Predicting Predatory Outcomes in the Context of Carryover Effects: Interactions between Juvenile Frogs and Spider Predators

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Abstract

As representatives of organisms with complex life histories, frogs provide an ideal system to study predator-induced carryover effects: how the risk of predation in one life stage can impact predator–prey interactions in a later stage. Invertebrate predation on frogs has been widely reported, although studies of the behavioral mechanisms underlying their interactions in the terrestrial stage have been lacking. We made detailed observations of interactions between a wolf spider (*Tigrosa helluo*) and Blanchard's cricket frog (*Acris blanchardi*) to determine factors that predict capture success and to evaluate potential carryover effects from aquatic predation risk. Juvenile frogs, reared with or without dragonfly predator cues, were placed in an arena with or without spider cues and allowed to interact with a spider. Spiders captured frogs, and an interaction between frog size and activity predicted frog survival. We found no evidence that either aquatic or terrestrial cues altered frog behavior or survival. By preying upon a demographically important life stage, spiders may contribute to population dynamics in frogs.

Introduction

Predation is a ubiquitous selection pressure that shapes the evolution of prey behavior, morphology, and life history. Antipredator behaviors typically represent trade-offs made by prey, such as forgoing foraging opportunities to exhibit vigilance for predators. Species with complex life histories represent particularly interesting cases of predator–prey interactions, as prey trade predation risk in the larval habitat for predation risk in the adult habitat (Benard 2004). Furthermore, the nature of the predation risks prey face in distinct habitats (e.g., aquatic and terrestrial) may be highly divergent because of dissimilarities in predator community composition. Carryover effects (i.e., latent impacts of an individual's early environment on performance of later life stages [Pechenik 2006; Earl & Semlitsch 2013]) serve as a working hypothesis for connecting predator-induced stresses across different life stages. Although considerable variation exists in the strength and direction of carryover effects, the majority of studies of carryover effects have found evidence supporting the importance of early experiences on success later in life (Earl & Semlitsch 2013). Predators may be important drivers of carryover effects in metamorphosing species, as non-consumptive effects of predators (i.e., predator cues) have been shown to strongly impact prey behavior, morphology, and life history (Benard 2004; Relyea 2007), often eliciting adaptive prey phenotypes (Persons & Rypstra 2001; Benard 2006; Storm & Lima 2008; Hettyey et al. 2011).

Understanding predation risk at multiple life stages is essential for predicting the abundance and distribution of prey species that undergo metamorphosis (Rubbo et al. 2006). Frogs (Amphibia: Anura) are a representative group of metamorphosing species that shift from aquatic to terrestrial habitats as juveniles prior to sexual maturity. Although a long tradition of research on anuran interactions with aquatic predators and the resulting effects on tadpoles and metamorphic endpoints exists, relatively little is

known about possible carryover effects of predator exposure in the larval environment to the terrestrial environment (Relyea 2007). Furthermore, reports of terrestrial predation are frequently anecdotal and there is a dearth of information detailing the encounters of juvenile amphibians with predators and the resulting antipredator behaviors (Toledo 2005; Toledo et al. 2007; but see Touchon et al. 2013). Juvenile anurans may play a disproportionate role in population persistence; sensitivity analyses have shown that post-metamorphic survival rates strongly influence population growth rates (Biek et al. 2002; Govindarajulu et al. 2005), and Berven (1990) demonstrated that breeding population size of wood frogs (*Lithobates sylvatica*) depended on juvenile recruitment in previous years. Juveniles are also at considerable risk of predation as they leave the aquatic environment (e.g., Wassersug & Sperry 1977); a study on mortality in recently metamorphosed amphibians indicated substantial terrestrial predation pressure in proximity to the aquatic habitat (Pittman et al. 2013). Given the relative importance of juvenile frog mortality to population dynamics and the lack of detailed observations of interactions with predators, we were motivated to conduct a study of predator–prey interactions at this life stage.

Although a wide diversity of vertebrates commonly consume anurans (Toledo et al. 2007), invertebrate predators also present a sizable mortality risk (Toledo 2005). While primarily insectivorous, spiders are known to consume both aerial and aquatic vertebrates across a wide geographic range (Nyffeler & Knörnschild 2013; Nyffeler & Pusey 2014) and may be the most important invertebrate predators of anurans (Toledo 2005). Wolf spiders (Araneae: Lycosidae) can reach high densities in near-aquatic habitats (Graham et al. 2003) where they are likely to encounter juvenile frogs exiting the pond and dispersing to upland habitats. Our study species were the large wolf spider *Tigrosa helluo* (formerly *Hogna helluo* [Brady 2012]) and Blanchard's cricket frog (*Acris blanchardi*) (Fig. 1). These co-occurring species utilize similar microhabitats at the edge of ponds, making *T. helluo* a likely predator of juvenile frogs. A report by Blackburn et al. (2002) on predation between these two species, our personal observation of *T. helluo* collected with frog remains in its chelicerae in proximity to a pond, and a recent study demonstrating the negative impact of this spider on another metamorphic anuran (DeVore & Maerz 2014) all suggest that *T. helluo* may incorporate Blanchard's cricket frogs into its diet. Blanchard's cricket frogs are experiencing declines across their range for unknown reasons

Fig. 1: Predation of Blanchard's cricket frog (*Acris blanchardi*) by the wolf spider *Tigrosa helluo*.

(Gray et al. 2005), and their annual life cycle may make populations particularly sensitive to factors that impact juvenile recruitment (Lehtinen & MacDonald 2011; McCallum et al. 2011).

The objective of this study was to document predator–prey interactions between wolf spiders and cricket frogs and determine what factors predict the outcome of those interactions within the framework of the carryover hypothesis. We addressed three specific questions: in the presence of a terrestrial predator, (i) Does prior tadpole exposure to cues from an aquatic predator affect cricket frog behavior and survival? (ii) Do cricket frogs alter their behavior in response to terrestrial predator cues? and (iii) Is there an interaction between exposure to predator cues in the aquatic and terrestrial environments that affects cricket frog survival? We predicted prior exposure to aquatic predator cues in the larval environment would alter cricket frog behavior (as documented by Barbasch & Benard 2011; in wood frogs) and reduce survival in the presence of a terrestrial predator. We also predicted that wolf spiders would readily attack and consume metamorphic cricket frogs, and that cricket frogs would detect and respond to spider cues in a manner that would increase their survival.

Methods

Collection and Maintenance

Cricket frogs

All cricket frog metamorphs were reared from tadpoles in outdoor mesocosms and had previously been

used in a study testing the effects of predator cues on metamorphosis in 2013 (A.M. Gordon, M.B. Young-quist, and M.D. Boone unpublished data). Ten am-plexed pairs were collected from a pond at Miami University's Ecology Research Center (39°31′33″ N, 84°43′20″W). The eggs were hatched and maintained in an outdoor rearing mesocosm before being trans-ferred to experimental mesocosms. Tadpoles were reared in 1000 L mesocosms. Mesocosms were filled with tap water, which was allowed to age 1 d prior to addition of 1 kg leaf litter; we then inoculated meso-cosms with algae from a fishless pond every other day for 2 wk prior to addition of tadpoles. Thirty tadpoles were added to each mesocosm and allowed to accli-mate for 1 wk before the addition of dragonfly naiads (*Erythemis simplicicollis*). Tadpoles were reared with or without caged dragonfly naiads, resulting in the pres-ence or absence of aquatic predator cues. We used a randomized block design for this study. In mesocosms with predator cues, three individually caged dragonfly naiads were added to each mesocosm and fed 180 g of cricket frog tadpoles weekly; in mesocosms without predator cues, we added three empty cages. Cricket frog tadpoles were exposed to predator cues throughout development. There were no effects of caged predator presence on cricket frog time to or size at metamorphosis (A.M. Gordon, M.B. Young-quist, and M.D. Boone unpublished data; Wilks' Lambda = 0.909, df = 2, p = 0.3859). After metamor-phosis, all cricket frogs were housed in groups of 10 in 30 L × 20 W × 25 H cm plastic containers with a damp paper towel, which was changed daily. Frogs were fed crickets (*Acheta domesticus*) dusted with cal-cium powder, as a nutrient supplement, *ad libitum*. Frogs were maintained in the laboratory 1–3 weeks of post-metamorphosis prior to predation trials.

Wolf spiders

Adult female *Tigrosa* were collected from the margins of agricultural fields at Miami University's Ecology Research Center. Spiders were housed individually in plastic containers (8 cm tall × 12 cm diameter) with a substrate of moistened peat moss and potting soil and maintained in an environmental chamber (13 L:11D light cycle at 25°C). We provided *Tigrosa* two appropri-ately sized crickets weekly, and spiders were used in trials 1 wk after their most recent feeding.

Predation Trials

All predation trials occurred in 30 L × 20 W × 25 H cm plastic containers (experimental arenas) that contained a

2-cm layer of rinsed pea gravel and 200 ml of water. The water level was just below the top layer of gravel and ensured appropriate levels of humidity for frogs and spi-ders. We used a full factorial design to test the effect of aquatic predator cues (reared with or without dragonfly naiads), terrestrial predator cues (experimental arenas with or without cues deposited by wolf spiders), and their interaction on frog behavior and survival in the presence of a spider. Each treatment was replicated 8–12 times, for a total of 40 trials. We added spider cues to the experimental arenas by placing a spider in the arena and allowing it free range to deposit cues (i.e., silk, feces, and other excreta) for 24 h prior to the start of a trial; control arenas (those without spider cues) were also setup 24 h before a trial.

Prior to the start of each trial, we weighed each frog and spider to the nearest 0.1 mg. Average (SE) frog mass was 0.262 (0.008) g and spider mass was 0.417 (0.017) g. Spiders used for cue deposition were subse-quently used as the predator in the same arena. At the start of each trial, the test spider was placed under a black vial on one side of the arena and allowed 3 min to acclimate. Cricket frogs were placed by hand into the arena on the side opposite the spider. The starting positions of the frog and spider were alter-nated between trials. Immediately after frog place-ment into the arena, we removed the vial covering the spider and started the trial.

Trials lasted 20 min and were recorded by a camera positioned above the arena. We scored videos for frog activity (jumps per second, proportion of time spent climbing), spider activity (lunges per second, time to orient to frog), attack direction (front, back, or side of frog), and frog survival (capture success). If frogs were not captured after 20 min, we ended the trial, and the frog was recorded as having escaped capture. When a spider captured a frog, we allowed the spider to hold the frog for 15 min to qualitatively evaluate the effi-cacy of venom and speed of digestion. A subset of spi-ders were allowed to digest frogs for 2 or 24 h after capture. No frogs or spiders were re-used in any trials. We conducted 2–10 trials on a single day, and all trials were completed within 3 wk.

Statistical Analyses

Because we were interested in predatory interactions between spiders and frogs, we excluded trials in which the spider did not orient toward the frog, as this behavior represents the onset of the predation sequence. We were thus left with 25 total trials for use in statistical analyses. The effects of aquatic predator cues, terrestrial predator cues, and their

interaction on frog behavior (jumps per second, proportion of time spent climbing) and spider behavior (lunges per second, time to orient to frog) were tested using two separate MANCOVAs, with frog and spider mass as co-variates, respectively. All analyses were carried out using R (R Core Team 2013).

To understand factors related to spider capture success, we compared nested logistic regression models of varying complexity. Specifically, we built (i) a *global model* including the main and interactive effects of aquatic and terrestrial predator cues along with variables that appeared influential after preliminary data analysis, (ii) a reduced *predator–prey model* including only the mass and behavior of both spiders and frogs, and (iii) a *prey-based model* including only the main and interactive effects of frog mass and number of jumps per second (Table 1). To address the presence of linear separation (i.e., when a combination of predictors are associated with a single response), we used Firth's penalized-likelihood logistic regression and compared the AICc values from penalized models using the packages logistf (Heinze et al. 2013) and MuMIn (Bartoń 2013).

We compared the observed frequency of all attack directions with an expected uniform distribution using a chi-squared goodness of fit test. Additionally, we compared the distribution of initial attacks made with the distribution of successful attacks using Fisher's exact test.

Results

Spiders captured frogs in 36% of the trials in which they oriented to their prey. On average (SE) spiders oriented to frogs after 336 (46) s, and, if they attacked, made their first lunge 66 (28) s later. Spiders lunged at frogs an average of 1.8 (0.3) times throughout the trial; of those with successful captures, 67% of frogs were captured on the first attack. Frogs jumped at an average rate of 0.02 (0.005) jumps/s and spent 16 (4) % of the time climbing (Video S1–S3).

Neither aquatic predator cues, terrestrial predator cues, nor their interaction affected the behavior of

frogs or spiders ($F_{1,19}$ ≤2.12; p ≥ 0.15). The nested logistic regression models indicated that the *prey-based model* (including only frog size, number of jumps made, and their interaction) was better than the other models at explaining the probability of a frog being captured (Table 1). Specifically, smaller frogs were more likely to survive if they jumped less often, but the survival of larger frogs was unaffected by jump frequency (Fig. 2; Table 2).

The direction from which spiders attacked followed a non-random pattern, with 49% of attacks occurring from behind the frog, 38% from either side, and only 13% from the front (χ^2 = 14.07, df = 2, p < 0.01). Successful attacks were not distributed differently from the first attack made (Fisher's exact test, p = 0.88). Within 15 min post-capture, frogs ceased moving their appendages, and most showed no evidence of cardio-respiratory function, suggesting potent, fast-acting venom. External digestion of tissues began quickly, and the digestive fluids in concert with cheliceral teeth were capable of rendering most of the skeleton (Fig. 3).

Discussion

Our study demonstrates that wolf spiders are capable terrestrial predators of newly metamorphosed anurans, although we did not find support for the carry-over hypothesis. Furthermore, we demonstrate that both size and behavior of the anuran prey affect survival probability. Our results indicate that frog jumping frequency is an important predictor of survival for smaller individuals, whereas the survival probability for larger individuals appeared unaffected by activity. The interaction of size and jumping frequency may be explained by differences in jumping performance. For most anurans, including cricket frogs, jump distance increases with size (Zug 1978; Miller et al. 1993; M.B. Youngquist unpublished data). Endurance also scales with size (Pough & Kamel 1984; Careau et al. 2014; but see Miller et al. 1993); species that have similar larval periods and metamorphic mass as cricket frogs show increased endurance with size after metamorphosis

Table 1: Summary of nested models used to describe the likelihood of frogs being captured by spiders

Model Name	Predictors of Capture	df	AICc
Prey-based	Frog + Jumps + Frog*Jumps	4	63.5
Predator–prey	*Prey based* + Time to orient + Spider + Frog*Spider	7	74.9
Global	*Predator–prey* + Aquatic + Terrestrial + Aquatic*Terrestrial	10	90.6

Terms included in the models: frog (frog mass), jumps (number of jumps per second), time to orient (time from start of trial until spider directed body toward frog), spider (spider mass), aquatic (the presence or absence of predator cues in the larval environment), and terrestrial (the presence or absence of cues deposited by spiders). Models with lower AICc values provide an improved fit to the data.
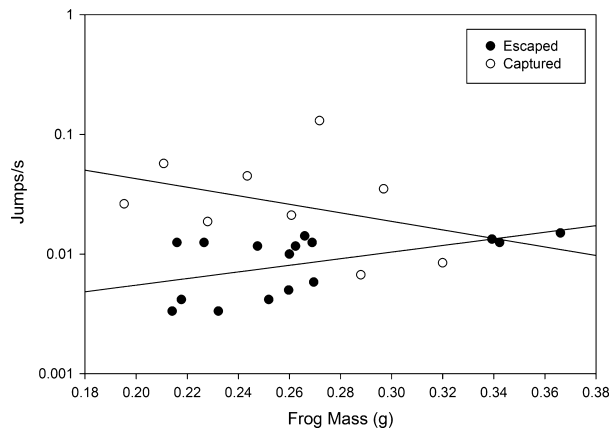
Fig. 2: Frog size, frog activity (number of jumps per trial duration), and their interaction best predict the likelihood of being captured by a spider. Frog activity is presented on a log scale.

Table 2: Parameter estimates and confidence intervals for predictors included in the *prey-based model*

Predictor	Parameter Estimate	Confidence Interval
Frog	1.8	1.5–1.9
Jumps	37.5	35.6–39.7
Frog*Jumps	−125.0	−132.8 to −117.2

Terms included in the model: frog (frog mass), jumps (number of jumps per second).

(Pough & Kamel 1984). It then follows that small individuals, that jump shorter distances and tire faster than larger individuals, may increase their odds of survival by not moving. Remaining immobile can increase survival in the presence of visually oriented predators (Heinen 1994; Persons et al. 2001; Touchon et al. 2013).

The higher survival likelihood for small frogs that were less active can be attributed to the mechanisms of spider hunting behavior. Spiders possess a sophisticated array of senses, including vision and vibration detection. Both sensory systems can be stimulated by moving prey, and spiders are capable of integrating these multimodal cues to shape their behavior (Uetz & Roberts 2002). For example, spiders increase their attention and spend more time near highly active prey than less active prey (Persons & Uetz 1997) and are more likely to attack moving prey (Touchon et al. 2013), which is consistent with our observation of higher capture success with more active frogs. Successful spider attacks were disproportionately initiated from behind the frog. We did not observe frogs adjusting their position relative to spiders, so spiders may have assessed their prey's body positioning and

decreased their likelihood of being detected by attacking from behind (Nelson et al. 2005). Because our study was conducted in the laboratory and the only refuge frogs had was to climb on the wall, our predation rates may not reflect those in nature. However, prey capture occurred in only 22.5% of trials (including trials without spider orientation), which is consistent with spider predation in the wild being rare (Wise 1993; Touchon et al. 2013). Despite the low probability of capturing prey at the level of the individual, spider predation on frogs (Toledo 2005) and other vertebrates (Nyffeler & Knörnschild 2013; Nyffeler & Pusey 2014) has been widely documented and may represent an important ecological interaction (DeVore & Maerz 2014).

While many amphibian species respond to cues from both aquatic and terrestrial predators (e.g., Belden et al. 2000; Van Buskirk 2001; Vonesh & Warkentin 2006), we found no evidence that cricket frogs respond to wolf spider cues. Similar results have been reported by Rubbo et al. (2003). Cricket frogs may not detect the chemotactile cues (i.e., silk, feces, and other excreta) deposited by spiders. Alternatively, cricket frogs may detect but not respond to spider cues. Our results also indicate that experience with aquatic predator cues does not affect the behavior or survival of cricket frogs in the presence of wolf spiders. Thus, we reject the carryover hypothesis in this system. Cricket frog tadpoles respond to fish predator cues by losing their characteristic tail spot and will alter their behavior in response to cues from both dragonfly naiads and fish (Carfagno et al. 2011). Therefore, the lack of a detected carryover effect in our study is unlikely to be caused by cricket frogs being unresponsive to predator cues in the larval stage. Similar to our results, Barbasch & Benard (2011) found no carryover effect of tadpole exposure to dragonfly naiad cues on the response of juvenile wood frogs to garter snake cues. While prior experience with predator cues can influence behavior with future encounters of the same species (Murray et al. 2004; Sitvarin & Rypstra 2012), it is possible that predator cue response is decoupled between aquatic and terrestrial environments and responses to predator cues are species specific (Murray et al. 2004), rather than a generalized response.

We have documented interactions between spider predators and juvenile frogs in a terrestrial environment, providing mechanistic details about a widely reported phenomenon that had previously consisted largely of anecdotal observations (Toledo 2005). Future studies would benefit from examining how relationships between frogs and spiders change
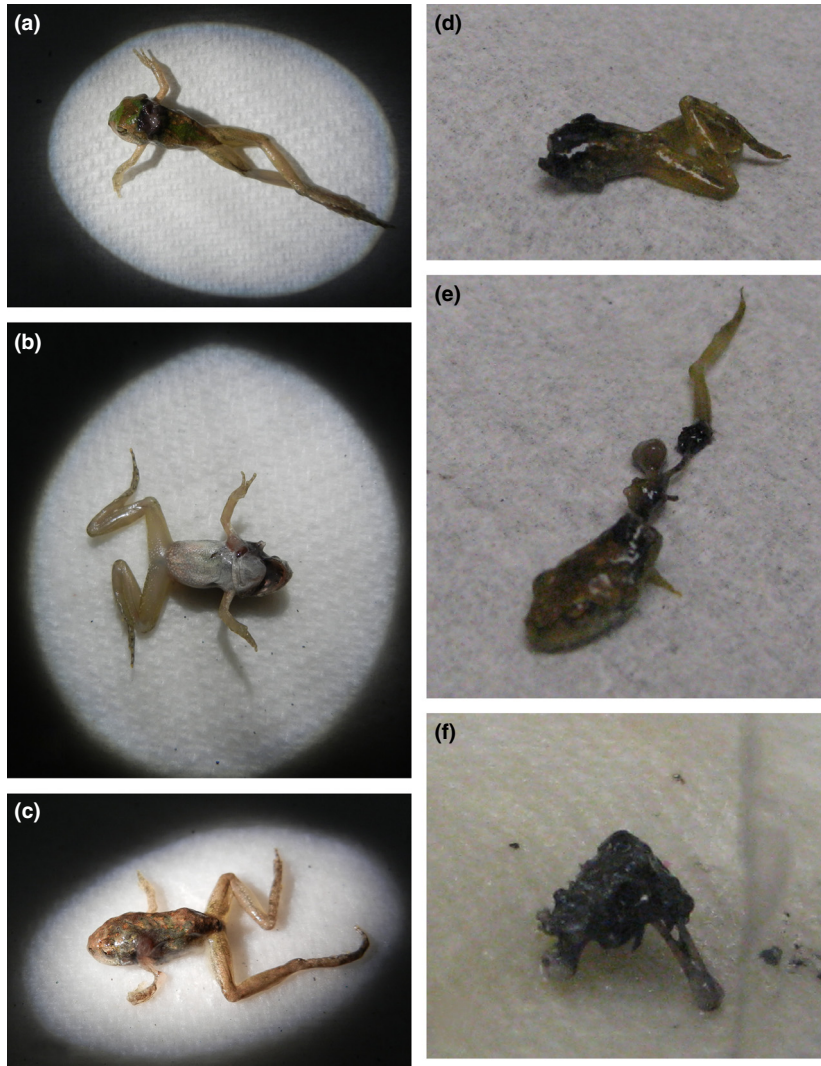
Fig. 3: Frog remains after capture and digestion for a–c 15 min, d–e 2 h, and f 24 h.

through ontogeny, as the roles of competitor, intra-guild predator, and intraguild prey are likely to shift over time (Rypstra & Samu 2005). Given the importance of juvenile frog survival for population persistence (Biek et al. 2002; Govindarajulu et al. 2005), the risk juveniles face as they exit the pond (Pittman et al. 2013), and the potential for high densities of spiders around ponds (Graham et al. 2003; Toledo 2005; Nyffeler & Pusey 2014), it is likely that our observed predation events are ecologically relevant for populations of cricket frogs and other amphibians. Furthermore, understanding the role of spiders as predators of amphibians may become increasingly important as habitats are modified by invasive species that can indirectly increase predation by spiders on metamorphic frogs (DeVore & Maerz 2014). Although the likelihood of an individual spider consuming a vertebrate

is likely low, these predators have effective paralytic and digestive capabilities that may be a byproduct of selection for the acquisition of large, nutritious meals (Blackledge 2011; Nyffeler & Knörnschild 2013; Nyffeler & Pusey 2014). Further exploration of mortality risks for metamorphic anurans, and the frequency of interactions with spiders, will provide insight into evolutionary forces shaping the behaviors of both frogs and spiders.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Video S1. Sequence of spider orientation toward frog, lunge, and escape.

Video S2. Series of evasions by a frog.

Video S3. Successful capture.