Daily temperature extremes play an important role in predicting thermal effects

Gang Ma, Ary A. Hoffmann and Chun-Sen Ma

ABSTRACT
Organisms in natural environments experience diel temperature fluctuations, including sporadic extreme conditions, rather than constant temperatures. Studies based mainly on model organisms have tended to focus on responses to average temperatures or short-term heat stress, which overlooks the potential impact of daily fluctuations, including stressful daytime periods and milder nighttime periods. Here, we focus on daily maximum temperatures, while holding night-time temperatures constant, to specifically investigate the effects of high temperature on demographic parameters and fitness in the English grain aphid *Sitobion avenae*. We then compared the observed effects of different daily maximum temperatures with predictions from constant temperature–performance expectations. Moderate daily maximum temperatures depressed aphid performance while extreme conditions had dramatic effects, even when mean temperatures were below the critical maximum. Predictions based on daily average temperature underestimated negative effects of temperature on performance by ignoring daily maximum temperatures, while predictions based on daytime maximum temperatures overestimated detrimental impacts by ignoring recovery under mild night-time temperatures. Our findings suggest that daily maximum temperature will play an important role in regulating natural population dynamics and should be considered in predictions. These findings have implications for natural population dynamics, particularly when considering the expected increase in extreme temperature events under climate change.

KEY WORDS: Average temperature, Climate change, Life history trait, Mild temperature, Model prediction, Temperature extreme

INTRODUCTION
Climate change is expected to increase temperature variability and lead to a substantial increase in temperature extremes such as the daily maximum temperature (*T*<sub>max</sub>) (Easterling et al., 1997; IPCC, 2013). While average temperatures in temperate regions are rarely expected to exceed optimum temperatures for many organisms (Deutsch et al., 2008), *T*<sub>max</sub> on summer days is often predicted to surpass critical thermal maxima (Kearney et al., 2009; Bale and Hayward, 2010), resulting in stressful conditions for many mid-latitude ectotherms (Hoffmann et al., 2013; Zhang et al., 2013; Vasseur et al., 2015). Even small increases in maximum temperature may impact organism phenology (Semenov, 2009), species distribution (Overgaard et al., 2014), population dynamics (Welbergen et al., 2008) and community structure (Ma et al., 2015). However, previous studies often model or predict effects on the distribution and population growth of organisms based on changes in average temperature (Cannon, 1998; Parmesan and Yohe, 2003; Rall et al., 2010; Vucic-Pestic et al., 2011) rather than *T*<sub>max</sub> (Easterling et al., 2000; Smith, 2011; Reyer et al., 2013).

Organisms in many natural terrestrial environments experience diel temperature fluctuations rather than constant temperatures (Colinet et al., 2015), including sporadic extreme conditions involving *T*<sub>max</sub>. Responses to constant conditions with no temperature fluctuations have been found to overestimate organisms’ optimal temperature, thermal safety margins and temperature-dependent fitness in both animals and plants (Clusella-Trullas et al., 2011, 2013; Paaijmans et al., 2013; Reyer et al., 2013), by overlooking the negative impact of *T*<sub>max</sub>. When natural temperature variation is simulated, *T*<sub>max</sub> is often deliberately avoided to minimize mortality (Bradshaw et al., 2004; Whitney-Johnson et al., 2005; Warren and Anderson, 2013; Jeffs and Leather, 2014). Temperature fluctuations that vary in amplitude to approximate extremes in nature depress fitness components such as development, survival and fecundity (Ragland and Kingsolver, 2008; Paaijmans et al., 2010; Carrington et al., 2013; Xing et al., 2014), pointing to adverse effects of *T*<sub>max</sub> on organism performance. However, predictions based on short periods of high-temperature stress may neglect the effect of mild night-time temperatures (Carter et al., 1982; Zhou et al., 1989; Triltsch et al., 1998), which allow organisms sufficient time to recover during intervals of successive episodes of thermal stress (Davis et al., 2006; Sentsis et al., 2013). Regimes used in previous studies on temperature fluctuations (reviewed by Colinet et al., 2015) tend to focus on the amplitude of fluctuating conditions and confound changes in *T*<sub>max</sub> with different daily minima, which also affect performance (Zhao et al., 2014). This makes it difficult to isolate the specific effects of changes in *T*<sub>max</sub>.

Aphids are important pests widely distributed in temperate areas (van Emden and Harrington, 2007). They have rapid rates of heat transfer and short life cycles and thus are highly vulnerable to variation in temperature (Brown et al., 2004; Danks, 2006; Angilletta, 2009). In this study, we used the English grain aphid *Sitobion avenae* (Fabricius 1775), as a model species. This aphid is one of the most important agricultural pests, not only in European countries, but also in China and the United States where average temperatures can be high and hot events occur frequently during the growing season. For instance, during mid June in 2013 near Beijing (40°N), a typical temperate region in China, changes in *T*<sub>max</sub> (31–41°C) were nearly twice as variable as daily average temperatures (*T*<sub>av</sub>, 22–27°C) and there were seven consecutive days with *T*<sub>max</sub> exceeding 30°C (Fig. 1A,B). Since these aphids mostly select microhabitats around plant spikelets, which are directly exposed to sunlight, the aphids may face extreme *T*<sub>max</sub>.

Here, we used a modified life-table experiment to test how different *T*<sub>max</sub> affect demographic parameters and fitness of the...
aphids. Life history data collected under different constant temperatures are available for building constant temperature–performance models, which can be compared with the observed effects of different $T_{\text{max}}$ values. By manipulating $T_{\text{max}}$ and fixing the same day-night temperatures to a mild constant value, our study aims to limit possible confounding effects of thermal changes not involving $T_{\text{max}}$ (c.f. Flynn et al., 2006; Folguera et al., 2009; Gillespie et al., 2012; Bannerman and Roitberg, 2014). Since organism responses to climate change can vary across life history traits (Radchuk et al., 2013; Ma et al., 2015), we tested multiple demographic parameters including development, survival, fecundity and adult longevity, and used the intrinsic rate of increase ($r_m$) as an overall fitness measure. Thus, the present study helps to indicate how changes in $T_{\text{max}}$ affect organism performance, along with implications for predicting the impact of climate change. We focus in particular on the following questions: (1) Does $T_{\text{max}}$ depress aphid performance when the means are below the critical maximum mean temperatures? (2) To what extent do different $T_{\text{max}}$ values affect aphid performance in contrast to corresponding constant temperatures? (3) How do these findings translate into population predictions and what are the implications for climate change studies?

RESULTS

Development

The developmental rate of nymphs at constant temperature estimated from the literature (Dean, 1974; Lykouressis, 1985; Li, 1990; Liu and Li, 1990; Sengonca et al., 1994; Yin et al., 2003) provided a good fit to the Lactin model (Lactin et al., 1995) (Fig. 2A, solid line; $D_T = e^{0.1377 - e^{4.514 - (32.947 - T)^7/267}}$, $R^2=0.864$). Based on this model, nymphal developmental rate was expected to be stable with temperature in our experiment when daily $T_{\text{av}}$ were considered, whereas these values were predicted to decrease dramatically when daylight temperatures ($T_{\text{day}}$) were considered (Fig. 2B). However, our data show that the nymphal developmental rate varied significantly ($F_{4,25}=16.83$, $P<0.0001$) and increased first and then decreased as the daily $T_{\text{max}}$ increased, with the values varying between 0.105 and 0.126 (Fig. 2B). In general, the observed values were higher than model predictions based on $T_{\text{day}}$, whereas they were lower than model predictions based on $T_{\text{av}}$.

Survival

Nymphal survival under constant temperatures (Dean, 1974; Lykouressis, 1985; Acreman and Dixon, 1989; Li, 1990; Asin and Pons, 2001; Yin et al., 2003) fitted a nonlinear model [Fig. 3A, solid line; survival = $1 - T/(316.118 - 0.314T^2)$, $R^2=0.888$]. Based on this relationship, nymphal survival is high across a range of different $T_{\text{av}}$ before dropping abruptly, whereas these values differ sharply from those observed under the range of $T_{\text{day}}$ tested (Fig. 3B). Our observed data also shows that $T_{\text{max}}$ over 36°C dramatically decreased survival (Fig. 3B; $\chi^2=63.51$, d.f.=4, $P<0.0001$).

Longevity

The best-fit equation for adult longevity at constant temperatures (Dean, 1974; Li, 1990; Sengonca et al., 1994; Zhang, 1994) was linear (Fig. 4A, solid line; longevity = $33.342 - 0.932T^2$, $R^2=0.651$). Our observed longevity under various regimes with different $T_{\text{max}}$ varied ($F_{4,25}=2.91$, $P=0.0461$) and was lower than model prediction under equivalent $T_{\text{av}}$, whereas the values were higher than the prediction under $T_{\text{day}}$ (Fig. 4B).

Fecundity

The best-fit equation for adult fecundity under constant temperatures (Dean, 1974; Lykouressis, 1984; Acreman and Dixon, 1989; Li,
overlook the potential impact of changes in $T_{\text{max}}$ or confound it with other thermal effects. Our study explicitly considers the impact of ecologically relevant $T_{\text{max}}$ on organism performance and fitness. The results point to aphid fitness declining with $T_{\text{max}}$ in contrast to predictions based on daily average temperature. The main driver of this decline is decreased survival at the maximum temperature treatments and to some extent, reductions in adult longevity and lifetime fecundity, although the effect of $T_{\text{max}}$ on development rate is relatively small. Aphids are more likely to be exposed to the most extreme temperatures and may not seek thermal refuges in the same way as other species. Therefore, $T_{\text{max}}$ may be more crucial for models on aphid thermal performance and other species that are less mobile compared with species that actively thermoregulate to avoid temperature extremes.

**Daily maximum temperatures depress aphid performance even when means are near the critical maximum mean temperatures**

An important finding of this work is that $T_{\text{max}}$ can clearly depress life history performance even when average temperatures are still below the critical maximum mean temperature. Our experiments isolated effects of $T_{\text{max}}$ by fixing night-time temperatures. As $T_{\text{max}}$ increased from 32°C to 40°C, the mean temperatures (24–26°C) used are still below or near the critical maximum mean temperatures (26–26.5°C) (Li, 1990; Asin and Pons, 2001), but aphid performance was dampered. Compared with observations from constant-temperature studies (see Ma et al., 2015), the observed
demographic parameters and fitness ($r_m$) of *S. avenae* were decreased to some extent when $T_{\text{max}}$ varied between 32°C and 36°C. When $T_{\text{max}}$ exceeded 36°C, the demographic parameters and fitness declined dramatically (Figs 2–6). This suggests that $T_{\text{max}}$ will reduce fitness to 0 when it reaches a critical threshold. During the daytime, episodic high temperatures can lead to a series of severe physiological and developmental problems in organisms (Denlinger and Yocum, 1998; Karl et al., 2011; Zhang et al., 2013) and further result in mass mortality (Welbergen et al., 2008).

In temperate regions with a large daily temperature range, moderate mean daily temperatures but high daytime maximum temperatures often occur during the growing season. For example, during 1 week in mid June in 2013 at Beijing, five out of seven days had moderate daily average temperatures, which were below the mean threshold (25°C) for the fitness of *S. avenae*. However, the $T_{\text{max}}$ of these days exceeded 36°C which are critical for the aphid (Fig. 1A). Thus, the temperature regimens we used can reflect $T_{\text{max}}$ under field conditions. These findings point to a crucial effect of $T_{\text{max}}$ even when the means are still below critical maximum mean temperatures.

**Intermediate effects of daily maximum temperatures on aphid performance in contrast to constant temperatures**

We found that $T_{\text{max}}$ generate particular effects on organisms and result in life-history performances that are lower than predicted based on daily average temperature ($T_{\text{av}}$), but higher than predicted based on average daylight temperatures ($T_{\text{day}}$). For the demographic parameters including development rate, survival, adult longevity and lifetime fecundity, the observed values were lower than model predictions based on $T_{\text{av}}$, especially when $T_{\text{max}}$ exceeded 36°C (Figs 2–5). As a consequence, the fitness ($r_m$) decreased as $T_{\text{max}}$ increased, in contrast to model predictions based on $T_{\text{av}}$ (Fig. 6). Even short-term extreme high temperatures can denature proteins and cause numerous physiological problems (Feder and Hofmann, 1999; Harmon et al., 2009). Our results, together with these findings, indicate detrimental effects of $T_{\text{max}}$ on organisms. However, the observed demographic parameters and fitness were stable under $T_{\text{max}} \leq 36°C$ and were much higher than predictions based on $T_{\text{day}}$ (Figs 2–6). This suggests that organisms can recover or even compensate for heat stress under mild temperatures during the night (Davis et al., 2006; Sentis et al., 2013; Colinet et al., 2015).

Predictions based on $T_{\text{av}}$ underestimate the impacts of temperature by neglecting the negative effects of $T_{\text{max}}$, while predictions based on $T_{\text{day}}$ overestimate the detrimental impacts of temperature by ignoring the recovery effects of mild night-time temperatures. Previous studies suggest a trade-off between thermal tolerance and energy allocation in organisms (Neargarder et al., 2003). On the one hand, when facing high daytime temperatures, organisms consume more resources and energy in producing and/or accumulating substances such as heat shock proteins (McMillan et al., 2005), exoskeletal proteins (Nguyen et al., 2009), mannitol and sorbitol (Hendrix and Salvucci, 1998) to enhance their heat resistance and rapidly adapt to daily maximum temperatures.

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**Fig. 4. Predictions for adult longevity based on daily average temperature and the differences between observed results and constant-temperature models.** (A) Linear relationship between adult longevity and constant temperature in *S. avenae* (Dean, 1974; Li, 1990; Sengonca et al., 1994; Zhang, 1994) (adapted from Zhao et al., 2014). (B) Comparison of adult longevity between our results (means$\pm$s.d.) and constant temperature models. Different letters in the plot represent significantly different daily maximum temperatures ($T_{\text{max}}$) at $P=0.05$. Solid and dashed lines represent models based on daily 24 h average temperatures ($T_{\text{av}}$) and daylight 8 h temperatures ($T_{\text{day}}$), respectively.

**Fig. 5. Predictions for lifetime fecundity based on daily average temperature and the differences between observed results and constant temperature models.** (A) Nonlinear relationship between lifetime fecundity and constant temperature in *S. avenae* (Dean, 1974; Lykouressis, 1984; Acreman and Dixon, 1989; Li, 1990; Asin and Pons, 2001) (after Zhao et al., 2014). (B) Comparison of lifetime fecundity between experimental results (means$\pm$s.d.) and constant temperature models. Different letters in the plot represent significantly different daily maximum temperatures ($T_{\text{max}}$) at $P=0.05$. Solid and dashed lines represent models based on daily 24 h average temperatures ($T_{\text{av}}$) and daylight 8 h temperatures ($T_{\text{day}}$), respectively.
(Overgaard and Sørensen, 2008). These substances, combined with excessive consumption of resources and energy in promoting heat resistance, in turn reduce performance for life history traits (Krebs and Feder, 1998; Silbermann and Tatar, 2000). Yet on the other hand, at mild night-time temperatures, organisms may spend more resources and energy on repairing and compensating performance such as development and reproduction (Davis et al., 2006; Sentis et al., 2013; Colinet et al., 2015). For example, some aphid species can buffer the negative impact of high daytime temperatures by recovering at relatively lower night-time temperatures (Ma et al., 2004a,b; Zhao et al., 2014). Therefore, our results emphasize the ecological significance of natural fluctuating temperatures with both daytime maximum temperatures and mild night-time temperatures.

**Population predictions and climate change**

Our findings indicate that daily maximum temperature plays an important role in regulating natural population dynamics and should be considered as an independent variable in predictive models. Effects of realistic daily $T_{\text{max}}$ are different from predictions based on constant temperatures which either overestimate or underestimate the impact of temperature (Overgaard et al., 2014). Previous studies on model organisms are mainly based on daily average temperatures, which either overlook daily maximum temperature (Rossberg et al., 1986; Freier et al., 1996; Tobin et al., 2008) or use the mean of the daily average and daily maximum temperatures (van Asch et al., 2007), and thus may underestimate the adverse impact of daily maximum temperature. By contrast, model predictions based on hourly or two-hourly average temperature (Carter et al., 1982; Zhou et al., 1989; Triltsch et al., 1998) focus on the immediate effect of temperature extremes rather than allowing for recovery at other times of the day, and thereby may overestimate the detrimental effect of daily maximum temperature. Our results may be useful for improving population dynamics prediction, as in the case of the aphid *Metopolophium dirhodum* (Ma, 2000). Data for daily maximum temperatures are easily accessed from most meteorological databases. Since even small changes in maximum temperature can dramatically influence organism phenology (Beebee, 1995; Semenov, 2009), distribution (Overgaard et al., 2014) and population dynamics (Welbergen et al., 2008), our findings highlight the importance for establishing $T_{\text{max}}$-dependent performance models.

Accurate prediction of the impact of climate change on organisms is a major challenge in this century. The present study emphasizes the need for taking daily maximum temperature into account in making these predictions. Warming is expected to lead to an increase in surface average temperature as well as in daily maximum temperature (IPCC, 2013). Temperate organisms are thought to have broader thermal tolerance and live in climates that are currently far from their optimal temperature (Deutsch et al., 2008). As a consequence, temperate organisms are expected to increase in abundance under climate change because fecundity and developmental rate are often enhanced by a small increase in mean temperature (Cannon, 1998; Parmesan and Yohe, 2003; Rall et al., 2010). However, previous studies on the impact of short-term heat stress (for several hours at constant high temperatures) show that temperate organisms are particularly vulnerable to extreme high temperatures (Tomanek, 2005; Huang et al., 2007) and predict a substantial decrease in these populations (Terblanche et al., 2008; Chidawanyika and Terblanche, 2011; Zizzari and Ellers, 2011). However, our results show that ecologically relevant daily maximum temperatures have an intermediate impact, in contrast to model predictions based on either mean daily temperatures or mean daylight temperatures. These novel findings point to the requirements for a comprehensive understanding of the impact of climate change in the context of increasingly extreme temperature events.

**MATERIALS AND METHODS**

**Experimental design**

We established five temperature regimens in climate chambers (PQX, Laifu Ltd., Ningbo, China; accuracy: 1°C), with different $T_{\text{max}}$ regimes with the same mean temperature ($T_{\text{max}}$ regimes with the same mean temperatures (van Asch et al., 2007), and thus may underestimate the adverse impact of daily maximum temperature. Our results may be useful for improving population dynamics prediction, as in the case of the aphid *Metopolophium dirhodum* (Ma, 2000). Data for daily maximum temperatures are easily accessed from most meteorological databases. Since even small changes in maximum temperature can dramatically influence organism phenology (Beebee, 1995; Semenov, 2009), distribution (Overgaard et al., 2014) and population dynamics (Welbergen et al., 2008), our findings highlight the importance for establishing $T_{\text{max}}$-dependent performance models.

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temperatures without changing any other part of the temperature regime, e.g. duration of peak temperatures, or minimum temperature for eliminating the disturbing impacts of mean temperature. Importantly, the daily means (24–26°C) used were below or near the critical maximum mean temperatures for population growth [intrinsically rate of increase \(r_m>0\) recorded for this species, i.e. 26–26.5°C (Li, 1990; Asin and Pons, 2001). Thus, the small differences in mean temperatures are unlikely to impact life history traits of this species, whereas changing other aspects of the temperature regime (e.g. reducing minimum temperatures) are known to alter life history traits and thereby lead to confounding effects of the \(T_{\text{max}}\) treatments (Zhao et al., 2014).

**Stock and experimental protocol**

Aphids were collected from a winter wheat field near Beijing (39°48’N, 116°28’E) during May 2010. *Sitobion avenae* was identified from the aphid samples, and then reared on 5–20 cm high winter wheat seedlings (CA0405) in screen cages (diameter 35 mm, with two window screens for ventilation) in five groups of five. The aphids in each clip-cage were fed on one fresh leaf in screen cages (60×60×60 cm) at 22±0.5°C, 50–60% RH, and a photoperiod of 16:8 h (L:D). Aphids were transferred to new seedlings weekly.

For each temperature regimen, 30 newborn aphids (0–6 h old) were monitored until death. These aphids were placed in six translucent clip cages (diameter 35 mm, with two window screens for ventilation) in groups of five. The aphids in each clip-cage were fed on one fresh leaf (clamped by the clip-cage) from a wheat seedling. Nymphal development and survival were checked twice per day at 07:00 and 19:00 h, respectively. Different instar nymphs were determined by their exuvia, which were removed (along with any dead nymphs) from the clip-cage. Reproduction and survival of adults were recorded once a day at 19:00 h, and dead adults and new offspring were removed. After each observation, the focal aphids from a clip-cage were placed into a new one and returned to the climate chambers. The aphids were transferred to new seedlings weekly. Within each chamber, photoperiod was 16:8 h (L:D), with light from 06:00 to 22:00 and darkness from 22:00 to 06:00, while relative humidity was 50–60%.

Developmental rate, proportional survival, lifetime fecundity and adult longevity were used as demographic variables, and the intrinsic rate of increase \(r_m\) was computed as a measure of relative fitness and population growth. For each variable, we calculated cage means by averaging across all five individuals within a cage. Survival was expressed as the proportion of live nymphs that developed into the adult stage. Developmental rate was given by the number of days until nymphs reached the adult stage. Lifetime fecundity (number of offspring per female) and adult longevity were calculated as the total number of offspring and days from adult emergence until death, respectively. The overall fitness measure \(r_m\) was calculated from the life table with PopTools 3.2.5 according to Hood (2017).

To reveal the extent to which the realistic temperature fluctuations affect aphid performance relative to temperature means and short-term heat stress, we compared the observed effects of these regimens with the predictions based on daily average temperatures \(T_{\text{av}}\) and the average temperature during daylight hours \(T_{\text{day}}\) reflecting heat stress. \(T_{\text{av}}\) under the five different regimens were calculated as the means of diel 24 h average temperatures (24, 24.4, 25, 25.3 and 26°C respectively), whereas \(T_{\text{day}}\) was calculated as the mean of daylight 8 h (08:00–16:00) temperatures coinciding with periods of high temperature (29.1, 29.2, 31.1, 32.4 and 33.1°C, respectively).

For nymphal developmental rate, survival, adult fecundity and longevity, the constant temperature-dependent performance models are the same as those used in Zhao et al. (2014). Nymphal development data (10–30°C) extracted from the literature (Dean, 1974; Lykouressis, 1985; Li, 1990; Liu and Li, 1990; Sengonca et al., 1994; Yin et al., 2003) were used. Survival data for nymphs (14–30°C) were extracted from the literature (Dean, 1974; Lykouressis, 1985; Acremen and Dixon, 1989; Li, 1990; Asin and Pons, 2001; Yin et al., 2003). Existing data for longevity (Dean, 1974; Li, 1990; Sengonca et al., 1994; Zhang, 1994) and fecundity (Dean, 1974; Lykouressis, 1985; Acremen and Dixon, 1989; Li, 1990; Asin and Pons, 2001) were used. For fitness \(r_m\), data extracted from the literature (Li, 1990; Asin and Pons, 2001) were used to construct a constant temperature-dependent second-order polynomial model (14–30°C) and the values of regression parameters were estimated with SigmaPlot 11:

\[
r_m(T) = a + bT + cT^2. \tag{1}
\]

**Statistical analysis**

The effects of different temperature regimens on developmental rate, adult longevity, lifetime fecundity and \(r_m\) were analyzed with one-way ANOVAs and normally distributed errors using the GLM procedure in SAS V8, and means separated with Duncan’s multiple range tests. Proportional survival was analyzed with a generalized linear mixed model (GLM) with binomial error distribution using the GENMOD procedure, and the levels of significant differences between regimens were compared using planned contrasts based on least-square means.

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**Competing interests**

The authors declare no competing or financial interests.

**Author contributions**

C.-S.M. conceived and designed the experiments. G.M. and C.-S.M. performed the experiments. G.M., A.A.H. and C.-S.M. analyzed the data and wrote the paper. All authors reviewed the manuscript.

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