

Resource limitation alters effects of phenological shifts on inter-specific competition

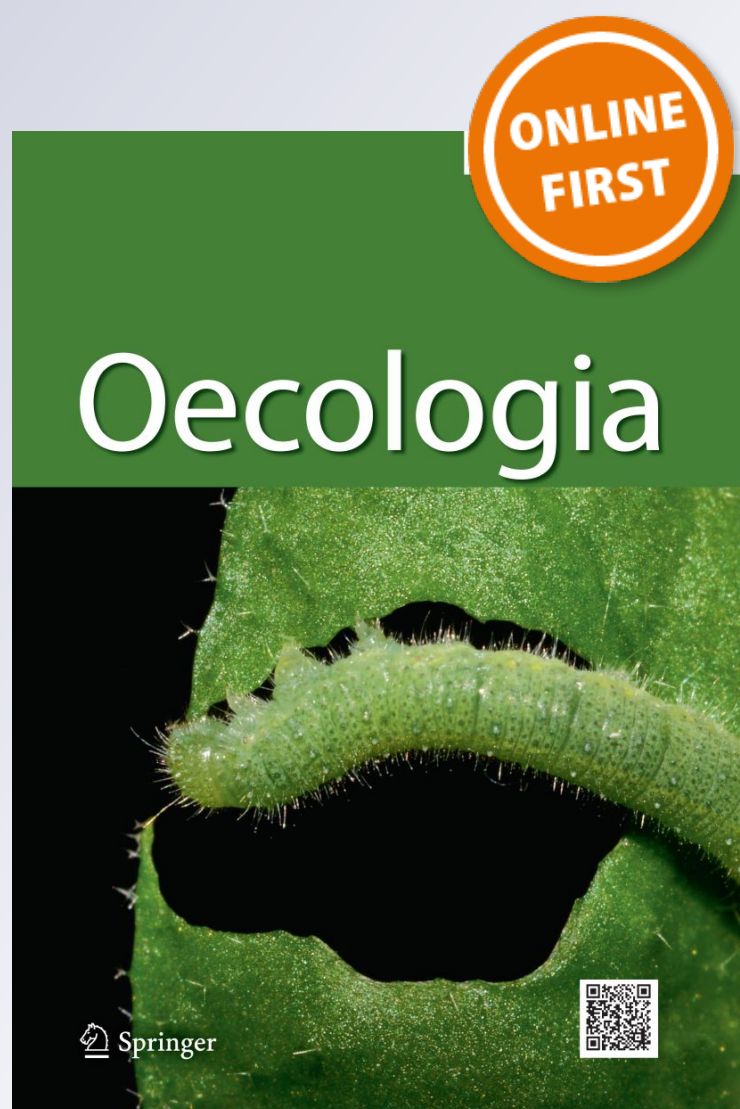
Volker H. W. Rudolf & Sena McCrory

Oecologia

ISSN 0029-8549

Oecologia

DOI 10.1007/s00442-018-4214-3



Your article is protected by copyright and all rights are held exclusively by Springer-Verlag GmbH Germany, part of Springer Nature. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".



Resource limitation alters effects of phenological shifts on inter-specific competition

Volker H. W. Rudolf¹ · Sena McCrory¹Received: 12 October 2017 / Accepted: 24 June 2018
© Springer-Verlag GmbH Germany, part of Springer Nature 2018

Abstract

Phenological shifts can alter the relative arrival time of competing species in natural communities, but predicting the consequences for species interactions and community dynamics is a major challenge. Here we show that differences in relative arrival time can lead to predictable priority effects that alter the outcome of competitive interactions. By experimentally manipulating the relative arrival time of two competing tadpole species across a resource gradient, we found that delaying relative arrival of a species reduced the interaction asymmetry between species and could even reverse competitive dominance. However, the strength of these priority effects was contingent on the abundance of the shared resource. Priority effects were generally weak when resources were limited, but increased at higher resource levels. Importantly, this context dependency could be explained by a shift in per capita interaction strength driven by a shift in relative body sizes of competitors. These results shed new light into the mechanisms that drive variation in priority effects and help predict consequences of phenological shifts across different environments.

Keywords Phenological shifts · Colonization · Historical contingency · Amphibian · Competition

Introduction

In nature, different species tend not to arrive simultaneously in a community. Instead, there is a clear sequence of arrival times, and this sequence can play a key role in determining the outcome of ecological interactions (Connell and Slatyer 1977; Wolkovich et al. 2014). For instance, the identity of the competitor that will be excluded from a community often depends on its relative arrival time (Drake 1991; Geange and Stier 2009; Rasmussen et al. 2014; Shorrocks and Bingley 1994). Such priority effects (or historical contingencies) are well documented in aquatic and terrestrial systems in both animal and plant communities and they are a key driver of the dynamics of communities, species coexistence, and spatio-temporal biodiversity patterns (Chase 2003; Drake 1991; Fukami 2015). However, the importance and consequences of priority effects vary considerably across systems and studies and we still have a limited understanding

of the mechanisms responsible for this variation (Alford and Wilbur 1985; Cleland et al. 2015; Kordas and Dudgeon 2011; Sharon and Morin 1993). Predicting priority effects is particularly important given that climate change is altering the relative phenologies of species around the globe (Walther et al. 2002; Yang and Rudolf 2010).

Priority effects arise when differences in relative arrival time alter (1) the relative abundance of species at the start of the interaction (numerical effects) (Olito and Fukami 2009; Robinson and Dickerson 1987), (2) per capita interaction strength (Geange and Stier 2009; Rasmussen and Rudolf 2016; Rasmussen et al. 2014; Rudolf and Singh 2013), or (3) environmental conditions (Hernandez and Chalcraft 2012). For instance, classical Lotka–Volterra competition models predict that when inter-specific density dependence is stronger than intra-specific effects, the outcome (i.e., which species persists) depends on the initial density of both competitors (Lotka 1932; Volterra 1926). Differences in per capita effects with relative arrival time can arise through a variety of mechanisms, but they are frequently linked to trait changes (Geange and Stier 2009; Rasmussen et al. 2014). Recent studies suggest that trait-mediated changes are particularly important source of priority effects in seasonal communities (Rasmussen

Communicated by Howard Whiteman.

 Volker H. W. Rudolf
Volker.rudolf@rice.edu¹ BioSciences, Rice University, Houston, TX 77005, USA

and Rudolf 2016; Rasmussen et al. 2014). Every year, seasonal communities are “colonized” by the new offspring of species, and the relative phenologies of species (e.g., germination, hatching, reproduction) determines when and at what size/stage individuals start interacting with each other (Yang and Rudolf 2010). The relative size of individuals typically determines per capita interaction strength, i.e., the effect of one individual on another. For example, larger individuals are often competitively dominant because they are better at exploiting or monopolizing shared resources (Persson et al. 2004; Rudolf and Singh 2013; Schwinning and Weiner 1998; Werner 1994). In these systems, priority effects can arise because differences in arrival sequence alter trait-differences (i.e., relative body size) of interacting species that determine per capita interaction strength (Rasmussen et al. 2014).

Given these underlying mechanisms, priority effects should not simply depend on who arrives first, but instead vary depending on how relative arrival times affect relative abundances or per capita effects. For instance, delaying arrival of a competitor gives the early arriver more time to increase in abundance (e.g., change in numerical effect) or in size (e.g., change in per capita effect). Thus, the strength of priority effects should be positively related with differences in relative arrival time (Kardol et al. 2013; Robinson and Edgemon 1988; Stier et al. 2013). However, the relationship between priority effects and arrival time should depend on how much the per capita effect (e.g., trait) or abundance changes during that time period. For instance, low growth rates will lead to smaller size differences at the onset of the interaction and thereby reduce the size-mediated advantage in per capita interaction strength of early arrivers while high growth rates should have opposite effects. Thus, any variation in environmental conditions that alter growth rates could also alter the strength of priority effects and how they scale with relative arrival time, but few studies have experimentally tested this hypothesis.

One key environmental condition that could alter priority effects is resource availability. Specifically, priority effects are often predicted to become more frequent and important at higher resource levels (productivity) (Chase 2003, 2010; Fukami 2015; Steiner and Leibold 2004). This is based on the assumption that higher resource levels allow early arriving populations to reach higher densities faster before other species arrive. However, during the early transient phase of the interaction (e.g., temporary, seasonal communities) higher resource levels can also reduce per capita interaction strength. Thus, higher productivity levels could increase numerical effects (e.g., increase in abundance or biomass of early arriver) but also reduce per capita effects. These contrasting forces make it difficult to predict how variation in relative arrival time across a productivity gradient will ultimately alter transient dynamics in temporary communities.

Here we take an experimental approach to test how variation in relative arrival time and productivity interact to determine the strength and consequences of competition and identify underlying mechanisms of priority effects. Specifically, we manipulated the relative hatching time of two competing tadpole species and the availability of their shared resource. This allowed us to examine (1) how priority effects scale with differences in relative arrival times of competing species, (2) how this relationship is modified by availability of a shared resource and whether effects are independent, and (3) the underlying mechanisms. Consistent with predictions we found that priority effects altered the competitive dominance in our system, and the strength of priority effects was context dependent and driven by the interaction of relative arrival time and resource availability. Importantly, this context dependency could be explained by differences in relative size and growth rates of species, indicating that variation in priority effects could be predicted by one simple mechanism.

Methods

Study species

We used two tadpole species *Rana sphenoccephala* and *Pseudacris triseriata* as a model system to examine consequences of phenological shifts. These two species are naturally coexisting in the wild in temporary ponds. *R. sphenoccephala* is larger in size and known to be the dominant competitor under most conditions, but the outcome of competition depends on relative hatching time of both species (Rudolf and Singh 2013). Like many amphibians, the breeding times of these two species are highly dependent on local weather conditions making them susceptible to climate change. The breeding phenology of *R. sphenoccephala* is mostly driven by rainfall, whereas *P. triseriata* breeding varies with temperature (Saenz et al. 2006). Therefore, tadpoles of both species often interact at different relative ages depending on the temperature and precipitation conditions during a breeding season (Rudolf 2018).

Study design

To examine the effect of phenological shifts under different food regimes, we independently manipulated phenology and food regimes using a 4 (relative arrival times) $\times$ 3 (food treatments) factorial design + 6 single species (no competition) control treatments each replicated four times (= 72 units). We used an additive competition design to estimate the change in inter-specific competition, with 15 tadpoles of *P. triseriata*, and 5 tadpoles of *R. sphenoccephala*. We used higher densities of *P. triseriata* to account for the 3–4

times smaller body size of *P. triseriata* at hatching relative to *R. sphenoccephala* and because they are known to be the inferior competitor with much lower survival rates (Rudolf and Singh 2013). This design keeps the respective species densities constant across all treatments and thus does not confound changes in intra-specific competition with inter-specific competition, allowing us to calculate per capita interaction coefficients (Goldberg et al. 1999; Inouye 2001). We manipulated the degree of phenological shift by delaying hatching of *R. sphenoccephala* relative to *P. triseriata*. Newly hatched *P. triseriata* were always added to the respective treatment on day zero. Newly hatched *R. sphenoccephala* were introduced to the appropriate replicates on days 0, 5, 10, and 15 depending on the phenology treatment. These four introduction times represent the different degrees of phenological mismatches that might be seen in the wild (Rudolf 2018). Previous studies indicate that *P. triseriata* is completely excluded (i.e., no survivors) by *R. sphenoccephala* when it arrives second (Rudolf and Singh 2013). Thus, we only focused here on the more informative scenario where *P. triseriata* arrives at the same time or earlier.

Every 3 days we fed tadpoles a mixture of ground up ©Purina rabbit chow and alfalfa and cleaned excess food and feces from the tanks. Initially, daily food levels were determined as 5, 10, and 20% of the average total body mass in each treatment (five *R. sphenoccephala* plus fifteen *P. triseriata*). Note that the total food levels differed in single (5 RS or 15 PT) vs. two species (5 RS + 15 PT) systems and increased over time to account for increase in body size and keep per unit-biomass food level as constant as possible throughout the experiment. The highest food level was reduced by 25% on February 11th due to issues with water fouling. On February 19th, all levels were increased by 50% because there was a very high starvation rate for *P. triseriata* at the lowest food levels. Medium and high food levels were returned to original levels again on March 4th to avoid water fouling.

In addition, to the competition/phenology treatments, we raised each tadpole species at all three food levels alone, i.e., in the absence of inter-specific competition. These control treatments of *P. triseriata* and *R. sphenoccephala* were all started at time zero and serve as a baseline to calculate species-specific growth and survival rates in the absence of inter-specific competition across food levels.

We collected eggs and pond water from several fishless ponds in the Davy Crockett National Forrest, TX on January 11, 2013. To delay the hatching for the late arrival treatments, we followed established protocols (Rudolf and Singh 2013) and incubated *R. sphenoccephala* egg clutches at 10 °C before being moved to 18 °C several days before their respective arrival time to accelerate hatching and growth. This allowed us to introduce all tadpoles at the same developmental stage and size to the experiment, approximately

5 days after hatching. Previous studies indicate that this procedure has no detectable side effect on tadpole growth, development, or mortality in all phenology treatments (Rudolf and Singh 2013; Rudolf & Rasmussen unpubl. data). We randomly assigned *R. sphenoccephala* clutches to one of the four phenology treatments. Each phenology treatment had multiple clutches, and tadpoles from each clutch within a given phenology treatment were distributed evenly among all replicates. All experiments were carried out in 11L aquaria setup in a temperature controlled room at 18 °C with a 10:14 h light:dark cycle. Each of the 72 tanks was filled with 7 L of 1 part filtered pond water to 3 parts reconditioned RO water. Treatments were set up in a completely randomized design and the experiment ran for 43 days from January 27 to March 11. This period covered most of the larval period of *P. triseriata* (~50–60 days) and assured that there were survivors in all treatments at the end of the study to measure growth rates and biomass production.

Tracking survival and growth rate

Mortality was recorded every 3 days in all tanks. Any dead tadpoles were also removed during this stage to prevent water fouling. To track growth rates, five tadpoles of each species from half of the tanks of each treatment were weighed individually every 6–9 days and returned to their respective tanks. For logistical reasons, we were not able to measure all tadpoles from all replicates, so we alternated which tanks were censored between samples. On the final days of the experiment, all surviving individuals from all tanks were weighed. In two replicates (both in low food level treatments, one with arrival times 10 and one with 15), all tadpoles died during the first 2 weeks of the experiment (for unknown reasons) and we excluded these replicates from all analyses. All applicable institutional guidelines for the care and use of animals were followed.

Data analysis

Survival We used a generalized linear model with binomial error structure with logit link function to determine the effect of arrival time, food level, and the interaction between these two factors as predictors for survival of *P. triseriata*. The time of *R. sphenoccephala* in experimental tanks inevitably varied across phenology treatments. To correct for these differences in treatment exposure, we calculated mortality rate of *R. sphenoccephala* tadpoles as $\log(N_t/N_0)/t$, with N_t the surviving individuals at time t , N_0 the initial number of individuals, and t the time present in a tank (27–42 days). We then tested for treatment effects on mortality rate of *R. sphenoccephala* with a general linear model with Gaussian distributed errors and identity link function. Statistical

significance for both species was assessed with type II Wald Chi-square tests using the “car” package in R.

Growth rates and biomass We calculated mean growth rates of tadpoles (g) as: $g = M/N/t$, with M the total mass summed across all surviving tadpoles in a tank, N the number of corresponding survivors, and t the time individuals were in the tank. Using the growth rate as response variable also allowed us to correct for differences in size of *R. sphenoccephala* simply due to differences in residence time within a given tank across phenology treatments. We used GLM with normal distributed errors with identify link function, food level and arrival time as fixed effects and survivors as weights to account for variable survival among treatments and mean growth rate (averaged across tadpoles within a tank) as response variable. Including weights did not alter qualitative patterns but significantly improved the fit of the model. Second, we repeated the same analysis but used total biomass production rate (b) as response variable. Biomass production was calculated in the same way as growth rate except we summed total biomass of all surviving tadpoles within a given tank at the end of the experiment, b the total biomass/ t . The difference between growth rates and biomass production is that the latter is also driven by survival, and differences between the two metrics can identify biomass compensation. Statistical significance was assessed with type II Wald Chi-square tests using the “car” package in R.

Finally, we also calculated the relative competition intensity (RCI) (Goldberg et al. 1999) for both survival and growth rate as $RCI = (X_{f,j(\text{two species})} - X_{f,j(\text{control})})/X_{f,j(\text{control})}$, where $X_{f,j}$ is the survival or growth rate of species j at food level f . This metric has a simple intuitive interpretation because it indicates the proportional change in a fitness metric due to the presence of the other species.

Results

Mortality In single species controls, survival increased with food for *P. triseriata* [low (L) = $35\% \pm 1.3$ SE, medium (M) = $45\% \pm 6.4$ SE, high (H) = $67\% \pm 3.3$ SE], but varied little for *R. sphenoccephala* (mean $\pm$ SE: $L = 90\% \pm 2.6$, $M = 95\% \pm 2.0$, $H = 95\% \pm 2.0$), suggesting *P. triseriata* had higher resource needs. In treatments with inter-specific competition, arrival time of the “late” competitor (*R. sphenoccephala*) significantly affected survival of both, the early and late competitor (Table 1). When both species arrived together, competition reduced survival of the early competitor (*P. triseriata*) by 25–75% depending on the food treatment. Longer delay in relative arrival time increased survival of the early competitor, *P. triseriata*, but decreased survival rate of the late competitor (Fig. 1). Competition had no clear effect on survival in the latest (15 days delay) and the earliest (0 day delay) arrival treatment for the early and late competitors, respectively (Fig. 1). The changes in relative competition intensity clearly indicate that shifts in relative arrival time altered the strength of inter-specific competition in this system, but effects were asymmetric. Priority effects were much stronger for early arriving species, increasing survival by up to three times (medium food level, 20 vs. 60%) with a 15-day delay of the late arriver (Fig. 1). In contrast, survival of the late arriver was always much higher and only decreased somewhat at the latest arrival time (Fig. 1). Food levels were positively related to survival of the early competitor but did not significantly differ for the late arriver (Table 1, Fig. 1). Food level had additive effects and did not significantly modify relationship

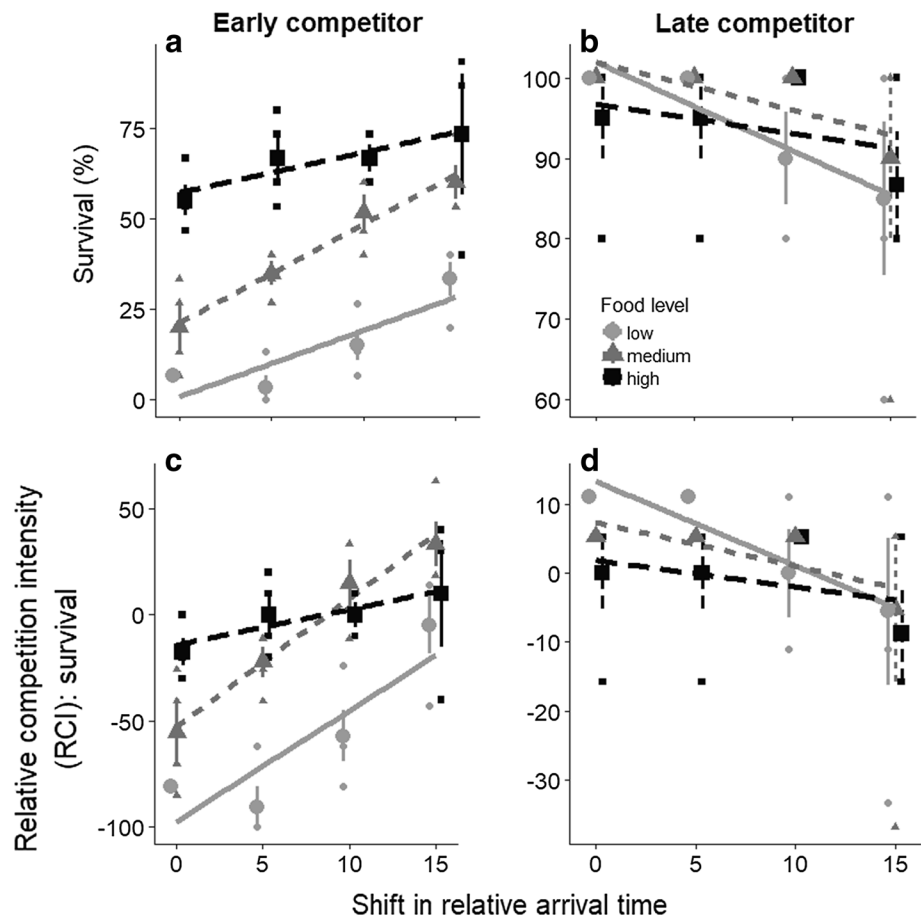
Table 1 Effects of relative arrival time and food availability on survival, growth rates and final biomass of two competing tadpole species

	Early competitor (<i>P. triseriata</i>)			Late competitor (<i>R. sphenoccephala</i>)		
	χ^2	df	P value	χ^2	df	P value
Survival						
Food availability	32.02	2	< 0.0001	0.91	2	0.6332
Arrival time	8.51	1	0.0036	8.49	1	0.0035
Food availability: arrival time	0.97	2	0.6171	1.02	2	0.6012
Growth rate						
Food availability	61.36	2	< 0.0001	66.36	2	< 0.0001
Arrival time	44.41	1	< 0.0001	88.91	1	< 0.0001
Food availability: arrival time	6.24	2	0.0441	31.15	2	< 0.0001
Total biomass production rate						
Food availability	180.44	2	< 0.0001	30.43	2	< 0.0001
Arrival time	69.59	1	< 0.0001	47.52	1	< 0.0001
Food availability: arrival time	11.77	2	0.0028	14.43	2	0.0007

χ^2 indicates Wald II Chi-square statistics

Bold values indicate significance with $P < 0.05$

Fig. 1 Survival and competitive effects of early (*P. triseriata*) and late (*R. sphenoccephala*) competitor as a function relative arrival time. Y-axis indicates delay of late competitor relative to arrival early competitor (in days) (0=arrival at same time, 15=15 day delay of late competitor). Symbols and color and shape indicate level of shared food availability in respective treatments (low = x, medium = 2x, high = 4x, with x based on % of tadpole mass, see “Methods” for details). Each treatment was replicated four times (= 72 units). Large symbols indicate mean $\pm$ 1 SE and small symbols individual replicates, lines indicate best fit relationships. Points were slightly horizontally offset to reduce overlap. Relative competition intensity (RCI) indicates the proportional change (%) in survival due to the presence of the other species



between priority effects and relative arrival times (no significant interaction, Table 1).

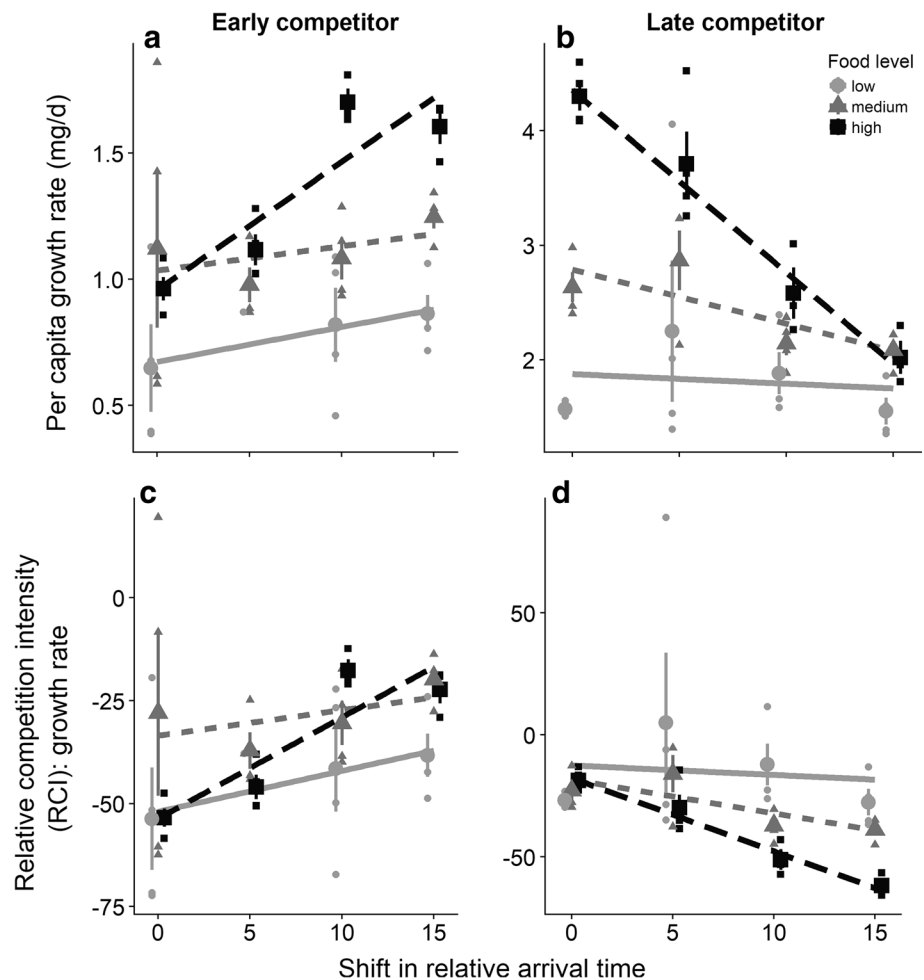
Growth rates Higher food levels resulted in faster growth rates in single species treatments ($\chi^2 = 136.5$, $P < 0.0001$), and *R. sphenoccephala* grew significantly faster ($\chi^2: 199.8$, $P < 0.0001$) than *P. triseriata* and this difference increased at higher food levels (species identity $\times$ food treatment, $\chi^2: 56.7$, $P < 0.0001$) (*P. triseriata* mean $\pm$ SE: food level low: 1.4 ± 0.05 mg/day, medium: 1.56 ± 0.08 mg/day, high: 2.01 ± 0.06 mg/day, *R. sphenoccephala*: low: 2.15 ± 0.08 mg/day, medium: 3.41 ± 0.06 mg/day, high: 5.29 ± 0.08 mg/day), confirming that our food manipulation successfully created differences in resource limitations.

The presence of the inter-specific competitor always reduced growth rates of both species, but the effect was contingent on their relative arrival time (Table 1, Fig. 2). Delaying arrival of the late competitor generally increased growth rates of early arriving competitors while it decreased growth of the late arriving competitor (Fig. 2). For both species, the effect of arrival times decreased with reduction in resource availability. For instance, delaying arrival of the later competitor by 15 days increased the competition intensity from ~18% (0 delay) to 60% at high resource levels, but the same delay did not alter the competitive intensity at

lowest resource level (0 days delay: 26% vs. 15 days delay: 27%) (Fig. 2). Total final biomass showed a very similar pattern to growth rates. Biomass increased in direct proportion to the difference in relative arrival time of the late competitor, but it decreased for the late competitor. For both species, the effect size of shifting relative arrival time increased with relative resource levels (Table 1).

To further elucidate how priority effects alter competition in this system, we examined the relationship in relative competitiveness of the two species by calculating the ratios of growth rates of both species and compared them to relative growth rates expected from single species treatments (Fig. 3). This analysis shows that the competitive dominance of the late competitor becomes generally weaker with delay in relative arrival time, but this effect was contingent on resource level (food $\times$ arrival: LR = 36.4.1, $P < 0.0001$). At low and intermediate levels, there was only a weak shift in relative growth rates, and only with 15 day difference in arrival time did growth rate ratios reach the ratios expected from single species control at medium food level (Fig. 3). However, at high resource levels, delaying arrival of the late competitor quickly shifted relative growth rates in favor of early competitor and even reversed competitive dominance at the latest two arrival times (i.e., growth ratio higher than

Fig. 2 Growth rates and competitive effects of early (*P. triseriata*) and late (*R. sphenoccephala*) competitor as a function relative arrival time. Y-axis indicates delay of late competitor relative to arrival early competitor (in days) (0 = arrival at same time, 15 = 15 day delay of late competitor). Symbols and color indicate level of shared food availability in respective treatments (low = x, medium = 2x, high = 4x, with x based on % of tadpole mass, see “Methods” for details). Symbols represent individual replicates and symbols’ size differences reflect differences in survivors. Relative competition intensity (RCI) indicates the proportional change (%) in survival due to the presence of the other species. Each treatment was replicated four times (= 72 units)



predicted based on single species ratios) (Fig. 3). Overall, this indicates that priority effects did not simply shift relative body size, but it altered how body size of both species changed over time, i.e., the trajectory itself.

Discussion

Phenological shifts can alter the relative arrival time of competing species in natural communities, but predicting the consequences for species interactions and community dynamics is a major challenge of the twenty-first century (Visser 2016). Here we show that differences in relative arrival time can lead to predictable priority effects that alter the outcome of competitive interactions. Specifically, delaying relative arrival of a dominant competitor reduced the competitive asymmetry among competitors and could even reverse competitive dominance. However, the strength of these priority effects was contingent on the abundance of the shared resource. Priority effects were generally weak when resources were limited, but increased at higher resource levels. These results shed new light into the mechanisms that

drive variation in priority effects and help predict consequences of phenological shifts across different environments.

Priority effects scale with relative arrival time

Priority effects play a key role in community assembly and ultimately species coexistence, but they are still highly understudied (Fukami 2015). As a consequence we still have a limited understanding of the different mechanisms that determine variation in the strength and consequences of priority effects. We found that the strength of priority effects was driven by the interaction of relative arrival time and resource availability. This variation in priority effects could be driven by several non-exclusive mechanisms: changes in density, changes in environmental conditions, or changes in per capita effects (Chase 2003; Fukami 2015; Rasmussen et al. 2014). Theory suggests that priority effects should increase when populations have more time to increase in abundance (Fukami 2015). In our experimental system, populations could not increase but either remained constant or declined. Differences in population size can therefore not predict the observed differences in priority effects.

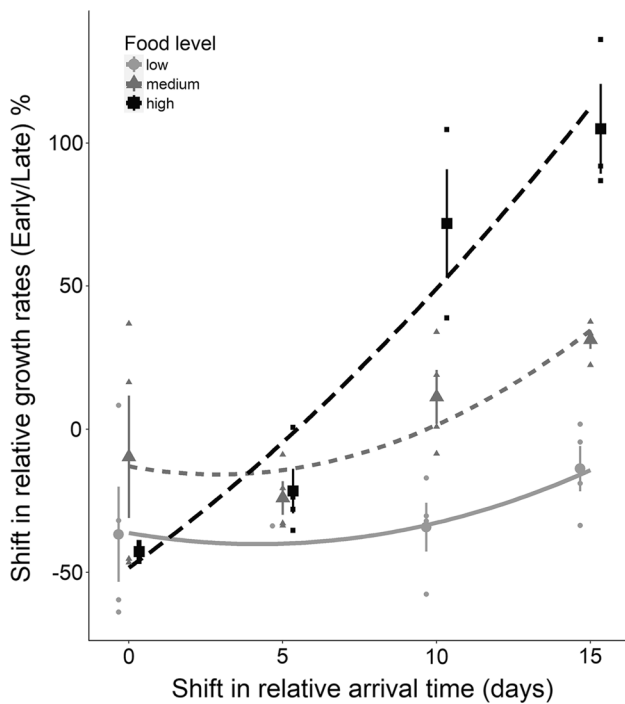


Fig. 3 Shift in relative growth rates of early vs. late competitors as a function relative arrival time of late competitor. X-axis, symbols and labels as described in Fig. 1. The y-axis indicates the proportional change in relative growth rates compared to ratios expected from single species controls

Alternatively, priority effects could also arise when early arrivers can modify the environment, including depletion or monopolization of shared resources (Hernandez and Chalcraft 2012). We were able to rule out this mechanism because we kept environmental conditions constant and renewed food in regular intervals. This setup prevented early arrivers from depleting or monopolizing the shared resource before the late competitor arrived in the system. Thus, priority effects could only be driven by changes in the per capita interaction strength of individuals.

Shifts in relative arrival time can alter the per capita strength of inter-specific interactions when the traits of individuals change over time. This can be driven by behavioral (Geange and Stier 2010) or morphological changes (Hoverman and Relyea 2008; Rasmussen et al. 2014). In many systems, including ours, body size is positively correlated with competitive ability (Yang and Rudolf 2010). Delaying arrival of a competitor allows the early arriving species to increase in size and thereby increase its per capita effect on the late arriver while decreasing the per capita effect of the late arriver on itself. Such “size-mediated priority effects” (sensu Rasmussen et al. 2014) are consistent with the patterns we observed in our system and help explain why the strength of priority effects varied across arrival times and changed the competitive dominance of early vs. late

arriver. Delaying arrival of the late competitor could potentially result in unintended experimental bias if it somehow also reduces competitive ability. However, previous studies demonstrate that delaying hatching of this species has no measureable negative effects (Alford and Wilbur 1985; Rudolf and Singh 2013). Furthermore, this potential bias could not explain why effects varied across food level within a given arrival time. Overall, our results suggesting that the observed pattern was driven by simple mechanism: size-mediated priority effects arising from shifts in the size of early competitor.

Context dependency of priority effects

A key challenge in community ecology is to predict when historical contingencies are more or less important, because they determine the importance of stochastic vs. deterministic processes and ultimately how biodiversity is partitioned across temporal and spatial scales (Chase 2003, 2010; Fukami 2015; Van Allen et al. 2017). Our results demonstrate that priority effects depend on the specific context, i.e., priority effects declined when shared resources were more limited. Importantly, this provides direct experimental evidence that priority effects should become more important in productive environments and helps explain why stochastic processes are becoming more dominant in driving community structure in productive environments (Chase 2010). However, our mechanism is somewhat different from the ones typically proposed for this relationship. Instead of productivity driving density-mediated priority effects (Chase 2010; Fukami 2015), productivity altered the per capita interaction strength of individuals via size-mediated priority effects (Rasmussen et al. 2014; Rudolf and Singh 2013). Note that this effect only arises because interactions occur among growing individuals. However, given that the vast majority of interactions occur among growing individuals, this is clearly a common scenario in nature and likely to play a key role in seasonal dynamics of communities (Kardol et al. 2013; Rasmussen et al. 2014; Stier et al. 2013).

Species interactions in a changing world

Competition is an important ecological interaction structuring natural systems, but current theoretical models typically assume that per capita interaction strength is an intrinsic trait of a species. Our results clearly demonstrate that this is not the case; the per capita interaction strength and even competitive dominance changed in our system depending on the relative arrival time. This variation in per capita effects is currently not included in theoretical models but could play a key role in determining long-term coexistence of competing species. The relative “arrival time” of offspring in a given community depends on the

respective phenologies of interacting species. However, phenologies can vary considerably across years with changes in environmental conditions leading to concurrent changes in relative arrival time (Visser 2016; Visser and Both 2005; Yang and Rudolf 2010). Our study suggests that this variation could help facilitate persistence of the inferior competitor, *P. triseriata*, in our system. Consistent with previous studies (Rudolf and Singh 2013) we found that *R. sphecephala* is clearly the better competitor and can readily competitively exclude *P. triseriata* when both species arrive at the same time. However, we show that *P. triseriata* can persist and even become competitively dominant if it arrives earlier relative to *R. sphecephala* at high resource levels. This reversal in competitive dominance could potentially facilitate long-term persistence of an inferior competitor if variation in relative arrival time allows the inferior competitor to arrive earlier than its competitor, especially if adults can live through multiple years (Chesson 2000) but more detailed models are needed to determine under which specific conditions this would occur.

Climatic change is driving shifts in the relative phenologies of species worldwide (Parmesan and Yohe 2003; Walther 2010; Walther et al. 2002), thus emphasizing the need for a temporally explicit approach to community ecology to understand and predict how these changes will affect natural ecosystems (Wolkovich et al. 2014; Yang et al. 2008). Our study adds to a growing body of empirical studies indicating that the outcome of species interactions are often highly sensitive to variation in relative arrival time of interacting species. Similar sensitivities to the timing of interactions are likely to be common in many natural systems, suggesting that climate-mediated shifts in phenologies could have dramatic consequences on the structure of natural communities. However, predicting the outcome will require a detailed understanding of the relationship between relative arrival time and interaction strength and how it is affected by different biotic and abiotic factors. For instance, our study suggests that if climate change drives a directional shift in the relative arrival this could either reduce or facilitate long-term coexistence depending on whether it decreases or increases the delay in arrival of the dominant competitor, respectively. Similarly, our results suggest that phenological shifts may need to be substantial to have noticeable consequences in less productive environments, but even small shifts may have dramatic effects in highly productive environments. Importantly, recent field experiments suggest (Rudolf 2018) that these findings hold under natural conditions in more complex communities with natural, dynamic resources, suggesting that general patterns observed in this study are relevant in natural systems. Future studies that examine the relationship between phenological shifts along different

environmental gradients will help to determine how general these patterns are across taxa and ecosystems.

Acknowledgements We thank C. Dibble for feedback and help on all aspects of the experiments and manuscript. This work was supported by NSF DEB-1256860 and DEB-1655626 to V.H.W. Rudolf.

Author contribution statement VHWR and SM design the experiment, SM conducted the experiment, and VHWR analyzed the data and wrote the manuscript with input from SM.

Compliance with ethical standards

Ethical approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. All applicable institutional and national guidelines for the care and use of animals were followed and approved under IACUC protocol A13101101.

References

- Alford RA, Wilbur HM (1985) Priority effects in experimental pond communities: competition between *Bufo* and *Rana*. *Ecology* 66:1097–1105
- Chase JM (2003) Community assembly: when should history matter? *Oecologia* 136:489–498
- Chase JM (2010) Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 328:1388–1391
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* 31:343
- Cleland EE, Esch E, McKinney J (2015) Priority effects vary with species identity and origin in an experiment varying the timing of seed arrival. *Oikos* 124:33–40
- Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *Am Nat* 111:1119–1144
- Drake JA (1991) Community-assembly mechanics and the structure of an experimental species ensemble. *Am Nat* 137:1–26
- Fukami T (2015) Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annu Rev Ecol Syst* 46:1–23
- Geange SW, Stier AC (2009) Order of arrival affects competition in two reef fishes. *Ecology* 90:2868–2878
- Geange SW, Stier AC (2010) Priority effects and habitat complexity affect the strength of competition. *Oecologia* 163:111–118
- Goldberg DE, Rajaniemi T, Gurevitch J, Stewart-Oaten A (1999) Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology* 80:1118–1131
- Hernandez JP, Chalcraft DR (2012) Synergistic effects of multiple mechanisms drive priority effects within a tadpole assemblage. *Oikos* 121:259–267
- Hoverman JT, Relyea RA (2008) Temporal environmental variation and phenotypic plasticity: a mechanism underlying priority effects. *Oikos* 117:23–32
- Inouye BD (2001) Response surface experimental designs for investigating inter-specific competition. *Ecology* 82:2696–2706
- Kardol P, Souza L, Classen AT (2013) Resource availability mediates the importance of priority effects in plant community assembly and ecosystem function. *Oikos* 122:84–94

- Kordas RL, Dudgeon S (2011) Dynamics of species interaction strength in space, time and with developmental stage. *Proc R Soc Lond B* 278:1804–1813
- Lotka AJ (1932) The growth of mixed populations: two species competing for a common food supply. *J Wash Acad Sci* 22:461–469
- Olito C, Fukami T (2009) Long-term effects of predator arrival timing on prey community succession. *Am Nat* 173:354–362
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42
- Persson L et al (2004) Cannibalism in a size-structured population: energy extraction and control. *Ecol Monogr* 74:135–157
- Rasmussen NL, Rudolf VHW (2016) Individual and combined effects of two types of phenological shifts on predator–prey interactions. *Ecology* 97:3414–3421
- Rasmussen NL, Van Allen BG, Rudolf VHW (2014) Linking phenological shifts to species interactions through size-mediated priority effects. *J Anim Ecol* 83:1206–1215
- Robinson JV, Dickerson JE (1987) Does invasion sequence affect community structure. *Ecology* 68:587–595
- Robinson JV, Edgemon MA (1988) An experimental evaluation of the effect of invasion history on community structure. *Ecology* 69:1410–1417
- Rudolf VHW (2018) Nonlinear effects of phenological shifts link inter-annual variation to species interactions. *J Anim Ecol*. <https://doi.org/10.1111/1365-2656.12850>
- Rudolf VHW, Singh M (2013) Disentangling climate change effects on species interactions: effects of temperature, phenological shifts, and body size. *Oecologia* 173:1043–1052
- Schwinning S, Weiner J (1998) Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113:447–455
- Sharon PL, Morin PJ (1993) Temporal overlap, competition, and priority effects in larval anurans. *Ecology* 74:174–182
- Shorrocks B, Bingley M (1994) Priority effects and species coexistence: experiments with fungal-breeding *Drosophila*. *J Anim Ecol* 63:799–806
- Steiner CF, Leibold MA (2004) Cyclic assembly trajectories and scale-dependent productivity-diversity relationships. *Ecology* 85:107–113
- Stier AC, Geange SW, Hanson KM, Bolker BM (2013) Predator density and timing of arrival affect reef fish community assembly. *Ecology* 94:1057–1068
- Van Allen BG, Rasmussen NL, Dibble CJ, Clay PA, Rudolf VHW (2017) Top predators determine how biodiversity is partitioned across time and space. *Ecol Lett*
- Visser ME (2016) Phenology: interactions of climate change and species. *Nature* 535:236–237
- Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proc R Soc Lond B* 272:2561–2569
- Volterra V (1926) Variations and fluctuations of the numbers of individuals in animal species living together. In: Chapman RN (ed) *Animal ecology*. McGraw-Hill, New York
- Walther G-R (2010) Community and ecosystem responses to recent climate change. *Philos Trans R Soc B Biol Sci* 365:2019–2024
- Walther GR et al (2002) Ecological responses to recent climate change. *Nature* 416:389–395
- Werner EE (1994) Ontogenic scaling of competitive relations—size-dependent effects and responses in two anuran larvae. *Ecology* 75:197–213
- Wolkovich EM, Cook BI, McLauchlan KK, Davies TJ (2014) Temporal ecology in the anthropocene. *Ecol Lett* 17:1365–1379
- Yang LH, Rudolf VHW (2010) Phenology, ontogeny, and the effects of climate change on the timing of species interactions. *Ecol Lett* 13:1–10
- Yang LH, Bastow JL, Spence KO, Wright AN (2008) What can we learn from resource pulses? *Ecology* 89:621–634