

The advantage of no defense: predation enhances cohort survival in a desert amphibian

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Abstract The impacts that predators have on prey behavior, growth, survival, and ultimately the composition of many ecological communities are mediated by prey defenses and the susceptibility of prey to predators. We hypothesized that prey populations inhabiting short-lived, species-poor, aquatic environments should lack significant morphological, developmental, and behavioral responses to predators and are therefore highly susceptible to predation. Furthermore, we predicted that the resultant decrease in prey density and increase in per capita resources due to high susceptibility to predators should enhance overall cohort survival because of enhanced growth of surviving prey. To test these ideas, we performed laboratory and outdoor mesocosm experiments to disentangle multiple effects of predators on an anuran (*Scaphiopus couchii*); a species highly adapted to breeding in ephemeral habitats and that has one of the

shortest larval periods of all anurans. Chemical (presence of predator) and lethal predator cues (predator plus consumed conspecific) elicited no response in behavior, development, or morphology, indicating a lack of defensive mechanisms. Survivorship was significantly reduced in treatments where tadpoles were exposed to predators. However, this reduction in prey density led to accelerated time to metamorphosis, conferring an advantage to survivors who must metamorphose before ephemeral ponds dry. Our experiments demonstrated that in short-lived environments, prey may exhibit little or no response to the presence of predators presumably because selection for anti-predator defenses is countered by selection for rapid metamorphosis. However, predation actually resulted in an increase in overall cohort survival. Although predators are relatively rare in highly ephemeral aquatic environments, they may play an important role in facilitating the long-term persistence of their prey by reducing prey density.

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Introduction

Predators play an important role in driving the structure of species assemblages through various mechanisms that come into play depending on prey

density, prey characteristics, anti-predator defenses, and resources available to prey (Paine 1974; Sih et al. 1985; Crooks and Soule 1999). In extreme cases, predators may entirely exclude species from a particular environment (Bohonak and Whiteman 1999; Knapp et al. 2001). Theoretical and empirical studies have revealed instances when predation may either positively or negatively affect surviving prey; effects depend on context. In most cases, the presence of predators has a negative impact on prey, as individuals are either killed or exhibit anti-predator defenses that reduce growth or development. It is thus intuitive that anti-predator defenses should enhance cohort survival and, in turn, that prey exhibit some degree of anti-predator defense. However, when the density of prey is reduced by predators (prey thinning), survivors may actually benefit (Morin 1983; Wilbur 1988; Fauth 1990). A positive effect of prey thinning is expected to be most evident in resource-limited environments because of the increase in per capita resources for surviving individuals. Because of the potential advantages of prey thinning in resource-limited environments, lack of defensive mechanisms (and the resulting high rates of predation) may actually have a positive influence on cohort survival.

Species that have been subjected to constant predation risk over many generations tend to evolve fixed defenses such as spines, cryptic coloration, noxious toxins, and low activity levels, which are manifested regardless of whether predators are present or absent. Fixed defense mechanisms are presumed to be costly because resources and/or time that could be allocated to growth, fecundity, foraging, or mating are allocated to predator defenses or result in reduced resource intake. An alternative strategy to fixed defenses is plasticity in the manifestation of developmental, morphological, and behavioral defensive mechanisms (Sih 1980; Lima and Dill 1990; DeWitt et al. 2000; Relyea and Werner 2000; Resetarits 2001). Plasticity can bear costs in terms of reduced growth (Johansson et al. 2001; Relyea 2002a; Teplitsky et al. 2003) and lower fecundity (Black and Dodson 1990; DeWitt 1998). Thus, although predator defenses can increase survivorship, organisms must balance conflicting demands between growth and costs of fixed and plastic predator defenses (Newman 1992; Laurila and Kujasalo 1999). This balance may be difficult to achieve for

aquatic organisms that inhabit highly ephemeral sites where the risk of desiccation is great and food resources are limited.

In resource-poor, highly ephemeral sites where prey experience very low predation risk but compete for limited resources, the costs of defense mechanisms may outweigh the fitness gains from maintaining them. However, the lack of either fixed or plastic anti-predator defenses should result in high mortality when predators are present (Sih et al. 2000). For example, high predation rates have been observed when non-native predators decimate organisms that lack the appropriate defenses for the novel predator (Case and Bolger 1991; Knapp and Matthews 2000). High rates of predation are also common for aquatic organisms exposed to predators that utilize short-lived habitats, where predators are typically rare or absent entirely. Organisms in ephemeral pools tend to be very active in order to maintain high feeding rates, which in turn facilitate rapid growth (Woodward 1983; Suhling et al. 2005). Rapid growth is crucial in ephemeral aquatic habitats because delayed development increases the risk of death due to pond desiccation (Newman 1987; Suhling et al. 2005). High activity, which is associated with growth, is costly when predators are present because it is also correlated with susceptibility to predation (Werner and Anholt 1993; Skelly 1994; Suhling et al. 2005).

Here, we discuss findings from a combination of laboratory and mesocosm experiments designed to test two separate, but related, hypotheses regarding the impact predators have on survivorship and species persistence throughout the landscape. Specifically, we examined multiple effects of predators on tadpoles of a xeric-adapted anuran, *Scaphiopus couchii* (Baird) that inhabits short-lived temporary pools in extremely arid habitats of the southwestern United States. Because *S. couchii* breed in highly ephemeral environments and pond desiccation is the primary cause of death for most cohorts of *S. couchii* larvae, we hypothesized that tadpoles would lack defensive mechanisms and predicted that predators would not cause lower activity rates, alter tadpole developmental rate, or cause changes in morphology. We further hypothesized that direct numerical effects of predators on tadpoles would facilitate growth of surviving individuals due to increased available resources resulting from the thinning of tadpole densities.

Materials and methods

Study area and organism

Our study took place in Bend National Park, TX, USA, in the Chihuahuan Desert Ecoregion. Annual precipitation averages 35 cm with approximately 70% of the rainfall occurring in the form of isolated downpours from May to September (Brown 1994). *Scaphiopus couchii* is among the most xeric-adapted anuran species in the world. Adults spend the majority of their life buried beneath the desert floor, coming to the surface for short periods during seasonal rains to breed in ephemeral pools in relatively homogeneous, sandy clay loam soil (Mayhew 1965; Dimmitt and Ruibal 1980; Dayton et al. 2004), and typically call only during the first night of a rain (Sullivan 1989). Eggs are deposited in ephemeral pools that usually last for only a few weeks. As few as 30 h is needed for eggs to hatch and time to metamorphosis typically takes 7–10 days (Mayhew 1965; Newman 1987; Morey and Reznick 2000), the shortest of any North American amphibian (Buchholz and Hayes 2000). Tadpoles are very active, constantly feeding, and are thus susceptible to aquatic predators (Dayton and Fitzgerald 2001).

Indirect effects of predators on growth and development

We collected *S. couchii* egg masses from three ephemeral pools in Big Bend National Park, Texas <24 h after they were deposited. Eggs were combined and placed into a single plastic swimming pool (1.2 m diameter, 0.3 m tall, filled with ~151 l of aged tap water) that was housed in the laboratory. Two days post-hatching ($N = 10$; total length $\bar{x} = 10.8$, $SD = 0.78$ mm; Gosner stage (Gosner 1960) $\bar{x} = 27$, $SD = 0.32$), we set up an experiment to test for the effects that chemical cues for predators and alarm cues for injured prey have on development (time to metamorphosis), behavior (activity), and morphology (head length/tail length ratio and tail depth). We chose these variables as they are either surrogates for anuran fitness (Berven 1990) or are plastic defense traits common in many aquatic species (Laurila et al. 1998; Lardner 2000; Bryan et al. 2002; Relyea 2004). The experiment was a completely randomized design consisting of three

treatments with eight tadpoles in each experimental unit (plastic tub $30 \times 15 \times 8$ cm deep filled with 3 l of aged tap water). Treatments consisted of a control group where tadpoles were reared without predators, a “nonlethal” experimental group where tadpoles were reared with a caged predatory larva (Insecta: Hydrophilidae) that had not eaten for at least 48 h, and a “lethal” experimental group where tadpoles were reared with a caged hydrophilid larva that was fed five *S. couchii* tadpoles on a daily basis. We chose hydrophilid (*Hydrophilus* sp.) larvae as the predator because they are common throughout the study region and are very effective predators on *S. couchii* tadpoles in the field (Newman 1987; Dayton and Fitzgerald 2001). Predators were enclosed in a 2-mm mesh cage that prevented access to tadpoles but permitted water exchange between predator cages and the rest of the experimental arena. Control tubs also had cages (no predators) to control for potential cage effects. All predators were starved for at least 48 h prior to being placed in cages. Treatments were replicated 10 times. A fixed diet of crushed TetraMin[®] tropical fish flakes of 15 mg/day/tadpole was maintained throughout the study. These rations are consistent with other laboratory studies that have reared *S. couchii* tadpoles (Morey and Reznick 2000). Water was changed on day 3 and 6. Larvae that did not consume tadpoles within a few hours were replaced. Temperature varied from approximately 21–32°C. The laboratory was a desert field station and room temperature fluctuated. All replicates were exposed to the same temperature fluctuations, and temperatures were well below maximum temperatures of naturally occurring pools in the area.

Every 2 days, we preserved one tadpole from each tub in order to compare growth (tip of snout to end of tail) and development (Gosner stage) among treatments throughout the experiment. Tadpoles were haphazardly selected from each treatment using an aquarium dipnet. This method enabled us to test for differences in growth and morphological traits at several intervals while not having to take multiple measurements on an individual tadpole. Experiments were terminated after 8 days when the first tadpoles reached Gosner stage 42 (emergence of forelimbs); tadpoles at Gosner stage 42 were not included in morphological analyses as these individuals are absorbing their tails and going through drastic morphological changes. There were four removal

periods: three during the experiment and one at the end of the experiment. The final removal consisted of five tadpoles per tub. In seven of the tubs, one or more tadpoles died during the experiment (Control = 2; Nonlethal Cue = 3; and Lethal Cue = 2). These tubs were removed from all analyses as tadpoles in experimental units had access to more food, which could influence growth and development. Seven tadpoles were damaged in preservation and excluded from analyses. We regressed head-to-tail ratio and tail depth against total length (tip of snout to end of tail) and saved the residuals. The mean residuals were used as response variables, and we used analysis of variance (ANOVA) to test for differences in morphology among treatments at each of the four intervals. We also used ANOVA to test for differences in development among the treatments. Because we removed tadpoles throughout the experiment, we were able to examine the variation in development across all treatments at several different time periods. This method enabled us to test for effects at every stage of the experiment and thus examine potential ontogenetic effects (i.e., nonlinear responses across developmental stages) rather than only testing differences at the end of the experiment. We measured activity on three occasions (days 1, 4, and 7) by counting the number of tadpoles moving at the instant each tub was examined. We used the mean proportion of tadpoles active per tub as our behavioral response and ANOVA to test for differences among treatments at each of the three sampling periods. All proportional data were arcsine transformed prior to analyses.

Direct effects of predators on growth, development, and survival

We used an outdoor mesocosm experiment to examine the direct impacts of predators on survivorship and development of *S. couchii* tadpoles. This experiment differs from the laboratory experiment described above in that predators living in the mesocosms were actively preying upon tadpoles. Thus, predators were reducing tadpole densities via predation throughout the entire experiment. We used plastic pools (1.2 m in diameter and 0.3 m deep) as our experimental arena. Each pool was filled with 151 l of well water, 19 l of loamy soil (frequently used soil type for *S. couchii* breeding), and covered

with 60% shade cloth to prevent colonization by aquatic invertebrates. Pools sat for approximately 3 days, whereupon a total of 104 tadpoles were placed in each pool. The experimental design consisted of a control (no predators) and a predator treatment (two hydrophilid larvae). Although this environment was artificial, the conditions were similar in depth and substrate to many natural breeding sites used by *S. couchii* in the Chihuahuan desert.

We used a completely randomized design with treatments randomly assigned to pools. Treatments were replicated four times each. *Scaphiopus couchii* eggs were collected from multiple clutches from three sites in the field and reared to hatching in the lab, at which time the tadpoles were introduced to the pools. Predators were collected from two temporary pools and introduced into the mesocosms on the same day as the tadpoles. Pools were monitored every other day for tadpoles undergoing metamorphosis, and experiments were terminated after 60 days. We used *t* tests to examine differences in three fitness measures: survival (successfully reaching metamorphosis), size (snout to urostyle), and time to metamorphosis between controls and experimental groups.

Results

There were no significant differences in tadpole development or morphology between predator and control treatments at any point during the laboratory experiments, indicating that *S. couchii* did not exhibit developmental or morphological responses to predator cues (Fig. 1). There also was no indication of a behavioral response to predators as the mean proportion of tadpoles active on any given sampling period did not differ among treatments on day 1 ($P = 0.534$), day 4 ($P = 0.186$) or day 7 ($P = 0.727$).

Tadpole survivorship was significantly higher in the no-predator mesocosm experiment ($t = 3.272$, $P < 0.011$; Fig. 2), but tadpoles took more than twice as long to reach metamorphosis in the no-predator treatment ($t = 6.016$, $P < 0.002$; Fig. 2). There were no significant differences in size between the two treatments ($t = 1.022$, $P < 0.342$; Fig. 2). Hence, tadpoles that survived in the predator treatment achieved metamorphosis in less than half the time as in the no-predator treatment and at similar sizes. The initial density of 104 tadpoles per pool decreased

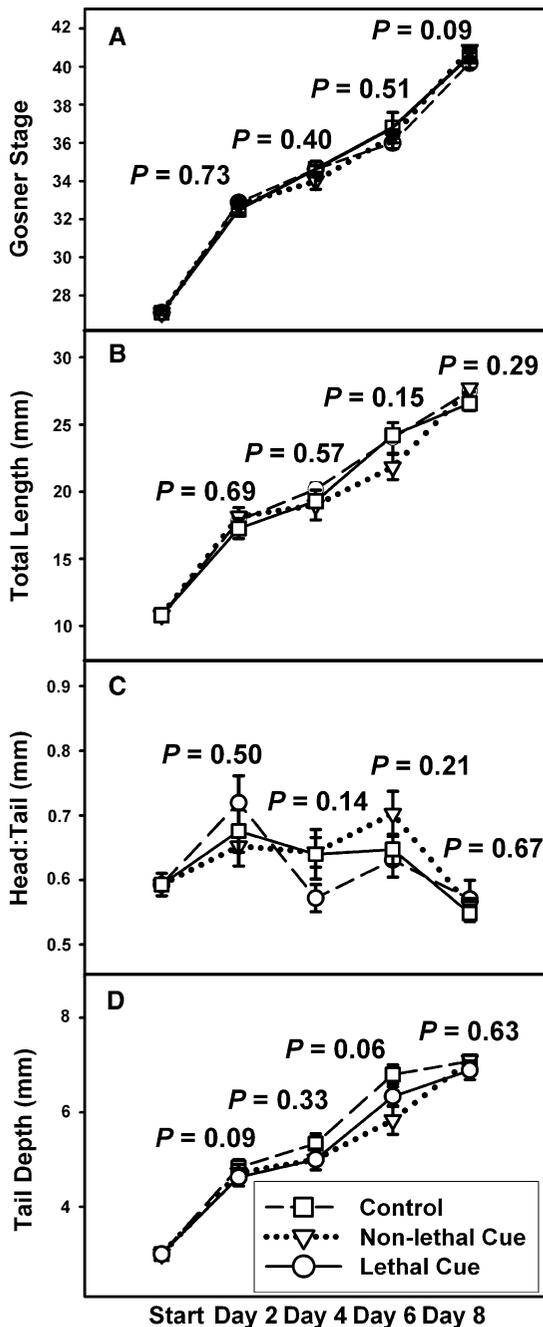


Fig. 1 Results from laboratory experiments examining indirect effects of predators on *S. couchii* tadpoles. **a** developmental stage; **b** total length; **c** head/tail ratio; and **d** tail depth of tadpoles raised without predators present (circles), in the presence of caged predators only (upside-down triangles), and in the presence of caged predators fed tadpoles on a daily basis (squares). *P* values were calculated using ANOVAs conducted on residuals; x-axes represent actual measurements from each sampling interval of the laboratory experiment. Error bars ± 1 SEM

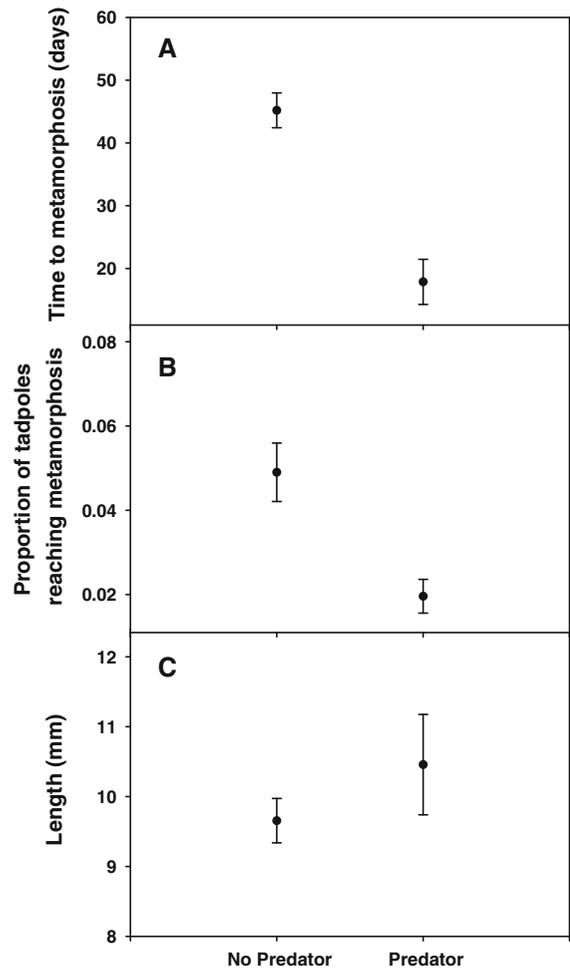


Fig. 2 Results from the mesocosm study examining the direct effects of predators on *S. couchii* tadpoles. **a** Mean time to metamorphosis, **b** mean proportion of tadpoles surviving, and **c** mean size of metamorphosing individuals. Error bars ± 1 SEM

in both treatments, but at a much higher rate in the predator treatment. Zero tadpoles remained in the predator mesocosms by day 60 (i.e., they had all died or metamorphosed) compared to an average of 17 tadpoles ($\bar{x} = 17$, $SD = 10$) in the no-predator mesocosms by day 60.

Discussion

Although predator-induced changes in behavior, development, and morphology are widespread among aquatic organisms, they are not ubiquitous. Our findings suggest that *S. couchii* tadpoles do not

exhibit fixed or plastic anti-predator defenses. As a result, they were very susceptible to predation in the mesocosm experiment. Susceptibility to predation in turn resulted in a rapid reduction in tadpole density and set the stage for surviving tadpoles to achieve metamorphosis in less than half the time as subjects in the no-predator treatment. We presume the reduction in time to metamorphosis for surviving tadpoles was due to increased availability of per capita food resources. Additionally, there was no cost of metamorphosing sooner in terms of size; tadpoles in both treatments metamorphosed at similar sizes. Shorter time to metamorphosis is linked to survivorship in anurans inhabiting ephemeral pools because of the risk of desiccation. We suggest the consequence of individuals being defenseless enhanced overall cohort survival.

Indirect effects of predators

Tadpoles in the laboratory experiments showed no developmental, morphological, or behavioral response to predator cues. The fact that predator-induced changes often occur early in ontogeny and disappear later can be problematic in interpreting experimental results (Van Buskirk and Yurewicz 1998; Relyea and Werner 2000). We circumvented this problem by measuring development, growth, and behavior at multiple periods throughout the laboratory experiment. Hence, we were able to compare responses at several ontogenetic stages and detected no differences in behavior, morphology, and development. Additionally, although tadpole density in our laboratory experiments changed throughout the study, we controlled for potential thinning effects that can alter morphology and behavior (Relyea 2002b) by holding density constant across treatments. We found no predator-induced changes in any of the response variables at any point during the study.

Direct effects of predators

Tadpole density decreased by approximately 95% in the predator treatment with a resultant decrease in time to metamorphosis by >30 days, with no effect on size at metamorphosis. The average time to metamorphosis of approximately 45 days in the no-predator treatment, which retained higher densities, was remarkably long compared to the mean time to

metamorphosis for *S. couchii* tadpoles of only 7–10 days in nature (Newman 1987; Morey and Reznick 2000). Time to metamorphosis for *S. couchii* can be significantly delayed or not take place at all when per capita resources are low (Newman 1987; Morey and Reznick 2000; Morey 2001). The increased time to metamorphosis in the no-predator treatment was also likely due to insufficient resources. *Scaphiopus couchii* tadpoles have also been shown to prolong development by a few days and metamorphose at larger sizes when resources are abundant (Newman 1989), but this was not the case in our experiments.

Our findings support the hypothesis that in resource-limited, ephemeral environments, the maintenance of anti-predator defenses, such as plasticity in behavior and development, may not incur a fitness advantage because of the overriding risk of desiccation. Thus, the presumed cost of plasticity (e.g., reduced growth and delayed development) can become a real disadvantage in rapidly drying habitats if time to metamorphosis is increased. Plastic defense mechanisms known to be manifested in other anuran larvae are expected to be greatest for individuals inhabiting environments with little resource competition (Van Buskirk and Yurewicz 1998), high predator loads (Lardner 2000), and stable environments (Maurer and Sih 1996). We created such an environment for *S. couchii* tadpoles in the laboratory and found no response to the presence of predators.

Although predator-induced shifts in behavior and growth are common for numerous organisms (Benard 2004), the costs of reduced growth and delayed time to metamorphosis are likely too costly for species such as *S. couchii* that inhabit extremely ephemeral aquatic environments. The primary cause of death for *S. couchii* tadpoles is desiccation, with approximately 60–90% of *S. couchii* cohorts failing due to desiccation and depleted resources (Newman 1987, 1989; Morey and Reznick 2000). Lack of predator-induced defenses renders individuals susceptible to predation, and it is this susceptibility that limits ephemeral pond-breeding organisms from utilizing longer-lasting sites where predators are more abundant (Werner et al. 1983; Woodward 1983). Although predators are not common in short-lived ephemeral pools, they are occasionally present and can eliminate entire cohorts of *S. couchii* larvae (Newman 1987).

Clearly, there is a fine line between too much predation and just the right amount. In ephemeral aquatic habitats where limited resources may significantly reduce survivorship by delaying time to metamorphosis and increasing the probability of death by desiccation, predation may serve as an important thinning mechanism that facilitates the persistence of prey species. That is, there is a potential for increased successful metamorphosis of tadpoles as a result of the combination of predator-caused thinning effects and subsequent increase in per capita resources due to release from intraspecific predation and lack of behavioral or morphological response to predators. Indeed, on several occasions, we have observed significant reductions in densities of *S. couchii* tadpoles in the field as a result of predation from hydrophilid larvae and *Kinosternon flavescens* (yellow-mud turtle). After these predation events, we have noticed increases in the size of surviving tadpoles. These observations are consistent with results of other studies (Newman 1987; Dayton and Wapo 2002), in which predators reduced or completely eliminated *S. couchii* clutches in natural pools. Our findings support previous work by Wilbur (1987, 1988) that showed predation can increase cohort survivorship via thinning and by Newman (1988) that showed slower growth and delayed metamorphosis can be disadvantageous to organisms inhabiting ephemeral aquatic environments. The positive effects of predation on surviving *S. couchii* tadpoles may be especially important during drought years when seasonal rains are less frequent and pool duration is even shorter compared to years when rainfall is abundant.

Richter-Boix et al. (2006) and Lardner (2000) used comparative approaches to examine developmental plasticity among several anurans along a pond permanency gradient. These studies found that species that use short-lived pools exhibited relatively little developmental plasticity compared to species that breed in pools with longer hydroperiods. Although comparative analyses were not part of our experimental study design, these findings support our conclusion that larval anurans that breed in highly ephemeral pools are in general less likely to exhibit plastic phenotypic responses that delay time to metamorphosis. We suggest this occurs because there is relatively small selective benefit of plasticity in highly ephemeral environments. The outcome of

delayed metamorphosis as a result of predator avoidance is not that advantageous in a drying pond. Newman (1994) showed that cohorts of *S. couchii* tadpoles do exhibit variation in larval period in response to hydroperiod and temperature; however, variation was genetically based and varied across families. This suggests that for some traits selection for plasticity may be constrained in *S. couchii*. Future studies examining behavioral and developmental impacts of predators on closely related species that inhabit opposite ends of the hydroperiod gradient, as well as studies examining diverse lineages of organisms that inhabit highly ephemeral aquatic environments, could provide important insight into the roles that phylogeny and environment play in influencing predator defenses.

Our experiments and field observations demonstrated that in resource-limited, ephemeral environments prey thinning was more important to cohort survival than predator defenses. The tradeoffs that come with anti-predator defenses in tadpoles, specifically longer time to metamorphosis and reduced competitive ability, are not viable for *S. couchii* in ephemeral pools in the Big Bend landscape, thus explaining the lack of predator defenses we observed. In the Chihuahuan desert it appears that for individual *S. couchii* tadpoles, hydroperiod, rapid growth, and ability to compete for limited resources trumps the need to defend against predators, and all of these are enhanced when population density is decreased by predation.

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