Priority effects and desert anuran communities

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Abstract: The roles of priority effects and predation in structuring anuran communities have not been considered important in desert environments characterized by highly ephemeral pools and anuran species that breed synchronously. Predation is one mechanism that can set the stage for priority effects to be important, especially in ephemeral pools where resources are limiting and densities are high. We observed oophagy by *Scaphiopus couchii* Baird, 1854 on eggs of *Bufo speciosus* Girard, 1854 in the field and conducted laboratory experiments to test the hypothesis that *S. couchii* tadpoles would reduce *B. speciosus* survivorship via predation. Three-day-old *S. couchii* tadpoles reduced hatching success of *B. speciosus* eggs by nearly 90%. When *S. couchii* and *B. speciosus* eggs were laid the same day, *S. couchii* tadpoles reduced *B. speciosus* egg survivorship by 56%. Our results indicate that priority effects and predation may play an important role in influencing species composition of anuran assemblages in desert regions. Our study provides more support for the need to reevaluate the current paradigm in aquatic ecology that suggests predation does not play a role in structuring community assemblages in highly ephemeral pools.

Résumé : Dans les environnements désertiques caractérisés par des mares très éphémères et habités par des espèces d'anoures à reproduction synchrone, les rôles des effets de la priorité et de la prédation sur la structure des communautés d'anoures ne sont pas considérés importants. La prédation est un mécanisme qui peut rendre les effets de priorité plus significatifs, particulièrement dans les mares éphémères où les ressources sont limitantes et les densités élevées. Nous avons observé l'oophagie des oeufs de *Bufo speciosus* Girard, 1854 par *Scaphiopus couchii* Baird, 1854 en nature et fait des expériences de laboratoire pour vérifier l'hypothèse selon laquelle les têtards de *S. couchii* réduisent par prédation la survie de *B. speciosus*. Des têtards de *S. couchii* âgés de 3 jours réduisent le succès de l'éclosion chez *B. speciosus* de presque 90 %. Lorsque les oeufs de *S. couchii* et ceux de *B. speciosus* sont pondus le même jour, les têtards de *S. couchii* réduisent la survie des oeufs de *B. speciosus* de 56 %. Nos résultats indiquent que les effets de la priorité et la prédation peuvent jouer un rôle important en influençant la composition spécifique des peuplements d'anoures dans les régions désertiques. Notre étude apporte des éléments additionnels qui soulignent la nécessité de réévaluer le paradigme courant en écologie aquatique qui veut que la prédation ne joue pas de rôle dans la structuration des communautés dans les mares très éphémères.

[Traduit par la Rédaction]

Introduction

A central goal in ecology is to understand what determines ecological patterns among species across space and time (MacArthur 1968), and steady progress has been made toward understanding abiotic and biotic factors that determine the structure of communities in very different settings (Hutchinson 1959; Dayton 1971; Belyea and Lancaster 1999). The general consensus is that so-called assembly rules vary from system to system, and different communities may operate under different rules (Simberloff 2004). In aquatic environments a paradigm of community assembly has emerged that is based on the interplay between hydroperiod, resource competition, and predation (Morin 1983; Woodward 1983; Wellborn et al. 1996). The result of this interplay largely determines which species may be present or absent at a given site. Communities of larval anurans fit well into this paradigm of community structure. Pools with short hydroperiods are utilized by species with short larval periods and rapid development and, in general, tend to be low in species richness in comparison with longer lasting sites (Babbitt and Tanner 2000; Snodgrass et al. 2000). Species that inhabit highly ephemeral pools in desert landscapes generally tend to be superior competitors, but very susceptible to predation (Woodward 1983; Dayton and Fitzgerald 2001). At the other end of the spectrum, species with relatively long larval periods require sites that persist long enough for metamorphosis to occur. However, pools with longer hydroperiods are colonized by predators, and the species with longer larval periods deal much better with predation. Hence, the balance between hydroperiod, predation, and competition appears to largely explain how tadpole communities are structured.

How well does the anuran community assembly paradigm apply to species that breed in extremely ephemeral environments? In desert regions, the majority of anuran species breed in highly ephemeral pools created by unpredictable seasonal thunderstorms (Sullivan 1989; Woodward and

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Mitchell 1991) and tend to exhibit behavioral, developmental, and morphological adaptations that enable them to persist in harsh environments. In xeric environments, anurans congregate in temporary pools following a rain event and exhibit explosive breeding behavior (Sullivan 1989). There is very little temporal segregation of breeding among species compared with temperate regions, where groups of species tend to breed asynchronously (Woodward and Mitchell 1991). The lack of asynchronous breeding in desert regions is presumably due to the fact that pools with very short hydroperiods do not last long enough for sequential use of the site by different species, or cohorts of the same species. Additionally, factors such as predation that are associated with regulating species persistence in temperate and tropical environments (Morin 1986; Petranka et al. 1994) were thought to be unimportant in highly stochastic and ephemeral environments (Woodward and Mitchell 1991). However, empirical evidence from the few studies that have examined the roles of predation on eggs and tadpoles of desert anurans does suggest that predation may be an important mechanism affecting anuran community structure in highly ephemeral desert pools (Newman 1987; Dayton and Fitzgerald 2001; Dayton and Wapo 2002). Results from these studies suggest that assembly rules regulating community composition of amphibians in temperate and tropical regions may also be important in determining the structure of amphibian communities in desert regions.

One process that has not been explored as a mechanism of community assembly in desert anurans is priority effects, the advantages that “early-arriving” species, or species that hatch sooner, may have over latecomers in an assembling community. In temperate regions, where species often breed asynchronously, early-arriving species have a potential competitive and predatory advantage over “late-arriving” species (Travis 1983; Alford and Wilbur 1985; Petranka et al. 1994). In communities with asynchronous breeding, early breeders may deplete resources for late-arriving species, thereby inhibiting their population growth (Wilbur and Alford 1985). In breeding pools where tadpoles vary in age and size, both intra- and inter-specific oophagy have been suggested as mechanisms for how predation may structure amphibian communities (Banks and Beebee 1987; Marshall et al. 1990; Tejedo 1991; Petranka and Kennedy 1999).

Oophagy by one species on another may affect community composition by altering densities or even the presence of species in the community. Being the first to breed should reduce the potential for predation on eggs and tadpoles by conspecifics and other species (Petranka and Thomas 1995). There are two potential benefits of oophagy. First, egg consumption reduces the number of future competitors, thus reducing resource depletion (Crump 1983). Second, oophagy provides a high-energy food source (Drewes and Altig 1996; Kam et al. 1998; Gibson and Buley 2004). These benefits may be especially important in highly ephemeral pools where resources are limited and tadpole density is high. Indeed, experiments have shown that food supplementation and lower densities of tadpoles increased the probability of metamorphosis as well as the size of *Scaphiopus couchii* Baird, 1854 (Couch’s spadefoot) metamorphs (Newman 1987, 1989).

In the Chihuahuan Desert, anuran species that use ephemeral breeding sites are not randomly distributed (Dayton and Fitzgerald 2001). Tadpoles of *S. couchii* have the shortest larval period and rarely occur with tadpoles of other species. Tadpoles of *S. couchii* are more susceptible to predation, presumably because of their high activity level (Dayton and Fitzgerald 2001). These findings help explain the lack of co-occurrence of larval anuran species across the Chihuahuan Desert landscape. However, other biotic mechanisms, such as oophagy, may also influence the co-occurrence of species.

Here we present results of experiments using *S. couchii* tadpoles and *Bufo speciosus* Girard, 1854 (Texas toad) eggs to test the hypothesis that a species with relatively fast development (*S. couchii*) will consume eggs and reduce the survivorship of a species with slower development (*B. speciosus*). Specifically, we examine the role of oophagy as a mechanism resulting in nonrandom associations of *S. couchii* and *B. speciosus* across the Chihuahuan Desert landscape in Big Bend National Park, Texas, USA.

Methods

Study area and organisms

Big Bend National Park is located in southwestern Texas along the Rio Grande in the Chihuahuan Desert Ecoregion. Annual precipitation averages 35 cm, with approximately 70% of the rainfall occurring from May to September (Brown 1994). Summer rains occur primarily as isolated downbursts that flood arroyos and create breeding pools. The two species used in our study, *S. couchii* and *B. speciosus*, are explosive breeders that use temporary pools created by summer monsoon storms (Bragg 1945). *Scaphiopus couchii* typically call during the first night of a rain (Sullivan 1989), whereas *B. speciosus* will call for up to 4 days after a rain event (Moore 1976). Eggs are deposited in temporary pools that typically last from a few days up to 2 months. *Scaphiopus couchii* deposit their eggs in gelatinous strings surrounding submerged vegetation; a single female will deposit several egg masses throughout a pond. As little as 30 h are needed for *S. couchii* eggs to hatch, and time to metamorphosis can be as short as 8 days (Newman 1987), the shortest of any North American anuran (Buchholz and Hayes 2000). *Bufo speciosus* lay eggs in thin strings at the base of submerged vegetation, often in a single locality within the pool. In Big Bend we have observed up to seven amplecting pairs depositing eggs at the base of a single submerged plant. *Bufo speciosus* eggs require approximately 2–3 days to hatch, and tadpoles reach metamorphosis in 18–60 days (Wright and Wright 1949; Moore 1976). These two species are regionally sympatric, but they show very little overlap in their use of breeding sites (Dayton and Fitzgerald 2001).

Laboratory experiments

In July 2003 we collected *S. couchii* tadpoles and eggs and *B. speciosus* eggs from two ephemeral pools in Big Bend National Park. The two pools differed in hydroperiod and species composition. The first pool filled on 5 July and had only *S. couchii* tadpoles that hatched on 6 July. The second pool filled on 7 July, at which time *S. couchii* and *B. speciosus* were heard chorusing. On 8 July we collected

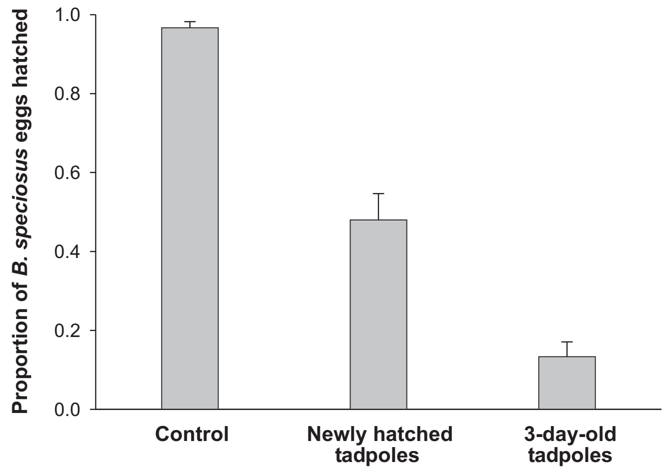
S. couchii tadpoles from the first pool and *B. speciosus* and *S. couchii* eggs from the second pool. Tadpoles and eggs were housed in separate 40-L buckets. On 9 July we set up an experiment to test for differences in survivorship of *B. speciosus* eggs reared with *S. couchii* tadpoles from two age classes. The experiment was a completely randomized design consisting of three treatments: (1) a control group of 30 eggs of *B. speciosus* with five newly hatched *S. couchii* tadpoles enclosed in a 2-mm mesh cage (no access to eggs); (2) an experimental group with 30 *B. speciosus* eggs (means calculated from a subset of 20 randomly sampled eggs; Gosner stage $\bar{x}$ = 15.9, SD = 0.22) and five newly hatched *S. couchii* tadpoles (means calculated from a subset of 20 randomly sampled tadpoles; length $\bar{x}$ = 7.05 mm, SD = 0.22 mm; Gosner stage $\bar{x}$ = 23, SD = 0.10); and (3) an experimental group with 30 *B. speciosus* eggs and five 3-day-old *S. couchii* tadpoles (means calculated from a subset of 20 randomly sampled tadpoles; length $\bar{x}$ = 15.4 mm, SD = 0.37 mm; Gosner stage $\bar{x}$ = 32.95, SD = 0.21). Eggs and tadpoles were randomized among treatments and treatments were replicated 10 times. Tadpoles and eggs were placed in plastic tubs (30 cm × 15 cm × 8 cm deep) filled with 1 L of aged tap water (aged for dechlorination). Experiments were terminated after 36 h, when the first *B. speciosus* eggs hatched. Our design enabled us to examine the variation in survivorship of *B. speciosus* eggs reared with *S. couchii* tadpoles of different age and size classes while controlling for potential indirect effects of the presence of newly hatched *S. couchii* tadpoles on the hatching success of *B. speciosus* eggs (i.e., the caged tadpoles in the control group). We used analysis of variance followed by Tukey's post hoc tests to test the hypothesis that egg survival differed among the three treatments. Percent survivorship data for each tub were arcsine square root transformed prior to analysis to meet assumptions of normality.

Results

Field observations

Over a 7-year period we observed >100 *S. couchii* and >15 *B. speciosus* breeding sites; at only 4 sites did we observe *S. couchii* and *B. speciosus* breeding in the same pool. In these instances, *S. couchii* eggs hatched first and thousands of *S. couchii* tadpoles swarmed the *B. speciosus* egg strings, biting and consuming *B. speciosus* eggs. Observation of *B. speciosus* eggs revealed that *S. couchii* were consuming *B. speciosus* embryos. Gosner stages of the *S. couchii* tadpoles at the 4 sites ranged from 25 to 40 (Gosner 1960). The disparity in Gosner stages among sites was due to the variation in development rates and time of oviposition. In all 4 cases, survivorship of *B. speciosus* was notably reduced, as inferred by the lack of viable eggs. In 2 of the pools, zero *B. speciosus* metamorphs were observed, indicating that oophagy by *S. couchii* may have completely eliminated those cohorts of *B. speciosus*. In the other 2 pools, although we do not have quantitative data on effects of *S. couchii* on *B. speciousus* eggs, we estimated a 75% reduction in metamorphosing *B. speciosus*.

Fig. 1. Proportion of *Bufo speciosus* eggs that hatched in each of the three treatments.



Experimental results

Scaphiopus couchii tadpoles in both experimental treatments consumed eggs of *B. speciosus*. There were significant differences in the survivorship of *B. speciosus* eggs among treatments ($F_{[2,27]}$ = 96.88, P < 0.00001). Tukey's tests revealed significant differences between all treatments (P < 0.05). An average of 97% of *B. speciosus* eggs hatched in the control group (n = 10, $\bar{x}$ = 0.97, SD = 0.02), significantly more than in the two treatment groups (P < 0.0001). Hatching success was also significantly different between the two experimental treatments (P = 0.001), with 44% (n = 10, SD = 0.17) of *B. speciosus* eggs reared with small *S. couchii* tadpoles hatching and 13% (n = 10, SD = 0.04) of eggs raised with large *S. couchii* tadpoles hatching (Fig. 1).

Discussion

Both inter- and intra-specific oophagy have been reported in several anuran species, and it is postulated that oophagy plays a role in regulating species co-occurrence in long-lived pools in temperate environments (Petranka et al. 1994). In our study, *S. couchii* tadpoles significantly reduced survival of *B. speciosus* eggs. *Scaphiopus couchii* tadpoles had a greater effect on *B. speciosus* egg survivorship when there was a lag period of a few days between hatching of the two species. Yet, even when hatching was offset by less than 24 h, *S. couchii* tadpoles significantly reduced *B. speciosus* egg survivorship via oophagy. Our laboratory experiments combined with field observations support the hypothesis that *S. couchii* tadpoles are effective predators on *B. speciosus* eggs.

It has been suggested that high rates of oophagy have led to the evolution of synchronized breeding in some systems (Petranka and Thomas 1995). The rationale is that explosive breeding reduces age and size variation among individuals in the tadpole community and should therefore reduce oophagy. In fact, studies examining oophagy have shown that "late-arriving" anurans avoid using breeding pools where "early-arriving" species are already present (Banks and Beebee 1987; Petranka et al. 1994). Our results imply that oophagy may also be important in a synchronously breeding community. *Scaphiopus couchii* and *B. speciosus* are explosive, synchronized breeders, yet there is sufficient variation in development rates to allow oophagy to manifest important effects on survival and density of species. The rapid development of *S. couchii* tadpoles creates a gap in Gosner stage (Gosner 1960) and size among species of co-occurring tadpoles. The short period between egg deposition and hatching provides *S. couchii* tadpoles with a potential competitive and predatory advantage over other species that require longer periods from egg deposition to hatching. In the Chihuahuan Desert landscape, the fast-growing *S. couchii* and relatively slower *B. speciosus* are functional analogs of early- and late-arriving species in asynchronously breeding anuran communities.

The benefits of oophagy to *S. couchii* and the associated costs to *B. speciosus* further set the stage for priority effects to structure the Chihuahuan Desert anuran community, especially when resources are limiting. Increased size and decreased time to metamorphosis of *S. couchii* tadpoles in the low-density, food-supplemented treatments in Newman's (1987) experiments suggest that resources are limited and that high densities lead to longer larval periods, which can be catastrophic in short-lived pools where the primary cause of mortality is desiccation. In natural pools, where densities of *S. couchii* tadpoles are often high and resources are limited (Newman 1987), the added nutrition provided by eggs and the corresponding reduction in density of *B. speciosus* may increase the likelihood of *S. couchii* tadpoles successfully reaching metamorphosis.

Due to the short-lived nature of highly ephemeral pools and the synchronous breeding of anurans in desert environments (Woodward and Mitchell 1991), the roles of priority effects and predation in structuring desert anuran communities have been largely overlooked (but see, for predation, Newman 1987; Dayton and Fitzgerald 2001; Dayton and Wapo 2002). Our results suggest that in the Chihuahuan Desert anuran community, resource limitation and variation in development rates facilitate oophagy by *S. couchii* on *B. speciosus*. These findings support previous research demonstrating that *S. couchii* tadpoles were effective predators on eggs of conspecifics when egg deposition was disjunct by a few days as a result of multiple rain events (Dayton and Wapo 2002). The effects of oophagy on use of breeding sites by anuran species, or cohorts, may be important in structuring amphibian communities in desert environments. Our results indicate that, as Petranka and Kennedy (1999) suggest, it is time to reevaluate the perception that pond tadpoles are primarily microphagous suspension feeders and herbivorous bottom grazers and realize that predation may in fact be an important mechanism structuring community composition even in highly ephemeral pools in desert environments.

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