CrossMark

HIGHLIGHTED STUDENT RESEARCH

# Isocline analysis of competition predicts stable coexistence of two amphibians

**Andrea Gazzola · Josh Van Buskirk**

**Abstract** We investigated the interaction between larvae of two anuran amphibian species (*Rana temporaria* and *Bufo bufo*) to test models of two-species competition. The study had a response surface experimental design with four replicates, each consisting of 24 density combinations. Larval performance—and, by assumption, change in population size—was defined by a linear combination of survival, growth, and development. We fit six competition models from the literature and discovered that density dependence was strongly non-linear, with the highest support for the Hassel–Comins model. *Rana temporaria* was competitively superior to *B. bufo*; the impacts of both species on growth and development were about five- to tenfold greater than those on survival. Isocline analysis predicted a stable configuration, which agrees with the observation that these two species are syntopic in nature. The results of this study confirm competition theory by identifying a model structure that agrees with data and making predictions that are broadly supportive of the observations.

Communicated by Steven Kohler.

A. Gazzola · J. Van Buskirk (✉)
Institute of Evolutionary Biology and Environmental Studies, University of Zürich, Winterthurerstrasse 190, 8057 Zurich, Switzerland
e-mail: josh.vanbuskirk@ieu.uzh.ch

A. Gazzola
Department of Earth and Environmental Sciences, University of Pavia, Pavia, Italy

**Keywords** Amphibian · Coexistence · Competition · Isoclines · Response surface modeling

## Introduction

In a classic study, Ayala et al. (1973) illustrated how interspecific competition models could be tested by fitting them to experimental data. Nevertheless, the great majority of experiments on competition have not been designed to address theory directly. While much experimental and comparative evidence demonstrates the importance of competition in diverse communities (Connell 1983; Schoener 1983; Simberloff and Dayan 1991; Wootton 1994; Kaplan and Denno 2007; Hibbing et al. 2010), the data from most studies cannot be used to test models of interspecific competition (Inouye 1999, 2001). A better relation between experimental results and theory would allow the validity of existing models, including their structure, assumptions, and predictions, to be tested. Ultimately, direct comparisons of theory and data might confirm the adequacy of existing theory (Vandermeer 1969) or justify developing more sophisticated models (Ayala et al. 1973).

Here we describe a model-based approach inspired by Ayala et al. (1973) and Inouye (2001) to investigate competition between two species of amphibian, *Rana temporaria* and *Bufo bufo*. These two anurans occupy freshwater wetlands across much of Western Eurasia during the larval stage of their life cycle and are usually found in the terrestrial environment during the juvenile and adult stages. The species coexist both at local spatial scales within breeding sites (Fig. 1) and at larger landscape scales (Nöllert and Nöllert 1992; Babik and Rafinski 2001; Van Buskirk 2005). Therefore, any successful model of the interaction between *R. temporaria* and *B. bufo* must predict that they
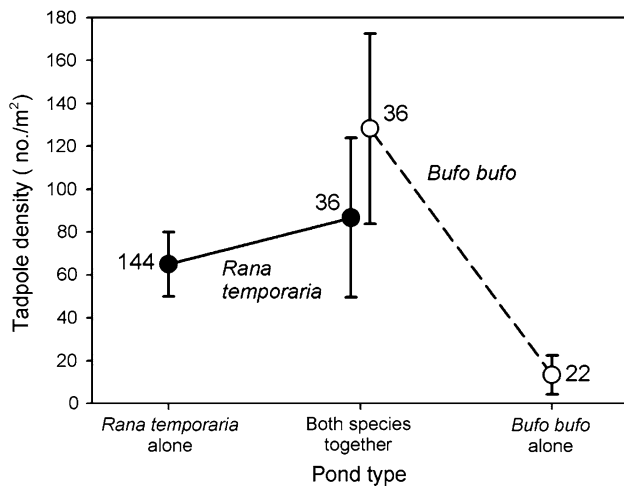
**Fig. 1** Average densities of *Rana temporaria* and *Bufo bufo* tadpoles in pond samples collected mid-way through the larval period of both species, near Zurich, Switzerland. Data are from 79 ponds that were sampled on 321 occasions between 1997 and 2003 (each pond was sampled an average of 4.1 years). Sample sizes are the number of pond-sampling occasions. Field methods are as described by Van Buskirk (2005). Both species occurred at a higher density when they occurred together than when each occurred alone. The two species were not associated in their presence/absence across all years ($G = 0.41$, $P = 0.52$, $df = 1$, $N = 79$ ponds; Sokal and Rohlf 1981). Nevertheless, larval densities of *R. temporaria* and *B. bufo* were somewhat positively correlated among ponds ($r = 0.17$, $P = 0.13$, $N = 79$ ponds) and among years within ponds ($r = 0.06$, $N = 14$ ponds with at least 4 years of data and both species present)

coexist stably. Because tadpoles of these species occur at relatively high densities in discrete ponds, it is reasonable to expect that interactions are especially severe during the larval stage (Wilbur 1980; Pechmann 1995; Altwegg 2003). Therefore, our experiment was designed to estimate competition among tadpoles within and between species. We first determined which of several competition models is the most appropriate to describe the interaction between *R. temporaria* and *B. bufo*, and then asked whether the estimated parameters predicted stable coexistence.

**Methods**

The experiment included four replicates, each consisting of 24 density combinations of *R. temporaria* and *B. bufo*. For each species, the design included a 4 × 5 complete factorial design (5, 10, 20, and 40 individuals of the target species, crossed with 0, 5, 10, 20, and 40 individuals of the other species). The treatment with zero individuals of both species was not included. One replicate of the treatment with ten *B. bufo* and zero *R. temporaria* was lost.

The experiment was conducted in ninety-six 80-l plastic mesocosms (0.28 m²) placed outdoors in a field located

on the campus of the University of Zurich, Switzerland. They were arranged in the field within two spatial blocks, with two replicates of each treatment per block. Two weeks prior to initiation of the experiment, we filled each mesocosm with tap water to which we added 40 g dried leaf litter and 2 g of commercial rabbit food; we then covered the mesocosms with lids made of 37 % shade cloth. Many features of natural ponds are not present in mesocosms established in this way, and these conditions might influence the outcome of interspecific competition (Wilbur 1987; Dunson and Travis 1991). However, the mesocosms described here supported diverse communities of microorganisms, zooplankton, and periphyton and provided sufficient food for the survival and growth of anuran larvae.

The tadpoles came from five clutches of each species, collected from a pond 30 km north of Zurich, Switzerland. The experiment began on 5 April 2012, when the tadpoles were 6–7 days old, weighed $25.4 \pm 6.6$ mg (mean ± standard deviation; *R. temporaria*) and $9.5 \pm 3.0$ mg (*B. bufo*), and were at Gosner (1960) stage 25. Tadpoles were randomly chosen from different clutches in equal proportions and groups were assigned to mesocosms also at random. The experiment continued until 8 May, at which point all tadpoles were removed and we recorded the number of survivors of each species, along with their mass and developmental stage. In mesocosms with more than ten survivors, we assessed Gosner stage in a randomly chosen sample of ten individuals of each species. The staged tadpoles were preserved in 10 % formalin.

Statistical analyses

First, we compared the ability of each of six competition models to describe the interaction between *R. temporaria* and *B. bufo* tadpoles. The models [listed in Electronic Supplementary Material (ESM) Table A1] consist of difference equations that describe how the number of individuals of a particular species present in the next time-step ($X_{t+1}$) change with the numbers of individuals of the two competing species present in the current time-step ($X_t$ and $Y_t$). Parameters of the models describe the population growth rates and carrying capacities of both species, competition between species, and the functional form of density dependence. Data can be used to differentiate these models by fitting the two surfaces that they describe: $X_{t+1}$ as a function of $X_t$ and $Y_t$, and the corresponding surface for $Y_{t+1}$ (Ayala et al. 1973; Inouye 2001). Changes in population size could not be determined in our study due to the complex life cycles and long generation times of the organisms under study. We therefore assumed that changes in population size are proportional to a composite measure of individual fitness, as defined below. The coefficients that scale individual fitness to change in population size cannot

be estimated from our data, and these are integrated into the model parameters for growth rate and carrying capacity; estimates of competition coefficients are unaffected by scaling (Inouye 2001; Hart and Marshall 2012).

"Fitness" was defined as survival to reproduction, which we predicted for each individual in the experiment using data from a different species of frog (*Pseudacris maculata*; Smith 1987). Smith (1987) estimated that survival to reproduction at age 2 years was related to size at metamorphosis (SM) and date of metamorphosis (DM) in the following way: logit[survival to age 2] = −1.16 + 0.601 × SM − 0.198 × DM. Both SM and DM are standardized [mean = 0, standard deviation (SD) = 1]. The intercept scales indicate mean survival which is therefore arbitrary. We substituted final mass for SM and final stage for DM, both standardized so that the units of measurement were the same as those in Smith's study. Individual fitness was estimated for each tadpole in the experiment; those that did not survive were assigned a value of 0. The exact coefficients are probably different in our study organisms than in *P. maculata*, but we are confident of the general form of this relationship because (1) coefficients relating size and age at emergence with 1-year survival in European water frogs (Altwegg and Reyer 2003) are similar to those estimated by Smith (1987) and (2) the link between larval and adult performance has been confirmed in other amphibian species (Berven and Gill 1983; Semlitsch et al. 1988; Berven 1990, 2009; Scott 1994). Nevertheless, we evaluated the sensitivity of our results to the values of the coefficients by exploring the effect of increasing or decreasing each coefficient by 20 % (ESM Fig. S2). These manipulations never affected the general configuration of the isoclines or caused more than a 2 % change in the predicted equilibrium densities of the two species, calculated as described below.

Using nonlinear least squares model fitting, we fit the six competition models onto the mean values of relative fitness at the level of the mesocosm, ignoring spatial blocks. Models were compared using a small-sample version of Akaike's information criterion (AICc; Burnham and Anderson 1998). The best model for both species was that of Hassell and Comins (1976). For *R. temporaria*, this model was 15 AICc units better than the next-best model, and for *B. bufo* it was 3 AICc units better (see ESM Table S1). The Hassel–Comins model fit the data reasonably well in both species (ESM Fig. S2). Therefore, we hereafter consider only the Hassel–Comins competition model because this model was well-supported by the data and has been successfully applied elsewhere (e.g., Inouye 1999). The modified model was

$$w = X \times \lambda \times [1 + c \times (X + \beta \times Y)]^{-b}, \quad (1)$$

where $w$ = relative fitness (=fitness/fitness of species × averaged over all treatments), $X$ and $Y$ are the numbers of conspecific and heterospecific tadpoles entering the experiment, respectively, $\lambda$ and $c$ are parameters related to population growth and carrying capacity, respectively, $\beta$ is the competitive effect of species Y on species X, and $b$ controls the functional form of density dependence.

The probable outcome of competition in this system was evaluated in several ways. As shown by Hassell and Comins (1976), coexistence is possible when the product of the two competition coefficients is <1. Also, the zero isocline for species A (plotted on the horizontal axis) must be steeper than the isocline for species B near their point of intersection (Fig. 1 in Hassell and Comins 1976). Because we do not know how population growth scales with fitness, we drew what we call "mean-fitness isoclines" connecting all points which predicted $w = 1$. The intersect of the isoclines is the point at which individuals of both species have equal relative fitnesses. Mean-fitness isoclines correspond to zero-growth isoclines only if the population sizes of the two species remain constant when individuals have average fitness (i.e., only if $R_0 = 1$ when mean $w = 1$). More often, the transition between population growth and decline will occur above or below the mean-fitness isoclines. This will influence their point(s) of intersection, but should not affect the general configuration of isoclines. Note that zero-growth isoclines are linear in the Hassell–Comins model, but mean-fitness isoclines are not because increasing conspecific density has both positive and negative effects; isoclines become linear after division on both sides by $X$ (Eq. 1). We explored the dynamical behavior of the system in two ways. First, we superimposed "displacement vectors" onto the phase diagram (Ayala et al. 1973), representing changes in population size between time-steps. As we did not measure population change in our study, the length of displacement vectors in each direction was proportional to $(w − 1)$. This again assumes that the population declines when $w < 1$ and increases when $w > 1$. Vectors were calculated separately for the two species and then summed to produce the displacement vector. We also simulated dynamics over 1,000 generations under the same assumption on population change, starting at all two-species combinations of density between 1 and 40 at intervals of 1.

Next we explored the influence of conspecific and heterospecific density on the separate components of individual performance assessed at the end of the experiment: survival, mass, and developmental stage. Using mixed-effects linear models on mean values at the level of the mesocosm, we regressed each component against $\log_{10}$-transformed numbers of *Rana* and *Bufo* + 1, and their interaction. Models included random effects for variation between blocks and heterogeneity between blocks in the effects of *Rana* density and *Bufo* density. In one set of models, performance components were transformed to improve the distributions of residuals (arcsine-square root-transformation
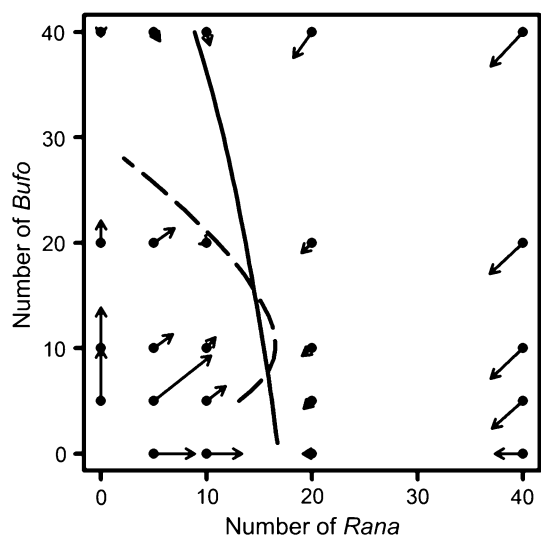
**Fig. 2** Mean-fitness isoclines of the Hassell and Comins (1976) model estimated for competition between tadpoles of *Rana temporaria* (*solid line*) and *Bufo bufo* (*dashed line*). Isoclines occur when relative fitness (*w*) is 1. *Filled symbols* The 24 density combinations in the experimental design, *axes* represent the number of hatchling tadpoles of the two species added to each 0.28-m² mesocosm, *arrows* show the direction and relative magnitude of change that the system is predicted to experience in the next time-step under the assumption that population size increases when *w* > 1, *arrow lengths* are proportional to (*w* − 1)

for survival, ln-transformation for mass, and no transformation for stage). We used these models to evaluate significance, which was determined by inspecting profile likelihood confidence intervals (CIs) (Venzon and Moolgavkar 1988). In a second set of models, performance traits were not transformed and the slopes were scaled by the pooled individual-level SD of the trait. These models were used for evaluating the magnitude of density effects because they produced estimates in comparable and easily interpretable units (SD units per ten-fold change in density). All analyses were implemented in R 3.1.2, using nls and lme4 R Core Team 2014).

## Results

Competition was strongly asymmetric. The competition coefficient representing the per capita effect of *R. temporaria* on *B. bufo* (0.218, 95 % CI 0.165−0.279) was nearly fivefold greater than that of *B. bufo* on *R. temporaria* (0.045, 95 % CI 0.027−0.064). The fitted models suggest that the two species should coexist. First, the product of the competition coefficients was well below 1, a condition for coexistence in the Hassell–Comins model (Hassell and Comins 1976). The mean-fitness isoclines intersected at two points (Fig. 2), with the upper intersection

characterized by relatively steep mean-fitness isoclines for both species in a configuration that implies stability, and the lower intersection implying damped cycles in the abundance of the two species. Displacement vectors originating at each of the 24 initial density combinations pointed towards the intersections of the isoclines (Fig. 2). This is a necessary consequence of high individual fitness at low density and lower-than-average fitness at high density, but the specific arrangement of vectors implies that the system is strongly attracted to the upper intersection. Indeed, simulations confirmed that the system always converges upon the upper intersection, at 14.5 *R. temporaria* and 15.7 *B. bufo*, assuming that change in population size from one time interval to the next is proportional to (*w* − 1).

Analysis of the separate performance measures indicated that competitive effects were stronger on tadpole size and development than on survival and confirmed that the per capita impact of *R. temporaria* was usually higher than that of *B. bufo*. Tests of significance on the left side of Table 1 show that, for both species, mass and stage were negatively influenced by increases in both conspecific and heterospecific density; survival was never significantly affected by density and interactive effects were weak (ESM Fig. S3). The right side of Table 1 confirms that density-dependent declines in growth and development were about four to tenfold greater than the declines in survival. A tenfold increase in density caused a decline in survival of roughly 0.0–0.3 SD units, a reduction in mass of 1.6–3.9 SD units, and a delay in development of 0.2–2.0 SD units. Competition affected the mass of *R. temporaria* at least twice as strongly as it affected development rate, and the impact of conspecific density was more than double that of heterospecific density. For *B. bufo*, mass also responded more strongly than stage, and the impacts of conspecific and heterospecific competitors were similar.

## Discussion

The observation that natural populations of *Rana temporaria* and *Bufo bufo* coexist during larval and adult stages implies that their interaction is stable. A variety of models have been proposed to describe the outcome of competition among two or more species and specify conditions under which coexistence is possible. The results of this study favor non-linear rather than linear forms of density dependence and specifically support the model of Hassell and Comins (1976), especially for *R. temporaria*. Many studies agree that linear density dependence, as represented by the Lotka–Volterra model, does not match empirical results (e.g., Wilbur 1977; Goldberg and Landa 1991; Hart and Marshall 2012). When data are compared explicitly with competition models, the models of Ricker (1954) or

**Table 1** Two assessments of the competitive effects of *Rana temporaria* and *Bufo bufo* tadpoles on survival, body size, and developmental stage measured on the last day of the experiment

| Source | Original/transformed units | | | Standard deviation units | | |
|---|---|---|---|---|---|---|
| | Survival | Mass | Stage | Survival | Mass | Stage |
| Responding species: *Rana temporaria* | | | | | | |
| *Rana* density | −0.066 | −0.934** | −3.048** | −0.316 | −3.839 | −1.864 |
| *Bufo* density | −0.040 | −0.295** | −0.305 | −0.235 | −1.581 | −0.186 |
| *Rana* × *Bufo* | 0.017 | 0.145 | 0.038 | 0.103 | 0.902 | 0.023 |
| Responding species: *Bufo bufo* | | | | | | |
| *Rana* density | −0.141 | −0.629** | −2.844* | −0.239 | −3.937 | −2.022 |
| *Bufo* density | −0.058 | −0.550** | −1.951* | −0.031 | −3.499 | −1.387 |
| *Rana* × *Bufo* | 0.076 | 0.147 | 0.757 | 0.124 | 1.546 | 0.539 |

Both methods estimate the effects of the $\log_{10}$-transformed density of conspecific and heterospecific tadpoles; slopes therefore represent the change in response with a tenfold increase in competitor density. All models include random effects for differences between blocks and heterogeneity between blocks in the effects of *Rana* density and *Bufo* density, but these effects were never significant in likelihood-ratio tests. The left side of the table is appropriate for evaluating significance: survival was arcsine-square root-transformed, mass was ln-transformed, and stage was untransformed. The right side of the table is appropriate for comparing effect sizes: responses were untransformed and slopes were rescaled to units of standard deviation among individual tadpoles pooled across treatments

Significant at * $P < 0.05$ and ** $P < 0.01$ judged from the profile likelihood confidence intervals

Hassell and Comins (1976)—with the parameter $b \geq 1$—are often well supported (Inouye 1999; Paini et al. 2008; Hart and Marshall 2012; Kim et al. 2013).

Given an appropriate structure of the underlying competition model, our experiment then estimated values of its parameters and suggested dynamic behavior of the system. The competition coefficients suggest that the interaction between tadpoles of the two species was asymmetric, with *R. temporaria* roughly fivefold stronger than *B. bufo* in terms of interspecific competition and twofold stronger in terms of intraspecific effect. Although asymmetric competition can cause competitive exclusion of a competitively inferior species (May 1975; Hassell and Comins 1976), this was not predicted in our system because interspecific competition was relatively weak in both directions (both βs well below 1). This result agrees with those reported in a sizeable portion of the relevant literature, indicating that asymmetric competition among coexisting species is widespread (Lawton and Hassell 1981; Connell 1983; Schoener 1983; Kaplan and Denno 2007), including in amphibians (Morin and Johnson 1988; Pearman 2002; Richter-Boix et al. 2004; Behm et al. 2013). The mechanism generating asymmetry in this case might be related to the difference in body size, as has been noted elsewhere (Richter-Boix et al. 2004). *Rana temporaria* tadpoles were about 2.5-fold larger than those of *B. bufo* at hatching and remained so throughout the experiment; the former therefore may have consumed more resources per capita. An alternative explanation is that the two species have settled upon different evolutionary solutions to the trade-off between competitive ability and resistance to predators. This trade-off, observed in a wide variety of taxa, arises because traits that enable success in

competitive interactions also confer high mortality from predators (Woodward 1983; McPeek 1990; Smith and Van Buskirk 1995; Wellborn 2002; Yoshida et al. 2004). Indeed, *B. bufo* tadpoles appear to be relatively weak competitors, and they typically occur in permanent wetlands with high densities of aquatic predators, especially fish (Van Buskirk 2003, 2005).

The locally syntopic occurrence of *R. temporaria* and *B. bufo* across much of Europe and the abundance patterns of larvae in our field sites are mostly consistent with the predictions of theory. Indeed, their completely independent patterns of occurrence imply that the two species pay little attention to each other (Fig. 1). The approximately equal densities of the two species in ponds where they co-occur are also consistent with the model (although this prediction depends on how population growth rate scales with relative fitness). However, the fact that *R. temporaria* and *B. bufo* larval densities were somewhat positively correlated in our field survey seems incompatible with the finding that tadpoles compete strongly. For *B. bufo*, the predicted equilibrium density in the absence of competition was well above the density under coexistence (Fig. 2), but the observed density in ponds without *R. temporaria* competitors was lower (Fig. 1). An obvious explanation is that wetlands vary in overall quality so that both species occur together at higher larval density in sites of higher quality; this produces a positive density correlation despite a negative interspecific interaction (e.g., Gascon 1992; Schmitz and Suttle 2001; Thurnheer and Reyer 2001). More generally, our experimental and field data highlight challenges associated with using non-experimental field data to test predictions on abundance from theory

and experiment (Werner 1998). In our case, it is clear that intra- and interspecific competition among larvae are not the only processes affecting the occurrence and abundance of these two species. Many environmental factors are known to influence amphibian larval abundance (Van Buskirk 2005; Werner et al. 2007a), and processes taking place during the terrestrial stage of the life cycle can influence occurrence and abundance (Joly et al. 2001; Werner et al. 2007b; Hamer and Parris 2011).

One value of linking experimental data and models in the study of species interactions is that explicit predictions on system dynamics can be made and tested. Applying this approach to organisms that have complex life cycles—such as amphibians—is difficult because of the uncertain connection between individual performance and population dynamics. This issue may be overcome by studying model species with relatively accessible life cycles, such as *Drosophila* (Ayala et al. 1973; Prout and McChesney 1985). In non-model organisms, the issue will have to be overcome by studying multiple life stages simultaneously (e.g., Altwegg and Reyer 2003), better connecting the performance of individuals with their contributions to population growth (e.g., Berven 2009), and developing appropriate models of species interactions in multi-stage organisms (e.g., Moll and Brown 2008).

**Author contribution statement**  AG and JVB conceived and designed the experiment. AG performed the experiment. JVB analyzed the data and wrote the manuscript with input from AG.

## References

Altwegg R (2003) Multistage density dependence in an amphibian. Oecologia 136:46–50

Altwegg R, Reyer HU (2003) Patterns of natural selection on size at metamorphosis in water frogs. Evolution 57:872–882

Ayala FJ, Gilpin ME, Ehrenfeld JG (1973) Competition between species: theoretical models and experimental tests. Theor Popul Biol 4:331–356

Babik W, Rafinski J (2001) Amphibian breeding site characteristics in the Western Carpathians, Poland. Herp J 11:41–51

Behm JE, Edmonds DA, Harmon JP, Ives AR (2013) Multilevel statistical models and the analysis of experimental data. Ecology 94:1479–1486

Berven KA (1990) Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). Ecology 71:1599–1608

Berven KA (2009) Density dependence in the terrestrial stage of wood frogs: evidence from a 21-years population study. Copeia 2009:328–338

Berven KA, Gill DE (1983) Interpreting geographic variation in life-history traits. Am Zool 23:85–97

Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer, New York

Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am Nat 122:661–696

Dunson WA, Travis J (1991) The role of abiotic factors in community organization. Am Nat 138:1067–1091

Gascon C (1992) Aquatic predators and tadpole prey in central Amazonia: field data and experimental manipulations. Ecology 73:971–980

Goldberg DE, Landa K (1991) Competitive effect and response: hierarchies and correlated traits in the early stages of competition. J Ecol 79:1013–1030

Gosner K (1960) A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16:183–190

Hamer AJ, Parris KM (2011) Local and landscape determinants of amphibian communities in urban ponds. Ecol Appl 21:378–390

Hart SP, Marshall DJ (2012) Environmental stress, facilitation, competition, and coexistence. Ecology 94:2719–2731

Hassell MP, Comins HN (1976) Discrete time models for two-species competition. Theor Pop Biol 9:202–221

Hibbing ME, Fuqua C, Parsek MR, Peterson SB (2010) Bacterial competition: surviving and thriving in the microbial jungle. Nat Rev Microbiol 8:15–25

Inouye BD (1999) Estimating competition coefficients: strong competition among three species of frugivorous flies. Oecologia 120:588–594

Inouye BD (2001) Response surface experimental designs for investigating interspecific competition. Ecology 82:2696–2706

Joly P, Miaud C, Lehmann A, Grolet O (2001) Habitat matrix effects on pond occupancy in newts. Conservation Biol 15:239–248

Kaplan I, Denno RF (2007) Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. Ecol Lett 10:977–994

Kim TN, Underwood N, Inouye BD (2013) Insect herbivores change the outcome of plant competition through both inter- and intraspecific processes. Ecology 94:1753–1763

Lawton JH, Hassell MP (1981) Asymmetrical competition in insects. Nature 289:793–795

May RM (1975) Stability and complexity in model ecosystems. Princeton University Press, Princeton

McPeek MA (1990) Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. Ecology 71:83–98

Moll JD, Brown JS (2008) Competition and coexistence with multiple life-history stages. Am Nat 171:839–843

Morin PJ, Johnson EA (1988) Experimental studies of asymmetric competition among anurans. Oikos 53:398–407

Nöllert A, Nöllert C (1992) Die Amphibien Europas: Bestimmung, Gefährdung, Schutz. Franckh-Kosmos Verlag, Stuttgart

Paini DR, Funderburk JE, Reitz SR (2008) Competitive exclusion of a worldwide invasive pest by a native: quantifying competition between two phytophagous insects on two host plant species. J Anim Ecol 77:184–190

Pearman PB (2002) Interactions between *Ambystoma* salamander larvae: evidence for competitive asymmetry. Herpetologica 58:156–165

Pechmann JHK (1995) Use of large field enclosures to study the terrestrial ecology of pond-breeding amphibians. Herpetologica 51:434–450

Prout T, McChesney F (1985) Competition among immatures affects their adult fertility: population dynamics. Am Nat 126:521–558

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Richter-Boix A, Llorente GA, Montori A (2004) Responses to competition effects of two anuran tadpoles according to life-history traits. Oikos 106:39–50

Ricker WE (1954) Stock and recruitment. J Fish Res Board Can 11:559–623

Schmitz O, Suttle K (2001) Effects of top predator species on direct and indirect interactions in a food web. Ecology 82:2072–2081

Schoener TW (1983) Field experiments on interspecific competition. Am Nat 122:240–285

Scott DE (1994) The effect of larval density on adult demographic traits in *Ambystoma opacum*. Ecology 75:1383–1396

Semlitsch RD, Scott DE, Pechmann JHK (1988) Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. Ecology 69:184–192

Simberloff D, Dayan T (1991) The guild concept and the structure of ecological communities. Annu Rev Ecol Syst 22:115–143

Smith DC (1987) Adult recruitment in chorus frogs: effects of size and date at metamorphosis. Ecology 68:344–350

Smith DC, Van Buskirk J (1995) Phenotypic design, plasticity, and ecological performance in two tadpole species. Am Nat 145:211–233

Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. W. H. Freeman, San Francisco

Thurnheer S, Reyer HU (2001) Spatial distribution and survival rate of waterfrog tadpoles in relation to biotic and abiotic factors: a field experiment. Amphib Reptil 22:21–32

Van Buskirk J (2003) Habitat partitioning of European and North American pond-breeding frogs and toads. Div Dist 9:399–410

Van Buskirk J (2005) Local and landscape influence on amphibian occurrence and abundance. Ecology 86:1936–1947

Vandermeer JH (1969) The competitive structure of communities: an experimental approach with protozoa. Ecology 50:362–371

Venzon DJ, Moolgavkar SH (1988) A method for computing profile-likelihood based confidence intervals. Appl Stat 37:87–94

Wellborn GA (2002) Trade-off between competitive ability and antipredator adaptation in a freshwater amphipod species complex. Ecology 83:129–136

Werner EE (1998) Ecological experiments and a research program in ecology. In: Resetarits WJ, Bernardo J (eds) Experimental ecology. Oxford University Press, New York, pp 3–26

Werner EE, Skelly DK, Relyea RA, Yurewicz KL (2007a) Amphibian species richness along environmental gradients. Oikos 116:1697–1712

Werner EE, Yurewicz KL, Skelly DK, Relyea RA (2007b) Turnover in an amphibian metacommunity: the role of local and regional factors. Oikos 116:1713–1725

Wilbur HM (1977) Density-dependent aspects of growth and metamorphosis in *Bufo americanus*. Ecology 58:196–200

Wilbur HM (1980) Complex life cycles. Annu Rev Ecol Syst 11:67–93

Wilbur HM (1987) Regulation of structure in complex systems: experimental temporary pond communities. Ecology 68:1437–1452

Woodward BD (1983) Predator–prey interactions and breeding-pond use of temporary-pond species in a desert anuran community. Ecology 64:1549–1555

Wootton JT (1994) The nature and consequences of indirect effects in ecological communities. Annu Rev Ecol Syst 25:443–466

Yoshida T, Hairston NG, Ellner SP (2004) Evolutionary trade-off between defence against grazing and competitive ability in a simple unicellular alga, *Chlorella vulgaris*. Proc R Soc Lond B 271:1947–1953