topminnows, (4) caged green sunfish, (5) caged pirate perch, (6) caged golden topminnows, and (7) control. Caged predators were free to consume invertebrates, but they were not fed larval mole salamanders. We added golden topminnows as an additional small-gaped predator after observing the strong consumptive effects of the large-gaped predators in the gray treefrog study 6 months prior (see *Results*). Each treatment was replicated six times ($n = 6$), and each treatment was represented once in each of the seven rows (=blocks) (7 treatments × 6 blocks = 42 mesocosms). Fish were collected from local ponds and streams at UMFS (number 144, green sunfish; Bay Springs Branch, pirate perch; Bramlett Pond, golden topminnows), weighed, and assigned to mesocosms (one per mesocosm) on 12 January so that all fish within a block were of similar relative size and mass (green sunfish: 2.59 ± 0.16 g; pirate perch: 3.73 ± 0.28 g; golden topminnows: 0.98 ± 0.05 g). Green

sunfish and pirate perch were relatively smaller in this experiment to account for expected growth over the longer experiment duration and to more closely match the small size of golden topminnows.

Egg masses of mole salamanders were collected from ponds at UMFS in December and reared until hatching in small outdoor wading pools. Eggs were separated by the date of oviposition. Each mesocosm received 12 randomly selected mole salamander hatchlings (typical total length < 6 mm; Semlitsch & Gibbons, 1990), which reflects natural mole salamander densities. This density is lower than in the gray treefrog study because mole salamanders, as predators, occupy a higher trophic position (Semlitsch, 1987c). We could not collect sufficient eggs from one night of oviposition for all mesocosms; thus, 12 randomly selected mole salamander hatchlings were added to mesocosms on 25 January for Blocks 1–4 and likewise on 31 January for Blocks 5 and 6. Hatchlings were acclimated to mesocosm water for 15 min prior to introduction. Screen lids were depressed into the water in early February to open the mesocosms for insect colonization and oviposition to add to the mesocosms' food supply.

Night checks for emerging metamorphs began on 12 May and occurred every 3 days until late October when metamorphs stopped emerging. Emerging metamorphs were collected by hand, weighed, photographed, and then released into the terrestrial environment at UMFS. During 12–14 December, the experiment was terminated and all remaining individuals (larvae, paedomorphs, and fish) were collected, weighed, and photographed. Paedomorphs were distinguished from larvae by conspicuously swollen cloacal glands on males and a protruding cloaca with a gravid body shape on females (Bohenek et al., 2021).

Tail color and shape analyses

During the fourth week of the gray treefrog experiment, when larvae were full sized (Gosner Stages 35–39; Gosner, 1960) and metamorphs began emerging, we sampled 10 gray treefrog larvae from each mesocosm using a small aquarium net, which was passed above the leaf litter for no more than 5 min to limit disturbance. Due to treatment effects, not all mesocosms contained larvae at the time of sampling. Larvae were weighed, photographed in standardized positions on a white balance card with scales for morphometric and color calibrations, and then returned to their respective mesocosm. Following methods of Touchon and Warkentin (2008), we measured larval body size (body length), tail size (tail length, tail depth, and tail muscle depth), and tail color, for which we utilized the hue (color), saturation (intensity),

and brightness (HSV) color model (Goedert et al., 2020). ImageJ (Schneider et al., 2012) was used for morphometrics and color measurements. For the mole salamander study, only salamanders collected at the end of the experiment (larvae and paedomorphs) were analyzed for tail color because handling larvae can induce a stress response and affect growth and phenotype (Bohenek et al., 2021). Salamanders were photographed and measured in the same way as gray treefrog larvae.

Statistical analyses

Mesocosms with missing fish were removed from analyses, which included three free-roaming pirate perch in the gray treefrog study and one free-roaming golden topminnow, one caged green sunfish, and three caged pirate perch in the mole salamander study. These replicates had values similar to controls, suggesting fish did not survive introduction into the experiments.

Binomial logistic regression was used to evaluate survival rates in each mesocosm with "predator species" (control, pirate perch, golden topminnow, or green sunfish) and "predator exposure" (free-roaming [+] or caged [−]) as crossed main effects and block as a random factor (Warton & Hui, 2011). Significance for binomial logistic regression models was determined with likelihood-ratio tests. Linear mixed effects models (LMMs) were used to evaluate body size (mass), growth rate, larval period, and body condition. Body condition was evaluated for the mole salamander study only, and it was modeled with snout–vent length (SVL) as a covariate to produce SVL-adjusted mass (Garcia-Berthou, 2001). All LMMs had predator species and predator exposure as crossed main effects, survival as a covariate (to control for density-mediated growth), and mesocosm nested within the block as random effects. Significance for LMMs was tested with approximate F tests (Type III Satterthwaite). Marginal means and Tukey post hoc pairwise tests were performed to identify treatment differences.

Permutational analysis of variance (PERMANOVA; Anderson, 2008) was used to assess tail coloration and shape for both studies and phenotype composition for the mole salamander study. Mean hue, saturation, and brightness (HSV model) of each individual were averaged per mesocosm (to prevent pseudoreplication), square-root transformed, and used to compute a Bray–Curtis dissimilarity matrix. In the PERMANOVA model, predator species and predator exposure were used as crossed fixed effects, survival was a covariate, and block was used to constrain permutations. Tail shape was analyzed much in the same way, using mean tail length, tail depth, and tail muscle depth as response variables, but also included

body size (body length for gray treefrog and SVL for mole salamander) as a covariate to ensure body size independence of tail shape. Permutational analysis of multivariate dispersion (PERMDISP) was used to check for homogeneity of group variances. Phenotype composition (number of larvae, metamorphs, and paedomorphs per mesocosm) was analyzed in the same way as tail color.

All analyses set α = 0.05 and used R 4.0.2 (R Core Team, 2020), lme4 1.1-26 (Bates et al., 2015) for mixed effects models, lmerTest 3.1-3 (Kuznetsova et al., 2015) for approximate F tests, tidyverse 1.3.1 (Wickham et al., 2019) for graphics and data manipulation, vegan 2.5-7 (Oksanen et al., 2018) for PERMANOVA, PERMDISP, and NMDS scores, ggsci 2.9 (Xiao, 2018) for plot color schemes, cowplot 1.1.1 (Wilke, 2020) for plot themes, ggConvexHull 0.1.0 (Martin, 2017) for NMDS convex hulls, emmeans 1.5.3 (Lenth, 2020) for marginal mean estimates, multcompView 0.1-8 (Graves et al., 2015) for multiple comparisons, kableExtra 1.3.1 (Zhu, 2020) for output formatting, psych 2.0.12 (Revelle, 2020) for data summaries, and car 3.0-10 (Fox & Weisberg, 2019) for model diagnostics.

RESULTS

Gray treefrog study

Across all treatments, 37.6% of treefrog larvae survived to metamorphosis; free-roaming predator treatments significantly reduced survival (Table 1), and all treatments significantly differed from each other, except for the two free-roaming predator treatments. Control survival (71.8 ± 1.9%; marginal mean ± SE) was highest among all treatments (Figure 1a), and similar to reported control values in other gray treefrog studies (Pintar & Resetarits Jr., 2017; Resetarits Jr. et al., 2004; Wilbur & Alford, 1985). Both free-roaming pirate perch (0.8 ± 0.4%) and free-roaming green sunfish (0.6 ± 0.0%) drastically reduced larval survival, nearly eliminating all larvae, with only 12 combined total individuals surviving to metamorphosis (0.7%). Survival in caged predator treatments varied by predatory fish species, with significantly greater survival with caged pirate perch (51.8 ± 2.5%) compared to that of caged green sunfish (10.1 ± 1.2%), which had surprisingly strong, true non-consumptive effects (Figure 1a).

There was a significant predator species × predator exposure effect on metamorph mass (Table 1), with most treatments being quite similar except for free-roaming green sunfish, which produced a low number of very small metamorphs even after controlling for density-mediated growth (i.e., survival rate covariate; Table 1, Figure 1b). There was a marginally nonsignificant difference in the larval period between predator species, but no effect of predator exposure, or the predator species × predator exposure interaction (Table 1). No treatments differed in larval period in post hoc tests ($p > 0.05$), but free-roaming green sunfish had the shortest larval period (20.65 ± 4.38 days), whereas all other treatment marginal means ranged from 27.53 ± 1.95 days for caged green sunfish to 32.38 ± 3.56 days for free-roaming pirate perch. There was a significant predator species × predator exposure effect on

TABLE 1 Univariate statistical results for the gray treefrog study

Response variable	Factor	SS	df	ddf	χ^2 or F	p
Survival (LRT)	Predator species × predator exposure		1		10.22	**0.001**
Body mass	Survival	2.27×10^{-2}	1	15.37	10.65	**0.005**
	Predator species	4.02×10^{-2}	2	21.06	9.43	**0.001**
	Predator exposure	8.42×10^{-3}	1	25.74	3.95	0.058
	Predator species × predator exposure	4.39×10^{-2}	1	28.40	20.58	**<0.001**
Larval period	Survival	1.30	1	16.80	0.04	0.838
	Predator species	189.10	2	22.04	3.13	0.064
	Predator exposure	21.24	1	26.66	0.70	0.409
	Predator species × predator exposure	40.20	1	28.72	1.33	0.258
Growth rate	Survival	7.69×10^{-6}	1	14.04	2.79	0.117
	Predator species	2.98×10^{-6}	2	16.83	0.54	0.591
	Predator exposure	2.62×10^{-6}	1	18.94	0.95	0.341
	Predator species × predator exposure	1.98×10^{-5}	1	19.61	7.18	**0.015**

Notes: Likelihood-ratio test (LRT) result for survival analyses, which does not assess the main effects given that the interaction is significant. Linear mixed model ANOVA results using Satterthwaite approximation for denominator degrees of freedom. Statistically significant results are in bold ($p < 0.05$).

Abbreviations: ddf, denominator degrees of freedom; df, numerator degrees of freedom; SS, sums of squares.
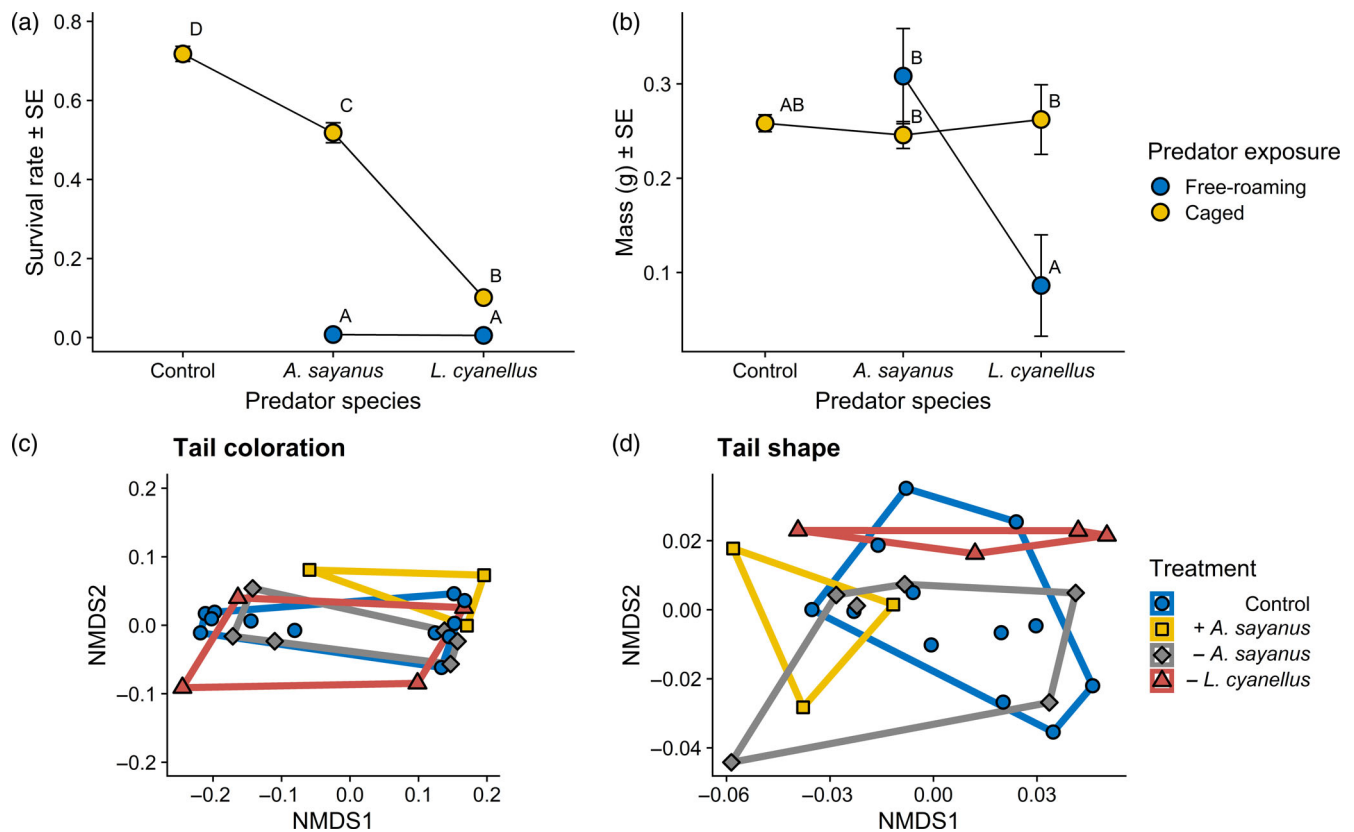
FIGURE 1 Responses of gray treefrogs to caged and free-roaming pirate perch and green sunfish relative to fishless controls. (a) Proportion of gray treefrogs that survived to metamorphosis (marginal mean $\pm$ 1 SE). (b) Gray treefrog mass at metamorphosis (marginal mean $\pm$ 1 SE). Different letters indicate significant differences ($p < 0.05$). (c) Nonmetric multidimensional scaling plot visualizing the difference in hue-saturation-brightness (HSV) values of larval gray treefrog tails across treatments. (d) Nonmetric multidimensional scaling plot visualizing comparisons of tail length, tail height, and tail muscle height of larval gray treefrog tails across treatments. Free-roaming predator exposure is indicated by [+], while caged predator exposure is indicated by [−]. Note that consumptive green sunfish are absent because insufficient individuals survived to this stage of the experiment

the growth rate, but post hoc tests revealed no differences among treatments ($p > 0.05$; Table 1). However, the marginal means of growth rate among treatments mirrored the mass results (Figure 1b), where free-roaming green sunfish was the lowest ($6.22 \times 10^{-3} \pm 2.66 \times 10^{-3}$ g day^{-1}).

Since no larvae from the free-roaming green sunfish treatment could be sampled for tail color or shape (due to consumptive effects), the predator species × predator exposure effect could not be estimated. This introduced design imbalance, and thus, we simply modeled "treatment" as the main factor of interest. Permutational analysis of variance revealed significant main effects of treatment on tail coloration, but no significant effect on the survival covariate (Table 2). Differences in color were primarily driven by free-roaming pirate perch, which produced more saturated gray treefrog tails compared to control, caged pirate perch, and caged green sunfish treatments (Figures 1c and 4a,c). There were no significant effects of treatment or survival on tail shape; tail shape metrics were scaled with body size (Table 2).

Permutational analysis of multivariate dispersion revealed no significant difference in group spatial median variances for either tail color or tail shape (Table 2).

Mole salamander study

Across all treatments, 52.0% of the salamanders survived to the end of the experiment; there was a significant treatment effect of predator species and predator exposure on salamander survival, but not their interaction (Table 3, Figure 2a). Salamander survival with free-roaming pirate perch ($9.4 \pm 3.6\%$) and free-roaming green sunfish ($12.1 \pm 4.1\%$) was reduced compared to free-roaming golden topminnows and all caged treatments. Free-roaming golden topminnows ($40.5 \pm 7.2\%$) had an intermediate effect that was between control/caged predator treatments and free-roaming green sunfish/pirate perch (Figure 2a). Differences in salamander metamorph body size (mass) (Figure 2b) were driven by

TABLE 2 Multivariate statistical results for the gray treefrog study including complete PERMANOVA results along with accompanying PERMDISP diagnostics

Response variable	Factor	SS	df	ddf	Pseudo-F	p
Tail color	Survival	8.07×10^{-4}	1	20	0.10	0.486
	Treatment	1.28×10^{-2}	3	20	0.54	**0.004**
	PERMDISP	3.10×10^{-3}	3	21	1.14	0.354
Tail shape	Body length	8.77×10^{-3}	1	19	11.15	**0.004**
	Survival	1.72×10^{-3}	1	19	2.19	0.073
	Treatment	3.46×10^{-3}	2	19	1.47	0.170
	PERMDISP	8.62×10^{-4}	3	21	1.03	0.399

Note: Statistically significant results are in bold ($p < 0.05$).
Abbreviations: SS, sums of squares; df, numerator degrees of freedom; ddf, denominator degrees of freedom.

TABLE 3 Univariate statistical results for the mole salamander study

Response variable	Factors	SS	df	ddf	χ^2 or F	p
Survival (LRT)	Predator species		1		23.81	**<0.001**
	Predator exposure		1		121.34	**<0.001**
	Predator species × predator exposure		1		3.45	0.179
Body mass	Survival	26.95	1	23.52	27.03	**<0.001**
	Predator species	16.31	3	23.28	5.45	**0.005**
	Predator exposure	8.43	1	25.74	3.95	0.058
	Predator species × predator exposure	32.02	2	26.14	16.05	**<0.001**
Larval period	Survival	649.80	1	48.861	0.298	0.588
	Predator species	9204.66	3	46.896	1.406	0.253
	Predator exposure	13,938.87	1	46.530	6.388	**0.015**
	Predator species × predator exposure	11,794.83	1	47.637	5.405	**0.024**
Growth rate	Survival	1.55×10^{-4}	1	22.85	29.38	**<0.001**
	Predator species	9.58×10^{-5}	3	20.05	6.06	**0.004**
	Predator exposure	7.01×10^{-5}	1	21.02	13.30	**0.002**
	Predator species × predator exposure	6.08×10^{-5}	2	21.91	11.53	**<0.001**
Body condition	Snout–vent length	197.51	1	207.73	966.32	**<0.001**
	Survival	1.81	1	30.64	8.85	**0.006**
	Predator species	1.41	3	20.86	2.30	0.107
	Predator exposure	0.06	1	25.92	0.315	0.579
	Predator species × predator exposure	3.19	2	29.52	7.80	**0.002**

Note: Likelihood-ratio test (LRT) result for survival analyses that include main effects because the interaction was not significant. Linear mixed model ANOVA results using Satterthwaite approximation for denominator degrees of freedom. Statistically significant results are in bold ($p < 0.05$).
Abbreviations: ddf, denominator degrees of freedom; df, numerator degrees of freedom; SS, sums of squares.

differential survival among treatments (Table 3, Figure 2a). However, there was also a significant predator species × predator exposure effect on mass (Table 3) as these growth-enhancing density-dependent effects were absent with free-roaming green sunfish, but apparent with free-roaming pirate perch (Figure 1b). There was a significant predator exposure, but not predator species, effect on the larval period, but this analysis was limited because it could only assess the limited number of individuals that metamorphosed and because free-roaming green sunfish produced no metamorphs, thereby eliminating an entire treatment (Table 3, Figure 2c). Growth rate followed the same patterns as body mass with a predator species × predator exposure effect (Table 3) driven by decreased growth rates with free-roaming green sunfish, but no other predators. There was also a predator species × predator exposure effect on body condition (Table 3) primarily driven by differences between free-
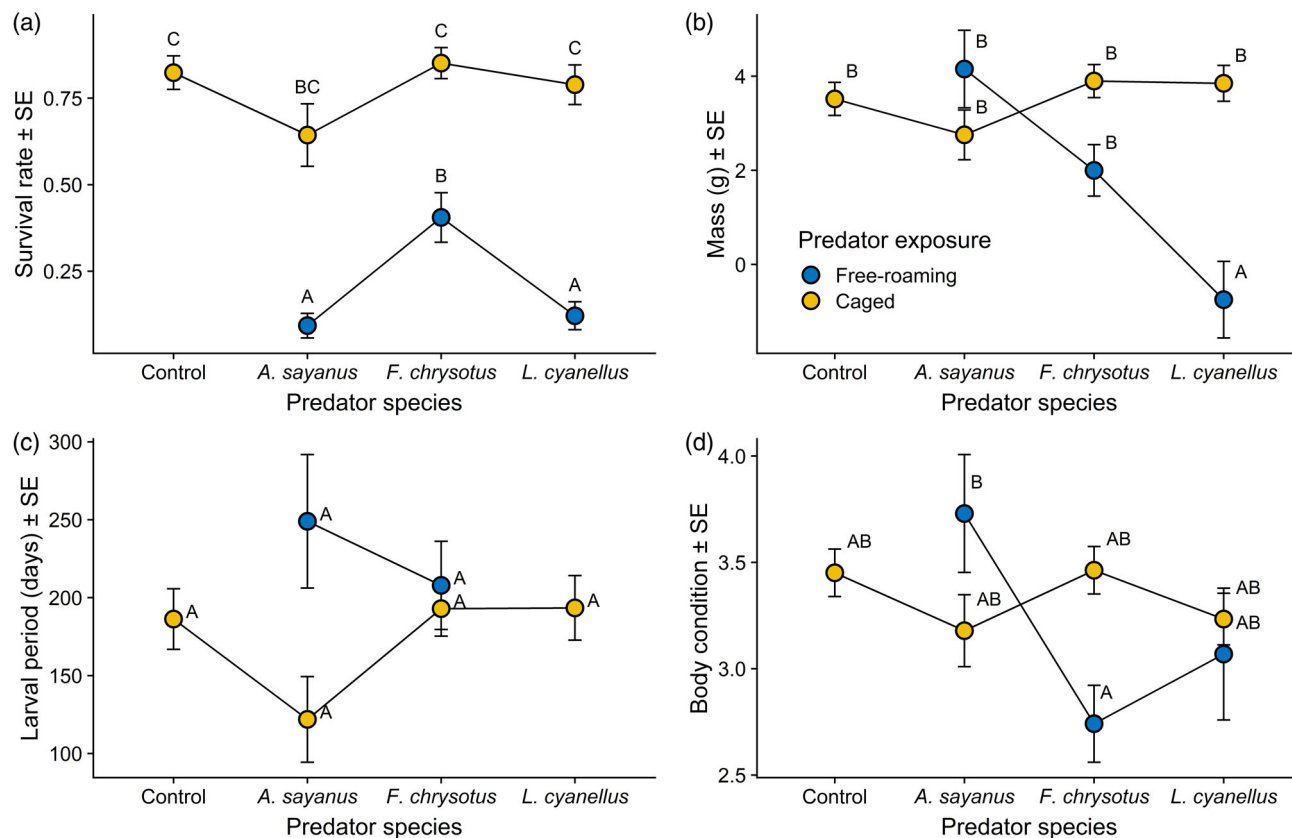
FIGURE 2 Responses of mole salamanders to caged and free-roaming pirate perch, golden topminnows, and green sunfish relative to fishless controls. (a) Proportion of mole salamanders that survived to the end of the experiment (marginal mean $\pm$ 1 SE). (b) Mole salamander mass at metamorphosis (marginal mean $\pm$ 1 SE). (c) Mole salamander larval period (days; marginal mean $\pm$ 1 SE). (d) Mole salamander body condition (SVL-adjusted mass; marginal mean $\pm$ 1 SE). Different letters indicate significant differences ($p < 0.05$)

roaming pirate perch and free-roaming golden topminnows, suggesting that golden topminnows may function more as a competitor than predator after larval salamanders eclipse golden topminnow gape limitation.

When comparing phenotype composition across treatments, PERMANOVA revealed that there was a significant predator species × predator exposure effect (Table 4, Figure 3a,b). Caged predator treatments and controls were similar in proportions of larvae, metamorphs, and paedomorphs (Figure 3a). All free-roaming predator treatments reduced the overall number of individuals compared to caged predator treatments, but each predatory fish species had its own effect. Free-roaming pirate perch produced fewer larvae than all other treatments and higher proportions of large-bodied adult phenotypes suggesting a density-dependent response that facilitated maximal growth rates. In contrast, free-roaming green sunfish had similar effects on survival, but most individuals remained as larvae and not a single individual metamorphosed, suggesting that free-roaming green sunfish elicited risk-induced trait responses that uniquely affected growth and phenotype. All three phenotypes occurred with free-roaming golden topminnows, which produced

phenotype compositions most similar to caged predator treatments (Figure 3a), but individuals were mostly small larvae with poor body condition (Figure 2b,c).

There was no interaction or main effects of predator species and predator exposure on salamander tail color or tail shape (Table 4). However, survival rate did affect mole salamander tail coloration; this significant effect was primarily driven by darker tails with free-roaming green sunfish compared to all other treatments (Figures 3c and 4b, d). Like with gray treefrogs, there were no significant effects of any variable on tail shape, as tail shape metrics only scale with body size (Table 4, Figure 3d). Permutational analysis of multivariate dispersion results revealed no significant difference in group spatial median variances for polyphenism, tail color, or tail shape (Table 4).

DISCUSSION

In aquatic environments, predation-risk effects are often driven by chemical cues (Ferrari et al., 2010), and gray treefrog larvae are known to recognize green sunfish chemical cues, which cause risk-induced trait

TABLE 4 Multivariate statistical results for the mole salamander study including complete PERMANOVA results along with accompanying PERMDISP diagnostics

Response variable	Factor	SS	df	ddf	Pseudo-F	p
Phenotype	Survival	0.87	1	29	9.82	**<0.001**
	Predator species × predator exposure	0.48	2	29	2.70	**0.039**
	PERMDISP	2.13	6	30	0.11	0.995
Tail color	Survival	5.95×10^{-3}	1	26	2.20	**0.043**
	Predator species	9.34×10^{-3}	3	26	1.15	0.276
	Predator exposure	1.95×10^{-3}	1	26	0.72	0.789
	Predator species × predator exposure	6.86×10^{-3}	2	24	1.30	0.206
	PERMDISP	1.44×10^{-3}	6	25	0.76	0.609
Tail shape	Snout–vent length	2.72×10^{-2}	1	25	350.85	**<0.001**
	Survival	6.50×10^{-5}	1	25	0.84	0.369
	Predator species	1.43×10^{-4}	3	25	0.61	0.633
	Predator exposure	6.84×10^{-5}	1	25	0.88	0.370
	Predator species × predator exposure	1.83×10^{-4}	2	23	1.19	0.324
	PERMDISP	9.82×10^{-4}	6	25	0.53	0.783

Note: Statistically significant results are in bold ($p < 0.05$).

Abbreviations: ddf, denominator degrees of freedom; df, numerator degrees of freedom; SS, sums of squares.

responses—increased refuge use and reduced foraging rates (Petranka et al., 1987). Recent work has demonstrated that predation-risk effects can directly increase prey mortality (true non-consumptive effects; Peacor et al., 2020) by making prey susceptible to other mortality factors (MacLeod et al., 2018; McCauley et al., 2011). These effects are thought to be mediated through a chronic stress response (Preisser, 2009), which can be lethal and have population effects as strong as (or stronger than) consumptive effects, particularly in aquatic environments (McCauley et al., 2011; Peacor & Werner, 2001; Preisser et al., 2005; Resetarits Jr. et al., 2004). The consumptive effects of both free-roaming pirate perch and green sunfish decimated larval amphibians (Figures 1a and 2a), but the predation-risk effects of our caged active predator, green sunfish, strongly decreased gray treefrog survival, a true non-consumptive effect that has rarely been documented (Sheriff et al., 2020). The caged ambush predator, pirate perch, had dramatically weaker effects on gray treefrog survival (though still different from controls; Figure 1a). This result is at odds with the idea that ambush predators uniformly have more reliable cues and stronger predation-risk effects on prey than active predators (Preisser et al., 2007). It also adds evidence to the hypothesis that pirate perch are cryptic to prey at both the colonization stage (Resetarits Jr. et al., 2021; Resetarits Jr. & Binckley, 2013; Resetarits Jr. & Pintar, 2016) and post-colonization stage (here). Free-roaming golden topminnows had an intermediate effect and all caged fish had

no effect on mole salamander survival. Growing salamander larvae would quickly escape golden topminnow gape limitations, and they may have attenuated responses to chemical cues of all predatory fish species over their longer larval period (Jackson & Semlitsch, 1993). The mole salamander life cycle (and this study) begins in the winter when predators are less active and aquatic stressors are less severe.

Both consumptive and predation-risk effects on body mass (Figures 1b and 2b) were largely absent across treatments when considering marginal mean adjustments for density-dependent growth generated by differential mortality (i.e., body mass was density-dependent; Wilbur & Collins, 1973). However, our free-roaming active predators, green sunfish, were the exception to this rule as they lowered amphibian body mass (and thus growth rates) substantially compared to density-adjusted expectations, suggesting behavioral changes, suppressed foraging, and/or general stress effects (Nakaoka, 2000; Pangle et al., 2007) that were not present with the ambush predator, small-gaped active predator, or any caged active or ambush predators. Interestingly, free-roaming golden topminnows had the largest effect on mole salamander body condition (Figure 2d), but their effect on overall growth was absent (Figure 2b) and their effect on survival was moderate (Figure 2a), suggesting that golden topminnows act as intraguild predators that pose transient, gape-limited predation-risk (Polis et al., 1989). Our results show consistent predator-driven mortality (Figures 1a and 2a) and growth (Figure 2a,b) effects on
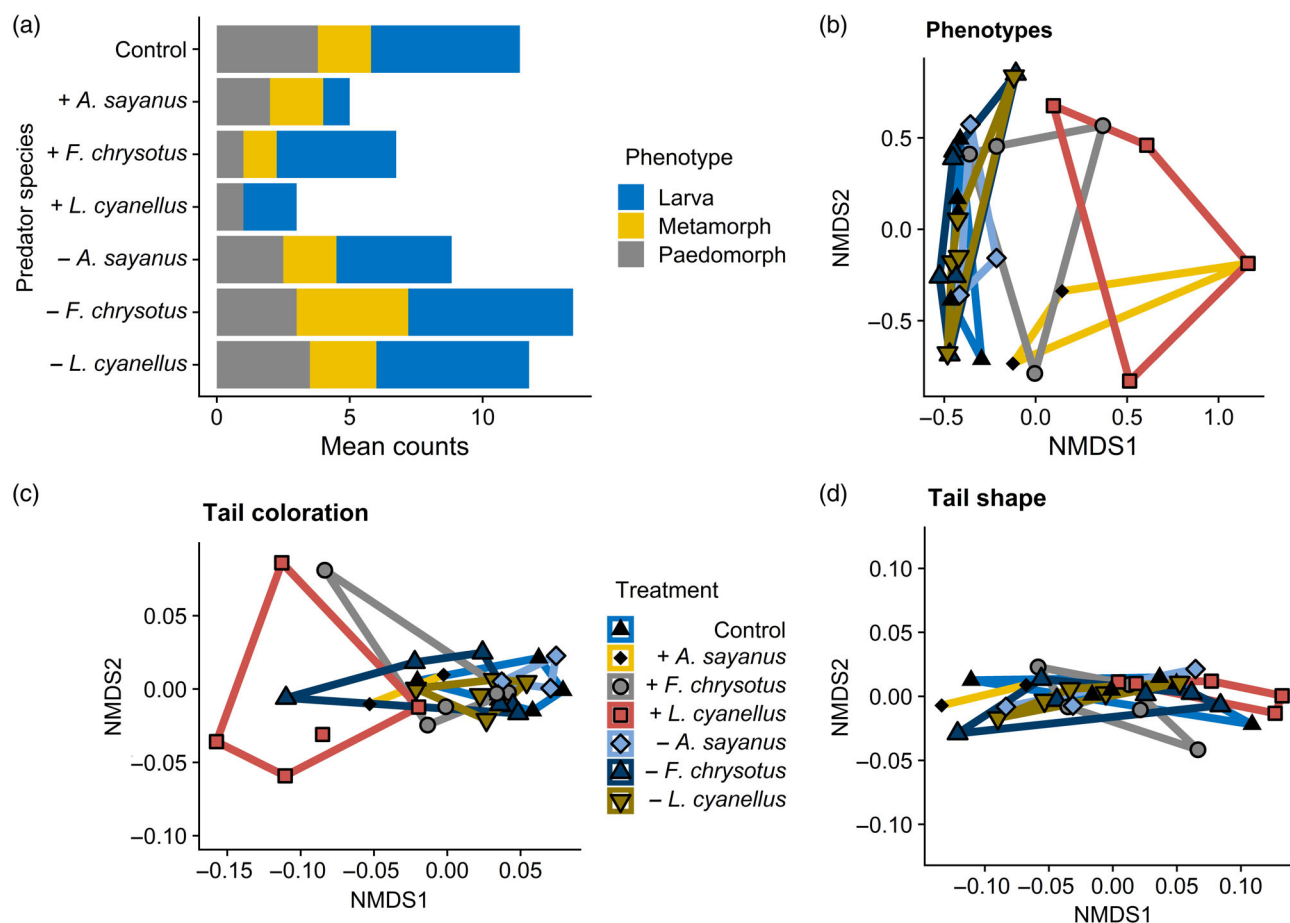
FIGURE 3 Responses of mole salamanders to caged and free-roaming pirate perch, golden topminnows, and green sunfish relative to fishless controls. (a) Mean phenotype counts of mole salamanders in each treatment. (b) Nonmetric multidimensional scaling plot visualizing the difference in phenotype proportions (larvae, metamorphs, and paedomorphs) of mole salamanders across treatments. (c) Nonmetric multidimensional scaling plot visualizing the comparison of hue-saturation-brightness (HSV) values of mole salamander tails across treatments. (d) Nonmetric multidimensional scaling plot visualizing the comparison of tail length, tail height, and tail muscle height of mole salamander tails across treatments. Free-roaming predator exposure is indicated by [+], while caged predator exposure is indicated by [−]

two different amphibian prey that occupy different trophic niches: one that does not compete with fish (herbivorous larval anurans) and one that may compete with fish (carnivorous larval mole salamanders). Thus, we rule out competition for food resources as a major factor driving mortality or growth effects.

"Effective" behavioral or morphological defenses appeared largely absent because of the very low survival rate in the presence of free-roaming pirate perch and green sunfish (Figures 1a and 2a), but these defenses may have greater utility in natural systems. Since effects on growth were only seen with the free-roaming active, large-gaped predator, it appears conspecific alarm signals, strong visual cues, and/or attacks from predators need to be paired with predator-released kairomones to elicit the full suite of risk-induced trait responses (Hossie et al., 2017; Schoeppner & Relyea, 2005). On the contrary,

free-roaming ambush predators did not differ from caged ambush predators in effects on mass in both studies (Figures 1b and 2b), despite other studies finding stronger predation-risk effects of ambush predators (Preisser et al., 2007; Schmitz, 2008) and the likely presence of conspecific alarm signals and attacks in these treatments (Richardson, 2006). This pattern provides evidence that defenses did not fully materialize with the ambush predator, pirate perch, and that ambush predators can be functionally cryptic to prey. However, there is evidence that pirate perch are detectable at least on some level as Albecker and Vance-Chalcraft (2015) have shown with risk-induced behavioral responses in southern leopard frogs (*Lithobates sphenocephalus*). But abandoning behavioral defenses and relying more on morphological traits (larger body mass, deeper tails, and shorter bodies) is a recognized strategy for larval amphibians late in
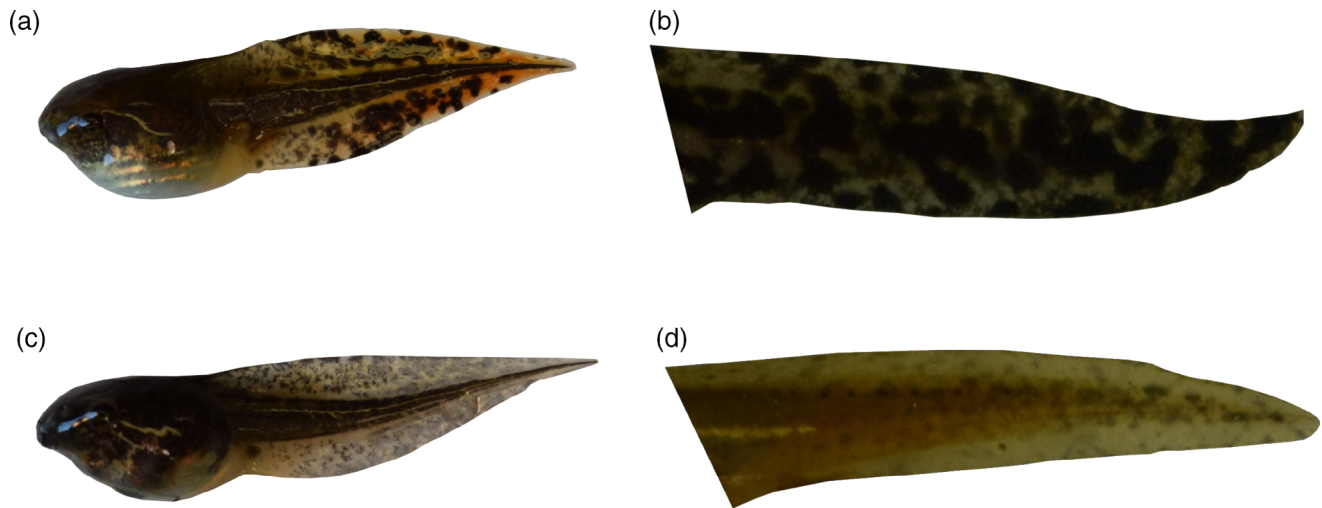
FIGURE 4 (a) Chromatic gray treefrog larva from a mesocosm with free-roaming pirate perch. (b) Pigmented mole salamander tail from a mesocosm with free-roaming green sunfish. (c) Achromatic gray treefrog larvae from a controlled mesocosm. (d) Nonpigmented mole salamander tail from a control mesocosm

ontogeny (Relyea, 2003). This change in strategy over ontogeny provides an alternative explanation that prey attenuated responses to predator cues in caged active predator treatments, for example, evidently for mole salamanders and at least for surviving individuals in the case of gray treefrogs. Nevertheless, the traits of cryptic, ambush predators themselves may facilitate response attenuation in prey (to either visual/chemical cues, conspecific alarm signals, or physiological stress) because they are simply not detectable.

For gray treefrog larvae, we expected more pigmented tail coloration in the presence of predators to camouflage themselves within the leaf litter, their primary predator refugia in the experiment. The free-roaming ambush predator, pirate perch, had absent risk-induced effects on gray treefrog mass, but they did induce more saturated tails compared to all caged predator treatments (Figures 1c and 4a,c). Unfortunately, no larvae survived long enough with the free-roaming active predator, green sunfish, for comparison due to strong consumptive effects. Since morphological responses are more enduring predictors of risk than behavioral responses (Relyea, 2003), prey may detect cryptic predators or their predaceous activity at least initially, but, evidenced by absent risk-induced effect on mass, ultimately attenuate responses. This attenuation may occur after prey mortality plateaus and conspecific alarm cues eventually degrade, but if that were true, then, we should expect prey to have similar response attenuation to both active and ambush predators, which had equivalent predation rates. However, our results on body mass suggest that no such response attenuation occurred with our active free-roaming predator, possibly due to chronic stress, but there was potential response

attenuation with the ambush predator, pirate perch. Since our predators diverged in this respect, it suggests that our active-foraging predator, green sunfish, affected prey directly, and not through conspecific alarm cues.

With mole salamanders, we also expected darker tails in the presence of predators to camouflage themselves in the leaf litter. Mole salamander tail coloration dissimilarity was directly related to larval survival rates, suggesting that conspecific cues, and not predator attacks, are the driving factor. Tails were darkest in the presence of free-roaming green sunfish (Figures 3c and 4b,d), which is similar to earlier studies with salamanders (Storfer & White, 2004; Van Buskirk & Schmidt, 2000), but more recent work has suggested that salamanders have greater variability in risk-induced morphological responses compared to anurans (Brossman et al., 2014; Shaffery & Relyea, 2015). For example, our results did not fit neatly into the two categories found by Touchon and Warkentin (2008), whom showed that fish induce long, shallow, achromatic tails and dragonfly naiads induce short, deep, chromatic tails. Here, larval amphibians showed changes in tail color, but not shape. Again, these responses only occurred with free-roaming predators, suggesting that additional cues, or the stress thereof (Middlemis Maher et al., 2013), need to be paired with predator kairomones or attacks to elicit a full suite of responses (Schoeppner & Relyea, 2005). Unfortunately, only a limited number of individuals could be sampled for tail coloration and morphology in free-roaming predator treatments, thus we advise caution in interpretation.

Following classic theories on ontogenetic niche shifts (Werner & Gilliam, 1984; Wilbur & Collins, 1973), along with theories on facultative paedomorphosis (Denoël

et al., 2005; Whiteman, 1994), we expected the frequency of metamorphosis to scale positively with predation threat, that is, larvae should abandon aquatic conditions that are unfavorable to growth and lifetime fitness. While mole salamander phenotype proportions were similar across all caged predator treatments, including controls (Figure 3a), we found that each free-roaming predatory fish had somewhat different effects. The free-roaming active predator, green sunfish, again, had the most intense effects, but instead of increasing metamorphosis, they prevented all mole salamanders from metamorphosing (Figure 3a,b). While this finding refutes theoretical models (Werner & Gilliam, 1984; Whiteman, 1994; Wilbur & Collins, 1973), it agrees with past studies that found active predators can reduce the frequency of paedomorphosis (Denoël & Ficetola, 2014) and prevent transition to either metamorphic or paedomorphic stages (Jackson & Semlitsch, 1993). The absence of metamorphosis, in this case, appears driven by risk-induced effects on growth (Figure 2b), since metamorphosis requires a minimum larval body size (35 mm SVL; Semlitsch & Wilbur, 1988). Free-roaming golden topminnows induced phenotype proportions most similar to controls and caged predator treatments, but produced a larger proportion of larvae overall (Figure 3a,b), unsurprisingly similar to bluegill sunfish effects found by Jackson and Semlitsch (1993) since both bluegill sunfish and golden topminnows function as intraguild predators of larval mole salamanders. Effects of the free-roaming ambush predator, pirate perch, diverged most from other predatory fish in that most mole salamanders reached metamorphosis or paedomorphosis and few remained as larvae (Figure 3a,b). Much like the absent effects on body size (Figure 2b), the effect of the ambush predator on mole salamander phenotype proportions appeared to strictly match density-adjusted expectations seen in other studies (Semlitsch, 1987b; Bohenek & Resetarits, unpublished data), with no apparent risk-induced trait responses to the ambush predator itself—a clear mismatch given the intense consumptive effects of the ambush predator (Figures 2a and 3a,b).

Breeding hylids generally avoid fish, including active predators like green sunfish, but they do not avoid pirate perch (Resetarits Jr. & Binckley, 2013). Mole salamander oviposition has been less extensively studied, though anecdotal observations also suggest fish avoidance (Pintar & Bohenek, personal observations), as has been observed with congeners (Davenport et al., 2017; Kats & Sih, 1992), but no studies in relation to pirate perch currently exist. Operating under the assumption that certain families of breeding amphibians avoid habitats with fish because they pose a significant predation threat to their offspring (Relyea, 2001a, 2001b), we should expect spatial segregation between predator and

prey and decreased selection pressure for anti-predator responses (Agrawal et al., 2010), thus, a negative correlation between prey life stages. However, here, we see mostly positive correlations where the strongest prey responses occur with the most strongly avoided predator, green sunfish, while behavioral and morphological responses to the ambush predator, pirate perch, are relatively absent. First, prey have a clear mismatch between the perceived and actual predation threat of the ambush predator (Figures 1a,b and 2a,b) (Albecker & Vance-Chalcraft, 2015; Resetarits Jr. & Binckley, 2013). Second, this pattern suggests that prey have a positive correlation of responses across life stages where they utilize multicomponent defenses against some predators (i.e., strong responses to green sunfish at the adult colonization stage and post-colonization larval stage), or absent or limited defenses in both life stages to other predators (i.e., relatively absent responses to pirate perch at the adult colonization stage and post-colonization larval stage; Andrade et al., 2017). Though, one may argue that prey defenses observed here may be so ineffectual (relative to other anurans) that these results may represent a negative correlation of functional defenses.

Predator-naïve prey or chemically camouflaged predator?

These observed divergent predation-risk effects in larval amphibians provide further evidence that prey have mismatched anti-predator responses to the cryptic ambush predator, pirate perch (Silberbush & Resetarits Jr., 2017). The high growth rates of larval gray treefrogs and mole salamanders in the presence of consumptive pirate perch are puzzling given the responses of larval amphibians to many other predatory fish species (Hossie et al., 2017; Kats et al., 1988; Relyea, 2001b; Resetarits Jr. & Binckley, 2013; Touchon & Warkentin, 2008) and the strong consumptive effects of pirate perch shown here. This can be explained by one of two alternative hypotheses—each of which focuses on one of the two participants in the interaction: predator-naïvete of the prey or chemical camouflage of the predator.

Predator-naïvete can occur for a number of reasons such as when predators and prey lack evolutionary history and predators are therefore unfamiliar and not inherently recognized (Cox & Lima, 2006; Diamond & Case, 1986; Freeman & Byers, 2006), as is common with invasive predators (Sih et al., 2010). Unfamiliarity can also apply if predators are sufficiently rare. Predators and prey may also occupy different habitat domains or predators may utilize novel hunting modes, both of which can contribute to predator-naïvete (Carthey & Banks, 2014).

Sih et al. (2010) posited that predator-naïve prey may experience intense consumptive effects, but limited predation-risk effects, from unfamiliar predators, which is what we see here with pirate perch. However, gray treefrogs and pirate perch naturally co-occur, utilize similar habitat domain, and have extensive, historical range overlap, and yet, there still seems to be no inherent or effective anti-predatory responses to pirate perch. Nor do pirate perch utilize a novel hunting mode as larval amphibians are faced with many ambush predators, from dragonfly naiads to turtles to other predatory fish species. That being said, we do not know if pirate perch are functionally "rare" relative to other fish species in the region, or if the concept of a functionally "rare" predator is even meaningful for a cryptic ambush predator.

Ambush predators, by definition, remain relatively motionless until prey are within range for attacks, and they employ a wide array of visual camouflage to conceal themselves from unsuspecting prey (Pembury Smith & Ruxton, 2020). These two strategies (motionlessness and camouflage) are immediately apparent to us as observers since we are highly visually oriented organisms. However, there is increasing evidence that camouflage is also operating in sensory modes that are less immediately apparent such as mechanoreception (e.g. silent flight in owls; Wagner et al. 2017; Clark et al., 2020) and chemoreception. Camouflage in chemoreception, where organisms conceal or modify their scent, is increasingly recognized in predator-prey interactions (Akino, 2005; Anton et al., 2016; Brooker et al., 2014; Lönnstedt & McCormick, 2013; Miller et al., 2015; Resetarits Jr. & Binckley, 2013). Both larval amphibians and ovipositing adults may not be able to sense pirate perch because they are chemically camouflaged, which is defined as an adaptation to modify or conceal chemical cues so as to be misidentified or remain undetected (Resetarits Jr. & Binckley, 2013; Ruxton, 2009). Pirate perch also appear to be chemically camouflaged to dispersing aquatic coleopterans and hemipterans and to ovipositing mosquitoes and gray treefrogs (Binckley & Resetarits Jr., 2003; Binckley & Resetarits Jr., 2005; Resetarits Jr. & Binckley, 2013; Resetarits Jr. et al. 2022; Silberbush & Resetarits Jr., 2017) and, based on this experiment, to larval gray treefrogs and mole salamanders in the aquatic environment. These disparate taxonomic groups show highly convergent veha However, while the divergent effects of pirate perch in this study may be attributable to chemical camouflage, there were still trace risk-induced trait responses to free-roaming pirate perch (Figure 1a,c,d), suggesting that chemical camouflage is imperfect or some additional mechanism may be operating, such as conspecific alarm signals. In our study, pirate perch never induced effects as strong as green sunfish or golden topminnows, even when consuming prey, suggesting the difference lies with the fish itself. Lastly, while we value the control and natural approximation afforded by mesocosm studies, they have limitations, especially when replicates are lost (e.g., pirate perch treatments), and support for chemical camouflage would improve with observations of this mechanism in natural systems.

CONCLUSIONS

Current theory and evidence posited in a meta-analysis by Preisser et al. (2007) suggests that ambush predators should elicit stronger predation-risk effects in prey than active predators because of differences in the reliability of cues between hunting modes. Ambush predators remain motionless until prey are within striking distance, thereby spatially concentrating their cues (e.g., waterborne kairomones) to their hiding position. Ambush predators typically do suppress prey foraging (Preisser et al., 2007) and because their cues are localized, they may provide more information and reliability of immediate predation-risk. Contrarily, active predators spatially disperse, rather than concentrate, their cues as they move throughout the environment. Active predators typically do not suppress the foraging of prey (Preisser et al., 2007) and because their cues are dispersed, their cues theoretically provide less information and are less reliable indicators of predation-risk (Preisser et al., 2007; Schmitz, 2008). However, a more recent meta-analysis by Davenport et al. (2014) focused on organisms with complex life cycles and suggests that large-gaped active predators have stronger effects on size at metamorphosis than large-gaped ambush predators. Here, we saw effects opposite of Preisser et al. (2007), but in line with Davenport et al. (2014), where a free-roaming active predator had strong effects on growth, while a free-roaming ambush predator had no effects on growth. One major assumption in this framework is that all ambush predators emit detectable information (e.g., waterborne kairomones) on which prey can eavesdrop to avoid consumption (Preisser et al., 2007, Schmitz, 2008). If prey have evolved sensory capabilities to detect ambush predators, then selection would also favor ambush predators that can conceal their cues (Resetarits Jr. & Binckley, 2013). Thus, it should be expected that ambush predators can evolve countermeasures to facilitate their success in the information wars of predator–prey interactions (Miller et al., 2015). We should also not expect prey to perfectly predict predation-risk as their information about any predator species is typically incomplete. For example, Symes et al. (2020) conclude that multiple

species of katydids can detect bat echolocation, but they do not distinguish between predatory and nonpredatory bats. Thawley and Langkilde (2017) found that eastern fence lizards (*Sceloporus undulatus*) learned to flee from invasive fire ants (*Solenopsis invicta*), but they have generalized this response to nonthreatening native ants that are otherwise consumed as prey by the lizards, an empirical example of ecological stimulus substitution (Fanselow, 1989).

Our results, here, demonstrate that predators with alternative hunting modes can have functionally equivalent consumptive effects, but divergent predation-risk effects, on prey. We show that the cryptic ambush predator, pirate perch, has equal predation rates to an active, dominant, widespread predator, green sunfish (Figures 1a and 2a). The non-consumptive effect of the caged, active predator on prey mortality (Figure 1a) was surprising and emphasizes how predation-risk effects are changing the way we think about classical predator–prey theory (Boonstra, Hik, et al., 1998; McCauley et al., 2011; Peckarsky et al., 2008). Most risk-induced trait responses manifested in free-roaming predator treatments, where active predators had much stronger effects on growth than ambush predators, refuting current models (Preisser et al., 2007). More limited predation-risk effects of caged predators suggest that predator kairomones alone were insufficient for a full range of anti-predator responses and effects. Since larval defenses appeared relatively ineffective, the most effective anti-predator strategy is for adults to choose predator-free oviposition sites, though gray treefrogs appear incapable of behaviorally avoiding pirate perch (Resetarits Jr. & Binckley, 2013).

Comparing consumptive and predation-risk effects is an area ripe for exploration, and we encourage researchers to continue exploring predators and prey with diverse traits, instead of utilizing overstudied model predator species (e.g., green sunfish). We also encourage researchers to consider all life stages (Krenek & Rudolf, 2014; Rudolf et al., 2014; Wilbur, 1988) so as to paint a more complete picture of the total impacts of consumptive and predation-risk effects on individuals, populations, and communities. The primary lesson, here, is that predation-risk effects cannot be reliably predicted based on the strength of consumptive effects, and while we would expect the converse to be true, predator adaptations like crypsis make the link between consumptive and predation-risk effects tenuous. Whether the mysterious effects of pirate perch are due to predator-naïvete or chemical camouflage cannot be fully resolved in this paper, but as more evidence accrues for chemical camouflage, we hypothesize that these cryptic strategies may be more common among ambush predators than previously understood.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data (Bohenek et al., 2022) are available from Figshare: https://doi.org/10.6084/m9.figshare.19216881.v1.

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