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Competition, predation, and the distributions of four desert anurans

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Abstract Several studies have shown that larval competition and susceptibility to predation affect distributions of amphibian assemblages across ephemeral and perennial habitats. However, few studies have examined mechanisms affecting distribution patterns and site use of anurans adapted to highly ephemeral habitats. This study examines hypotheses about competition and predation as mechanisms creating non-overlapping patterns of site use in four anurans that breed in highly ephemeral habitats: *Scaphiopus couchii* (Couch's spadefoot toad), *Gastrophryne olivacea* (narrow-mouthed toad), *Bufo speciosus* (Texas toad), and *Bufo punctatus* (red-spotted toad). These four anurans showed a significantly nonrandom pattern of co-occurrence. Only 12% of 95 ephemeral breeding sites surveyed were occupied by more than one species. We tested the hypotheses that non-overlapping use of breeding sites was due to activity rates of their tadpoles that in turn reflect their competitive ability and susceptibility to predation. Tadpoles of *S. couchii* were significantly more active and more susceptible to predation than were tadpoles of *G. olivacea*, *B. speciosus*, and *B. punctatus*. The masses of *G. olivacea*, *B. speciosus*, and *B. punctatus* were less when they were reared with *S. couchii*, demonstrating the possible competitive dominance of *S. couchii*. These results suggest that the competitive ability of *S. couchii* may play a role in excluding *G. olivacea*, *B. speciosus*, and *B. punctatus* from very ephemeral breeding sites, and that susceptibility to predation could play a role in excluding *S. couchii* from breeding sites of longer duration that are more likely to be colonized by aquatic predators.

Keywords Amphibians · Predation · Competition · Desert · Distributions

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Introduction

Understanding mechanisms that determine patterns in ecological communities has been a focal point in ecology for decades (Hutchinson 1959; MacArthur and Levins 1968; Dayton 1971). Many amphibian species appear to be limited in their use of breeding sites by abiotic and biotic constraints on aquatic larvae such as hydroperiod, predation, and intra- and interspecific competition (Woodward 1982; Newman 1987; Sredl and Collins 1994; Skelly 1995a; Kupferberg 1997; Skelly et al. 1999). By determining mechanisms that influence the persistence of a species at local sites, we can gain insight into ecological processes that give rise to emergent patterns of species distribution across the landscape and processes that govern the structure of ecological communities.

Several studies suggest that amphibian species that breed in predator-free ephemeral pools are highly susceptible to predation by aquatic predators that inhabit perennial water sources (Woodward 1983; Skelly 1996). Conversely, species that breed in perennial pools often have longer larval periods, lower activity rates, and slower growth rates than ephemeral adapted species. High activity rates give tadpoles a competitive advantage in resource acquisition leading to greater growth, but also make them more susceptible to predation (Woodward 1983; Morin 1983). This trade-off between competitive dominance (high activity) and predator avoidance (low activity) has been proposed as an important mechanism resulting in segregation of amphibian species into ephemeral and permanent pool species (Morin 1983).

Few experiments have been done to identify factors that determine local distribution patterns of ephemeral breeding amphibians and whether competition and predation are important mechanisms. Herein, we present a study of the occurrence of four desert anurans in a desert landscape and results of laboratory experiments designed to elucidate whether competition-predation trade-offs are operating to determine use of sites by anuran species in ephemeral pools, and if the pattern helps explain the distribution of species across the landscape.

If competition-predation trade-offs are operating to determine site use of anuran species in ephemeral pools, species that cannot withstand predation should occur in highly ephemeral pools that are not readily colonized by predators (Woodward 1983). Moreover, time to acquire resources might be limiting in pools of short duration. Consequently, tadpoles should have experienced strong selection for quick growth to metamorphosis. Thus, it is expected that species inhabiting relatively predator-free environments with short hydroperiods should be good competitors. We hypothesized that more active species may have a competitive advantage over less active species. Because high activity increases susceptibility to predation (Morin 1983; Woodward 1983), we also hypothesized that more active tadpoles would suffer greater mortality in the presence of an aquatic predator. To test these hypotheses, we measured activity levels, growth rates, and susceptibility to predation of tadpoles of four different anuran species that use very ephemeral breeding sites.

Materials and methods

We conducted laboratory experiments in Big Bend National Park, Texas, to test competition and predation as potential mechanisms resulting in nonrandom use of breeding sites by four ephemeral adapted anurans: *Scaphiopus couchii* (Couch's spadefoot toad), *Gastrophryne olivacea* (narrow-mouthed toad), *Bufo speciosus* (Texas toad), and *Bufo punctatus* (red-spotted toad). Breeding events for these species are extremely explosive and take place during summer monsoon storms (Newman 1987; Degenhardt et al. 1996). Eggs are deposited in ephemeral pools that range in duration from a few hours to several months. Larval periods range from as little as 8 days for *S. couchii* to up to 50 days for *B. speciosus* (Garret and Barker 1987; Degenhardt et al. 1996). Pools often dry before metamorphosis occurs (Newman 1994; G. H. D. unpublished data). Density of tadpoles ranges from <1 to >1,000 tadpoles/l (Newman 1994). Density of aquatic predators, for example odonates and hydrophilid beetles, are highest in larger sites that retain water for longer periods (Woodward 1983; Kubly 1992). All tadpoles used for experiments were collected from multiple clutches in the field and experiments were conducted from 1 June to 19 August 1999. Tadpoles were fed a 3:1 ratio of Purina rabbit chow and Tetra fish food every 4 days (Alford and Harris 1988). Food rations consisted of 10% of the mean tadpole weight per tub per day (mean tadpole mass \times 0.10 \times 4). Aged tap water was used for all laboratory experiments. Water was changed and the tubs were cleaned every 4 days.

Breeding site surveys

From 15 June to 30 July 1999, within 4 days following rain, anuran breeding sites along 31 road segments in Big Bend National Park, Texas, were surveyed for amphibian larvae. Each plot was 1.61 km long and 0.80 km wide. All areas with potential to retain water (i.e., washes, tanks, and draws) were surveyed; when water was found, tadpoles were surveyed by intensive dip netting. Tadpoles were identified to species (Altig and McDiarmid 1998).

We tested the null hypothesis that the observed distribution of anurans among breeding sites was random using the computer program, Ecosim (Gotelli and Entsminger 2000). Rejection of the null hypothesis would indicate that the distribution of the four anuran species among breeding sites was not readily explained by chance. The null model preserved the number of sites where each species was found (row totals). The probability a site could be oc-

cupied by a species was proportional to the number of species at each site (column total). With this option, the column totals were not fixed, but on average, the rank order of sites matched the rank order of sites in the original matrix. These assumptions were robust to type I errors, yet permitted the species to vary in their colonization pattern (Gotelli 2000). The model generated 5,000 random matrices and calculated a C-score to test for differences between the observed and simulated patterns of distribution (Stone and Roberts 1990). The C-score deals well with random "noise" in co-occurrence patterns and measures the tendency for species not to occur together; larger scores reflect less average co-occurrence among species (Gotelli 2000).

Activity

Activity trials were conducted by separately placing five tadpoles of each species, all of similar size and Gosner stage 25 (Gosner 1960), into ten randomly placed 2-l tubs. We quantified activity by standing with our eyes closed at 0.5 m above each tub, then opening our eyes and counting how many tadpoles were moving at that instant (Skelly 1995b). Trials were replicated 20–23 times, allowing at least 2 h between observations. From these data we calculated proportions of the number of tadpoles active per trial. We arcsine-transformed proportional data and used ANOVA followed by Tukey's multiple comparisons to test the hypothesis that species would differ in the number of active tadpoles per trial.

Predation

We conducted predation experiments to test whether tadpole species differed in their susceptibility to a natural predator, water-scavenger beetle larvae (Hydrophilidae). We observed hydrophilid larvae preying on tadpoles in the field, and they are known to be effective predators on a variety of aquatic animals (Wilson 1923; Borror et al. 1992; G. H. D. personal observation). Hydrophilid larvae have a short larval cycle, facilitating their colonization of very ephemeral sites as well as long-lasting pools (Wilson 1923; Merritt and Cummins 1996; G.H.D. personal observation). Several other predators typically found in longer lasting ephemeral pools in the Big Bend region included diving beetles and their larvae (Dysticidae), giant water bugs (Belostomatidae), back swimmers (Notonectidae), water scorpions (Nepidae), dragon fly larvae (suborder Anisoptera), damselfly larvae (suborder Zygoptera), black-neck garter snakes (*Thamnophis crytopsis*), and yellow mud turtles (*Kinosternon flavescens*). Among the suite of predators available, hydrophilid larvae were common throughout the landscape and worked well in the experiments.

We predicted that more active species of tadpoles should be more susceptible to predation. Similarly sized tadpoles of *G. olivacea*, *S. couchii*, *B. speciosus*, and *B. punctatus* were randomly selected from 5-gallon plastic buckets and one individual of each species was randomly placed into one of thirteen, 3-l plastic tubs. Hydrophilid larvae were collected in the field from several sites then randomly selected from a 5-gallon bucket and placed into the 3-l tubs containing the tadpoles. Tub was monitored continuously until a predation event occurred. Elapsed time to predation and species preyed upon were recorded. Surviving tadpoles and predators were immediately removed and kept separately. After each experiment, water was discarded and the tubs were cleaned and filled with aged tap water. Experiments were replicated 8 times with at least 2 h between trials (total of 104 tubs). Because the availability of tadpoles, especially *G. olivacea*, as well as hydrophilid larvae, was the limiting factor for these experiments, some individuals may have been used in more than one trial (probabilities of re-use per trial for *G. olivacea*=0.16, *B. speciosus*=0.07, *B. punctatus*=0.03, and *S. couchii*=0.03). However, the identity of individual tadpoles and predators was not known, and individuals were always selected at random. Tadpoles and hydrophilid larvae used in predation experiments were kept in 5-gallon plastic buckets and tadpoles were fed equal amounts of 3:1 Purina rabbit chow

and Tetra fish food mixture. We arcsine-transformed proportional data and used an ANOVA followed by a Tukey's multiple comparisons test to test for differences in the number of times each species of tadpole was preyed upon during each experiment.

Competition

Competition experiments were conducted in 2-l plastic tubs with 8 tadpoles/container. Each treatment consisted of three tubs: one tub with eight *S. couchii* tadpoles, one tub with eight tadpoles of species *B. punctatus*, *B. speciosus*, or *G. olivacea*, and a third tub with four *S. couchii* tadpoles and four tadpoles of either *B. punctatus*, *B. speciosus*, or *G. olivacea*. Each treatment group was replicated 6–8 times with tubs randomly placed on three shelves. We measured wet mass every 4 days. Competition was assessed by analyzing differences between mean tadpole mass at the start and end of each trial (to the nearest 0.01 g on an electronic scale). Trials were terminated when the first tadpole reached Gosner stage 41 (Gosner 1960) because tadpoles after this stage decrease in mass as they begin to metamorphose (Wilbur and Collins 1973). One trial ended before tadpoles reached Gosner stage 41 due to the contamination of water. In this instance, weights were compared from previous measurements prior to the termination of the experiment. As *S. couchii* has the shortest larval period of the four species, we predicted it would be the most competitive (Morin 1983), and used two tailed *t*-tests to test the hypotheses that differences of start and end masses of *B. punctatus*, *B. speciosus*, and *G. olivacea* tadpoles would be less when they were reared with *S. couchii*.

Results

Of the 95 pools searched, only 12% had multiple species of tadpoles (Table 1), 11 sites had two species and no sites had three or four species combinations. This pattern of co-occurrence was significantly non-random based on the null model simulations ($P < 0.001$). There was much less co-occurrence among species in the observed data (C-score=494.00) than in the 5,000 simulated matrices (C-score=230.67).

There were significant differences among species in mean number of tadpoles active (ANOVA, $F_{3,81}=61.25$, $P < 0.001$). Tukey's test revealed that *S. couchii* had the highest proportion of tadpoles active per tub ($n=23$, mean=3.85, SD=0.17) and was significantly more active than all other species ($P < 0.001$). Mean number of tadpoles active per tub for *B. punctatus* was 2.05 ($n=20$, SD=0.13), which was significantly different than that for *G. olivacea* ($n=20$, mean=1.0, SD=0.12, $P < 0.001$) but not for *B. speciosus* ($n=20$, mean=1.56, SD=0.08, $P < 0.205$). The mean number of tadpoles active per tub for *G. olivacea* tadpoles was 1.0, which was significantly different than that for *B. speciosus* ($P < 0.02$).

There were also significant differences among mean number of times each species was preyed upon (ANOVA,

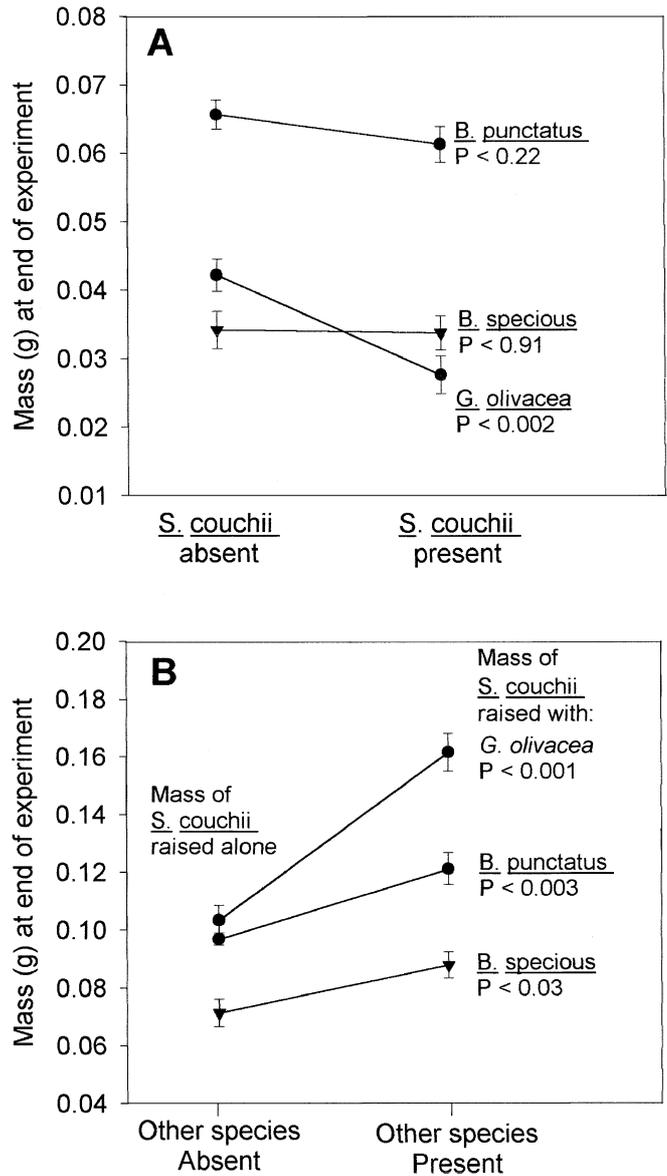


Fig. 1 A Interspecific competition experiments resulted in lowered mean mass at termination of the trials for *Gastrophryne olivacea*, *Bufo punctatus*, and *Bufo speciosus* tadpoles raised with *Scaphiopus couchii* tadpoles. B Intraspecific competition experiments showed that the mean mass of *S. couchii* at the termination of competition experiments was highest in the presence of other species and lowest when raised alone. Density was held constant at 8 tadpoles/l. Error bars represent 1 SE. Probability values are given for each experiment

$F_{3,28}=19.01$, $P < 0.001$). Tukey's tests showed *S. couchii* was the most frequent species to be preyed upon first ($n=8$, mean=8.58, SD=0.17), and was significantly different than all the other species ($P < 0.001$). There were no

Table 1 Number of times tadpoles of each species were found alone or with another species. No combinations of more than two species were found

Species	<i>n</i>	<i>Scaphiopus couchii</i>	<i>Bufo punctatus</i>	<i>Gastrophryne olivacea</i>	<i>Bufo speciosus</i>
<i>S. couchii</i>	44	33	4	7	0
<i>B. punctatus</i>	43		38	0	1
<i>G. olivacea</i>	15			8	0
<i>B. speciosus</i>	5				4

significant differences between *G. olivacea* ($n=8$, mean=0.62, SD=0.07, $P>0.20$), *B. punctatus* ($n=8$, mean=2.18, SD=0.14), and *B. speciosus* ($n=8$, mean=1.66, SD=0.12). Mean differences in mass of *G. olivacea*, *B. punctatus*, and *B. speciosus* tadpoles were all less in the presence of *S. couchii* than when reared alone. However, the difference was statistically significant only for *G. olivacea* ($t_{0.05,14}=4.061$, $P<0.002$, Fig. 1A). *S. couchii* tadpoles showed a significant reduction in mean mass when raised with conspecifics compared to when they were reared with *B. punctatus* ($t_{0.05,14}=4.127$, $P<0.003$), *B. speciosus* ($t_{0.05,10}=2.537$, $P<0.03$), and *G. olivacea* ($t_{0.05,14}=7.051$, $P<0.001$) (Fig. 1B).

Discussion

The results presented here support the idea that competition and predation can influence the distributions of anuran species across a desert landscape, but the pattern is complex and variable among species. *S. couchii* tadpoles were generally found alone, were the most active, and also the most susceptible to predation. These results are consistent with the hypothesis that predation may prevent active species from using sites that retain water for relatively long periods, due to high predator density coupled with their inherent susceptibility to predation (Skelly 1995b), and that tadpole species with high activity rates have a competitive advantage over less active tadpole species.

Inter- and intraspecific competition undoubtedly play a role in reducing growth and survival rates of larval amphibians (Wilbur 1972; Debenedictis 1974; Morin 1983; Travis 1984). We suggest that for species that breed in ephemeral habitats with high tadpole densities (frequently greater than 100 tadpoles/l), such as *B. speciosus*, *G. olivacea*, *S. couchii*, and *B. punctatus*, resource limitation is a real possibility that can potentially affect survival of amphibians in natural communities. Thus, it would be expected that in a resource-limited environment such as ephemeral pools in Big Bend (Newman 1987), active species like *S. couchii* would have a competitive advantage over less active, slower growing, species. Our results affirmed this, although only *G. olivacea* showed a significant reduction in weight when raised with *S. couchii*, weights of *B. punctatus* and *B. speciosus* were also reduced when they were raised with *S. couchii*. Intraspecific competition was apparent in *S. couchii*; mean differences in starting and ending mass of its tadpoles decreased significantly in all trials when it was raised alone compared to when it was raised with any of the other three species.

Scaphiopus couchii tadpole densities exceed 1,000 tadpoles/l in ephemeral pools (G. H. D. personal observation; Newman 1994), hence it may be expected that intraspecific competition for resources, chemically mediated growth inhibition, or other density effects may be important in nature. The demonstrated effect of reduced mass in tadpoles raised with *S. couchii* compared to tadpoles

raised with conspecifics is consistent with the hypothesis that such effects may increase time to metamorphosis, or mass at metamorphosis, for *S. couchii*, and reduce time to metamorphosis, or mass at metamorphosis, for *G. olivacea*, *B. punctatus*, and *B. speciosus*. In harsh environments, such as the Chihuahuan Desert, where ephemeral pools often dry before metamorphosis occurs (Newman 1994; G. H. D. personal observation), sufficient time for metamorphosis is essential for survival. Other research showed that increased time to metamorphosis (Travis 1984) and decreased mass at metamorphosis reduced chances of survival of metamorphs (Brevin 1990). Thus, in pools where other species co-exist with *S. couchii*, a reduction in weight leading to an increased time to metamorphosis, puts tadpoles at greater risk.

There were significant differences in activity between *G. olivacea* and the two *Bufo* species; however, no significant differences were found in time to predation among these three species. We therefore expected that these species should co-occur at breeding sites. However, 79% ($n=63$) of the breeding sites surveyed that were occupied by either *B. punctatus*, *B. speciosus*, or *G. olivacea*, had only a single species. Non-overlapping use of breeding sites by species with similar activity rates, larval periods, and susceptibility to predation (i.e., *B. punctatus*, *G. olivacea*, and *B. speciosus*) suggests factors other than competition, and predation may also play a role in forming distribution patterns of these species across the Big Bend landscape. *S. couchii*, *B. punctatus*, *B. speciosus*, and *G. olivacea* are sympatric throughout the Big Bend region, but at the local scale of breeding sites we found little co-occurrence. Different species can be found breeding in isolation in pools that are within a few hundred meters of each other, hence it seems that large-scale factors such as vegetation type and geology probably do not play a significant role in forming the nonrandom patterns of occurrence that we observed.

It is unlikely hydroperiod per se could explain the distribution of these species at Big Bend. *S. couchii* tadpoles need pools that last for at least 10 days to successfully metamorphose, and they are well known to inhabit very ephemeral breeding sites with relatively few aquatic predators (Woodward 1983). However, even in ephemeral pools, richness of aquatic invertebrate predators is correlated with duration and volume of the pools (G. H. D. unpublished data; Kubly 1992; Spencer et al. 1999). *G. olivacea*, *B. speciosus*, and *B. punctatus* require at least 30 days to metamorphose, and are therefore limited to pools that persist for at least 30 days (G. H. D. personal observation; Degenherdt et al. 1996). Pools lasting for less than 30 days constrain *G. olivacea*, *B. punctatus*, and *B. speciosus* from using sites that can be occupied by *S. couchii*. However, hydroperiod is not likely to play a role in the observed lack of co-occurrence of *G. olivacea*, *B. punctatus*, and *B. speciosus* because they have similar larval periods and they did not differ in susceptibility to predation.

Our results from laboratory experiments gave insight into species interactions that may be important in the

field, but did not take into account abiotic factors that may also be operating in nature. The trade-off between realism in field experiments and precision of laboratory experiments is often debated. Field experiments allow for habitat and abiotic factors to play a role in the outcome of species interactions but often lack precision in testing predictions made by theory, have high variability among replicates, and low levels of replication (Morin 2000). Laboratory experiments, on the other hand, allow us to disentangle effects of abiotic and biotic factors. By controlling for confounding variables that exist in natural settings we were able to isolate and test specific hypothesis about predation, competition, and activity rates. Although it appears predation determines breeding site use by *S. couchii*, abiotic factors related to microhabitat at particular breeding sites may also influence distributions of *G. olivacea*, *B. speciosus*, and *B. punctatus*. Several studies showed that abiotic variables limited the local distribution of amphibians across landscapes (Gascon 1991; Skelly et al. 1999; Alford 1999). Abiotic factors may act as a filter for species composition at particular sites, allowing and rejecting species admittance to the assemblage, whereas biotic mechanisms, such as predation and competition, may act as secondary filters affecting community composition. Clearly, both laboratory and field approaches help us to understand mechanisms operating in nature. The laboratory experiments and field observations presented here suggest that competition and predation may be important mechanisms that influence the distribution of *S. couchii*, *B. speciosus*, *B. punctatus*, and *G. olivacea*, and highlight the need for future research in a field setting. Future research needs to be aimed at disentangling the interactions among habitat type, abiotic variables, and species interactions in order to be able to understand processes that operate at macro (regional) and micro (breeding site) scales, in order to understand the determinants of distributions of *S. couchii*, *B. punctatus*, *B. speciosus*, and *G. olivacea* across the Big Bend landscape.

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