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Night warming alters mean warming effects on predator–prey interactions by modifying predator demographics and interaction strengths

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Abstract

1. Temperatures are increasing globally, but this increase is not symmetrical; instead, night-time minimum air temperatures increase faster than daytime maximum temperatures. However, we still know little about when and how this differential increase in maximum versus minimum air temperatures affects ecological interactions between species. Understanding the connection between different types (night vs. day) of warming and interspecific interactions is essential to predict the ecological consequences of climate change for natural ecosystems.

2. Here we used experiments in a common predator (lady beetle)–prey (aphid) system to examine how night warming, thermal regime (constant vs. fluctuating) and prey density influence demographic rates and per capita feeding rate and thus predation pressure. We mainly focused on the demographic variables and prey consumption as well as energy-related variables of the predators to understand how changes in night-time temperature, temperature regime and prey density affect predator performances and to differentiate these effects between constant and fluctuating thermal conditions.

3. We found that warming effects on most of the individual demographic rates and per capita consumption rates of the predator differed between constant and fluctuating regimes. These differences scaled up to alter population stage structure and population growth rate of the predator and ultimately the predation pressure in our system. Furthermore, warming had stronger and negative consequences on predator population growth and thus predation pressure in constant regime, but little or even positive effects under fluctuating conditions. Importantly, these results are consistent across prey densities.

4. Our results suggest that compared to night warming, predictions based on mean warming can under- or overestimate species demographic rates and per capita predation effects, causing inaccurate or even misleading expectations on population structure, long-term population growth and interspecific interactions. These results emphasize the importance of accounting for both ecologically relevant diurnal temperature cycle and lifelong demographics and per capita consumption when assessing how warming affects interspecific interactions. Our findings thus provide better understanding of how night warming will affect predator–prey

interactions and energy flux within trophic cascades and also have implications for predicting the consequences of top-down control in natural and agricultural ecosystems under climate change.

1 | INTRODUCTION

The global mean surface air temperature has risen substantially during the 20th century (IPCC, 2012), and this temperature increase can affect trophic interactions around the globe (Daugaard et al., 2019; Harmon et al., 2009; Petchey et al., 1999). Importantly, the rise in mean air temperatures is largely driven from a faster rate of increase in daily minimum (night) than maximum (day) temperatures (Donat & Alexander, 2012; Easterling et al., 1997). However, most previous work on warming has focused on increase in average temperature (either constant or equal night and day) or just day temperature (Rall et al., 2010; Uszko et al., 2017; Vucic-Pestic et al., 2011). Recent studies indicate that daytime versus night-time warming may lead to different or even misleading thermal effects on organisms' performance (Ma, Ma, et al., 2021; Speights et al., 2017; Zhao et al., 2014) and interspecific interactions (Barton & Schmitz, 2018; Higashi et al., 2020; Speights & Barton, 2019), but it is still poorly understood how this differential increase in maximum versus minimum temperature affects long-term population structure, per capita prey consumption and interspecific interaction dynamics. Yet, understanding the connection between different types (night vs. day) of warming and interspecific interactions is essential given that interspecific interactions can be more important than responses of individual species in predicting the ecological consequences of climate change for natural ecosystems (Ockendon et al., 2014).

Night warming can influence interspecific interactions in two key ways: via direct effects on species physiologies (Dell et al., 2014; Gilman, 2017) and via changes in per capita interaction strength (Boukal et al., 2019; Gibert, 2019; Ma et al., 2020). Night warming represents an increase in the minimum temperature, and this increase can have different effects on a species' physiology than an increase in mean or max (Speights et al., 2017). For example, in areas with colder climates, warmer nights are expected to reduce cold stress and thus may have positive effects on organisms (Barton & Schmitz, 2018). In contrast, in areas with hot climates, lower night temperatures may allow individuals to recover from heat stress experienced during day time (Bai et al., 2019; Zhao et al., 2014). In this scenario, night warming is likely to cause decreased probability of recovery and thus exacerbate the negative impacts of daily extreme high temperatures (Ma, Ma, et al., 2021; Speights et al., 2017). Therefore, changes in night-time temperatures are expected to be of similar or even greater importance in determining warming effects on demographic traits (and thus population structure and abundance) than changes in daytime temperatures (Barton & Schmitz, 2018; Ma, Ma, et al., 2021; Speights et al., 2017; Zhao et al., 2014).

Besides these physiological effects, night warming has also the potential to change per capita interaction strength (Barton & Schmitz, 2018; Ma et al., 2020; Speights & Barton, 2019), leading to both bottom-up and top-down effects that influence predator–prey interactions (Barton & Schmitz, 2018; Fussmann et al., 2014). On the one hand, night warming may directly increase the temperature-dependent prey consumption by nocturnal predators (Miller et al., 2017) and thus result in strengthened top-down effects influencing interspecific interactions (Speights et al., 2017). On the other hand, night and day warming may lead to different predator–prey interactions indirectly via constraining species foraging activity due to the differential thermal sensitivities between prey and their predators (Barton & Schmitz, 2018; Dell et al., 2014; Gilman, 2017). For example, day warming may force heat-sensitive predators to seek thermal refuges in lower part of the plant canopy and away from their heat-tolerant prey, which may result in an increased prey density. However, night warming may not affect predator thermoregulatory behaviour and instead lead to an increased activity and thus cause the prey population to decrease (Barton & Schmitz, 2018).

Overall, this suggests that night warming may have different effects on interspecific interactions than what would be expected from a similar increase in mean or daytime temperature. If true, neglecting the potential positive or negative effects of night warming may thus either under- or overestimate the realistic warming effects (Barton & Schmitz, 2018; Zhao et al., 2014) and lead to inaccurate predictions (Ma, Ma, et al., 2021; Speights et al., 2017). However, previous research mainly concentrated on the effects of increased mean or day temperatures on predator–prey interactions (Rall et al., 2010; Uszko et al., 2017; Vucic-Pestic et al., 2011) or night warming on predator traits for only a single life stage (Barton & Schmitz, 2018; Higashi et al., 2020; Speights & Barton, 2019). Since each life stage matters in assessing the response of species to climate warming (Pandori & Sorte, 2019; Radchuk et al., 2013), we still lack a comprehensive understanding of how night warming affects long-term per capita consumption rates, abundance and population structure of species across species lifetime, and to what extent the joint effects of night warming ultimately differ from those predicted under increasing constant temperatures.
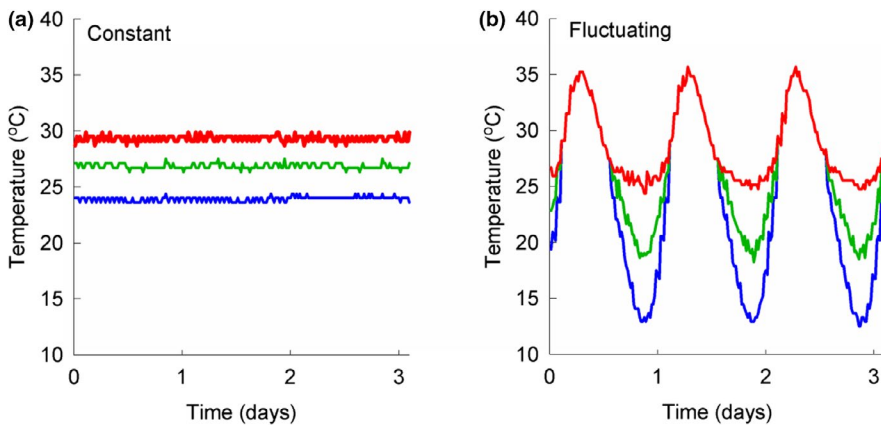
FIGURE 1 Thermal regimes used for creating different temperatures under constant and fluctuating conditions (shown only for 3 consecutive days during the experiment). (a) Constant regimes with different mean temperatures. (b) Fluctuating regimes with a similar daytime temperature fluctuation but different night-time temperatures. Red, green and blue lines represent different regimes of temperature with equal means respectively

Prey density naturally varies across sites and time, and this variation in prey density could alter the response of predators to changes in temperatures (Murrell & Barton, 2017; Veselý et al., 2019), thus the possible interactive effects of warming and food availability would also matter in predicting interspecific interactions under climate warming. Here we used a common predatory lady beetle species, *Propylea japonica*, and a global cereal aphid species, *Sitobion avenae*, as our model predator–prey system. Previous work already showed that night warming can over- or underestimate thermal performances in this aphid species relative to mean warming (Zhao et al., 2014). Here we experimentally manipulated mean temperature and temperature regime (uniform warming vs. night warming) across different prey densities to test how changes in night-time temperature affect key demographic rates and long-term population structure of predators and their effects on prey.

2 | MATERIALS AND METHODS

2.1 | Study system

Here we focus on predatory lady beetles *P. japonica* and its prey, the grain aphid *S. avenae*. Both species co-occur throughout East Asia (Zhang, Fu, et al., 2015). *Sitobion avenae* is an economically important pests infesting cereal crops. *P. japonica* is the dominant natural predator of *S. avenae* in this region and is therefore often used as an important biological agent in integrated pest management to control this aphid (Bai et al., 2019; Zhang, Fu, et al., 2015). We collected lady beetles from a wheat field at Langfang Experimental Station (39.51°N, 116.61°E), Hebei Province, China. We placed beetles into screen cages (60 × 60 × 60 cm) in a rearing room with 22 ± 1°C, 60%–70% relative humidity and a photoperiod of 16:8 (L:D). Larvae and adult beetles were fed with the grain aphid reared on 5- to 10-cm high winter wheat seedlings. We collected beetle eggs and put them into Petri dishes (diameter: 5 cm; height: 1 cm) with moist filter papers to allow them to hatch. After hatching, the first-instar larvae were transferred into new screen cages and fed with the grain aphids. Larvae, pupae and adults were transferred to new cages weekly.

2.2 | Experimental design

To discover the effects of night warming on performance of *P. japonica*, we considered the mean temperatures and regime (constant vs. fluctuating) as independent factors in our experiments. Additionally, since night warming may lead to declined aphid abundance and thereby limited prey resources (Zhao et al., 2014), prey densities (low vs. high) were also incorporated in the experiment due to its potential interaction with warming. We used a factorial design to test how these independent factors affect demographic parameters and energetic efficiency of the predators. We crossed three mean temperatures with two different thermal regimes: one with constant temperatures (i.e. 24, 27 and 29°C) and another with corresponding fluctuating temperatures (13–35°C with mean 24°C, 19–35°C with mean 27°C and 25–35°C with mean 29°C; Figure 1a,b). The fluctuating thermal regimes simulated night warming by increasing the minimum night-time temperature (with daily minimum temperatures increased from 13 to 25°C across treatments) while keeping the maximum daytime temperature constant at 35°C. By keeping mean temperature constant across thermal regimes (fluctuating vs. constant), comparing both treatments allowed us to isolate the effects of night warming independently of the mean.

Six climate chambers (RXZ-280B, Jiangnan Ltd.; accuracy: ±1°C) were used to establish the temperature × regime treatments. In fluctuating treatments, we changed temperature gradually over a 24-hr period to simulate daily temperature cycles in nature (Figure S1). Daily temperature increased and peaked at 35°C, and then decreased and reached at the lowest of 13, 19 and 25°C respectively (Figure S2). Relative humidity in the chambers was set 50%–70% and the photoperiod was set to 16:8 (L:D).

To account for the potential interaction between warming and food availability, we exposed predators to two prey densities: (a) low prey density or (b) high prey density. Pilot experiments indicated that per capita consumption rates varied substantially across individual stages. Thus, we adjusted prey density for each stage: first-, second-, third-, fourth-instar larvae, an adult beetle or one paired adults (1 female and 1 male) received 2, 4, 7, 10, 10 and 20 aphids every day at low prey density and 8, 12, 25, 30, 30 and 60 aphids every day at high prey density respectively. This adjustment ensured that each

predator stage would be affected by food limitation under low prey density but not at high prey density. We used fourth-instar nymphs or adults (with similar body sizes) of aphids *S. avenae* as prey for the predator *P. japonica* in all trials.

2.3 | Experimental manipulation

To obtain sufficient amount of first-instar larvae of the lady beetle at the same time, newly reproduced beetle eggs (within 24 hr) were selected from the rearing cages and randomly placed into 12 different Petri dishes (diameter: 5 cm; height: 1 cm) containing moist filter papers, with about 300 eggs in each dish (12 × 300 = 3,600 eggs). These Petri dishes were then randomly assigned to the six climate chambers with designed thermal regimes, with two dishes in each chamber. Eggs were checked twice a day at 08:00 and 20:00, respectively, to see if they had hatched. When the eggs hatched, we transferred newly emerged first-instar larvae into tubes (diameter: 1 cm; height: 4 cm) containing a certain amount of aphids (depended on the low or high prey density) for feeding and placed into the respective climate chambers and the experiment started.

For each treatment, 36 first-instar beetle larvae were tested, resulting in a total of 432 tested predators (3 mean temperatures × 2 thermal regimes × 2 prey density treatments × 36 larvae = 432 first-instar larvae). Aphids were added at 08:00 every day and one piece of wheat seedling leaf was added into each tube for aphid feeding. At this time, the number of aphids that had not been eaten was also recorded and these aphids were removed from the tube. We checked larval development and survival twice a day at 08:00 and 20:00 respectively. We measured the weight of pupae ((pupa + tube) − tube (after the pupae became adults)) using an electronic scale (Sartorius BP 221S, Sartorius AG Ltd.; accuracy: ±0.0001 g) 24~36 hr after pupating. When the pupae reached the premature adult stage, we determined their sex and measured their weights. We then put one female and one male premature adults into a Petri dish for mating, and added the treatment-specific amount of aphids for feeding. We recorded the number of eggs and survival of these adults and removed all eggs and dead adults twice a day at 08:00 and 20:00. Only mated adults of the tested predators were included in the final analysis (see Table S1 for more details).

2.4 | Response variables

We examined a range of key response variables to gain a comprehensive understanding for how temperature, regime and prey density affect predator demographic rates and their impact on the prey. Specifically, we analysed survival, development rate of larva, pupa and premature adult, growth rate of larva, adult weight and longevity of both males and females and lifetime reproduction. In addition, we analysed larval and adult daily and total prey consumption and energy efficiency to quantify predator–prey interactions.

We calculated survival time (days) until the deaths of the predator. We defined the premature adult stage as the duration from adult emergence until the first oviposition of the paired adults. We determined the development rate (1/day) of larva, pupa and premature adult by the inverse number of days until the predators completed their respective stages. We calculated the larval growth rate (mg/day) as the weight of pupa divided by the duration of larval period. We defined adult weight (mg) as the mass of male or female beetles just after adult emergence. We calculated adult longevity as the days from adult emergence until death. We determined the reproduction as the total number of eggs produced by female beetles.

We determined larval and adult daily consumption by the average number of daily prey consumed by the predators during larval and adult stage respectively. We calculated larval energy efficiency as the adult weight divided by the prey mass consumed by the predator during larval period. We calculated the adult energy efficiency as the egg mass produced divided by the prey mass consumed by adult females. We determined lifetime consumption as the number of prey consumed by the predator during their lifetime summed across all stages. We estimated the lifetime energy efficiency as the sum of the adult weights and egg mass of the adult females divided by the prey mass consumed by the predator during its lifetime. We calculated the prey mass consumed as the number of prey consumed multiplied by the average weight of each prey. We estimated the egg mass produced as the lifetime reproduction of adult females multiplied by the average weight of each egg.

2.5 | Statistical analysis

We analysed the effects of warming, thermal regime and prey density on each response variable of the predator by using GLMs and the CAR package in R to test for significant treatment effects (Type II Wald chi-squared tests), where temperature, regime and prey density were all treated as fixed factors. Each model involves all possible interactions between fixed factors. For the adult weight and longevity, we also included 'sex' as fixed factors. We analysed how temperature, regime and prey density and their interactions affected the survival of aphids, by fitting the Cox proportional hazard model using the SURVIVAL package and tested the significance of each factor using the CAR package. We fitted the models with different error distributions of each response variable, and selected the most parsimonious model with the lowest AIC value for further analysis in Table S2.

To get a more holistic understanding of how night warming affect predator–prey dynamics, we integrate the individual life-history metrics using a life-table approach to calculate the expected population growth rate of predators and predation pressure. Specifically we used the experiments to parameterize a stage-specific transition matrix. We can describe the change in the predator population between time steps as $n_{t+1} = M \times n_t$, where n_t is the stage vector:

$$n_t = \begin{bmatrix} L \\ P \\ PM \\ A \end{bmatrix},$$

with L represents larvae, P represents pupae, PM represents premature adults and A represents adults. The transition matrix is given by:

$$M = \begin{bmatrix} 1-p_L & 0 & 0 & F \\ p_L & 1-p_P & 0 & 0 \\ 0 & p_P & 1-p_{PM} & 0 \\ 0 & 0 & p_{PM} & s_A \end{bmatrix},$$

with F indicating the per capita production of new larvae per adult per day, and p_L, p_P, p_{PM} indicate the probability to transition from the larva to pupae stage, pupae to premature adult stage and premature to mature adult stage, respectively, and s_A indicates the survival probability of adults. We used our experimental data to parameterize the matrix assuming 1-day time step intervals and averaged each vital rate across males and females (to reflect natural 50:50 sex ratio). Transition probabilities are derived from the inverse of the average duration of each developmental stage multiplied by the average survival probability of that stage (i.e. $p_L = 1/DevL*SurL$; $p_p = 1/DevP*SurP$; and $p_{PM} = 1/DevPM*SurPM$, where SurL, SurP and SurPM indicate the survival probability of larval, pupal and premature adult stage respectively; DevL, DevP and DevPM represent the average duration of larval, pupal and premature adult stage respectively). Survival probabilities of adults are calculated as $(1-1/Al)$, with AL given by the average adult life span (assumed Type II survivorship curve, Figure S3). We calculated the transition matrix separately for each treatment.

Once fully parameterized, we used the characteristic equation of the transition matrix to calculate three key metrics of the predator population: (a) the long-term population growth rate (dominant eigenvalue λ), (b) the stable stage distribution (dominant right eigenvector) and (c) 'predation pressure' for each temperature scenario. Predation pressure was calculated by combining the stable stage distribution (giving us proportion of individuals of each stage within a population) with the stage-specific per capita predation rates (estimated in the experiments) to estimate the total per capita predation pressure expected for a growing predator population under a given temperature scenario. Note that these estimates of temperature effects on per capita rate are independent of predator density and thus best apply to early period of predator–prey dynamics and scenarios where predator population density is low and does not affect per capita rates. The advantage of this predation pressure metric is that it integrates temperature effects on per capita consumption rates across all predator life stages while accounting for natural differences in the relative abundances of stages, allowing a holistic comparison across temperature scenarios.

3 | RESULTS

Overall, warming and its interaction with regime influenced most of the life-history traits as well as prey consumption and energy efficiency of the predator (Tables 1 and 2). Prey density also had significant effects on almost all the response variables of the predator.

4 | Demographic rates

Generally, an increase in mean temperature accelerated the development rate of larva and pupa by 38% and 47% (% changes in the average effect sizes between 24 and 29°C), respectively (Figure 2b,c), decreased body weight at maturity (male: 11%; female: 16%; Figure 3a,b), shortened adult longevity (male: 30%; female: 18%; Figure 3c,d) and decreased lifetime reproduction by ~56% (Figure 3e). In contrast, warming either had positive or negative effect on survival time (Figure 2a), development of premature (Figure 2d) and larval growth rate (Figure 2e) depending on thermal regime.

The regime (constant vs. fluctuating) significantly influenced most of the demographic rates directly or via interactions with temperature (Tables 1 and 2). Overall, demographic rates or traits were generally lower in fluctuating regimes than in constant regimes at low temperatures. However, this difference often disappeared or was even reversed at high temperatures (Figures 2 and 3), leading to significant interaction between warming and regime for most demographic rates (Tables 1 and 2). For instance, an increase in mean temperature had a negative effect on growth rate in constant environments (−14%), but positive effect in fluctuating environments (+18%; Figure 2e). This indicates that the effects of night warming are different (and sometimes even opposite) to those effects predicted from an increase in mean temperature.

Overall, prey density affected almost all the demographic rates and traits of the predator and typically did not qualitatively alter the effects of temperature or regime treatments (Tables 1 and 2). Compared to low prey density, high prey density accelerated the development rate of larva and premature by 13% and 27%, respectively (Figure 2b,d), as well as larval growth rate (42%; Figure 2e), increased adult weight (male: 22%; female: 27%; Figure 3a,b) and reproduction (~83%; Figure 3e). However, female longevity shortened to some extent (~23%) under high prey density (Figure 3d).

5 | Prey consumption and energy efficiency

Both prey consumption and energy efficiency of the predator were affected by mean temperature and these effects were often contingent on thermal regime. Prey consumption rates of larva and adult increased with temperature and similar across regimes (Figure 4a,c). In contrast, efficiency decreased with mean temperature (Figure 4b,d), but this effect was contingent on regimes in adults: energy efficiency

TABLE 1 Effects of simulated warming on performances of the predator lady beetle *Propylea japonica*. (T: mean temperature, R: thermal regime (constant vs. fluctuating) and D: prey density)

Source	Survival curve	Development rate				Reproduction
		Larva	Pupa	Premature	Larval growth rate	
T	$\chi^2 = 39.14, p < 0.001$	$\chi^2 = 691.83, p < 0.001$	$\chi^2 = 810.26, p < 0.001$	$\chi^2 = 0.05, p = 815$	$\chi^2 = 0.00, p = 0.982$	$\chi^2 = 37.66, p < 0.001$
R	$\chi^2 = 3.72, p = 0.054$	$\chi^2 = 2.28, p = 0.131$	$\chi^2 = 0.64, p = 0.425$	$\chi^2 = 0.63, p = 0.428$	$\chi^2 = 34.48, p < 0.001$	$\chi^2 = 33.36, p < 0.001$
D	$\chi^2 = 7.218, p = 0.007$	$\chi^2 = 197.82, p < 0.001$	$\chi^2 = 7.25, p = 0.007$	$\chi^2 = 16.41, p < 0.001$	$\chi^2 = 262.83, p < 0.001$	$\chi^2 = 25.88, p < 0.001$
T × R	$\chi^2 = 9.02, p = 0.002$	$\chi^2 = 13.95, p < 0.001$	$\chi^2 = 51.54, p < 0.001$	$\chi^2 = 7.77, p < 0.001$	$\chi^2 = 34.33, p < 0.001$	$\chi^2 = 0.45, p = 0.501$
T × D	$\chi^2 = 10.56, p = 0.001$	$\chi^2 = 21.35, p < 0.001$	$\chi^2 = 2.04, p = 0.154$	$\chi^2 = 0.12, p = 0.891$	$\chi^2 = 17.17, p < 0.001$	$\chi^2 = 3.34, p = 0.068$
R × D	$\chi^2 = 2.37, p = 0.123$	$\chi^2 = 1.75, p = 0.186$	$\chi^2 = 0.38, p = 0.537$	$\chi^2 = 4.14, p = 0.042$	$\chi^2 = 0.21, p = 0.65$	$\chi^2 = 1.91, p = 0.167$
T × R × D	$\chi^2 = 2.57, p = 0.108$	$\chi^2 = 22.11, p < 0.001$	$\chi^2 = 0.11, p = 0.743$	$\chi^2 = 0.23, p = 0.632$	$\chi^2 = 13.59, p < 0.001$	$\chi^2 = 2.40, p = 0.121$

Source	Larva daily consumption	Larva energy efficiency	Adult daily Consumption	Adult energy efficiency	Lifetime consumption	Lifetime energy efficiency
T	$\chi^2 = 100.33, p < 0.001$	$\chi^2 = 0.03, p = 0.845$	$\chi^2 = 128.01, p < 0.001$	$\chi^2 = 28.74, p < 0.001$	$\chi^2 = 5.83, p = 0.016$	$\chi^2 = 28.33, p < 0.001$
R	$\chi^2 = 0.18, p = 0.671$	$\chi^2 = 2.80, p = 0.094$	$\chi^2 = 0.00, p = 0.932$	$\chi^2 = 51.35, p < 0.001$	$\chi^2 = 1.84, p = 0.175$	$\chi^2 = 51.77, p < 0.001$
D	$\chi^2 = 3{,}106.18, p < 0.001$	$\chi^2 = 177.40, p < 0.001$	$\chi^2 = 44{,}308, p < 0.001$	$\chi^2 = 0.16, p = 0.686$	$\chi^2 = 147.29, p < 0.001$	$\chi^2 = 1.40, p = 0.235$
T × R	$\chi^2 = 0.01, p = 0.916$	$\chi^2 = 0.28, p = 0.594$	$\chi^2 = 9.00, p = 0.003$	$\chi^2 = 9.28, p = 0.002$	$\chi^2 = 8.74, p = 0.003$	$\chi^2 = 9.92, p = 0.001$
T × D	$\chi^2 = 1.12, p = 0.289$	$\chi^2 = 1.99, p = 0.157$	$\chi^2 = 16.00, p < 0.001$	$\chi^2 = 0.48, p = 0.484$	$\chi^2 = 0.94, p = 0.331$	$\chi^2 = 0.42, p = 0.512$
R × D	$\chi^2 = 0.88, p = 0.349$	$\chi^2 = 0.956, p = 0.328$	$\chi^2 = 0.00, p = 0.690$	$\chi^2 = 0.09, p = 0.757$	$\chi^2 = 1.72, p = 0.190$	$\chi^2 = 0.33, p = 0.563$
T × R × D	$\chi^2 = 0.33, p = 0.568$	$\chi^2 = 3.59, p = 0.107$	$\chi^2 = 1.00, p = 0.287$	$\chi^2 = 2.02, p = 0.155$	$\chi^2 = 0.16, p = 0.693$	$\chi^2 = 2.05, p = 0.152$

Bold value indicates statistical significance ($p < 0.05$) of the experimental factors and their interactions based on Chi-square tests.

TABLE 2 Effects of simulated warming on body weight and adult longevity of the predator lady beetle *Propylea japonica*. (T: mean temperature, R: thermal regime (constant vs. fluctuating), D: prey density and S: sex)

Source	Body weight	Adult longevity
T	$\chi^2 = 41.18, p < 0.001$	$\chi^2 = 39.48, p < 0.001$
R	$\chi^2 = 2.52, p = 0.113$	$\chi^2 = 8.37, p = 0.004$
D	$\chi^2 = 151.75, p < 0.001$	$\chi^2 = 5.77, p = 0.016$
S	$\chi^2 = 49.86, p < 0.001$	$\chi^2 = 3.67, p = 0.055$
T × R	$\chi^2 = 4.88, p = 0.027$	$\chi^2 = 27.91, p < 0.001$
T × D	$\chi^2 = 2.80, p = 0.094$	$\chi^2 = 1.67, p = 0.197$
R × D	$\chi^2 = 4.40, p = 0.036$	$\chi^2 = 0.55, p = 0.460$
T × S	$\chi^2 = 3.09, p = 0.079$	$\chi^2 = 1.49, p = 0.222$
R × S	$\chi^2 = 4.93, p = 0.026$	$\chi^2 = 13.08, p < 0.001$
D × S	$\chi^2 = 4.31, p = 0.038$	$\chi^2 = 16.36, p < 0.001$
T × R × D	$\chi^2 = 0.10, p = 0.758$	$\chi^2 = 0.12, p = 0.734$
T × R × S	$\chi^2 = 0.08, p = 0.772$	$\chi^2 = 0.50, p = 0.478$
T × D × S	$\chi^2 = 1.29, p = 0.256$	$\chi^2 = 0.84, p = 0.360$
R × D × S	$\chi^2 = 0.35, p = 0.56$	$\chi^2 = 5.90, p = 0.015$
T × R × D × S	$\chi^2 = 1.41, p = 0.235$	$\chi^2 = 0.01, p = 0.938$

Bold value indicates statistical significance ($p < 0.05$) of the experimental factors and their interactions based on Chi-square tests.

was much higher in constant environments at low temperatures, but it quickly declined at higher temperatures, while warming had little effect in fluctuating environments (Figure 4). Similarly, taken together, the warming effects on lifetime prey consumption and energy efficiency showed very different trends between regimes (Figure 4e,f). As temperature increased, the lifetime prey consumption and energy efficiency decreased on average by 30% and 47%, respectively, under constant regime, while that under fluctuating regime remained stable.

Prey density had significant effects on prey consumption of the predator (Table 1). Not surprisingly, the predator consumed more preys at high prey density (Figure 4a,c). However, prey density only affected the energy efficiency of larva, with lower larval energy efficiency at higher prey density (reduced by 30%; Figure 4b). Generally, prey consumption and energy efficiency were little affected by the interaction between prey density and temperature or regime (Table 1).

6 | Population-level effects

The calculated model parameters for the transition metrics used to predict the stable stage distribution, per capita consumption rate and long-term population growth rate of the predator were shown in Table 3. Overall, the effects of temperature and thermal regime on key life-history traits of larva and adult scaled up to alter the demographic (stage) structure and growth rate of the predator population and predator pressure on its prey (Figure 5a–c). Specifically, predator populations are predicted to consist of a large proportion of

premature and mature adults (+0.14 on average) and smaller proportion of larvae (−0.13) at higher temperature, and when exposed to fluctuating regimes at lower temperature (+0.08 and −0.06 respectively; Figure 5a). Combined with temperature-dependent per capita consumption rates, this predicts a higher total predation pressure for a given predator density at higher temperatures and in populations in fluctuating regimes at lower temperature (Figure 5b). Furthermore, warming had a context-dependent effect on the intrinsic growth rate of the predator: warming led to increased or stable population growth rates under fluctuating regimes but decreased growth rates (−0.05) substantially under constant regimes (Figure 5c). As a consequence, population growth rates were substantially higher (+0.05) under constant regimes at low temperatures, but the similar or even opposite at high temperatures. Together, this suggests that warming should strengthen or stabilize predator effect (top-down control) in fluctuating environments, but destabilize or even weaken predator effect under constant regimes due to the negative effects on population growth rates. The changes in population structure, predation pressure and population growth rate with temperature showed similar trends at high and low prey densities. Higher prey density was found to cause increased proportion of larva (+0.04), predation pressure (+5.0) and population growth rate (+0.06) of the predator.

7 | DISCUSSION

7.1 | Thermal regimes determine warming effects on predator–prey interaction

Elucidating how climate warming alters interspecific interactions is essential to predict how ongoing climate change will affect biodiversity and ecosystem functioning (Blois et al., 2013; Daugaard et al., 2019; Petchey et al., 1999). In the present study, the consequences of warming for demographic rates and predator–prey interactions were largely contingent on the thermal regime. The energy efficiency of the predator decreased with warming under constant regimes and thus led to a decreased population growth rate. These negative effects of warming are consistent with previous studies, where increasing mean temperatures decreased energetic efficiencies of the predator (Frances & McCauley, 2018; Iles, 2014; Rall et al., 2010; Vucic-Pestic et al., 2011). Such negative effects are expected to destabilize predator–prey interactions (Daugaard et al., 2019; Dell et al., 2014). In contrast, we found that under night warming fluctuating regimes, lifetime consumption and energy efficiency remained stable and population growth rate of the predator increased, thereby strengthening the top-down control of predator–prey interaction. Comparable contrasting effects have been shown in spider–grasshopper interactions, where day and night warming caused weakened and strengthened top-down control respectively (Barton & Schmitz, 2018). Given that diurnal temperature cycles are ubiquitous in natural system and nights are warming faster than days, these results emphasize the importance of night warming to accurately predict the effects of climate change on interspecific interactions.

FIGURE 2 Effects of simulated warming on (a) survival time, (b–d) development rate of larva, pupa and premature and (e) larval growth rate of the predator under low and high prey density conditions. Data shown are means and *SD*
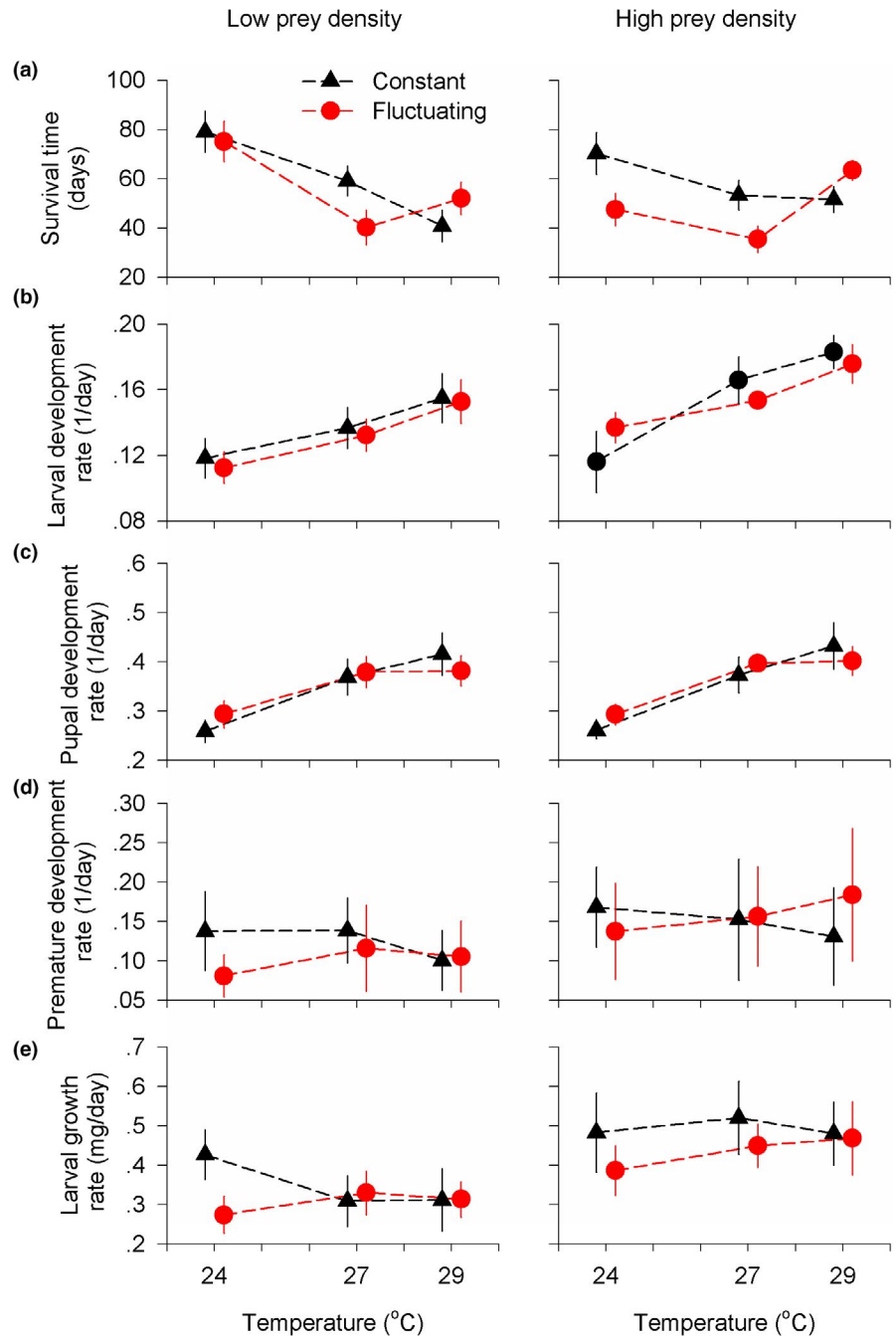
Along with thermal regimes, warming effects on interspecific interactions may also be system-specific and dependent on the respective baseline climate (Ma, Ma, et al., 2021; Speights et al., 2017). If the climate is not too warm for the persistence of the predator–prey system, we may expect similar results in other systems. For instance, our findings that night warming can strengthen top-down control in trophic cascades also can be found in a spider–grasshopper system in temperate climates (Barton & Schmitz, 2018). However, warming effects may differ from ours when the baseline temperature is already high in a system. For example, warming can have negative effects on a symbiont–host–parasitoid system regardless of increases in night or day temperatures due to high vulnerability of the symbiont to warming (Higashi

et al., 2020). In the present predator–prey system, the predatory beetle is a heat-tolerant species (Bai et al., 2019). In this case, night warming may alter the trophic interaction strength in this system under current warming trend. In addition, night warming may have different effects on nocturnal and diurnal predators and interspecific interactions (Miller et al., 2017). Increases in night-time temperature might lead to increased temperature-dependent prey consumption by nocturnal predators and thereby strengthened predator–prey interactions. By contrast, night warming might increase the energy cost at night and subsequently reduce the body mass in diurnal predators and thus result in weakened interspecific interactions. The system-specific features and other profiles of climate warming such as changes in daily and seasonal temperature
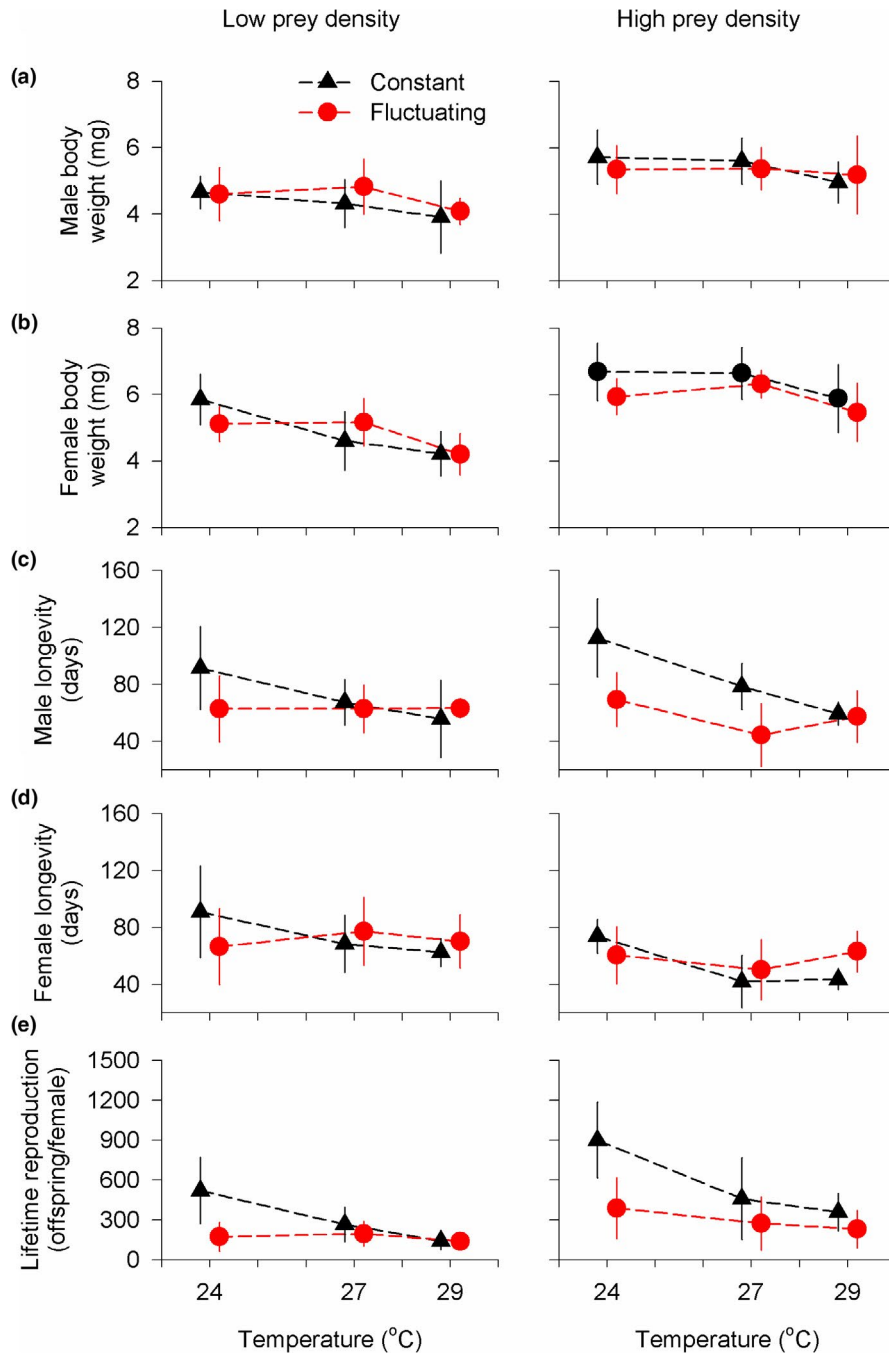
FIGURE 3 Effects of simulated warming on (a, b) body weight, (c, d) adult longevity and (e) lifetime reproduction of the predator under low and high prey density conditions. Data shown are means and *SD*

variability and in the severity of extreme climate events should also be taken into account in the future studies.

7.2 | Long-term thermal effects matter in predicting the warming effects on interspecific interactions

The effects of warming on interspecific interactions ultimately depend on how both species physiology and per capita consumption respond to temperature changes (Boukal et al., 2019; Dell et al., 2014; Gilman, 2017). Previous studies mainly focused on short-term consumption rate (e.g. metabolic rates and/or ingestion

rates; Daugaard et al., 2019; Iles, 2014; Rall et al., 2010; Vucic-Pestic et al., 2011) while often neglected relative long-term thermal effects on key physiological traits and demographic rates across lifecycle that determine the population abundance of predators. Yet, we need to know how both abundance and per capita effect of predators are responding to predict long-term dynamics of predator–prey interactions. For example, when we just focused on short-term warming effects on interspecific interaction, we found that daily prey consumption of both larvae and adults increased with warming. This result is not surprisingly in accordance with previous research (Frances & McCauley, 2018; Rall et al., 2010; Vucic-Pestic et al., 2011) and may suggest a strengthening of top-down control. However, when we also considered the

FIGURE 4 Effects of simulated warming on prey consumption and energy efficiency of (a, b) larva, (c, d) adult and (e, f) whole lifetime of the predator under low and high prey density conditions. Data shown are means and *SD*
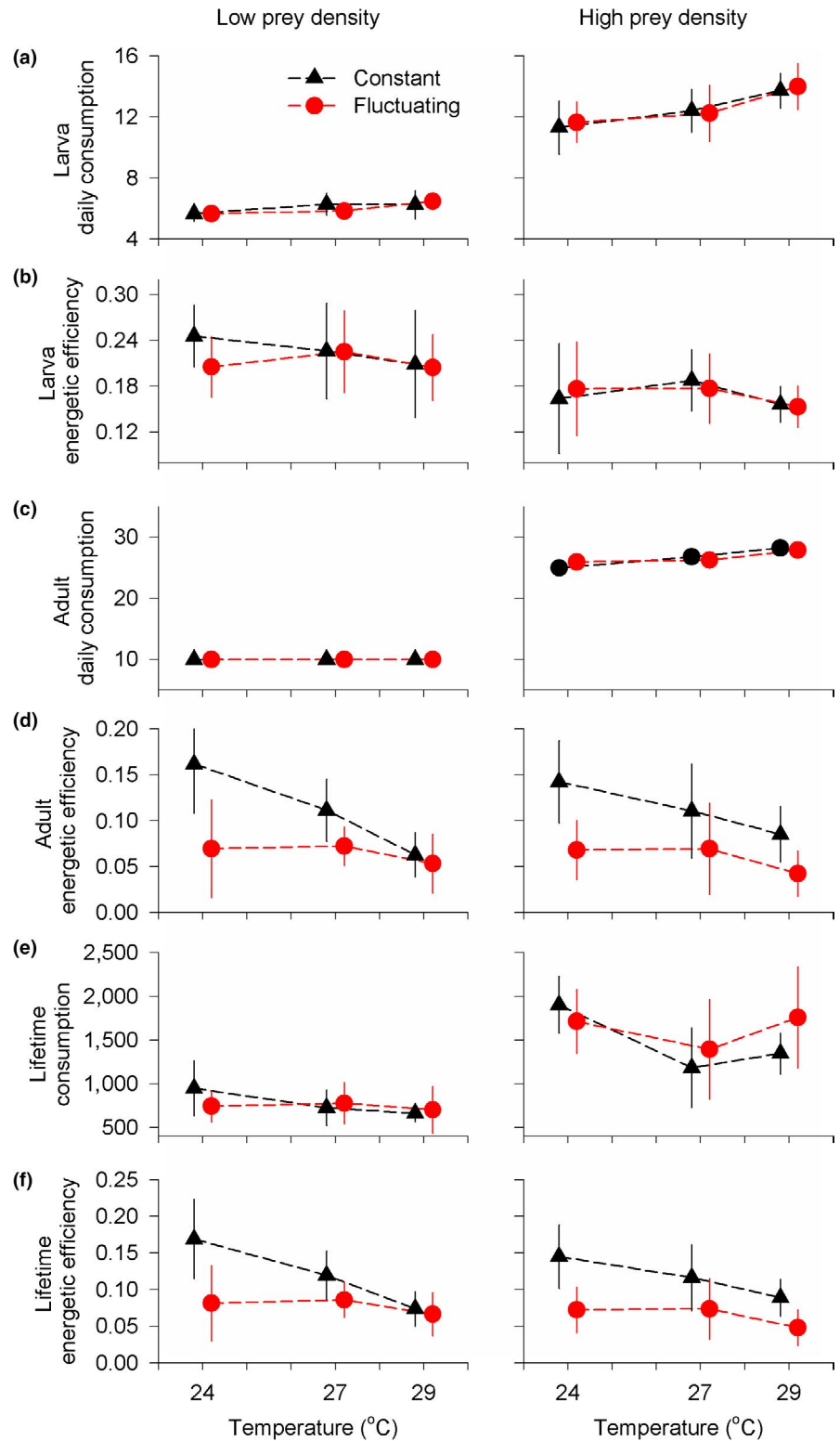
different long-term warming effects on adult longevity between regimes (constant regime reduced adult longevity but fluctuating regime did not), we found that the lifetime prey consumption actually remained stable under fluctuating regimes and decreased under constant conditions.

Moreover, most previous studies have mainly focused on a single life stage of the predator such as adult stage (Barton &

Schmitz, 2018; Rall et al., 2010; Vucic-Pestic et al., 2011). Consistent with previous studies, we found that warming effects on organisms are stage specific (Zhang, Rudolf, et al., 2015). Testing species traits across lifetime may allow us to avoid biased predictions of species responses to climate warming (Pandori & Sorte, 2019; Radchuk et al., 2013). Furthermore, we found that warming and thermal regimes influence the stage structure of populations, and this altered

TABLE 3 Model parameters for the transition metrics used to predict the stable stage distribution, per capita consumption rate and long-term population growth rate of the predator

| Temperature	Regime	Prey density	Model parameters				
			p_L	p_P	p_{PM}	F	S_A
24	Constant	Low	0.091	0.246	0.055	260.0	0.989
		High	0.088	0.241	0.051	450.5	0.989
	Fluctuating	Low	0.074	0.291	0.030	85.7	0.985
		High	0.080	0.292	0.038	194.2	0.985
27	Constant	Low	0.113	0.353	0.053	132.6	0.985
		High	0.133	0.369	0.050	229.7	0.983
	Fluctuating	Low	0.069	0.376	0.036	97.4	0.986
		High	0.098	0.379	0.054	136.8	0.979
29	Constant	Low	0.094	0.411	0.028	69.9	0.983
		High	0.142	0.427	0.025	179.2	0.981
	Fluctuating	Low	0.105	0.379	0.028	68.6	0.985
		High	0.170	0.400	0.064	115.2	0.983
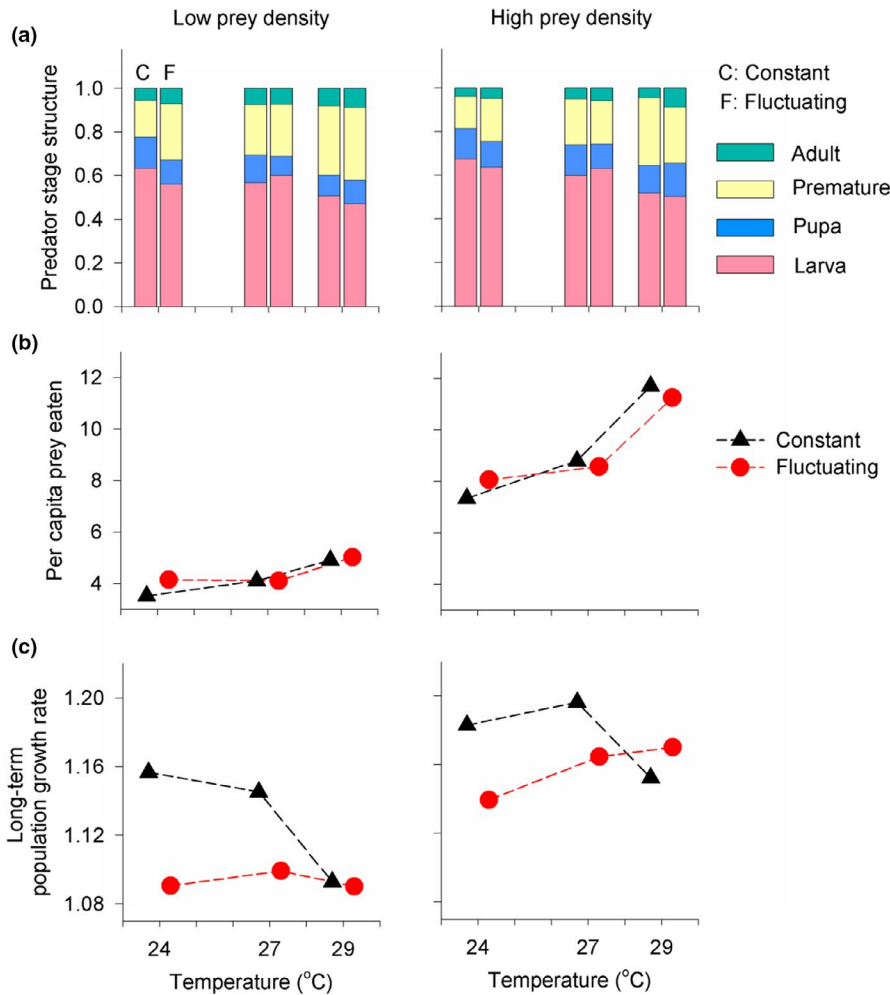
FIGURE 5 Effect of simulated warming on predator population traits: (a) Stable stage structure, (b) per capita prey eaten per day and (c) long-term population growth rate (lambda) of the predator under low and high prey density conditions. Stage structure and growth rate were calculated from the transition matrix, and per capita prey eaten reflects the expected per capita consumption rate in a predator population given stage-specific consumption rate and a stable-age distribution (see Section 2 for details)

the predicted population-level predation pressure and how this changes with warming. Thus, our results emphasize the importance of accounting for both species demographic rates and per capita

consumption across species lifetime when assessing how warming affects interspecific interactions. Nevertheless, other biological factors such as species dispersal ability in field open systems as well as

prey population composition should also be considered in the future studies (Wang et al., 2017).

7.3 | Constant temperatures can lead to over- or underestimations of warming effects

The effects of temperature on an organism's performances are usually described as thermal performance curves (Ruel & Ayres, 1999). However, the ambient temperatures are naturally fluctuating over time (24-hr cycles) in most terrestrial and aquatic environments (Potter et al., 2013). Our results indicate that effects in constant regimes typically either over-or underestimated warming effects in fluctuating regimes, even though mean temperatures were held the same for both regimes. This discrepancy between constant versus fluctuating regimes can be explained by the fact that most temperature performance curves are typically asymmetrical and nonlinear; performance/fitness often smoothly increases with temperature until an optimum is reached, but then it rapidly drops off. Thus, when predicting thermal performances based on mean temperatures, we likely either overestimate the true values by neglecting the possible negative impacts of heat stress at daytime (Ma, Hoffmann, et al., 2015; Ma, Rudolf, et al., 2015) or underestimate the values by overlooking the potential recovery and compensation at mild night temperatures (Bai et al., 2019; Speights et al., 2017; Zhao et al., 2014). Given that nonlinear temperature performance curves are ubiquitous in natural (especially ectothermic) systems, the results observed in this study should hold true for a wide range of natural systems and emphasize the importance of accounting for diurnal temperature cycles to predict the consequences of warming.

7.4 | Consistent warming effects across prey densities

Prey density can play a key role in warming effects on predator–prey interactions (Costa-Pereira et al., 2018; Rall et al., 2010). These effects can be driven by changes in per capita consumption effects or from numerical response of the prey. On the one hand, prey density naturally varies over the course of the seasons, the fact that the phenology (date of first appearance) of the ladybeetle is later than the aphid (our unpublished field observations) implies sufficient food availability for the predator. On the other hand, previous research showed that the effects of night warming on thermal performance and population growth of the aphid differed from mean warming (Zhao et al., 2014) which may cause declined population growth in the aphid (Figure S4) and lead to limited prey availability. Thus, the predator is likely to face either sufficient or insufficient prey availability. Here we decoupled the per capita consumption from the numerical physiological effects by keeping temperature and regime constant, but testing two different prey densities (low vs. high). We found that warming affected most of the demographic rates, prey

consumption and energy-related variables. Furthermore, population traits of the predator showed similar trend within constant or fluctuating regimes at both low and high prey densities. These consistent results under different prey densities indicate that warming has consistent effects on the predator–prey interactions in our system, regardless of any potential changes in prey population growth with climate warming. However, ultimately demographic responses of both prey and predator for generations, as well as the density-dependent population growth of the predator, need to be considered when predicting the long-term dynamics of the system.

8 | CONCLUSIONS

Understanding how species and interspecific interactions respond to natural realistic changes in global temperatures is essential for predicting the impacts of ongoing climate change on natural ecosystems. Although global warming is mainly due to a larger increase in night-time minimum than daytime maximum air temperatures (Donat & Alexander, 2012; Easterling et al., 1997), this asymmetrical warming between night and day is rarely considered when studying ecological consequences of warming climate (Barton & Schmitz, 2018; Ma, Ma, et al., 2021; Speights & Barton, 2019). Our results clearly show that night warming under realistic fluctuating temperature conditions has different consequences than those predicted from mean warming on species and interspecific interactions, modifying demographics, per capita consumption and population growth of predator and herein altering top-down control. These findings emphasize the importance of the nuanced changes in temperature such as night versus day warming in modelling the warming effects on interspecific interactions and consequent community structure and ecosystem functions.

AUTHORS' CONTRIBUTIONS
G.M., V.H.W.R. and C.-S.M. conceived of the study and designed the experiments; G.M. and C.-M.B. conducted the experiments and the data analyses; G.M., V.H.W.R. and C.-S.M. wrote the manuscript. All the authors gave final approval for publication.

DATA AVAILABILITY STATEMENT
Data are deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.z612jm6c2 (Ma, Bai, et al., 2021).

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REFERENCES

Bai, C. M., Ma, G., Cai, W. Z., & Ma, C. S. (2019). Independent and combined effects of daytime heat stress and nighttime recovery determine thermal performance. *Biology Open*, 8, bio038141. https://doi.org/10.1242/bio.038141

Barton, B. T., & Schmitz, O. J. (2018). Opposite effects of daytime and nighttime warming on top-down control of plant diversity. *Ecology*, 99, 13–20. https://doi.org/10.1002/ecy.2062

Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C., & Finnegan, S. (2013). Climate change and the past, present, and future of biotic interactions. *Science*, 341, 499–504. https://doi.org/10.1126/science.1237184

Boukal, D. S., Bideault, A., Carreira, B. M., & Sentis, A. (2019). Species interactions under climate change: Connecting kinetic effects of temperature on individuals to community dynamics. *Current Opinion in Insect Science*, 35, 88–95. https://doi.org/10.1016/j.cois.2019.06.014

Costa-Pereira, R., Araújo, M. S., Olivier, R. S., Souza, F. L., & Rudolf, V. H. W. (2018). Prey limitation drives variation in allometric scaling of predator-prey interactions. *The American Naturalist*, 192, E139–E149. https://doi.org/10.1086/698726

Daugaard, U., Petchey, O. L., & Pennekamp, F. (2019). Warming can destabilize predator–prey interactions by shifting the functional response from Type III to Type II. *Journal of Animal Ecology*, 88, 1575–1586. https://doi.org/10.1111/1365-2656.13053

Dell, A. I., Pawar, S., & Savage, V. M. (2014). Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *Journal of Animal Ecology*, 83, 70–84. https://doi.org/10.1111/1365-2656.12081

Donat, M. G., & Alexander, L. V. (2012). The shifting probability distribution of global daytime and night-time temperatures. *Geophysical Research Letters*, 39, L14707. https://doi.org/10.1029/2012GL052459

Easterling, D. R., Horton, B., Jones, P. D., Peterson, T. C., Karl, T. R., Parker, D. E., Salinger, M. J., Razuvayev, V., Plummer, N., Jamason, P., & Folland, C. K. (1997). Maximum and minimum temperature trends for the globe. *Science*, 277, 364–367. https://doi.org/10.1126/science.277.5324.364

Frances, D. N., & McCauley, S. J. (2018). Warming drives higher rates of prey consumption and increases rates of intraguild predation. *Oecologia*, 187, 585–596. https://doi.org/10.1007/s00442-018-4146-y

Fussmann, K. E., Schwarzmueller, F., Brose, U., Jousset, A., & Rall, B. C. (2014). Ecological stability in response to warming. *Nature Climate Change*, 4, 206–210. https://doi.org/10.1038/nclimate2134

Gibert, J. P. (2019). Temperature directly and indirectly influences food web structure. *Scientific Reports*, 9, 5312. https://doi.org/10.1038/s41598-019-41783-0

Gilman, S. E. (2017). Predicting indirect effects of predator-prey interactions. *Integrative and Comparative Biology*, 57, 148–158. https://doi.org/10.1093/icb/icx031

Harmon, J. P., Moran, N. A., & Ives, A. R. (2009). Species response to environmental change: Impacts of food web interactions and evolution. *Science*, 323, 1347–1350. https://doi.org/10.1126/science.1167396

Higashi, C. H. V., Barton, B. T., & Oliver, K. M. (2020). Warmer nights offer no respite for a defensive mutualism. *Journal of Animal Ecology*, 89, 1895–1905. https://doi.org/10.1111/1365-2656.13238

Iles, A. C. (2014). Toward predicting community-level effects of climate: Relative temperature scaling of metabolic and ingestion rates. *Ecology*, 95, 2657–2668. https://doi.org/10.1890/13-1342.1

IPCC. (2012). *Managing the risks of extreme events and disasters to advance climate change adaptation. A special report of Working Groups I and II of the Intergovernmental Panel on Climate Change*. Cambridge University Press.

Ma, C. S., Ma, G., & Pincebourde, S. (2021). Survive a warming climate: Insect responses to extreme high temperatures. *Annual Review of Entomology*, 66, 163–184. https://doi.org/10.1146/annurev-ento-041520-074454

Ma, G., Bai, C. M., Rudolf, V., & Ma, C. S. (2021). Data from: Night warming alters mean warming effects on predator–prey interactions by modifying predator demographics and interaction strengths. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.z612jm6c2

Ma, G., Hoffmann, A. A., & Ma, C. S. (2015). Daily temperature extremes play an important role in predicting thermal effects. *Journal of Experimental Biology*, 218, 2289–2296. https://doi.org/10.1242/jeb.122127

Ma, G., Le Lann, C., van Baaren, J., & Ma, C. S. (2020). Night warming affecting interspecific interactions: Implications for biological control. In Y. Gao, H. Hokkanen, & I. Menzler-Hokkanen (Eds.), *Integrative biological control. Progress in Biological Control* (Vol 20). Springer. https://doi.org/10.1007/978-3-030-44838-7_3

Ma, G., Rudolf, V. H. W., & Ma, C. S. (2015). Extreme temperature events alter demographic rates, relative fitness, and community structure. *Global Change Biology*, 21, 1794–1808. https://doi.org/10.1111/gcb.12654

Miller, C. R., Barton, B. T., Zhu, L., Radeloff, V. C., Oliver, K. M., Harmon, J. P., & Ives, A. R. (2017). Combined effects of night warming and light pollution on predator–prey interactions. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20171195. https://doi.org/10.1098/rspb.2017.1195

Murrell, E. G., & Barton, B. T. (2017). Warming alters prey density and biological control in conventional and organic agricultural systems. *Integrative and Comparative Biology*, 57, 1–13. https://doi.org/10.1093/icb/icx006

Ockendon, N., Baker, D. J., Carr, J. A., White, E. C., Almond, R. E. A., Amano, T., Bertram, E., Bradbury, R. B., Bradley, C., Butchart, S. H. M., Doswald, N., Foden, W., Gill, D. J. C., Green, R. E., Sutherland, W. J., Tanner, E. V. J., & Pearce-Higgins, J. W. (2014). Mechanisms underpinning climatic impacts on natural populations: Altered species interactions are more important than direct effects. *Global Change Biology*, 20, 2221–2229. https://doi.org/10.1111/gcb.12559

Pandori, L. L. M., & Sorte, C. J. B. (2019). The weakest link: Sensitivity to climate extremes across life stages of marine invertebrates. *Oikos*, 128, 621–629. https://doi.org/10.1111/oik.05886

Petchey, O. L., Mcphearson, P. T., Casey, T. M., & Morin, P. J. (1999). Environmental warming alters food-web structure and ecosystem function. *Nature*, 402, 69–72. https://doi.org/10.1038/47023

Potter, K. A., Woods, A., & Pincebourde, S. (2013). Microclimatic challenges in global change biology. *Global Change Biology*, 19, 2932–2939. https://doi.org/10.1111/gcb.12257

Radchuk, V., Turlure, C., & Schtickzelle, N. (2013). Each life stage matters: The importance of assessing the response to climate change over the complete life cycle in butterflies. *Journal of Animal Ecology*, 82, 275–285. https://doi.org/10.1111/j.1365-2656.2012.02029.x

Rall, B. C., Vucic-Pestic, O., Ehnes, R. B., Emmerson, M., & Brose, U. (2010). Temperature, predator–prey interaction strength and population stability. *Global Change Biology*, 16, 2145–2157. https://doi.org/10.1111/j.1365-2486.2009.02124.x

Ruel, J. J., & Ayres, M. P. (1999). Jensen's inequality predicts effects of environmental variation. *Trends in Ecology & Evolution*, 14, 361–366. https://doi.org/10.1016/S0169-5347(99)01664-X

Speights, C. J., & Barton, B. T. (2019). Timing is everything: Effects of day and night warming on predator functional traits. *Food Webs*, *21*, e00130. https://doi.org/10.1016/j.fooweb.2019.e00130

Speights, C. J., Harmon, J. P., & Barton, B. T. (2017). Contrasting the potential effects of daytime versus nighttime warming on insects. *Current Opinion in Insect Science*, *23*, 1–6. https://doi.org/10.1016/j.cois.2017.06.005

Uszko, W., Diehl, S., Englund, G., & Amarasekare, P. (2017). Effects of warming on predator–prey interactions – A resource-based approach and a theoretical synthesis. *Ecology Letters*, *20*, 513–523. https://doi.org/10.1111/ele.12755

Veselý, L., Boukal, D. S., Buřič, M., Kuklina, I., Fořt, M., Yazicioglu, B., Prchal, M., Kozák, P., Kouba, A., & Sentis, A. (2019). Temperature and prey density jointly influence trophic and non-trophic interactions in multiple predator communities. *Freshwater Biology*, *64*, 1984–1993. https://doi.org/10.1111/fwb.13387

Vucic-Pestic, O., Ehnes, R. B., Rall, B. C., & Brose, U. (2011). Warming up the system: Higher predator feeding rates but lower energetic efficiencies. *Global Change Biology*, *17*, 1301–1310. https://doi.org/10.1111/j.1365-2486.2010.02329.x

Wang, Y. J., Nakazawa, T., & Ho, C. K. (2017). Warming impact on herbivore population composition affects top-down control by predators. *Scientific Reports*, *7*, 941. https://doi.org/10.1038/s41598-017-01155-y

Zhang, S., Fu, W., Li, N., Zhang, F., & Liu, T. (2015). Antioxidant responses of *Propylaea japonica* (Coleoptera: Coccinellidae) exposed to high temperature stress. *Journal of Insect Physiology*, *73*, 47–52. https://doi.org/10.1016/j.jinsphys.2015.01.004

Zhang, W., Rudolf, V., & Ma, C. S. (2015). Stage-specific heat effects: Timing and duration of heat waves alter demographic rates of a global insect pest. *Oecologia*, *179*, 947–957. https://doi.org/10.1007/s00442-015-3409-0

Zhao, F., Zhang, W., Hoffmann, A. A., & Ma, C. S. (2014). Night warming on hot days produces novel impacts on development, survival and reproduction in a small arthropod. *Journal of Animal Ecology*, *83*, 769–778. https://doi.org/10.1111/1365-2656.12196

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