As temperature increases, predator attack rate is more important to survival than a smaller window of prey vulnerability

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Abstract. Climate change can have strong effects on species interactions and community structure. Temperature-dependent effects on predator–prey interactions are a major mechanism through which these effects occur. To understand the net effects of predator attack rates and dynamic windows of prey vulnerability, we examined the impacts of temperature on the interaction of a caterpillar (*Arctia virginalis*) and its ant predator (*Formica lasioides*). We conducted field experiments to examine attack rates on caterpillars relative to temperature, ant abundance, and body size, and laboratory experiments to determine the effects of temperature on caterpillar growth. We modeled temperature-dependent survival based on the integrated effects of temperature-dependent growth and temperature- and size-dependent predation. Attack rates on caterpillars increased with warming and ant recruitment, but decreased with caterpillar size. Caterpillar growth rates increased with temperature, narrowing the window of vulnerability. The model predicted that net caterpillar survival would decrease with temperature, suggesting that *A. virginalis* populations could be depressed with future climate warming. Theoretical work suggests that the net outcome of predator–prey interactions with increasing temperature depends on the respective responses of interacting species in terms of velocity across space, whereas the present study suggests the importance of effects of temperature on prey window of vulnerability, or "velocity" across time.

Key words: ants; caterpillars; climate change; predation; temperature dependence; trophic interactions; window of vulnerability.

Introduction

Climate change is causing widespread alteration to species' ranges, life histories, and phenologies (Parmesan 2006). These changes impact species interactions, population dynamics, and, ultimately, community structure and function (Cramer et al. 2001, Tylianakis et al. 2008). Altered phenologies have received the most study but climate change can also have direct impacts on interactions, independent of phenological effects (Tylianakis et al. 2008). There are various mechanisms through which climate change can affect species interactions, but the effects of temperature are particularly pervasive due to the strong effects of temperature on metabolism. While all aerobic organisms have the same basic biochemical mechanisms of metabolism, ectotherms, which have metabolic rates directly tied to ambient temperatures, make up a majority of the planet's biodiversity and biomass (Gillooly et al. 2001). Increased metabolic rates can cause increased attack rates by predators (Rall et al. 2010); this can in turn cause increased interaction strength with prey, leading ultimately to changes in density or dynamics of prey and to cascading effects on broader community structure (Berlow et al. 2009, Petchey et al. 2010). Temperature-augmented metabolic rates can also result in increased growth rates of prey (Kingsolver et al. 2011), which can also have broader effects through altered interactions with predators (Benrey and Denno 1997, Culler et al. 2015). For

example, larger prey are often less vulnerable to predation and temperature-augmented growth rates decrease the time for prey to reach a size refuge.

A body of theoretical work has investigated the effects of warming on ectothermic predator–prey systems (Dell et al. 2014, Uszko et al. 2017). Modeling and experimental studies make diverse predictions, depending on model assumptions or system-specific temperature responses. These predictions include increased population stability (Fussmann et al. 2014), decreased stability (Beisner et al. 1997, Vasseur and McCann 2005), extinction (Petchey et al. 1999, Rall et al. 2010, Vucic-Pestic et al. 2011), increased top-down control (O'Connor et al. 2009, Hoekman 2010), or complex responses to temperature in predator–prey systems (Amarasekare 2015). These varied predictions have more recently been synthesized in a unified model based on assumptions about the effects of temperature on carrying capacity and predator performance (Uszko et al. 2017). This body of work is largely founded on laboratory and microcosm studies. These studies have repeatedly shown that increased temperatures result in increased predation rates by invertebrate predators (e.g., Rall et al. 2010, Vucic-Pestic et al. 2011, Culler et al. 2015, Karban et al. 2015) at least within a "biologically relevant temperature range" before thermal performance maxima are reached (Englund et al. 2011). However, fewer studies have tested the effects of increased temperature on predation rates in the field (but see Barton and Schmitz 2009).

Temperature can have strong effects on prey development rates. This can in turn have strong effects on prey survival. The slow-growth–high-mortality hypothesis (Benrey and

Denno 1997) proposes that longer development times can expose vulnerable stages of insects to natural enemies for a longer time, resulting in higher mortality. If vulnerability to predation varies with ontogeny, the more rapid escape of prey from vulnerable stages can potentially offset increased predator attack rates entirely. Variable vulnerability to predation over ontogeny can occur through various mechanisms. Juveniles of taxa that undergo metamorphosis may be more vulnerable than adults and thus will experience less predation risk if they reach adulthood faster (Culler et al. 2015). Consumption of prey is often size dependent, sometimes due to gape-limited predators, such that if prey grow faster, they will reach a size refuge at which predation risk is minimal (Anderson et al. 2001, Taylor and Collie 2003). Because a wide range of taxa may have both stage or size-dependent predation risk and have temperature-dependent growth it is important to examine the combined effects of increased attack rates by predators and increased development rate of prey to understand the net effect of temperature on predator–prey systems.

In this study, we examined the effect of experimental warming on the interaction between the ant *Formica lasioides* and its prey, caterpillars of the tiger moth, *Arctia virginalis* (formerly *Platyprepia virginalis*). Previous long-term work on *A. virginalis* at Bodega Marine Reserve, Sonoma, California, has shown large annual fluctuations in caterpillar densities (Karban and de Valpine 2010), and suggested that precipitation and ant predation may be important drivers of observed dynamics (Karban et al. 2017). Ant predation has been shown in the laboratory to be affected by temperature (Karban et al. 2015), and by the depth and quality of litter substrate (Karban et al. 2013). The region where these studies have been conducted, the central coast of California, is expected to become warmer and drier with future climate change (Weare 2009, Li et al. 2014). Given these climate projections and the importance of temperature for this system, we expect that *A. virginalis* dynamics will change as a result of increased predator attack rate and accelerated larval development at warmer temperatures. We tested the effects of experimental warming on this interaction in the field and laboratory, and created a model using our experimental data to help understand how these interacting climate-driven factors are likely to impact the dynamics of *A. virginalis*.

METHODS

Warming tent predation experiment

To determine the effects of temperature on caterpillar predation by ants in the field, we exposed caterpillars in enclosures to ants inside and outside warming tents. Experimental warming tents were constructed at Bodega Marine Reserve, Sonoma, California (38°19′7.16″ N, 123°4′17.43″ W) on 17–18 July 2017. Ten tents, measuring 2 × 2 × 2 m were constructed at or near long-term monitoring plots for *A. virginalis* caterpillars. Tents were domes with PVC frames covered by clear polyethylene plastic sheeting (6 mil; Home Depot, Atlanta, Georgia, USA) on their sides up to 1 m and open tops. On 18 July, four deli containers (11 cm diameter), each with 3 s instar *A. virginalis*

caterpillars and approximately 1 g of fresh lupine (*Lupinus arboreus*) flowers were placed inside and an equal number were placed 0.5 m outside the tents. Containers had plastic lids and window screen bottoms that allowed ants to enter and leave but prevented caterpillars from leaving. Temperature loggers (iButton; Maxim Integrated, San Jose, California, USA) were placed inside and outside of each tent at the same time and recorded temperatures every 1 h. On 21 July, the number of missing caterpillars in each container was recorded (Trial 1), any missing or dead caterpillars were replaced, and fresh lupine petals were added to each container. To account for spatial variation of ant density, we recorded the number of ants recruiting to bait stations to use as a covariate in our model. This was calculated as the total number of ants recruiting to bait at each tent site, both inside and outside of tents. Ant baits consisting of supersaturated sugar-water-soaked cotton balls on petri dishes were placed out at the same time at sites inside and outside of each tent. These baits were revisited after several hours when the number of *F. lasioides* recruiting to baits was recorded. We have previously found that when caterpillars are placed out in the field they were usually discovered and killed by ants within a few hours or remained safe for the duration. On 24 July, the number of missing caterpillars in containers was measured for a second time (Trial 2), and temperature loggers were retrieved. Since caterpillars were too large to leave the containers, any missing caterpillars were assumed to have been killed and consumed by ant predators. We have observed ants killing, dismembering, and removing these dismembered caterpillars from our experimental containers on many occasions.

Data were analyzed using mixed effects models in R (v. 3.4.3, R Core Team, 2017), using the lme4 package (Bates et al. 2014). All models included site (tent location) as a random effect. The average warming effect of tents was assessed using daytime temperature measurements, from 07:00 to 21:00, in a linear mixed effects model. The effect of warming treatment on ant recruitment was tested with a Poisson mixed model, with trial included as a fixed effect, and an individual-level random effect to account for overdispersion (i.e., each replicate was a level in the random effect; see Harrison 2014). Predation on caterpillars by warming treatment was assessed using a binomial mixed model, with total number of *F. lasioides* recruiting to baits at each site, trial, an interaction between treatment and ant recruitment, and an individual level random effect to account for overdispersion included as predictors.

Temperature-dependent growth experiment

To assess the effects of temperature on caterpillar growth rates, we reared early instar caterpillars in the laboratory over a range of temperatures. On 6 June 2017, caterpillars, each weighing 1 or 2 mg, were placed in individual vented plastic containers (7 cm diameter condiment cups) and reared in growth chambers at constant temperatures of 10°, 15°, 20°, and 25°C. These temperatures reflect the natural range of summer temperatures at Bodega Bay (July and August average daily minimum 11°C to maximum 15°C) and temperatures in the field-warming experiment (average 21.7°C control and 22.9°C warming). Fifty-two caterpillars

were reared at each temperature. Caterpillars were fed organic romaine lettuce and occasional lupine petals and foliage every 3 d. Caterpillars were weighed every three weeks, with a total of four subsequent weighings ending on 26 August 2017. Individual growth rates from each weighing period to the next were calculated for each caterpillar as ln (W_t/W_{t+1}). The dependence of caterpillar growth rate on temperature as a categorical predictor was tested using a mixed effects model, with weighing date as a random effect. Temperature as a continuous predictor was also included in a second linear model of caterpillar growth rate.

Size dependent predation experiment

To measure the effects of caterpillar size on predation rates in the field, we conducted experiments exposing caterpillars of different sizes to ant predators. Lab-reared caterpillars ranging from 10 to 571 mg were placed singly in mesh-screened deli containers (11 cm diameter) at Bodega Bay Marine Reserve to assess size-dependent predation rates. Caterpillars could not escape through the mesh although ants were able to enter and leave. Sixty-six caterpillars were deployed on 13 August 2017 and retrieved after 6 d, and 81 caterpillars were deployed on 27 August and retrieved after 7 d. Caterpillars were counted as consumed or survived when deli containers were recovered. Survival was compared to the log of caterpillar mass with and without trial as a covariate in a binomial generalized linear model.

Model of temperature-dependent survival

A model of temperature-dependent survival of caterpillars was constructed to assess survival as affected by temperature-dependent growth, predation, and size-dependent predation. Functions of daily growth and predation rates by temperature and size-dependent predation were derived from data using generalized linear models. Size-dependent predation was expressed as a fraction of the maximum predation rate by size, which was for the smallest individuals. Data for temperature-dependent predation were from Karban et al. (2015), but modeled with temperature as a continuous predictor in a binomial generalized linear model. The form of the model of temperature-dependent survival was as follows:

$$P = \prod_{i=1}^{n} \frac{\exp\left\{a\left(x_0^{r(T)t_i}\right)\right\}}{1 + \exp\left\{a\left(x_0^{r(T)t_i}\right)\right\}} \left(\frac{\exp\{b(T)\}}{1 + \exp\{b(T)\}}\right) \quad (1)$$

where t is time in days, x_0 is initial caterpillar mass (10 mg), T is temperature, r is instantaneous daily caterpillar growth rate as a function of temperature, a represents size-dependent daily predation, and b is daily temperature-dependent predation rate. The first term is the inverse logit transformed size-dependent predation rate derived from a binomial model, with caterpillar size growing each day at a temperature-dependent rate. The second term is the inverse logit-transformed temperature-dependent predation rate also derived from a binomial model (see Appendix S1). The model calculates the daily temperature and size-dependent predation risk of a caterpillar that is iteratively grown at a temperature dependent growth rate. The predation risks of all the days are then multiplied together to determine predation risk across the entire larval stage. The product of the daily predation risk of each consecutive day was generated for values of caterpillar masses <400 mg ($x_0^{r(T)t} < 400$) for temperatures from 10° to 25°C.

To illustrate the relative contribution of the different components of the model to larval predation risk with temperature, sensitivity analyses were conducted. Versions of the model without size-dependent predation, temperature-dependent growth, and temperature-dependent predation were run. For the model without size-dependent predation risk, we used the predation rate for the smallest caterpillars from our laboratory predation trials for all caterpillar sizes. For the model without temperature-dependent growth, the growth rate of caterpillars was fixed at that measured for 10°C. For the model without temperature-dependent predation, the predation rate was fixed at the rate measured in the laboratory at 10°C, but it was modified by increasing caterpillar size.

RESULTS

The tents were successful at raising daytime temperatures at ground level. The ground temperature inside of tents was 1.2° ± 0.4°C (mean ± SE) above average ambient temperature (β = 1.2 [95% CI:0.42–1.99], $t = 3.0$, $P = 0.002$). These elevated temperatures are conservative relative to climate change models of coastal California for the near future, with one study projecting 2°C of warming by the 2060s (Li et al. 2014).

Rates of predation were affected by elevated temperatures in the field experiment. After controlling for ant density, caterpillars were more likely to survive at ambient temperatures than at elevated temperatures in both experimental trials (Fig. 1). Predation of caterpillars by ants was significantly higher in trial 2 in both treatments than in trial 1 (β = 0.2 [95% CI, 0.09–0.35], $z = -3.4$, $P < 0.001$, Fig. 1). There was a significant interaction between total *F. lasioides* recruiting to baits and treatment effect in both trials (β = 0.49 [95% CI, 0.48–0.50], $z = -2.76$, $P = 0.02$, Fig. 1). This means that at higher rates of ant recruitment, survival of caterpillars in the warming treatment became lower than controls. Ant recruitment to baits was not affected by elevated temperatures in the field experiment ($P > 0.05$).

Caterpillar survival rates in size-dependent field predation trials increased significantly with log caterpillar mass (β = 0.76 [95% CI, 0.38–0.46], df = 106, $z = 3.17$, $P = 0.001$, Fig. 2a), and were not significantly different between trials. Caterpillar growth rates were significantly higher at higher temperatures (mixed model, $\chi^2 = 214.5$, $P < 0.001$; linear model, β = 0.058 ± 0.005, df = 547, $t = 11.33$, $P < 0.001$, Fig. 2b). Caterpillar survival rates in laboratory predation trials were significantly lower at higher temperatures (β = 0.76 [95% CI, 0.54–0.91], df = 146, $z = -4.15$, $P < 0.001$, Fig. 2c).

In the model of temperature-dependent survival, caterpillar survival continuously declined with increasing temperature (Fig. 2d). This model included temperature-dependent caterpillar growth as well as temperature- and size-dependent predation rates. The sensitivity analyses illustrated that
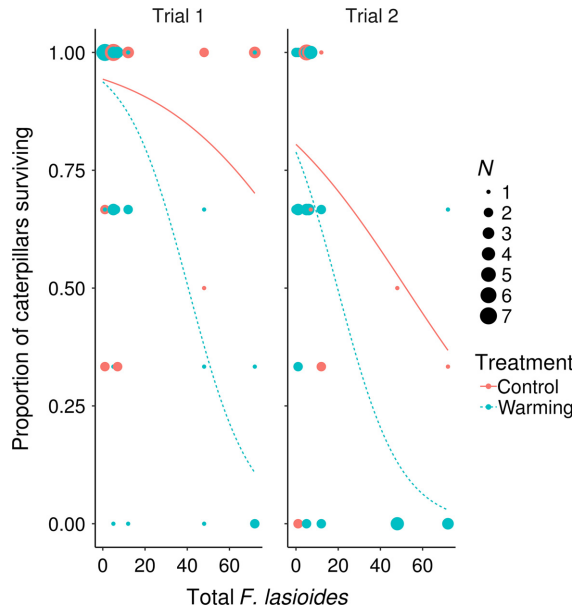
FIG. 1. The proportion of caterpillars remaining in deli containers are shown by treatment (red, controls; blue, warming), and number of *Formica lasioides* recruiting to baits at each container (*N*). Proportions are out of three caterpillars and the number of samples falling on each position is represented by the size of the circle.

size- and temperature-dependent predation rates had the largest impact on caterpillar survival (Fig. 3). In the model without size-dependent predation, caterpillar survival was much lower and declined quickly to zero. In the model without temperature-dependent predation, caterpillar survival was higher and increased with temperature. In the model

without temperature-dependent growth, caterpillar survival declined somewhat more quickly with temperature than in the full model.

DISCUSSION

The warming experiment showed that caterpillar predation by ants was higher with experimentally elevated temperature under field conditions. The interaction between ant recruitment and caterpillar survival demonstrated that the effect of the warming treatment on caterpillar survival was due to ant predation; caterpillar survival was lower in warming tents than controls only when ants were present, and this effect was stronger with increasing ant abundance. The decreasing rate of predation with caterpillar body size provides a mechanism by which increased caterpillar growth rates as temperature increases can increase overall survival. However, the integrated model of caterpillar survival (Eq. 1) showed that the net effect of warmer temperatures was negative for caterpillars; increased growth and lower predation at larger caterpillar size did not compensate for increased attack rates with higher temperature, leading to decreasing survival with temperature. This contrasts with other studies in which prey growth rates increased enough with temperature that prey species reached a size refuge fast enough to overcompensate for the increased attack rates of ectothermic predators, leading to increasing prey survival with temperature (Anderson et al. 2001, Taylor and Collie 2003). The relative effects of temperature on predator attack rate and prey window of vulnerability determined the net effect of temperature on the predator–prey interaction. This is seen in the sensitivity analyses (Fig. 3), where the removal of the
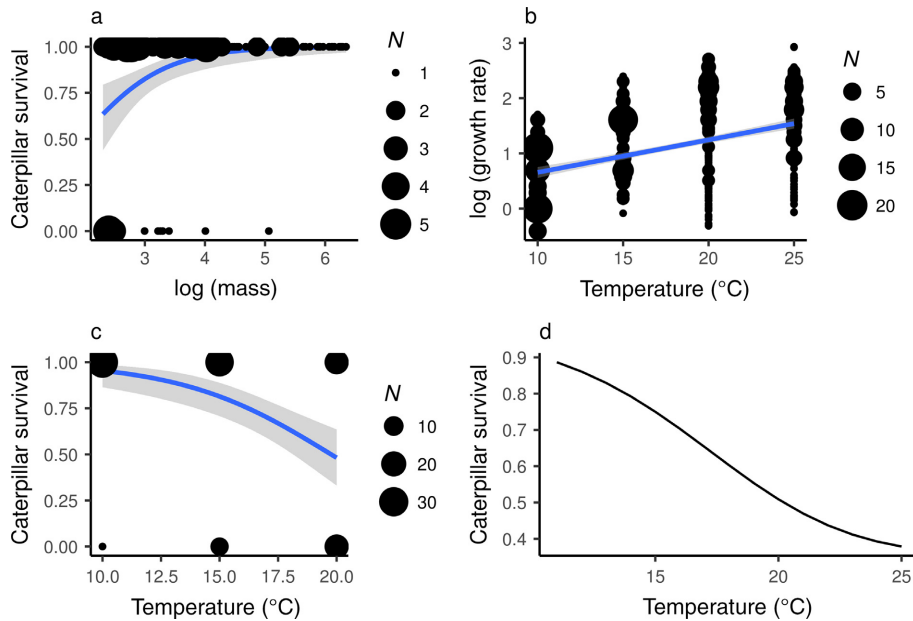

FIG. 2. (a) Survival of caterpillars preyed upon by *Formica lasioides* as a function of log caterpillar mass (measured in mg) in the field with 95% confidence intervals. (b) Log growth rate of caterpillars by temperature with 95% confidence intervals. (c) Survival of caterpillars preyed upon by *F. lasioides* by temperature in the laboratory with 95% confidence intervals, from Karban et al. (2015). (d) Predicted survival probability of caterpillars by temperature from a model (Eq. 1) based on a combination of temperature-dependent growth rates, size-dependent predation rate, and temperature-dependent predation rate.
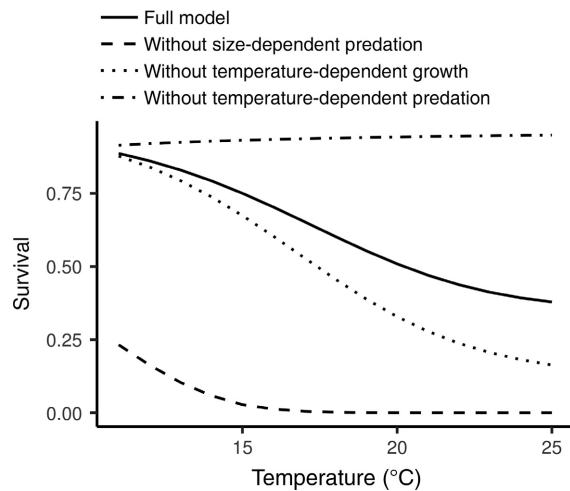
FIG. 3. Sensitivity analysis of models of temperature-dependent caterpillar survival by removing parameters. Line type shows (1) the full model, (2) the model without size-dependent predation rate, (3) the model without temperature-dependent growth, and (4) the model without temperature-dependent predation.

temperature dependence of the predator attack rate had a much larger effect on caterpillar survival than removing temperature dependence of caterpillar growth rate. This result suggests that the comparison of positive effects on prey growth but negative effects of predation is important to understand the effects of temperature on predator–prey interactions.

In this study. we measured an overall predation rate rather than a per-individual attack rate as typically measured in laboratory studies (e.g., Vucic-Pestic et al. 2011). This means that we sacrificed precision in our ability to calculate the per capita effects of temperature on predators in favor of ecological realism. However, our statistical model of the field warming experiment included ant recruitment to baits as an index of ant density, so the significant interaction between the effects of ant recruitment and warming treatment on caterpillar survival showed that for a given index of ant abundance, attack rates were higher with higher temperatures. Furthermore, temperature-dependent increases in attack rate may be caused both by higher activity rates and by faster gut evacuation times (Vucic-Pestic et al. 2011). *Formica lasiodes* is a colonial species that brings most foraged food items back to the colony and does not directly consume acquired food, so temperature-dependent gut evacuation time is unlikely to be relevant in this case. Therefore we assume that higher activity rate was the mechanism driving increases in attack rate in this system.

In this work, we assumed ad-libitum food access for growing caterpillars in the field; this assumption is typically true of later instar caterpillars (Karban et al. 2017). However, this may not be the case in the summer when early instars are developing, given highly variable precipitation in California. Organisms with limited food resources are likely to have unimodal responses of growth rate to temperature, where the maximum growth rate is below maximum metabolic rate (Elliott 1982). This violates our assumption of linearly increasing growth rates with temperature, and would

likely increase the observed negative impact of temperature on caterpillar survival rates. Increased temperatures also have the potential effect of decreasing adult sizes even while increasing growth rates (Sweeney et al. 2018). Our work did not consider such possible effects; however a larval size refuge was reached at sizes considerably lower than normal pupation mass (Fig. 2a), so this process was unlikely to affect predation rate by ants. Decreased adult body sizes caused by increasing temperatures however could potentially negatively affect population growth rates due to lowered adult fecundity as has been suggested in other system (Sweeney et al. 2018); in the present paper, however, we focus on predator–prey interactions within the larval stage.

The increase in predation rate (~75%) at sites with higher ant densities that resulted from a relatively small amount of warming (avg. 1.2°C) in the field experiment suggests that climate warming could result in increased top-down control of caterpillars. This matches the predictions of some previous work regarding temperature-dependent effects on predator–prey interactions (O'Connor et al. 2009, Hoekman 2010). If the future climate of coastal California is warmer and drier as models have predicted (Weare 2009, Li et al. 2014), populations of *A. virginalis* could be depressed relative to current levels. Models and experiments presented here predict increased predation by ants due to augmented attack rates associated with higher temperature. Previous work that focused on expectations of lower future precipitation predicted higher predation by ants due to higher ant densities and fewer refuges for caterpillars (Karban et al. 2017).

Similar work comparing the net effects of temperature-augmented predation vs. development rates on survival rates in Arctic mosquitoes suggested that, at higher temperatures, mosquitoes would have higher survival, ultimately resulting in higher mosquito populations and impacts on ungulates in the surrounding ecosystem (Culler et al. 2015). Work on damselfly larvae feeding on larval amphibians similarly showed that faster tadpole growth allowed prey to escape predators and attain higher survival rates at higher temperatures (Anderson et al. 2001). Another study examining sand shrimp preying on larval winter flounder found similarly that winter flounder escaped stages vulnerable to sand shrimp faster, though these benefits to flounder disappeared at higher temperatures (Taylor and Collie 2003). The present study, in contrast, found an opposing result, that increased growth rates of prey did not compensate for higher attack rates of predators.

Modeling work has suggested that the relative response rates of predators and prey to temperature will determine the outcome of predator–prey interactions (Dell et al. 2014, Ohlund et al. 2014). However, such work has thus far only considered the effects of temperature on the velocity of predator and prey movements and not effects of augmented prey growth rate on the window of prey vulnerability. Many ectothermic species are likely to experience stage- or size-dependent predation. Stage-dependent predation has been found to be important for many insects and amphibians that have complex lifecycles and undergo metamorphosis (Werner 1986, Benrey and Denno 1997), whereas size-dependent predation is probably important for many taxa but has been best documented in aquatic systems (e.g., Paine 1976,

Mittelbach 1981, Christensen 1996). Since these effects may be common in ectothermic species, the effect of temperature through increased prey growth rates on the window of vulnerability, or the "velocity" of prey through time as a means of escaping predators, is a good candidate to be included in future models of predator–prey interactions.

Besides size- and stage-dependent predation, complex lifecycles are an important life-history trait that is likely to impact the effects of temperature on population dynamics, but they have not generally been examined in theoretical work. This is probably because the temperature-dependent responses of growth and survival of ectothermic organisms with complex lifecycles are not well understood (Kingsolver et al. 2011). Species with complex lifecycles often undergo ontogenetic niche shifts (such as *A. virginalis*; Grof-Tisza et al. 2015) and experience different abiotic and biotic environments during different stages. In addition, different life stages can be differentially sensitive to temperature (Amarasekare and Sifuentes 2012). As such, the effects of temperature on species with complex lifecycles relative to those of their predators or prey are likely to be hard to predict in generalized temperature-dependent predator–prey models. Analyses thus far have not examined broader patterns of temperature effects on organisms with complex lifecycles to identify key factors or traits that affect survivorship and growth rate. One study examining three species suggested that the most temperature-sensitive life stage should have the greatest effect on survivorship (Amarasekare and Sifuentes 2012). The effects of some traits on temperature-dependent predator–prey interactions, however, have been considered in theoretical and experimental work: predator size (Brose 2010, Rall et al. 2010) and predator hunting mode (Barton and Schmitz 2009, Dell et al. 2014) have both been found to be important factors that impact how temperature affects predator–prey population dynamics.

In summary, this study represents a rare field demonstration showing increased attack rates by an ectothermic predator on its prey at higher temperature in which the net outcome is dependent on the relative impact of temperature on predator attack rates and prey window of vulnerability. Our analysis considered temperature-augmented prey growth and differed from other similar studies by finding a negative net outcome for the prey associated with biologically relevant elevated temperatures predicted for future climates. That increased temperature can increase attack rates of predatory ectotherms is a key assumption of a growing body of modeling literature, which has thus far mostly relied on laboratory and microcosm work; these data are not always accurate representations of how species and interactions will perform in situ. This and other studies that included the effects of temperature on the prey window of vulnerability showed that this is an important factor that might influence the net effects of temperature in many predator–prey systems. Finally, more field experiments and detailed work considering the broader effects of temperature will better serve to test the predictions of existing theoretical and laboratory work on the effects of climate warming on predator–prey systems. This will help solidify our understanding of how climate warming is likely to reshape ecological communities through altering these interactions.

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