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Interspecific competition between tadpoles of *Bufo gargarizans minshanicus* (STEJNEGER, 1926), and *Rana kukunoris* NIKOLSKII, 1918
(Anura: Bufonidae, Ranidae)

Zwischenartliche Konkurrenz bei Larven von *Bufo gargarizans minshanicus* (STEJNEGER, 1926) und *Rana kukunoris* NIKOLSKII, 1918
(Anura: Bufonidae, Ranidae)

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KURZFASSUNG

Der Autor untersuchte im Laborexperiment die Konkurrenz zwischen Larven von *Bufo gargarizans minshanicus* (STEJNEGER, 1926) und *Rana kukunoris* NIKOLSKII, 1918 aus dem Hochland von Tibet im Südwesten Chinas. Wachstums- und Entwicklungsraten, Dauer der Larvalzeit, Körpermasse zu Metamorphosebeginn, Körperkondition und Überlebensrate bis zur Metamorphose dienten als Maße für die Reaktion auf inner- und zwischenartliche Konkurrenz.

Bei Anwesenheit von *Rana*-Larven zeigten die *Bufo*-Larven wenig Veränderung hinsichtlich Wachstums- und Entwicklungsraten, Körpermasse zu Metamorphosebeginn, Körperkondition und Überlebensrate gegenüber einer reinen *Bufo* Kontrollgruppe. Demgegenüber erzielten Froschlarven bei Anwesenheit von Krötenlarven eine geringere Körperkondition aber höhere Überlebensraten als in einer reinen *Rana*-Kontrollgruppe. Die Ergebnisse legen nahe, daß die Konkurrenz zwischen den Larven dieser beiden Arten symmetrisch ist. Die symmetrische Konkurrenz zwischen *B. g. minshanicus* und *R. kukunoris* war nicht durch die untersuchten Faktoren zu erklären und basiert offenbar auf einem Wechselspiel zahlreicher, schwerer faßbarer Parameter wie Aktivität, Körpergröße, Wachstumsrate und bewohnte Nische, die noch auf ihre Untersuchung warten.

ABSTRACT

Competition between tadpoles of *Bufo gargarizans minshanicus* (STEJNEGER, 1926), and *Rana kukunoris* NIKOLSKII, 1918, from the Tibetan High Plateau in southwestern China was studied in a laboratory experiment. Growth rate, development rate, length of larval period, mass at metamorphosis, body condition, and survival rate until metamorphosis were used as measures of response to intra- and interspecific competition.

In the presence of ranid individuals, bufonid larvae showed largely unchanged growth, development, size at metamorphosis, body condition and survival as compared to a *Bufo* only control. While toad individuals present, frog larvae attained less body condition, but higher survival rates until metamorphosis compared to a *Rana* only control. The results suggested that competition between these two larval species was symmetric. The symmetric competition between *B. g. minshanicus* and *R. kukunoris* was not sufficiently explained by the studied factors but is rather controlled by a trade-off among a variety of more subtle traits such as activity level, body size, growth rate and niche that still awaits exploration.

KEY WORDS

Amphibia: Anura: Bufonidae, Ranidae; *Bufo gargarizans minshanicus*, *Rana kukunoris*, tadpoles, larvae, symmetric competition, trade-off, population ecology, China

INTRODUCTION

Competition in amphibian larvae has been a focus of research in laboratory experiments (e. g., WILBUR 1977; TRAVIS 1980) and artificial ponds (e. g., WILBUR 1987; MORIN & JOHNSON 1988; GRIFFITHS et al. 1993; WERNER 1994). Competitive situations are ubiquitous in nature and usually classified into symmetric competition (ecological competition between two species in which both suffer similar declines in fitness) and asymmetric competition (ecological competition between two species in which one species suffers a much greater fitness decline than the other). The outcomes of competitive situations often depend on traits which influence or indicate competitive ability, such as body size, body mass, armament, locomotion velocity, body color or costly signals of strength (reviewed by SIMMONS & SCHEEPERS 1996).

Although substantial evidence is chiefly available for asymmetric competition (MORIN & JOHNSON 1988; WERNER 1994; BEEBEE 1995; PETRANKA 1995; BARDSLEY & BEEBEE 1998; KIESECKER & BLAUSTEIN 1999; SINSCH et al. 1999; LAURMA 2000; WONG et al. 2000; PAKKASMAA & AIKIO 2003; SMITH et al. 2004; JONSSON et al. 2008; CHARTER et al. 2013), symmetric competition is common in nature (LAWTON & HASSELL 1981) and is therefore likely to be an important force of natural selection (reviewed by ZU et al. 2008). Anuran larvae provide a convenient tool for investigating interspecific and intraspecific competition (ALFORD & WILBUR 1985; GRIFFITHS et al. 1991; WERNER 1992; BARDSLEY & BEEBEE 1998).

Competition mechanisms in tadpoles are attributed to social interactions including the effect of pheromones (GROMKO et al. 1973; JOHN & FENSTER 1975; SCHOENER 1983; GRIFFITH 1991), food limitation (DEBENEDICTIS 1974; SEALE 1980; MORIN & JOHNSON 1988; MURRAY 1990;), body size and activity (CONNELL 1983; SCHOENER 1983; PERSSON 1985) or behavior and habitat choice (TILMAN 1987; WERNER 1992). Larval growth rate is a valid measure of an individual's competitive ability (WILBUR & COLLINS 1973; COLLINS 1975; SMITH-GILL & GILL 1978).

Bufo gargarizans minshanicus (STEJNEGER, 1926) and *Rana kukunoris* NIKOLSKII, 1918, are distributed throughout the Tibetan Plateau in southwestern China (FEI & YE 2001), where they are found in permanent large wetlands. The spawning periods of both species are almost overlapping (early-April to late-April) and as typical explosive breeders (WELLS 1977), both species exhibit short breeding seasons (*B. g. minshanicus*: 5-18 days; *R. kukunoris*: 9-21 days). *Rana kukunoris* is usually the first to arrive at the pond, about five days earlier than *B. g. minshanicus* which do not avoid spawning in pools occupied by *R. kukunoris* (YU, personal observation).

Since population numbers of both species are declining due to human encroachment and habitat degradation (FELLERS et al. 2003), understanding the mechanisms of competition between *B. g. minshanicus* and *R. kukunoris* tadpoles has important implications for the conservation of these two species.

The aim of the present study was to examine whether coexisting larval development of *B. g. minshanicus* and *R. kukunoris* produces competitive effects manifesting in modified growth, developmental rates or body condition. To exclude environmental and predatory effects, an experimental approach in the laboratory was chosen.

MATERIALS AND METHODS

The author collected 3,000 and 1,000 fertilized eggs from 30 clutches of *B. g. minshanicus* and 10 clutches of *R. kukunoris*, respectively, found in a pond located at 36° 40'N, 101°20'E (altitude 2546 m), in Huangyuan County, Qinghai, China, in April 2012. The egg masses were taken to the laboratory (1,272 km from the sampling site; altitude 130 m) to reduce the number of influencing variables such as predation during the experiments. Within 24 hours and separated by species, the clutches were transported to the lab in two large plastic containers, each being shallowly filled with 15 L holding-water. From each clutch, 100 embryos were taken and kept in plastic containers filled with 10 L holding-water that was aerated automatically. Although the *R. kukunoris* eggs were about five days older, the larvae of both species arrived synchroneously at developmental stage 26 (earliest free swimming and feeding stage - GOSNER 1960) after about seven days of keeping them at a water temperature of 20 °C.

From both species, only tadpoles of developmental stage 26 entered the experiment. Out of these, fifteen tadpoles of each species were selected randomly and weighed (to the nearest 0.001 g) after blotting dry to obtain comparative data on the mass of tadpoles of stage 26. These tadpoles were not used in the experiment prop-

Table 1: Summary of the laboratory experiment data of the monospecies and multispecies treatments of tadpoles of *Bufo gargarizans minshanicus* (STEJNEGER, 1926), and *Rana kukunoris* NIKOLSKII, 1918. NS - not significant ($p > 0.05$); * - significant ($p < 0.05$); ** - highly significant ($p < 0.01$). Developmental stages according to GOSNER (1960). Data is presented as arithmetic mean values ± one standard error of the mean.

Tab. 1: Datenzusammenfassung aus den Laborexperimenten der Monospezies- und Multispezies-Behandlungen mit Larven von *Bufo gargarizans minshanicus* (STEJNEGER, 1926) und *Rana kukunoris* NIKOLSKII, 1918. NS - nicht signifikant ($p > 0.05$); * - signifikant ($p < 0.05$); ** - hoch signifikant ($p < 0.01$). Larvenstadien nach GOSNER (1960). Die Daten repräsentieren den arithmetischen Mittelwert ± den einfachen Standardfehler des Mittelwertes.

Variables studied / Untersuchte Variablen	*Bufo gargarizans. minshanicus*		*Rana kukunoris*	
	monospecies treatment / Monospezies-Behandlung	multispecies treatment / Multispezies-Behandlung	monospecies treatment / Monospezies-Behandlung	multispecies treatment / Multispezies-Behandlung
Duration of larval feeding period (stage 26-42) [d] / Dauer der Larvalperiode mit Nahrungsaufnahme (Stadium 26-42) [d]	41.48 ± 1.85 NS	41.87 ± 2.60 NS	47.17 ± 2.08 NS	45.73 ± 2.37 NS
Body mass at stage 42 [g] / Körpermasse bei Stadium 42 [g]	0.097 ± 0.003 NS	0.100 ± 0.004 NS	0.210 ± 0.006 NS	0.225 ± 0.012 NS
Body condition at stage 42 [g/mm^3] / Körperkondition bei Stadium 42 [g/mm^3]	0.160 ± 0.005 NS	0.167 ± 0.008 NS	0.152 ± 0.004 *	0.139 ± 0.004 *
Growth rate [g/d] / Wachstumsrate [g/d]	0.25 ± 0.01 NS	0.26 ± 0.02 NS	0.47 ± 0.02 NS	0.50 ± 0.02 NS
Survival rate (%) / Überlebensrate (%)	80.00 NS	73.33 NS	60.00**	86.67**

er. *Bufo g. minshanicus* tadpoles (0.0223 ± 0.0022 g, $N = 15$) were significantly smaller than *R. kukunoris* tadpoles (0.0333 ± 0.0016 g, $N = 15$; Mann-Whitney Test: $Z = -3.33$, $P = 0.001$).

For the study of interspecific competition, five *R. kukunoris* tadpoles and five *B. g. minshanicus* tadpoles were put together into a plastic circular transparent aquarium (5 L holding-water) and allowed to contact freely. To evaluate the effects of intraspecific competition, another container of the above type was stocked with 10 tadpoles of *R. kukunoris* and a third one with 10 of *B. g. minshanicus.* Treatments were simultaneously replicated six times resulting in 18 replicates. The tadpoles in each treatment were placed on a same food regimen (50 mg per tadpole per day; commercial fish food, Bieyanghong, Biological Co. Ltd., Hangzhou, China: 30 % protein, 10 % lipids, 18 % algae, 4 % fibre, 10 % ash) plus filamentous algae (*Spirogyra*) and waterweeds such as *Potamogeton crispus.* The aquaria were exposed to a room temperature of 25.8 ± 1.4 °C and an 11 : 13 hours (light : dark) photoperiod throughout the study period; the water was changed weekly.

After the first metamorph (defined by the emergence of at least one forelimb, stage 42 - GOSNER 1960) was discovered, the 18 circular aquaria were checked daily and metamorphs found were taken out to avoid drowning. The metamorphs were kept separately in plastic vials (8 cm diameter) with sandy ground and a shallow (5 mm) layer of water on top until tail resorption was completed to ensure their survival until release.

Several variables were measured [units in brackets]: (1) 'duration of larval feeding period [d]' (i.e., number of days from the beginning of the experiment at Gosner stage 26 until beginning of metamorphosis at stage 42); (2) 'body mass at the beginning of metamorphosis (stage 42) [g]' (body mass was weighed with an electric balance to the nearest 0.001 g); (3) 'growth rate [g/d]' (measured as the 'body mass at the beginning of metamorphosis' divided by the 'duration of larval feeding period'); (4) 'survival rate [%]' (percentage of tadpoles that survived the experiment to enter metamorphosis at stage 42) and (5) 'body condition' at the beginning of metamorphosis at stage 42 [g/mm³] using the formula (body mass / SVL^3) × 1000 (Veith 1987; Walsh et al. 2008). Snout-vent-length (SVL) was measured with digital calipers (to the nearest 0.1 mm).

Within species, duration of larval feeding period (1), body mass at the beginning of metamorphosis (2), body condition at stage 42 (5), and growth rate (3) were analyzed by multifactor analysis of variance for differences between mono- and multispecies treatments. Survival rate (4) was analyzed using a Chi-square test (SPSS 13.0, SPSS Inc., 2004, Chicago, IL, USA). The *P*-values given are from two-tailed tests, with results presented as mean ± standard error.

All animal experiments were made in full agreement with the Animal Scientific Procedures Act 1988, legislated by the State Department of China; the Huangyuan county people's government approved the study protocol; approval number HY/10-07. Most metamorphic individuals were returned to the original breeding pond at the end of the experiments.

RESULTS

Mean duration of the larval feeding period was clearly shorter in *B. g. minshanicus* than *R. kukunoris* ($F_{1, 81} = 4.12$, $P = 0.046$). Within species, this value did not differ significantly between mono- and multispecies treatments (*Bufo*, $F_{1, 69} = 0.044$, $P = 0.90$; *Rana*, $F_{1, 59} = 0.21$, $P = 0.65$, Table 1); i.e., larvae in monospecies groups did not develop significantly faster or slower than in multispecies groups.

Mean body mass at the beginning of metamorphosis was clearly lower in *B. g. minshanicus* than *R. kukunoris* ($F_{1, 81} = 310.13$, $P < 0.001$). Within species, this value did not differ significantly between mono- and multispecies treatments (*Bufo*, $F_{1, 69} = 0.38$, $P = 0.54$; *Rana*, $F_{1, 59} = 1.51$, $P = 0.23$, Table 1); i. e., larvae in monospecies groups were not significantly heavier or lighter than in multispecies groups.

Mean growth rate was clearly higher in larvae of *R. kukunoris* than *B. g. minshanicus* ($F_{1, 81} = 72.46$, $P < 0.001$). Within species, this value did not differ significantly among mono- and multispecies treatments (*Bufo*, $F_{1, 69} = 0.032$, $P = 0.86$; *Rana*, $F_{1, 59} = 1.47$, $P = 0.23$, Table 1); i. e., larvae in monospecies groups did not grow significantly faster or slower than in multispecies groups.

The tadpoles' body condition values at Gosner stage 42 were similar among monospecies treatments ($F_{1, 81} = 1.79$, $P = 0.19$). There was no significant difference between mono- and multispecies treatments in *Bufo* ($F_{1, 69} = 0.57$, $P = 0.46$) whereas, in *Rana* monospecies treatments showed significantly ($F_{1, 59} = 5.41$, $P = 0.023$) higher body condition values than multispecies treatments; i. e., the body condition of *R. kukunoris* larvae was better when *B. g. minshanicus* larvae were absent.

Survival rate was high in *B. g. minshanicus* and not significantly different in mono- and multispecies treatments ($\chi^2 = 0.51$, $df = 1$, $P = 0.47$, Table 1). Remarkably, in *R. kukunoris* multispecies treatments, survival rate was high and significantly higher than in monospecies treatments ($\chi^2 = 6.64$, $df = 1$, $P = 0.01$).

DISCUSSION

The results show that coexisting tadpoles of *B. g. minshanicus* and *R. kukunoris* respond symmetrically to the presence of the complementary heterospecific. This symmetry appears to be the result of *B. g. minshanicus* tadpoles being relatively unaffected by the presence of both conspecific and heterospecific and *R. kukunoris* by heterospecific competitors. Interestingly, the survival rate of *R. kukunoris* larvae in heterospecific competition was clearly higher than in conspecific competition and the presence of *Bufo* larvae enhanced (although not significantly) other metamorphosis traits (e.g., body mass and growth rate). The results indicated that *R. kukunoris* tadpoles profited from the presence of *B. g. minshanicus* larvae. In fact, the author found nine of 10 *R. kukunoris* natural populations to coexist with *B. g. minshanicus* and other heterospecific competitors such as *Bufo raddei* STRAUCH, 1876.

WILBUR (1980) suggested that in amphibian communities coexistence of species may be controlled by stochastic environmental factors. Thus, priority effects, such as order of colonization may dictate the degree of niche overlap and the strength of interspecific competition. What could explain the symmetric heterospecific competition between simultaneously developing larvae of *B. g. minshanicus* and *R. kukunoris*?

(i) Differences in activity level are believed to explain coexistence in other species (reviewed by SMITH et al. 2004). In general, *B. g. minshanicus* tadpoles are more active than *R. kukunoris* larvae (ZHANG et al. 2007), suggesting *B. g. minshanicus* to be competitively superior to *R. kukunoris* in the habitats studied. Similarly, WERNER (1992) found that the more active tadpoles of *Lithobates pipiens* (SCHREBER, 1782) were competitively superior to the less active larvae of *Lithobates sylvaticus* (LECONTE, 1825). If activity is a measure of competitive advantage, one would expect the competition between *B. g. minshanicus* and *R. kukunoris* to be asymmetric.

(ii) The above assumption however neglects differences in body size as large individuals may be physically superior competitors (reviewed by ZU et al. 2008). Indeed, previous experiments on tadpole competition found that the larger species was the superior competitor (SMITH et al. 2004). At the beginning of the experiment, the *R. kukunoris* tadpoles were 1.49 times as heavy as the toad tadpoles; this difference gradually increased as the tadpoles' development proceeded (2.25 times at the beginning of metamorphosis). The larger larvae of *R. kukunoris* possess a wider mouth opening, and thus probably can feed more efficiently than their competitors, but *B. g. minshanicus* larvae may compensate for it by higher foraging activity.

(iii) Feeding niche was spatially different in the species of this experiment. *Bufo g. minshanicus* tadpoles were observed to graze on the water surface, whereas *R. kukunoris* larvae often fed in deeper water layers. This observation in the lab is largely consistent with the larval feeding behavior in the wild (Yu, personal observation). In this study, a mixture of fish food, pond weed and filamentous algae was administered. Fish food initially floated on the water surface before sinking to the bottom of the tanks, pond weed always floated on the water surface. Thus, most of the protein-rich fish fodder was probably taken by *B. g. minshanicus* larvae before reaching the feeding grounds of *R. kukunoris*. Additionally, *B. g. minshanicus* larvae fed on low protein pond weed, and, thus utilized a wider array of food resources. It was never observed that the larger *R. kukunoris* tadpoles actively hindered smaller *B. g. minshanicus* larvae in feeding. However, it cannot be excluded that the bottom-dwelling *R. kukunoris* larvae alimentarily profited from the sunken feces of the surface-feeding *B. g. minshanicus* tadpoles.

(iv) Competitive ability often correlates positively with growth rate in anurans (RICHARDSON 2001). In multispecies treatments, growth rate of *R. kukunoris* was higher than of *B. g. minshanicus* suggesting that *R. kukunoris* could be more efficient than *B. g. minshanicus* at exploiting and utilizing resources under competition conditions.

The observed symmetric competition between *B. g. minshanicus* and *R. kukunoris* larvae was not sufficiently explained by activity level, body size, growth rate, and feeding niche, but may play a role in successful colonization of habitats. Competition can be mediated by the production of toxic chemicals or inhibitory cells discharged into the ambient water by tadpoles (SCHOENER 1983; GRIFFITH 1991). Such a subtle mechanism could however not be detected with the methods applied. As a consequence, the author has to conclude that there is a yet unexplained interplay of trade-offs among a variety of traits that resulted in symmetric heterospecificity of the competition between *B. g. minshanicus* and *R. kukunoris*. Better understanding of its mechanism may have important implications for the conservation of these species.

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