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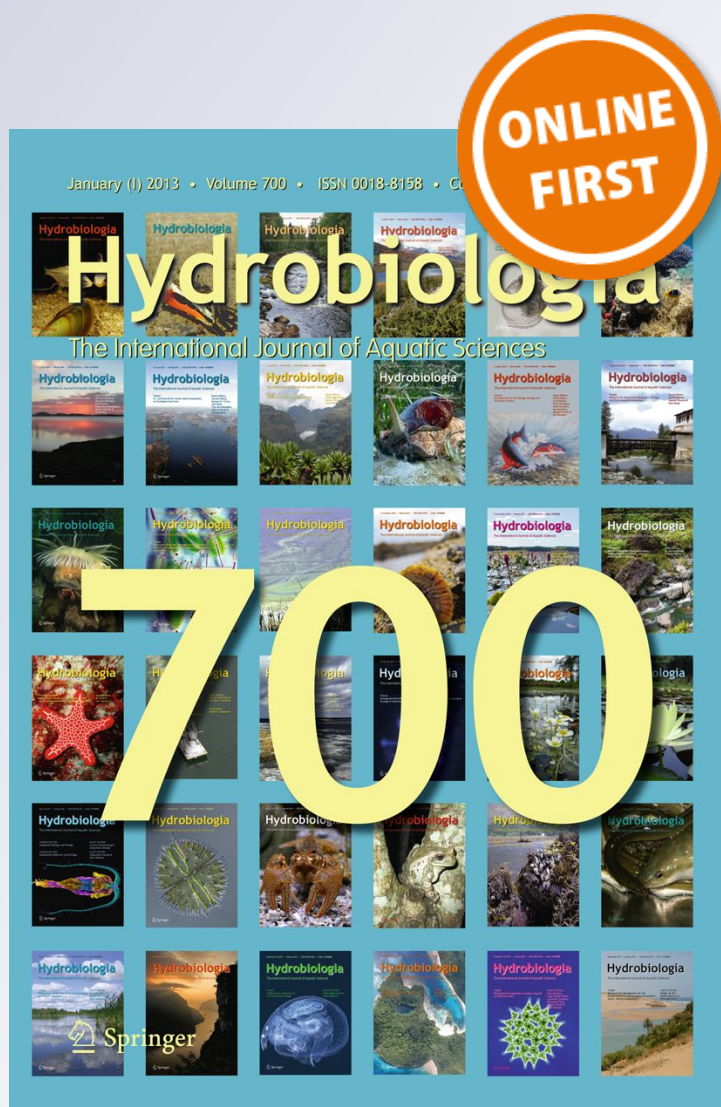
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# Testing for intraspecific and interspecific larval competition between two anurans: *Hyla savignyi* and *Bufo viridis*

Meital Stein · Shomen Mukherjee · Claire Duchet · Gail M. Moraru · Leon Blaustein

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**Abstract** Intraspecific and interspecific competition can be important factors affecting anuran tadpoles in temporary pools. We focus on two co-occurring anuran species that are of conservation concern in Israel and may negatively interact: *Bufo viridis* (Laurenti, 1768) and *Hyla savignyi* (Audouin, 1829). We conducted a replacement design mesocosm experiment to examine intraspecific and interspecific competition between tadpoles of these two species. Plastic tubs were assigned to five replacement design treatments: 0 *Hyla* + 20 *Bufo*; 0 *Hyla* + 40 *Bufo*; 20 *Hyla* + 20 *Bufo*; 20 *Hyla* + 0 *Bufo*; and 40 *Hyla* + 0 *Bufo*, and a control with no tadpoles which was used to test for effects of the tadpoles on invertebrate community structure. While *H. savignyi* was significantly affected by intraspecific density, with smaller body mass and longer time to metamorphosis at the high-density treatment, *B. viridis* showed

no intraspecific or interspecific density-dependent effects. However, *B. viridis* time to metamorphosis was negatively correlated with water temperature, while its survivorship was positively correlated with water temperature. The tadpoles affected neither abundance nor taxon richness of invertebrates. Our results suggest that stronger intraspecific competition than interspecific competition may contribute to the common co-occurrence of these two anurans in the same pools.

**Keywords** Replacement design · Amphibians · Temporary pools · Larval performance

## Introduction

Amphibian decline is a well-known issue, widely reviewed, and explored (Alford & Richards, 1999; Houlahan et al., 2000; McCallum, 2007; Hayes et al., 2010; Monastersky, 2014). Since this decline is reflected in populations of many anuran species and is occurring rapidly worldwide, a better understanding of their ecology can aid in their conservation (Young et al., 2001).

Competition is generally considered one of the most important ecological processes since it strongly affects population dynamics and community structure (Connell, 1961). In anurans, both intraspecific and interspecific competition are often important

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processes affecting larval performance and community composition (Griffiths, 1991; Dayton & Fitzgerald, 2001). Strong inter- and intraspecific competition can reduce growth (Light, 1967), affect morphology (Relyea, 2002) and can also affect behavior (Relyea, 2004), which in turn can indirectly affect demography and community structure. However, since interspecific competitive effects are often asymmetric, it is important to understand the relative strengths of intra- and interspecific competition in a given community. This can help in the understanding of a fundamental ecological question of whether stable coexistence among competitors possible (Hutchinson, 1959; Chesson, 2000; Chase & Leibold, 2003).

Competition between individuals in a population is often density dependent, which is caused by limited availability of resources such as food or space or may also be due to interference competition (Begon et al., 1990). Theory suggests that if interspecific competition is weaker than intraspecific competition, then stable local coexistence is possible (Chesson, 2000). However, if interspecific competition has a greater impact on survivorship for one or both competitors, local competitive exclusion is expected (Chesson, 2000). In contrast, when both types of competition have the same effects, the competitors are equivalent, and neutral competitive dynamics may determine species diversity (Hubbell, 2001; Adler et al., 2007). Only a small fraction of studies on competition are designed to assess the relative strengths of intra- and interspecific competition (Juliano, 2010). We follow Goldberg & Scheiner (2001) and Juliano (2010) study designs (see explanations in methods below) to understand density-dependent, inter- and intraspecific competition between two sympatric species of anurans.

Of interest here are the intraspecific and interspecific competitive interactions between tadpoles of two anuran species—the green toad, *Bufo viridis* (Laurenti, 1768), and the tree frog, *Hyla savignyi* (Audouin, 1829)—whose interactions are poorly understood. These species have high temporal and spatial overlap. They breed between late winter and mid-spring in the mountainous regions of northern Israel. Both breed in temporary pools, and to survive, larvae of both species must metamorphose and exit these pools before the pools dry. Both species are of conservation concern in Israel: the green toad is

listed as “endangered” while the tree frog is listed as “vulnerable” (Dolev & Perevolotsky, 2004). *B. viridis* larvae are predominantly periphyton grazers and have been shown to compete strongly with another periphyton grazer—the larval mosquito *Culiseta longiareolata* Macquart (Blaustein & Margalit, 1994, 1996). Larval *H. savignyi* appears to be primarily a periphyton grazer based on preliminary observations (M. Stein, personal observations). Gravid *H. savignyi* females have been shown to mitigate intraspecific competition among tadpoles by choosing to oviposit in pools with no or low densities of conspecific tadpoles (Stein & Blaustein, 2015).

The objectives of this study were to determine: (1) the relative importance of intraspecific competition and interspecific competition for larval performance (time to, size at, and survival to metamorphosis) of equal developmental stage cohorts of *B. viridis* and *H. savignyi* tadpoles; and (2) the effects of *B. viridis* and *H. savignyi* tadpoles on aquatic invertebrate community structure in temporary habitats. Exploring these relationships will not only provide an understanding of how these two anuran species interact and affect community structure, but also it may assist in understanding the mechanisms of coexistence and therefore have implications for conservation management.

We predicted strong intra- and interspecific competitive effects since the two sympatric species appear to be predominantly periphyton grazers. We predicted a stronger intraspecific-negative density-dependent effect, likely due to higher degree of dietary overlap among conspecifics. At high density, we predicted that survival and size at metamorphosis would be lower, while time to metamorphosis would be longer. We also predicted that both anurans will reduce invertebrate relative abundance and richness not only because of likely exploitative competition, but also due to predation on invertebrates (Blaustein & Margalit, 1994, 1996).

For anuran species, larval competition may be indirectly affected by water temperature, as this may also have an effect on their performance (Alvarez & Nicieza, 2002). For instance, temperature not only determines the desiccation rate of the ponds, thereby ultimately influencing phenotypic plasticity in metamorphic responses (Crump, 1989), but it also affects algal growth. Thus, we also assessed how temperature was related to larval performance.



## Methods

### Experimental design and sampling

A replicated outdoor mesocosm experiment, using a replacement design, was conducted at the Haifa University campus ( $\sim 460$  m above sea level,  $+32^{\circ}45'35.17''$ ,  $+35^{\circ}1'17.32''$ ). The mesocosms (pools) were dark green plastic tubs (length  $\times$  width  $\times$  depth:  $45 \times 55 \times 20$  cm; 40 L capacity) initially filled with 20 L of rain water in mid-January 2013. This volume was maintained initially by rains and then by refilling evaporated water with aged tap water. Both anuran species are known to oviposit into natural temporary pools of this size (Blaustein & Margalit, 1995; L. Blaustein, personal observations). An inoculation of natural pond water (0.5 L per tub) from a constructed temporary pond in the Hai-Bar Nature Reserve (Mount Carmel, Haifa) introduced microbes, algae, and invertebrates. Artificial-outdoor mesocosms, compared to natural pools, reasonably approximate natural conditions and allow for ease in replication, which in turn reduces within-treatment variance (Morin, 1998; Blaustein & Schwartz, 2001).

A 1 mm mesh net was added to each pool that lined the shape of the tub and was held to the bottom by two rocks that displaced  $\sim 0.925$  L. The mesh net, which contained small folds, also added heterogeneity to the tubs and, when lifting the net, allowed easy detection of tadpoles that were approaching metamorphosis (see Stein & Blaustein, 2015). In addition, we added organic matter to each pool in the form of fresh *Bromus sterilis* L., a common local annual plant (mean wet mass per mesocosm for all 36 mesocosms: 6.35 g, SE = 0.12) on 13 February 2013 (one week prior to anuran tadpole introduction).

The pools were covered with a 1.2 cm mesh metal net in order to reduce among-pool heterogeneous accumulation of leaf litter from nearby trees, and to avoid disturbance from animals such as mongoose, jackals, and cats, which commonly entered the experimental field (S. Mukherjee, C. Duchet and M. Stein, personal observations). These 1.2 cm openings were large enough for mosquitoes and other dipterans to penetrate and oviposit. The mesh openings were not large enough to allow colonization by large invertebrate predators and anurans, but previous works have demonstrated that colonization by insect predators and anurans in this particular experimental field are rare

(e.g., Eitam et al., 2002; Silberbush & Blaustein, 2011).

On 19 February 2013, *B. viridis* and *H. savignyi* tadpoles (Gosner stage 20–21; Gosner, 1960) were collected from nearby temporary waters on Mount Carmel. These sites contained a large number of *H. savignyi* egg clutches and *B. viridis* egg strings, ensuring that larvae collected were from multiple females. For each species, random individuals were weighed in 4 groups of 40 tadpoles, a total of 160 per species. These tadpoles were not used in the experiment but only for determination if species differ in initial weight; the sum of 40 *B. viridis* tadpoles averaged 0.29 g [SE: 0.019] and the sum of 40 *H. savignyi* tadpoles averaged 0.25 g [SE: 0.006]. The two species of tadpoles were not initially significantly different in mass (*t* test,  $t = -2.103$ ,  $P = 0.08$ ). The next day (20 February), we mixed the larvae of the same species together and took random samples to assign individuals to the different pools according to the experimental design described below.

We used a replacement-series experimental design with five different density treatments (Table 1). In addition, we used a “control” treatment of no tadpoles to check how the tadpoles may have influenced invertebrate community structure. These densities (20 or 40 tadpoles per 20 L) are well within the range of densities found in identical tubs that were naturally colonized by *H. savignyi* (L. Blaustein, unpublished data) and by *B. viridis* in natural temporary pools (Blaustein & Margalit, 1995). Preliminary work also showed that the experimental densities of 40 tadpoles per 20 L under similar conditions of this experiment

**Table 1** Experimental replacement design to assess intraspecific and interspecific competition for anurans *Hyla savignyi* and *Bufo viridis*

# <i>H. savignyi</i>	# <i>B. viridis</i>	Total
0	0	0
0	20	20
0	40	40
20	20	40
20	0	20
40	0	40

Number of early-stage (Gosner stage 20–21) tadpoles introduced into the various treatments of the outdoor mesocosm experiment

resulted in moderate to strong intraspecific density-dependent effects in *H. savignyi* (Stein & Blaustein, 2015). For potential spatial variation, we used a randomized block design. A total of six blocks were set up, and hence each of the six treatments was replicated six times ( $6 \times 6 = 36$  pools). Each pool was assigned randomly to a treatment within a block. The five density treatments (excluding the control with no tadpoles; Table 1) represent the minimum design that allows one to measure both inter- and intraspecific competition (see Goldberg & Scheiner, 2001; Juliano, 2010).

We measured larval performance in the form of time to, mass at, and survival to metamorphosis. Once we observed the first tadpoles approaching metamorphosis (detection of two fully developed hind limbs), we then checked the pools every day. As soon as tadpoles reached the stage of partially developed forelimbs (Gosner stage 42), they were removed from the mesocosm and brought to the lab. Taking them out prior to full metamorphosis prevented escapes from the tubs. When metamorphosis occurred (full absorption of tail—Gosner stage 46), the date was documented and the metamorphs were weighed, and then released back to their original site. During the few days in which tadpoles were kept in the lab until completion to metamorphosis, some unexplained mortality occurred. Since we saw no such mortality in the mesocosms, we assumed that this mortality was related to the transfer to the lab or conditions in the lab, and that these tadpoles would have metamorphosed normally at the experimental field. Therefore, since they were collected very shortly before metamorphosis, they were included in the analyses for survival to and time to metamorphosis. A one-way ANOVA indicated that laboratory mortality of tadpoles ( $F_{4,22} = 0.714$ ,  $P = 0.591$ ) was not different among the treatments. Analyses of survival and time to metamorphosis did not change when these larvae were not used in the analysis. For each dead individual, an estimation of time to metamorphosis was made by extrapolation of remaining time based on tail length at capture. Using the tail length recorded at day of death, we estimated the Gosner stage of each individual at day of death and calculated the time remaining to metamorphosis, where remaining time for individuals with full forelegs and full tails was 7 additional days.

After anuran introduction, generally every two weeks (until all tadpoles had metamorphosed from the

majority of the pools and only a few were left in the rest of the pools), we measured the following parameters in each of the pools: pH, temperature, and conductivity (HANNA instruments, model # HI9813-6). We also monitored invertebrate abundance (insects and crustaceans). We took invertebrate samples by taking eight random dips per tub using a 400 ml dipper, filtering the eight dips together for a combined single sample per mesocosm through an aquarium net (mesh size 250  $\mu\text{m}$ ), and then preserving the sample in  $\sim 90\%$  ethanol. Invertebrates were identified and counted under a dissecting microscope (Stereomicroscope SZX-ILLB200, Olympus Corporation, Japan).

### Statistical analysis

Anuran larval performance data were analyzed as an analysis of covariance using SPSS software, where the density treatment was the fixed factor, and temperature was used as a covariate. Temperature is likely to affect tadpole development as has been shown previously for *H. savignyi* (Blaustein et al., 1999). ANCOVA was carried out for each species separately. The factor (density treatment) had three levels—low density (20 conspecifics), high density (40 conspecifics), and combined (20 conspecific + 20 competing species). The dependent variables were time to metamorphosis, mass at metamorphosis, and proportion surviving to metamorphosis, with each variable being calculated as a mean per mesocosm. The temperature value used was the mean from all 9 sampling dates, for each pool. If the covariate was found to not be statistically significant, it was removed from the analysis. Temperatures among mesocosms varied spatially ( $\sim 4^\circ\text{C}$  range on a given date) because of heterogeneity of shade by pine trees (*Pinus halepensis* Mill). Temperature also increased as the season progressed. For example, temperatures, taken in early afternoon, averaged  $11.33^\circ\text{C}$  (SE 0.18) during 15 January (a pre-anuran introduction date),  $15.94^\circ\text{C}$  (SE: 0.21) on 18 March, and  $27.31^\circ\text{C}$  (SE 0.32) on 2 July. Because block was not statistically significant in any of the analyses, it was removed from all analyses and absorbed into the error term. Data for proportion surviving to metamorphosis were arcsine square root transformed before analysis. Mass to metamorphosis data were square root transformed in order to meet the assumptions of ANCOVA. Time to metamorphosis data were natural log-transformed for *H. savignyi*. If

the covariate was found to be significant, we used regression analysis to determine whether it had a positive or a negative effect on the dependent variable. When density treatment was significant, we used Tukey's HSD post-hoc test to look for differences between the different treatments. We used a two-tailed alpha level of 0.05 although, because of *a priori* hypotheses, one-tailed tests would also be considered legitimate.

We used a repeated measures ANOVA to determine whether the total invertebrate richness and abundance of various invertebrates in the experimental pools were affected by time and treatment. Assumptions of sphericity were met.

## Results

### *Bufo viridis* larval performance

*Bufo viridis* mass at metamorphosis did not statistically differ between density treatments (ANOVA:  $P = 0.19$ ; Table 2; Fig. 1a), nor was it correlated to temperature (regression:  $F_{1,13} = 1.94$ ,  $P = 0.187$ ,  $R^2 = 0.13$ ; Fig. 1b). Time to metamorphosis was not affected by density (ANCOVA:  $P = 0.687$ ; Table 2; Fig. 1c) but was significantly correlated to temperature (ANCOVA:  $P = 0.002$ ; Table 2). Regression analysis indicated a negative relationship between temperature and time to metamorphosis (regression:  $F_{1,14} = 17.63$ ,  $P = 0.001$ ,  $R^2 = 0.56$ ; Fig. 1d). Survivorship was not affected by treatment (ANCOVA:  $P = 0.518$ ; Table 2; Fig. 1e) but was correlated with temperature (ANCOVA:  $P = 0.02$ ; Table 2).

Regression showed a positive relationship between temperature and survivorship (regression:  $F_{1,13} = 8.57$ ,  $P = 0.01$ ,  $R^2 = 0.40$ ; Fig. 1f).

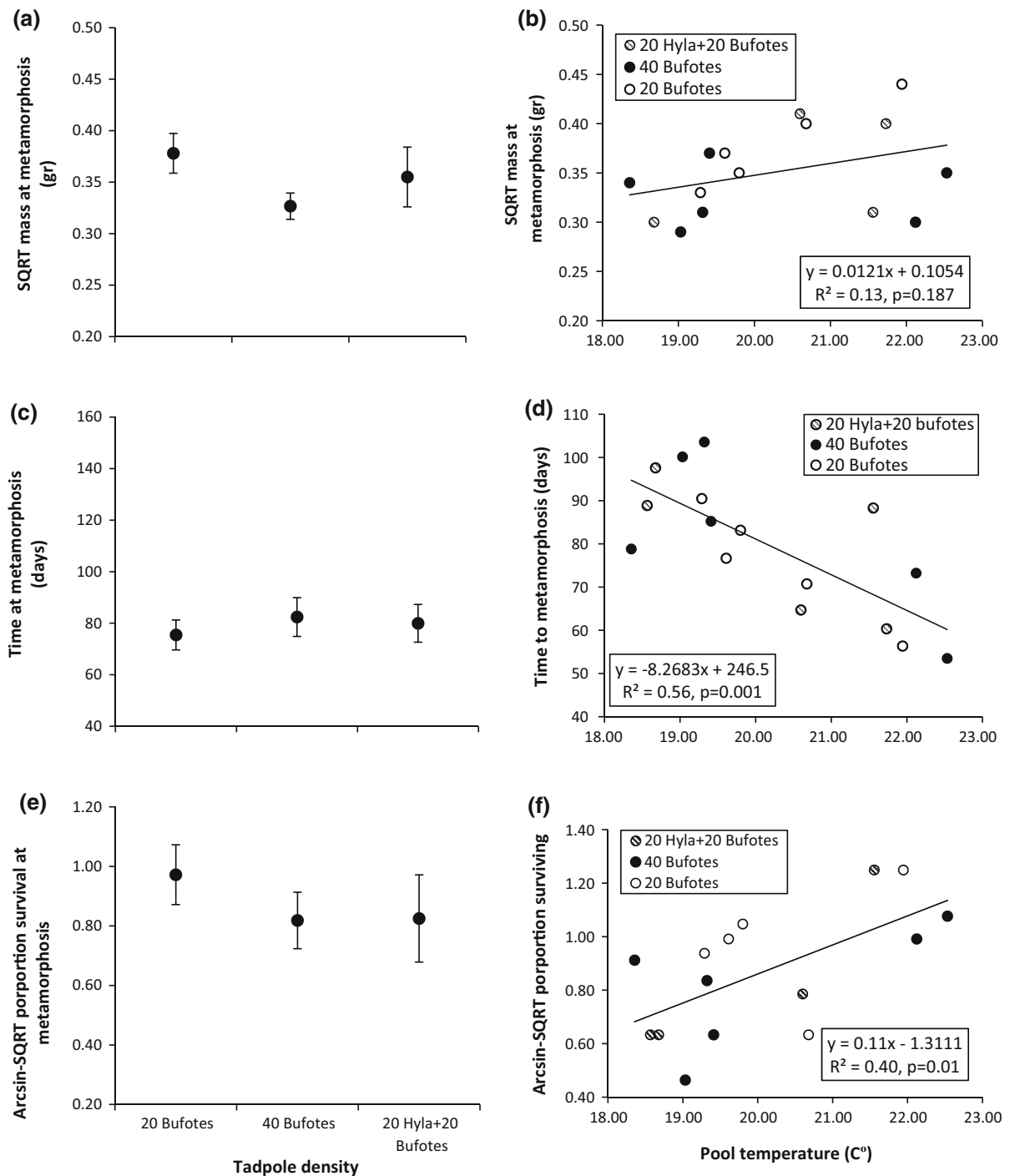
### *Hyla savignyi* larval Performance

Mass at metamorphosis was significantly affected by higher conspecific density (ANOVA:  $P = 0.04$ ; Table 2; Fig. 2a). Tukey's HSD post-hoc test indicated a strong intraspecific effect. Metamorphs were significantly lighter in the high conspecific density treatment (Tukey's HSD:  $P = 0.05$ ; Fig. 2a). However, no difference was found between low density and combined species high density treatment ( $P = 0.984$ ), nor was there a statistically significant difference between conspecific high density and combined species high density ( $P = 0.105$ ). Temperature was not correlated with mass at metamorphosis (regression:  $F_{1,13} = 1.97$ ,  $P = 0.184$ ,  $R^2 = 0.13$ ; Fig. 2b). Effects of density on time to metamorphosis was marginally significant (ANOVA:  $P = 0.05$ ; Fig. 2c). Tukey's HSD post-hoc test indicates a trend of longer time to metamorphosis in the high *Hyla* density treatment compared to the low *Hyla* density treatment, but this difference was not statistically significant based on a two-tailed test (Tukey's HSD:  $P = 0.06$ ; Fig. 2c). No correlation was found with temperature (regression:  $F_{1,13} = 0.83$ ,  $P = 0.378$ ,  $R^2 = 0.06$ ; Fig. 2d). The proportion surviving tended to be lower in the high *Hyla* density and in the combined *Hyla-Bufo* treatment, but these differences were not statistically significant (ANOVA:  $F_{2,12} = 2.18$ ,  $P = 0.15$ ; Fig. 2e). Temperature was not correlated to survivorship (regression:  $F_{1,13} = 0.67$ ,  $P = 0.43$ ,  $R^2 = 0.05$ ; Fig. 2f).

**Table 2** Analysis of covariance or analysis of variance for larval performance of *Hyla savignyi* and *Bufo viridis*

	Mass at metamorphosis			Time to metamorphosis			Survival to metamorphosis		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
<i>Bufo</i>									
Treatment	2, 12	1.94	0.19	2, 12	0.39	0.69	2, 11	0.7	0.52
Temperature	–	–	–	1, 12	15.79	0.002	1, 11	7.63	0.02
<i>Hyla</i>									
Treatment	2, 12	4.10	0.04	2, 12	3.85	0.05	2, 12	2.18	0.15
Temperature	–	–	–	–	–	–	–	–	–

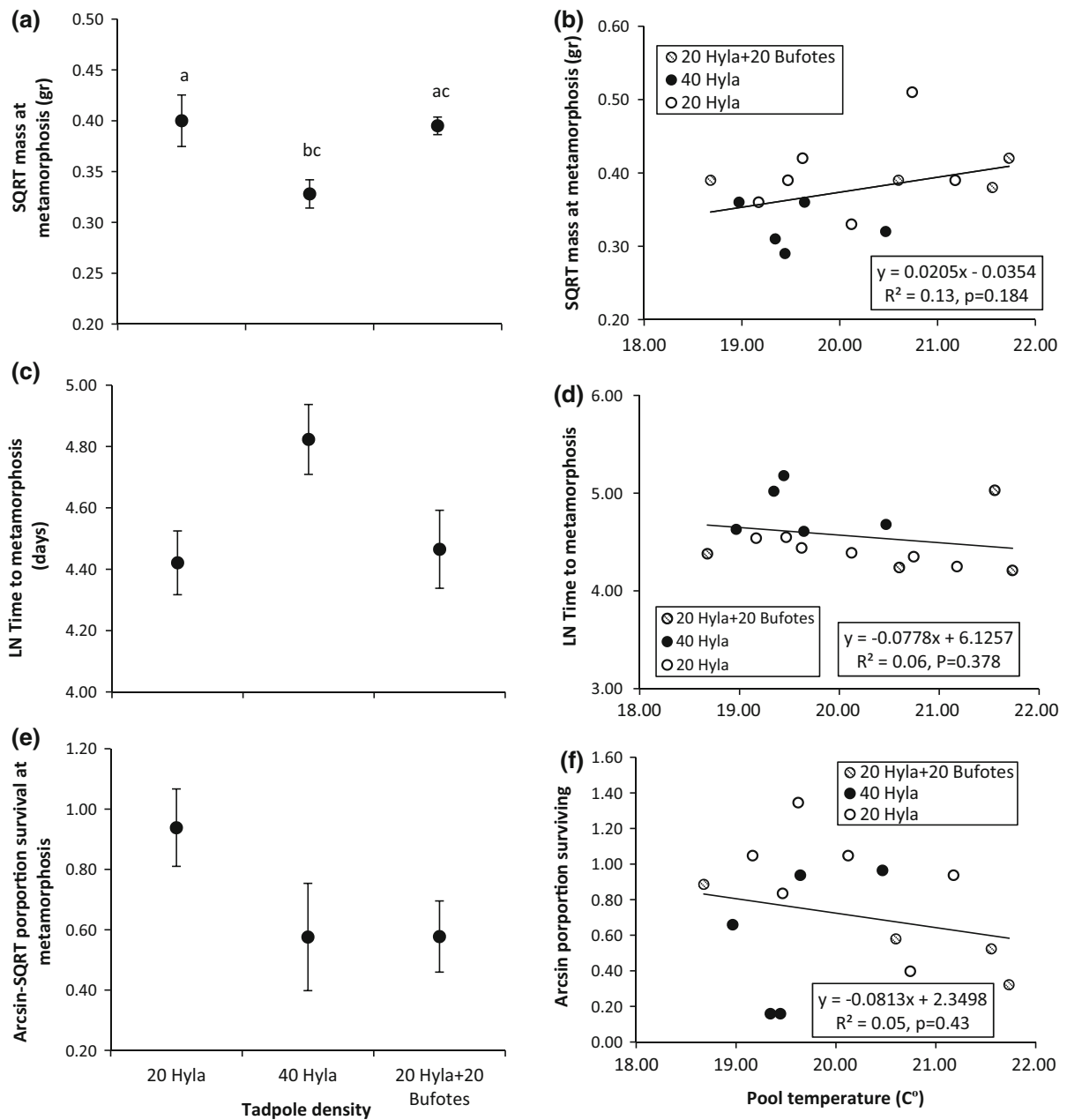
Dashed lines signifies that the covariate was not significant and removed from the analysis. *P* values are from two-tailed tests



**Fig. 1** *Bufotes viridis* larval performance across three density treatments (20 conspecifics, 40 conspecifics and 20 conspecifics + 20 *Hyla savignyi*): **a** mass at metamorphosis (square root transformed) and **b** relationship between mass at metamorphosis and pool temperature; **c** time to metamorphosis and **d** relationship between time to metamorphosis and pool temperature; **e** proportion survival (arcsin-square root

transformed) at metamorphosis and **f** relationship between proportion surviving and pool temperature. None of the three treatments for the three dependent variables were statistically significantly different. Error bars in the graphs on the left side are  $\pm 1$  SE. Number of replicate mesocosms is six for all treatments





**Fig. 2** *Hyla savignyi* larval performance across three density treatments (20 conspecific, 40 conspecific and 20 conspecific + 20 *B. viridis*): **a** mass at metamorphosis (square root transformed) and **b** relationship between mass at metamorphosis and pool temperature; **c** time to metamorphosis (natural log-transformed) and **d** relationship between time to metamorphosis and pool temperature; **e** proportion survival (arcsin-square root

transformed) at metamorphosis and **f** relationship between proportion surviving and pool temperature. Error bars in the graphs on the left side are  $\pm 1$  SE. Number of replicate mesocosms is six for all treatments. Different letters on the left-sided graphs above means signify statistically significant differences by Tukey's HSD test

## Invertebrates

No abundance of individual invertebrate taxa that were counted—mosquitoes (*Culiseta longiareolata*, *Culex* spp), chironomids, ceratopogonids, cladocerans (*Moina*, *Ceriodaphnia*, *Daphnia*, *Alona*), cyclopoid copepods, calanoid copepods, and ostracods (*Cypris* sp. plus *Potomocypris* sp.)—showed any statistically significant treatment effects ( $P > 0.05$  for all taxa). Invertebrate taxon richness increased over time (Wilk's Lambda = 0.16,  $F_{3,69} = 42.86$ ,  $P < 0.001$ ) (Fig. 3), but invertebrate richness was not affected by treatment ( $F_{5,27} = 0.82$ ,  $P = 0.55$ ) or by treatment  $\times$  time interaction (Wilk's Lambda = 0.52,  $F_{15,69} = 1.24$ ,  $P = .26$ ).

## Discussion

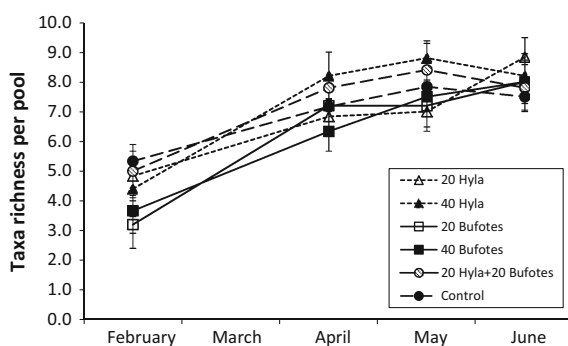
Anurans in temporary pools develop in unpredictable environments, and many studies have shown that increased intraspecific density causes time to metamorphosis to be longer, mass at metamorphosis to be smaller, and growth rate to be slower (reviewed in Wells, 2010). Few studies have used replacement design experiments to simultaneously compare intra- and interspecific competition (Juliano, 2010). Our results indicate that *B. viridis* tadpoles were neither affected by intra- nor interspecific competition. This is in contrast to other studies for *B. viridis* (and other Bufonidae species) where *Bufotes* intraspecific competition was demonstrated (Blaustein & Margalit, 1996; Katzmann et al., 2003). It is possible that the

amount of organic matter that we added (*Bromus sterilis*) combined with the very heavy allochthonous input of organic matter, in particular pine pollen, which may be highly nutritious to some but not all anuran tadpoles (Wagner, 1986; Britson & Kissell, 1996), did not provide a food-limited environment for *B. viridis*. Intraspecific competition of *B. viridis* may also have been observed had we allowed experimental pools to dry naturally (which would likely have increased individual mortality to endangered species) rather than maintain constant water volume. However, some pools containing both these species do not dry out until late summer (L. Blaustein, personal observations).

We found, as expected, that temperature had a positive correlation with *B. viridis* survival and a negative correlation with *B. viridis* time to metamorphosis. These results are consistent with other studies that have also shown that temperature influences anuran growth, development, and metamorphosis (Smith-Gill & Berven, 1979; Blaustein et al., 1999; Alvarez & Nieceza, 2002). Higher temperatures can also cause increased desiccation rates, which often induces tadpoles to metamorphose faster before the pool dries completely (Crump, 1989).

Larval performance of *H. savignyi* tadpoles was significantly influenced by larval density. Mass at metamorphosis of *H. savignyi* was significantly reduced at high conspecific density. Time to metamorphosis also tended to be higher for the higher density. These findings are consistent with our previous study, showing that mass at metamorphosis of *H. savignyi* larvae is lower when density of conspecific is higher (Stein & Blaustein, 2015). The design of the study does not allow for differentiating whether the differences were due to exploitative competition or to interference competition. Interference competition—both intraspecific and interspecific—may also be density-dependent and the mechanisms in other studies have been hypothesized to be due to various factors including chemical cues, mechanical cues, or release of growth inhibiting organisms (e.g., Bardsley & Beebe, 2001).

*Hyla savignyi* tadpoles at the low density were significantly larger than *H. savignyi* tadpoles at the high density, but *H. savignyi* tadpoles were not larger when combined with *B. viridis*, which also had high anuran tadpole density. This implies that for *H. savignyi*, conspecific competitors have a greater



**Fig. 3** Invertebrate taxa richness for each treatment combination across the experiment. In all cases, mean values are calculated based on six replicate pools and error bars are  $\pm 1$  SE. Number of replicate mesocosms is six for all treatments

impact than *B. viridis* competitors. Our results ultimately show that for this study specifically, intraspecific competition is stronger than interspecific competition.

Surprisingly, none of the anuran treatments compared to the control significantly affected invertebrate abundance or taxon richness (Fig. 3). Mosquito oviposition site selection has been known to be negatively affected by amphibian larval presence, e.g., in *B. viridis* (Blaustein & Kotler, 1993), *H. savignyi* (L. Blaustein, unpublished data), and other anuran larvae (Mokany & Shine, 2003). Other habitat traits apart from tadpole density might have affected invertebrate abundance or richness (Eitam et al., 2004) though this was not investigated here. As also suggested for the lack of interspecific competition among the two anuran species, the lack of a negative effect of these anuran tadpoles on invertebrate community structure could be due to the allochthonous input of pine pollen.

There are few studies which have been explicitly designed to test effects of interspecific and intraspecific competition. By following a replacement experimental design, we could test density-dependent competition between two anuran species. A stronger effect of intraspecific competition, compared to interspecific competition in *H. savignyi* suggests a stable coexistence between species. Microhabitat selection can also help coexistence among larval *H. savignyi* and *B. viridis*. Preliminary observations indicate that *H. savignyi* larvae in natural earthen pools utilize vegetated areas within the pool (M. Stein & L. Blaustein, personal observations), while *B. viridis* larvae are found more in the open waters (Blaustein & Margalit, 1995). Future studies should also test for effects of variation in food availability (e.g., high vs low food) on the different densities used in this experiment. Such studies about relations between species and their coexistence, along with understanding the full spatial and temporal distribution of each species, can contribute to the field of conservation management (e.g., Parris & Semlitsch, 1998).

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