

# Individual and combined effects of two types of phenological shifts on predator–prey interactions

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**Abstract.** Timing of phenological events varies among years with natural variation in environmental conditions and is also shifting in response to climate change. These phenological shifts likely have many effects on species interactions. Most research on the ecological consequences of phenological shifts has focused on variation in simple metrics such as phenological firsts. However, for a population, a phenological event exhibits a temporal distribution with many attributes that can vary (e.g., mean, variance, skewness), each of which likely has distinct effects on interactions. In this study, we manipulated two attributes of the phenological distribution of a prey species to determine their individual and combined effects on predator–prey interactions. Specifically, we studied how shifts in the mean and variation around the mean (i.e., synchrony) of hatching by tadpoles (*Hyla cinerea*) affected interactions with predatory dragonfly naiads (*Tramea carolina*). At the end of larval development, we quantified survival and growth of predator and prey. We found that both types of shifts altered demographic rates of the prey; that the effects of synchrony shifts, though rarely studied, were at least as strong as those due to mean shifts; and that the combined effects of shifts in synchrony and mean were additive rather than synergistic. By dissecting the roles of two types of shifts, this study represents a significant step toward a comprehensive understanding of the complex effects of phenological shifts on species interactions. Embracing this complexity is critical for predicting how climate change will alter community dynamics.

**Key words:** climate change; community assembly; dragonfly; *Hyla cinerea*; size–structured interactions; synchrony; tadpole; *Tramea carolina*.

## INTRODUCTION

Phenology is increasingly recognized as an important factor driving the dynamics of ecological communities (Forrest and Miller-Rushing 2010). It determines when during the year organisms become active within a habitat via events such as birth, migration, and emergence from dormancy. Therefore, phenology also determines when and at which ontogenetic stage organisms interact (Both et al. 2009, Yang and Rudolf 2010, McKinney et al. 2012). Variation among years in environmental conditions can cause substantial variation in the timing of phenological events, and the nature of these phenological responses frequently differs among species within a community (Todd et al. 2011, Ovaskainen et al. 2013, CaraDonna et al. 2014). Therefore, the timing of intraspecific and interspecific interactions can also vary among years. These phenological shifts likely have a host of effects on the outcome of interactions, but many of these effects remain largely unknown (Yang and Rudolf 2010). Linking phenology to species interactions is critical not only for understanding the dynamics of communities but also for predicting how those dynamics will be affected by

climate change, which is altering phenologies worldwide (Parmesan 2007, Miller-Rushing et al. 2010).

To determine how phenological timing affects interactions, it is important to recognize that a phenological event exhibits a temporal distribution, at the population level (Miller-Rushing et al. 2010, CaraDonna et al. 2014). The shape of this distribution is determined by year-specific seasonal patterns in environmental conditions and responses by individuals within a population to them. Variation among years in attributes of a phenological distribution, such as the mean, variance, and skewness, determine the temporal overlap of phenological events for populations of interacting species (e.g., plant flowering and pollinator activity, bird breeding and insect prey abundance), which can have a variety of effects on interactions. For example, variation in relative timing of two phenological events (i.e., shifts in mean) can affect predation (Fincke 1999, Rasmussen et al. 2014), herbivory (Liu et al. 2011), interspecific competition (Shorrocks and Bingley 1994, Hernandez and Chalcraft 2012, Rudolf and Singh 2013), and pollination (Rafferty and Ives 2011). Similarly, variation in the degree of temporal clustering (i.e., shifts in synchrony) of a phenological event can affect intraspecific interactions including cannibalism (Hopper et al. 1996) and intraspecific competition (Rasmussen and Rudolf 2015). Despite these advances in our understanding, much about the

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ecological consequences of phenological shifts remains unknown.

Ecologists are just beginning to understand how different attributes of phenological distributions vary among years. However, it is becoming clear that patterns of interannual variation in one attribute do not necessarily facilitate prediction of the patterns in other attributes for a given distribution. For example, a study of 60 plant species revealed that first, peak, and last flowering usually shifted independently among years (CaraDonna et al. 2014). In a study of arrival phenology for three migratory bird species, changes in some attributes generally were significantly correlated (e.g., first and mean), whereas changes in other attributes generally were not (e.g., mean and standard deviation) (Sparks et al. 2005). Virtually nothing is known about the relative importance of changes in one attribute of a phenological distribution vs. another (e.g., mean vs. synchrony) for the demographic rates of interacting populations. We also do not know whether simultaneous changes in multiple attributes have effects on interactions that are independent or synergistic. If concomitant shifts have independent effects, then the net effect of these shifts on the demographic rates of interacting populations could be determined by simply adding or subtracting their individual effects. If, however, their effects are synergistic, then determining the net effect becomes more complex (e.g., effects on survival of one shift could amplify those of another).

In this study, we took an experimental approach to determine the individual and combined effects of two types of shifts in prey phenology on predator–prey interactions. Specifically, we used a factorial manipulation of the degree of hatching synchrony of tadpoles and the mean hatching time of tadpoles relative to a dragonfly predator to answer two main questions: (1) What is the relative magnitude of the effects of shifts in the mean vs. synchrony of prey phenology on predator–prey interactions, and (2) are the combined effects of these two types of shifts independent or synergistic? While some mechanisms by which these two types of phenological shifts can affect predator–prey interactions are known, it is difficult to predict which type of shift would more strongly affect this interaction. As mean arrival of hatchling tadpoles shifts later relative to dragonflies, tadpoles likely suffer higher predation because they encounter increasingly larger dragonflies, and larger dragonflies can consume more tadpoles (Travis et al. 1985). As tadpoles arrive with higher synchrony, they can potentially satiate dragonflies (i.e., dragonflies do not exhibit linear functional responses, Rudolf 2008), which could allow a high proportion of tadpoles to survive to metamorphosis. Shifts in the mean and synchrony of tadpole arrival could result in synergic effects on tadpole demographic rates because the effectiveness of high arrival synchrony in satiating dragonflies could decline or even disappear with increasingly later mean tadpole arrival (higher tadpole densities are required to satiate larger dragonflies). By dissecting

the roles of two different types of shifts, this study represents a significant step toward a comprehensive understanding of the complex effects of phenological shifts on species interactions.

## METHODS

### *Study system*

We studied the consequences of shifts in prey hatching phenology for predator–prey interactions using tadpoles of *Hyla cinerea* (prey) and naiads of the dragonfly *Tramea carolina* (predator), hereafter referred to as tadpoles and dragonflies, respectively. These two species commonly co-occur in permanent ponds in eastern Texas (NLR, unpublished data, Garton and Brandon 1975, Wissinger and Mcgrady 1993). In this region, both species arrive in ponds as hatchlings between mid-spring and late summer, and dragonflies arrive before tadpoles (NLR, unpublished data). However, there exists substantial interannual variation in tadpole mean arrival time (can shift earlier or later) and arrival synchrony (can shift higher or lower) (NLR, personal observation). The strong predation pressure imposed by dragonfly naiads on tadpoles has been demonstrated in many studies (Smith 1983, Travis et al. 1985, McCoy et al. 2011). These features of the two species and the interactions between them lend themselves well to experimental tests of the effects of phenological shifts on species interactions.

### *Experimental design*

We conducted an outdoor mesocosm experiment using a full factorial design with three prey mean arrival treatments (early, medium, late) crossed with three prey arrival synchrony treatments (low, medium, high). We set up our treatments to capture nearly the full range of scenarios of prey mean arrival and arrival synchrony that would result in interactions between these two species in their natural habitat. To simulate variation in mean arrival of tadpoles relative to dragonflies, we used three size classes of dragonflies (see Table 1). Dragonflies increase in size with age, so larger dragonflies represent later arrival by tadpoles. Our estimates of dragonfly age based on size were informed by our previous work with

TABLE 1. Size classes of the predator, *Tramea carolina* dragonfly naiads, used to simulate relative shifts in mean arrival time of the prey, *Hyla cinerea* tadpoles.

	Mean prey arrival		
	Early	Medium	Late
Estimated predator age (days)	10	14	30
Predator head width (mm)	2.73	3.54	5.39
Predator body length (mm)	6.11	7.85	14.11
Predator dry mass (mg)	2.45	5.60	30.03

this species (Rasmussen et al. 2014). The smallest dragonfly size class represented the minimum capable of consuming hatchling tadpoles (NLR, *unpublished data*). The largest size class represented the maximum expected to interact with the latest-arriving cohort of tadpoles (see description of synchrony treatments below) for at least a week before completing development. Each experimental unit received three dragonflies belonging to one of these three size classes. Following the methods of Rasmussen et al. (2014), we controlled for density instead of biomass for three reasons: (1) we were interested in per capita, not per unit biomass, effects; (2) we anticipated that dragonfly survival would be high regardless of initial size; and (3) we expected that small dragonflies would catch up in size to large ones over time because small/young dragonflies grow faster than larger/older ones. If our assumptions about dragonflies held (they did, see *Results*), then controlling for density would result in similar densities and biomasses across treatments over the duration of the experiment.

To create prey arrival synchrony treatments, we manipulated the amount of temporal variation in tadpole hatching around a mean hatching date (June 24, 2012), following the methods of Rasmussen and Rudolf (2015). In the high synchrony treatment, all tadpoles were hatched on the mean date (no variation in hatching). For both the medium and low synchrony treatments, hatching was evenly divided among three dates. This included the mean date as well as one date before and one date after the mean date (medium synchrony =  $\pm 2$  d, low synchrony =  $\pm 4$  d). Even lower synchrony treatments, though possible, likely would have resulted in additions of tadpole cohorts after the largest dragonflies had already begun to complete development. In total, each experimental unit received 180 tadpoles. We used realistic densities of both tadpoles and dragonflies but employed somewhat low densities of dragonflies. These dragonfly densities facilitated natural predator-prey interactions, while reducing the risk that these voracious predators would completely eliminate all prey in our simple, but realistic, communities (see *Experimental setup* below). The nine treatment combinations were replicated six times in a randomized complete block design.

#### *Experimental setup*

Study organisms were collected from local field sites. We collected dragonflies from a pond in the Davy Crockett National Forest on June 18, 2012, and we obtained hatchling tadpoles from eggs laid by pairs of adults collected at a pond at the Sam Houston State University Center for Biological Field Studies. These eggs were collected on three evenings following rain events (June 14, 15, and 20) and from at least 10 pairs of adults on each evening. All clutches were initially maintained at 20°C to slow development. Then 48 h prior to introduction of a cohort of tadpoles to the experiment, eggs were gradually warmed to 30°C to induce hatching.

These temperatures are well within the range experienced by eggs in natural ponds. Using this approach, we were able to introduce cohorts of tadpoles of the same stage (Gosner stage 25,  $\sim 2.35$  mm snout-to-vent length) on all five dates needed to create the three synchrony treatments. To reduce the risk of incubation time and/or genetic composition confounding the synchrony treatments, the five cohorts generally included hatchlings from most clutches laid on each of two different dates. In addition, we conducted a supplementary laboratory experiment to compare survival among the five cohorts. Twenty hatchlings from each cohort were raised in groups of five on a diet of ground alfalfa pellets for 16 d. We found no differences in survival among the cohorts (mean  $\pm$  standard deviation [SD] = 4.75 tadpoles  $\pm$  0.55;  $\chi^2 = 6.9135$ ,  $P = 0.1405$ ).

The main experiment was conducted in an open field in Houston, TX. We used an array of 54 cylindrical plastic cattle watering tank mesocosms (volume = 360 L) configured into a grid of six square spatial blocks. Our mesocosms overlap in size with the bodies of water that these species naturally colonize, making these containers a useful venue for studying interactions between this prey and predator. Within these mesocosms, we created simple pond communities. We filled mesocosms with water on June 15, 2012 and immediately fitted them with lids made of 60% shade cloth to prevent colonization by amphibians and large, predatory insects. These lids did, however, allow colonization by small insects (e.g., small beetles, chironomid larvae), which served as alternative prey for dragonflies. On June 16, we added to each mesocosm 650 mL of concentrated phytoplankton and zooplankton from local fishless ponds and  $\sim 75$  g air dried mass of leaf litter. On June 21, we added 3 g dry mass of alfalfa pellets per mesocosm for nutrients. To simulate mats of vegetation, we added enough bunches of plastic deer fencing mesh to fill 30% of the water volume. We frequently observed dragonflies and tadpoles foraging in this artificial vegetation.

We initiated the experiment on June 20 by adding all the dragonflies, and later the same day, the first cohort of tadpoles for the low synchrony treatment. The remaining four tadpole cohorts were added over the following eight days (see *Experimental design*). On July 10, the first dragonflies and tadpoles completed development (20 d after experiment initiation). This suggested that the interaction between these two species was coming to a close, and therefore we used this as the end point of the experiment. All remaining dragonflies and tadpoles were collected and preserved in 10% buffered formalin. Preserved specimens were later counted to determine the proportion of survivors and measured to determine mean size (dragonflies: head width, tadpoles: snout-to-vent length). We found that the vast majority of remaining dragonflies, regardless of initial size, were in the final naiad stage and that generally tadpole densities had been reduced to low levels (see *Results*). These facts suggest that the experiment end date closely corresponded to the date when the

interaction would have concluded and that further changes to the response variables likely would have been small (except mean tadpole size).

### Statistical analysis

All analyses were performed using the R statistical computing environment (R Development Core Team 2016). Using the 'lme4' package (Bates et al. 2016), we ran generalized linear mixed models to analyze the effects of variation in prey mean arrival, prey arrival synchrony, and their interaction on proportion of survivors (binomial error structure) and mean size (Gaussian error structure) for both predator and prey. For the tadpole survival analysis, we included an observation-level random effect to deal with overdispersion (Zuur et al. 2013). Spatial block was included as a random effect in all models. For all analyses, we evaluated significance of fixed effects and their interactions by generating analysis of variance/deviance tests with the 'car' package (Fox and Weisberg 2011) and removed non-significant interaction terms from final models ( $P > 0.25$ , Quinn and Keough 2002).

When both mean arrival and arrival synchrony were significant, we compared the relative magnitude of their effects on the given response. For each spatial block, we calculated the mean values of each level of one predictor over the three levels of the other. Then, within each block, we determined the relative change in the response (synchrony: [high – low] / high; mean: [early – late] / early). These values were then divided by the corresponding number of days of shift (synchrony = 8 d, mean = 20 d) and multiplied by 100 to yield percentages. This metric, the per-day relative change in the response, allowed us to most directly compare the effects of these two types of phenological shifts.

## RESULTS

### Prey survival

Overall, tadpole survival was low (10.2%), as expected in the presence of dragonfly predators. Survival was driven by the effects of arrival synchrony and mean arrival (Fig. 1A, Synchrony:  $\chi^2 = 28.86$ ,  $P < 0.0001$ ; Mean:  $\chi^2 = 20.15$ ,  $P < 0.0001$ ) but not the interaction between them (Synchrony  $\times$  Mean:  $\chi^2 = 0.88$ ,  $P = 0.927$ ), indicating that their effects were independent rather than synergistic. Survival declined with later mean arrival (early: 14.4%, medium: 8.4%, late: 7.9%; averaged across arrival synchrony treatments) and with lower synchrony (high: 14.9%, medium: 10.0%, low: 5.7%; averaged across mean arrival treatments). We compared the relative magnitude of the effects of mean and synchrony using the per-day relative change in survival (see *Methods: Statistical analysis*). For mean arrival, each additional day of shift later resulted in a 2.0% (95% confidence interval [CI]: 0.0%, 4.1%) decline in survival relative to early arrival (i.e., ten-day difference in relative arrival). For synchrony,

each additional day of shift in arrival (i.e.,  $\pm 0.5$  d outward from the mean arrival date) resulted in a 7.3% (95% CI: 5.3%, 9.3%) decline in survival relative to high synchrony (i.e.,  $\pm 0$  d). Therefore, the effects of shifts in synchrony were 3.7 $\times$  stronger than those in mean arrival.

### Prey mean size

Mean tadpole snout-to-vent length (SVL) decreased as arrival synchrony became higher but did not depend upon mean arrival (Fig. 1B, Synchrony:  $\chi^2 = 70.88$ ,  $P < 0.0001$ ; Mean:  $\chi^2 = 3.83$ ,  $P = 0.1477$ ). With low synchrony, mean SVL was 13.80 mm, which was 1.3 $\times$  and 1.6 $\times$  that for medium and high synchrony, respectively. Tadpole mean size was inversely correlated with tadpole survival ( $r = -0.62$ ,  $t = -5.65$ ,  $df = 52$ ,  $P < 0.0001$ ), likely because density determines per capita resource availability, and consequently growth rates.

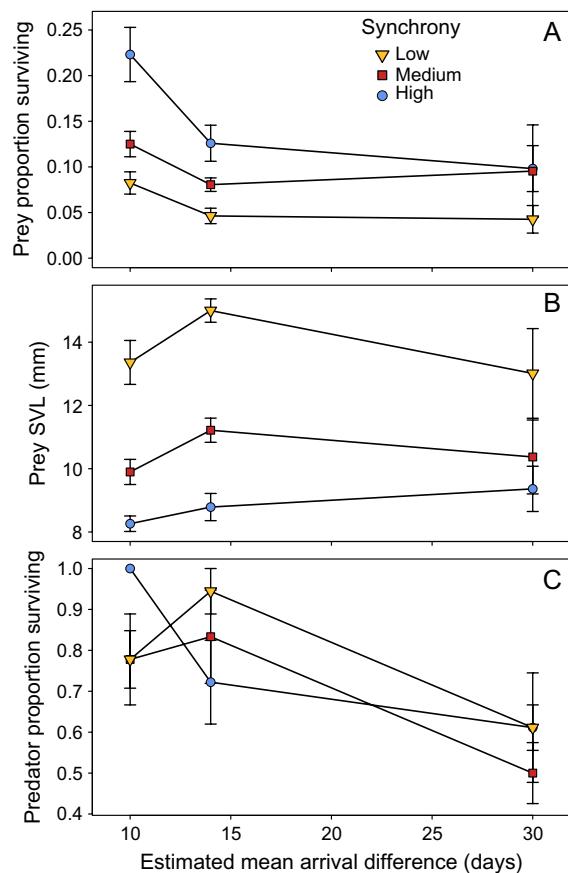


FIG. 1. Responses of the prey, *Hyla cinerea* tadpoles, and the predator, *Tramea carolina* dragonfly naiads, to variation in the mean and synchrony of prey arrival phenology. (A) Proportion of tadpoles that survived out of 180 per mesocosm. (B) Mean snout-to-vent length (SVL) of tadpoles. (C) Proportion of dragonfly naiads that survived out of three per mesocosm. There was no significant effect of prey phenological variation on predator mean size (see *Results*). Points represent treatment means  $\pm 1$  standard error (6 replicates). (Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com).)

### *Predator survival*

Across treatments, dragonfly survival was high (75.3%) and depended upon tadpole mean arrival only (Fig. 1C, Synchrony:  $\chi^2 = 1.24$ ,  $P = 0.5381$ ; Mean:  $\chi^2 = 14.07$ ,  $P = 0.0009$ ). When mean tadpole arrival was late (i.e., initial dragonfly size was large), there were 1.72 dragonfly survivors, which was 67% and 69% of that for early and medium tadpole arrival treatments, respectively. However, we think this effect is an artifact of the experiment (see *Discussion*), supported by the lack of correlation between dragonfly and tadpole survival ( $r = 0.09$ ,  $t = 0.64$ ,  $df = 52$ ,  $P = 0.5256$ ).

### *Predator mean size*

There was no effect of either mean arrival or arrival synchrony of tadpoles on mean dragonfly head width (data not shown;  $7.32 \text{ mm} \pm 0.51 \text{ SD}$ ; Synchrony:  $\chi^2 = 2.05$ ,  $P = 0.3580$ ; Mean:  $\chi^2 = 4.21$ ,  $P = 0.1218$ ). Of the 122 survivors, 85% were in the final instar, and the remaining individuals were in the penultimate instar.

## DISCUSSION

Phenologies can vary among years in diverse ways. Few studies have examined how these different types of phenological shifts affect species interactions, and to our knowledge, no others have evaluated the effect of two types of shifts simultaneously. In this study, we determined the consequences of changes in the mean and synchrony of prey phenology for predator–prey interactions. For the prey, we found that both types of shifts affected demographic rates, that their effects were independent, and that synchrony shifts had effects as strong, if not stronger, than mean shifts. Conversely, we found little effect of prey phenology on the predator. These results provide novel insight into the relative importance and net effect of different types of phenological shifts on the demographic rates of interacting populations.

### *Relative strength of different types of phenological shifts*

Studies of how phenological shifts affect species interactions have focused primarily upon how shifts in the timing of one species relative to another affect the outcome of interactions (Alford and Wilbur 1985, Wilbur and Alford 1985, Liu et al. 2011, Rafferty and Ives 2011). This is analogous to the shifts in mean timing employed in our study. Previous work on predator–prey interactions has demonstrated that as the phenology of a prey species shifts later relative to its predator, performance of the prey usually declines, oftentimes because the predator is growing (Brundage et al. 2014, Rasmussen et al. 2014, Nosaka et al. 2015). As the prey arrives later, it encounters larger predators, which can eat more and larger prey. In agreement with previous studies, we found that tadpole survival declined by 45% as dragonfly head width

doubled, which represented an estimated 20-d shift later in tadpole mean arrival (Table 1). Shifts in mean phenological timing alter the ontogenetic stage at which species encounter one another across a diversity of systems, ranging from plants (Korner et al. 2008, Kardol et al. 2013) to fishes (Geange and Stier 2010) to sessile marine invertebrates (Dean and Hurd 1980). This growing body of work spanning a broad spectrum of taxonomic groups and types of interactions suggests that changes to interaction strength could be predicted, in part, from knowledge of how variation in phenological timing affects relative body size.

Few experimental studies have examined how prey synchrony affects predator–prey interactions (Tucker et al. 2008), even though changes in synchrony should be just as likely as changes in the mean. Observational studies have often suggested that synchronization of phenological events by prey can reduce losses to predation via predator satiation (Findlay and Cooke 1982, Lalonde and Roitberg 1992, Williams et al. 1993). However, some theoretical (Ims 1990) and experimental work (Tucker et al. 2008) suggests that synchrony might not effectively satiate predators in many contexts. Our experimental results corroborate the idea that high prey synchrony can satiate predators. Across a range of mean arrival times, high prey arrival synchrony resulted in significantly higher prey survival, compared to low synchrony (Fig. 1A). Not only is this one of the few experiments to examine the consequences of synchrony for predator–prey interactions, but it is also, to our knowledge, the first to compare the relative importance of two different types of shifts. It is therefore noteworthy that our results show that the effects of synchrony shifts on prey survival can be even stronger than those of mean shifts (3.7× stronger in this case). One caveat that complicates comparison between these two types of shifts is that the mean shifted over a larger time range than did synchrony (20 vs. 9 d, respectively). If the effects of phenological shifts on survival are decelerating, then our metric could overestimate the strength of synchrony shifts relative to mean shifts. Regardless, the effects of synchrony shifts on survival were also strong enough to significantly affect prey growth rates, while the effects of mean shifts were not. These results indicate that synchrony shifts can be at least as important as mean shifts for predator–prey interactions.

### *Net effect of different types of phenological shifts*

Multiple attributes of a phenological distribution can vary among years (e.g., mean, synchrony, skewness) (Sparks et al. 2005, CaraDonna et al. 2014). However, we know almost nothing about the net effect of these concomitant phenological shifts on populations of interacting species. Different types of phenological shifts could differ in the magnitude and direction of their effects on demographic rates, and they could interact to have synergistic effects on these rates. These complexities

make it difficult to predict their net effect a priori. In this study, we found that shifts in the mean and synchrony of tadpole phenology had independent, rather than synergistic, effects on tadpole survival. Survival declined with later mean arrival and lower arrival synchrony. This has important implications for annual recruitment of individuals into the adult population. When tadpole phenology is asynchronous and late relative to predators, recruitment likely will be very low (Fig. 1A; 4.3% survival), and when it is synchronous and early, recruitment likely will be relatively high (Fig. 1A; 22.3% survival). The combination of either early arrival with low synchrony or late arrival with high synchrony could yield similar recruitment rates because of the opposing effects on survival of mean and synchrony in these scenarios (Fig. 1A; 8.2% vs. 9.8% survival, respectively). Our results emphasize that we often cannot predict effects of phenological shifts using simple metrics (e.g., first occurrence of phenological event) but instead need to account for changes in phenological distributions.

Although we observed that shifts in mean and synchrony had independent effects, synergistic effects are still likely possible. For example, the effects of variation in prey arrival synchrony on prey survival could disappear if prey mean arrival occurred even later than in our study (i.e., predators were even larger) or if densities of predators relative to prey were higher. In both scenarios, the number of prey arriving, even with high synchrony, likely would be insufficient to satiate predators, and therefore might not significantly increase the proportion of prey surviving to a size refuge. Thus, while our study provides first insights into the net effect of concomitant phenological shifts, we need more studies like ours across a range of conditions, systems, and interaction types to get a general understanding of when to expect independent vs. synergistic effects.

#### *Consequences of phenological shifts for prey vs. predator*

When phenological shifts occur, it remains unclear whether the two species involved in an interaction experience similarly-strong effects on their populations or whether the effects are asymmetric. For predator-prey interactions, timing likely has stronger implications for prey than predator because the prey is risking its life, while the predator is only risking a meal (Dawkins and Krebs 1979). Previous studies on the consequences of shifts in mean timing for predator-prey interactions suggest that prey do experience stronger effects due to timing than do predators (Sredl and Collins 1991, Brundage et al. 2014, Nosaka et al. 2015). For example, in a study of interactions between a tadpole prey and a salamander predator, Nosaka et al. (2015) found that phenological shifts affected survival, development time, and size at metamorphosis of the prey while none of these responses were significantly affected for the predator. In our study, the effects of phenological shifts on the prey were also stronger than those on the predator. Shifts in

the mean affected prey survival and shifts in synchrony affected prey survival and growth. Conversely, only shifts in mean prey arrival affected predator survival, and there was no effect of prey phenology on predator growth. Importantly, we argue that the effect of mean shifts on predator survival was an experimental artifact. The effect was driven by the relatively lower predator survival in the late mean prey arrival treatments. Dragonflies stocked in these treatments were the largest/oldest and therefore closest to completing development. No emergence structures were provided for dragonflies to eclose as adults, so dragonflies in these treatments were more prone to drowning than those in other treatments. Overall, the dragonfly predator was likely unaffected by prey phenology because dragonfly densities were low (but realistic) and because alternative prey were available to these generalist predators (e.g., zooplankton, chironomid midge larvae). It is possible that the demographic rates of generalist predators are not strongly affected by the phenological timing of any one potential prey species as long as other prey species are present in sufficient abundances. However, we hypothesize that the demographic rates of specialist predators would show a stronger response to shifts in the phenology of their prey.

#### CONCLUSIONS

To understand the impacts of climate change on natural communities, it is essential that we determine how phenological variation affects interactions among species. Our study demonstrates the power of manipulative experiments for addressing some of the many outstanding questions about the ecological consequences of phenological shifts. We evaluated the independent and combined effects of shifts in the mean and synchrony of prey phenology on predator-prey interactions, which yielded novel insight. We determined that synchrony shift effects were at least as strong as those caused by mean shifts and that the combined effect of these two types of shifts was additive rather than synergistic. Studies such as this are important for understanding the net effect that phenological shifts have on species interactions. When incorporated with field observations and theoretical models, experiments like this should prove valuable for developing a predictive framework to understand how phenological shifts affect community dynamics (van Asch et al. 2007, Rafferty et al. 2013).

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