

Night warming on hot days produces novel impacts on development, survival and reproduction in a small arthropod

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Summary

1. An asymmetric increase in night-time temperatures (NTs) on hot days is one of the main features of global climate change. But the biological effects of an increased night-time temperature combined with high daytime temperature are unclear.

2. We used six thermal regimens to simulate NTs on hot days and investigated the effects of night warming on life-history traits of the English grain aphid *Sitobion avenae*. Experimental temperatures fluctuated in continuous diurnal cycles, increasing from 27 °C to a maximum 35 °C and then declining to 27 °C gradually before further dropping to different minima (13, 16, 19, 21, 23 or 25 °C) representing NTs.

3. When compared to expectations based on constant temperatures, night warming raised the optimum temperature for development by 3 °C, in contrast to results from experiments where temperature variability was altered symmetrically or in a parallel manner. Night warming also reduced aphid survival under heat from 75% to 37% and depressed adult performance by up to 50%. Overall, night warming exacerbated the detrimental effects of hot days on the intrinsic rate of population increase, which was predicted to drop by 30% when night-time minimum temperatures exceeded 20 °C.

4. Our novel findings on development challenge the ‘Kaufmann effect’, suggesting this is inapplicable to night warming likely to be encountered in nature. Although many average temperature models predict increasing pest outbreaks, our results suggest that outbreaks of some species might decrease due to the effects of night warming on population dynamics.

Key-words: asymmetric warming, biology, climate warming, fluctuating temperature, heat stress, insect, phenology, thermal ecology

Introduction

Under global climate change, the increase of mean temperature over land is characterized by diurnal asymmetric patterns with greater trends of night warming than day warming (Karl *et al.* 1993; Easterling *et al.* 1997; Caesar, Alexander & Vose 2006), as well as an increase in intensity, duration and frequency of hot days (Frich *et al.* 2002; Luterbacher *et al.* 2004; IPCC 2007). In this context,

large-scale night warming coupled with hot days are starting to occur in many regions of the world (Easterling *et al.* 2000; Meehl & Tebaldi 2004) including agricultural areas. For instance, during the winter wheat growing season (April–June) at Wuhan (31°N) and Beijing (40°N), two main winter wheat regions in China, organisms living in field crops have experienced a marked increase in the number and average night-time temperatures (NTs) of hot days (daily maximum temperature exceeding 30 °C) for the last four decades (Fig. S1).

Despite this, night warming has not been considered much in modelling and predicting changes in populations of insects and other ectotherms, in contrast to brief heat

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exposure that causes multiple deleterious physiological and developmental effects (Denlinger & Yocum 1998). High daytime temperatures (DTs) on hot days increase the chance of individual death (Ma, Hau & Poehling 2004a), and the likelihood of a population crash (Kieckhefer, Elliott & Walgenbach 1989; Debarro & Maelzer 1993). Comparative studies suggest that thermal limits of many ectotherms will often be exceeded in the future (Hoffmann *et al.* 2012), highlighting an increased risk of species extinction (Deutsch *et al.* 2008). Night-time temperatures (NTs) are usually moderate even when DTs become extreme. These moderate temperatures alone generally do not depress the fitness of organisms (Huey & Kingsolver 1989). However, it is not known whether changes of these moderate NTs have much biological impact when combined with hot days.

In most studies undertaken so far, changes in NTs have been investigated by parallel or symmetrical changes in the nature of temperature fluctuations. In some studies, mean temperatures have been increased by simultaneously increasing DTs and NTs in a parallel manner (Naranjo, Gibson & Walgenbach 1990; Flynn, Sudderth & Bazzaz 2006). This can result in beneficial effects on organisms within an intermediate temperatures range (Fantinou & Chourdas 2006), and any effects of NTs being overwhelmed by negative impacts of daytime warming at high mean temperatures. In other studies, symmetric changes of daily thermal amplitude with constant mean have been considered, involving an increase of NT means an equivalent decrease in DTs affecting the daily thermal range (Georges *et al.* 2005; Folguera, Bastías & Bozinovic 2009; Folguera *et al.* 2011). Temperature changes in these studies involved both DTs and NTs, so the relative impact of changing DTs vs. NTs cannot be evaluated.

In few previous studies related to impacts of the asymmetric changes in NTs, night warming usually plays a positive role in life-history responses of ectotherms, such as accelerating the development in eggs of three grasshopper species (Wu *et al.* 2012), third larvae of *Manduca sexta* (Yang & Stamp 1995) and fifth larvae and pupae of *Pieris rapae* (Whitney-Johnson, Thompson & Hon 2005) and raising reproductive success and shortening reproductive cycle in *Uta stansburiana* (Clarke & Zani 2012). To minimize mortality, high DTs are avoided in these studies. Higher NTs therefore provide extra heat units and affect mainly rate processes, rather than affecting repair from heat lesions which may be one important function altered by NTs (Pétavy *et al.* 2001, 2004; Rohmer 2004; David *et al.* 2005).

In this study, we specifically consider the impact of changing NTs on hot days by testing the combined effects of daytime heat stress and night warming on life-history traits and population dynamics of English grain aphid *Sitobion avenae* (Fabricius). This species is an important global cereal pest common in temperate climates (van Emden & Harrington 2007). Small free-living arthropod herbivores like aphids are thought particularly susceptible to fluctuating ambient temperatures because they undergo

large metabolic shifts (Brown *et al.* 2004), have rapid rates of heat transfer (Angilletta 2009) and short life cycles (Danks 2006) that make them sensitive to brief heat exposure (Huey & Bennett 1990).

We address a series of questions. (i) Does night warming on hot days affect development and in what direction? (ii) Do the intermediate NTs on hot days decrease the survival? (iii) To what extent do different NTs ameliorate any detrimental effects of DTs on adult performance? (iv) How do these findings translate into phenology and population predictions? We tested life-history traits in *S. avenae* at six different NTs on hot days, and report on three novel findings: (i) night warming on hot days raises the optimum temperature for development; this finding challenges the 'Kaufmann effect'. (ii) Night warming within a moderate range reduces nymphal survival linearly; NT is an important predictor of survival. (iii) Night warming on hot days further depresses adult performance under daytime heat stress.

Materials and methods

TEMPERATURE REGIMES

Daytime temperatures and NTs used in the experiments are based on conditions observed in the field around Beijing on winter wheat crops when they are reaching maturity in late spring – early summer. In April–June, DTs often exceed 30 °C or more are recorded at weather stations on the outskirts of the city, and we have found that daytime maximum temperatures (DT_{max}) are around 5 °C higher in wheat crops when loggers are placed on spikes where most *S. avenae* are found. An example (Fig. S2a) provides data from a wheat crop located 16 km from a weather station near Yizhuangzhen (39°48'N, 116°28'E), with crop temperatures recorded using data – loggers (U23 – 001; Onset Ltd., Bourne, MA, USA) in April–June 2005. At the time that DT_{max} values in the field were 35 °C or higher, corresponding night-time minimum temperatures (NT_{min}) were in the range 13–25 °C (Fig. S2b).

Based on these types of data, we created six night-time temperature patterns (DT_{max} 35 °C and six different NT_{min} between 13–25 °C) to separate the thermal effects of NTs on aphid fitness during hot days. We examined development, survival, eclosion, fecundity and population increase. One growth chamber (RXZ-280B; Jiangnan Ltd., Ningbo, China) mimicked changes of DTs and six chambers simulated fluctuations of different NTs. During the day, temperatures in the chamber were increased from 27 °C to peak at 35 °C (at 09.00–15.00 h) and then decreased to 27 °C (at 15.00–21.00 h). During the night, temperatures in the six chambers dropped from 27 °C to different minima (13, 16, 19, 21, 23 and 25 °C) at 21.00–03.00 h and then rose to 27 °C (at 03.00–09.00 h). Temperature regimens in each growth chamber were controlled to change gradually in 12 steps in an hourly interval and cycled continuously during the experiment. Temperatures were recorded at 20-min interval using temperature/humidity data loggers (U23 – 001; Onset Ltd. Bourne, MA, USA) and were shown in Fig. 1. Relative humidity in chambers was set at about 40% during the day and 60% during the night. Photoperiod was set to 16 : 8 (L : D), with lighting for 12 h in the daytime chamber and for the last 4 h in the night-time chambers.

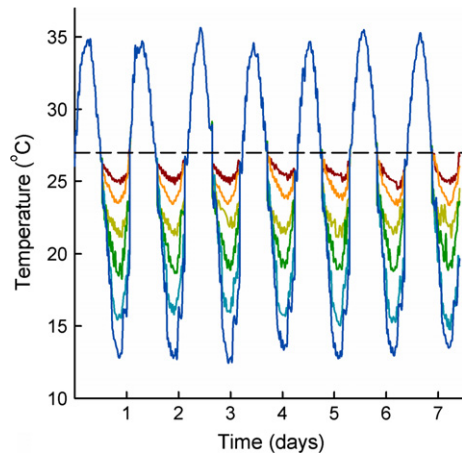


Fig. 1. Daily temperature variation in the experiments, as reflected by a 7 day-long sample recorded by Hobo dataloggers (at 20 min sampling intervals).

STOCK AND EXPERIMENTAL PROTOCOL

Aphids were collected from a winter wheat field near Beijing (39° 48' N, 116° 28' E) during May 2010. The English grain aphid was identified from the aphid samples, and then, the aphids were reared on 10–20 cm high winter wheat seedlings in screen cages (60 × 60 × 60 cm) at 22 ± 0.5 °C, 50–60% relative humidity, and a photoperiod of 16 : 8 (L : D). Aphids were transferred to new seedlings weekly.

At the beginning of the experiment, new nymphs (<6 h old) were placed into clip cages (3.5 cm diameter × 2 cm height) and then fixed on leaves of wheat seedlings with one nymph per cage. The host plants with prepared aphids were moved into six night chambers (21.00 h) and rotated between the day chamber and night chambers at 09.00 and 21.00 h every day. The development and survival of 30 individual nymphs per temperature regimen were recorded twice a day at 08.00 and 20.00 h. When aphids had developed to the adult stage, the number of offspring and the survival of adults in each cage were checked daily at 20.00 h. Mortality in clip cages was kept low in the absence of stress by (i) using well-ventilated clip cages to keep the aphids from escape, (ii) cleaning out exuviae and newly born nymphs without disturbing tested aphids during daily checking, and (iii) transferring tested aphids carefully to fresh seedlings every 4 days.

Apart from few escaped individuals, all aphids were used to determine the following traits: developmental times of the nymph stage, survival rate, adult longevity, fecundity and fecundity rate. Survival of different developmental stages was estimated as the percentage in individuals still alive entering the next stage or molting. Fecundity was measured as the number of nymphs per adult, and fecundity rate was estimated as adult fecundity divided by its longevity, i.e. the number of nymphs per adult per day.

To consider the possible effect of local thermal adaptation in *S. avenae* on thermal responses (Griffiths & Wratten 1979), we compared our results separately with previous studies for west European clones and Chinese clones at constant temperatures. Nymphal development data (10–30 °C) extracted from literature for west European clones (Dean 1974; Lykouressis 1985; Li 1990; Sengonca, Hoffmann & Kleinhenz 1994) and Chinese clones (Li 1990; Liu & Li 1990; Yin *et al.* 2003) were applied to construct a

constant temperature – dependent developmental rate model based on a Lactin nonlinear model (Lactin *et al.* 1995):

$$\text{Dr}(T) = e^{\rho T} - e^{\rho T_{\max} - (T_{\max} - T)/\Delta} \quad \text{eqn 1}$$

Where $\text{Dr}(T)$ is the mean nymphal developmental rate at temperature T (°C), ρ is the rate of increase at optimal temperature, T_{\max} is the upper developmental threshold, Δ is the difference between optimal and upper developmental threshold. The Marquardt algorithm in SYSTAT 6.0.1 (SPSS Inc, Chicago, IL, USA) was used to estimate the values of parameters.

Survival data for nymphs (14–30 °C) extracted from literature (Dean 1974; Lykouressis 1984; Acreman & Dixon 1989; Li 1990; Asin & Pons 2001; Yin *et al.* 2003) were applied to construct a constant temperature – dependent survival model:

$$\text{Sur}(T) = 1 - T/(\alpha - \beta T^2) \quad \text{eqn 2}$$

where $\text{Sur}(T)$ is the survival at temperature T (°C), α is the parameter that determines the inflexion point of temperature at which survival starts to decline rapidly, and β is the parameter that determines the speed of the decline. The Marquardt algorithm in SYSTAT 6.0.1 (SPSS Inc, Chicago, IL, USA) was used to estimate the values of parameters.

Existing longevity (Dean 1974; Li 1990; Sengonca, Hoffmann & Kleinhenz 1994; Zhang 1994) and fecundity (Dean 1974; Lykouressis 1984; Acreman & Dixon 1989; Li 1990; Asin & Pons 2001) data were used to construct constant temperature – dependent linear or second – order polynomial model (14–30 °C) and the values of regression parameters were estimated with SIGMAPLOT 11 (SPSS Inc):

$$\text{Longevity}(T) = a + bT \quad \text{eqn 3}$$

$$\text{Fecundity}(T) = a + bT + cT^2 \quad \text{eqn 4}$$

STATISTICAL ANALYSIS

Effects of the temperature regimens on development time, adult longevity, fecundity and fecundity rate were analysed with one-way analysis of variance (PROC GLM, SAS V8; SAS Institute Inc., Cary, NC, USA) and means separated with Duncan's multiple range test. Survival of whole nymph stages at different temperature regimes was determined with the Kaplan–Meier procedure. Differences between survival curves were compared using a Cox's proportional hazards model. The Dunn–Šidák technique was applied to adjust critical significance levels for multiple pairwise comparisons. Life table statistics, consisting of the intrinsic rate of increase (r_m), finite rate of increase (λ), net reproductive rate (R_0), doubling time (D) and mean generation time (T) were calculated through POP TOOLS 3.2.5 (Hood 2011).

Results

DEVELOPMENT

Nymphal developmental time was affected by NTs ($F_{5,85} = 15.92$, $P < 0.0001$); as average and minimum temperature increased, there was a linear relationship with these variables (Fig. S3, $y = 27.49 - 0.70x$, $R^2 = 0.478$). The longest development time (10.3 ± 1.5 day) was

observed at the lowest NT_{min} of 13 °C and this decreased to 7.5 ± 0.8 day at 25 °C.

The development rate of nymphs at constant temperature estimated either from Chinese clones (Li 1990; Liu & Li 1990 and Yin *et al.* 2003) or west European clones (Dean 1974; Lykouressis 1985; Sengonca, Hoffmann & Kleinhenz 1994) provided a good fit to the Lactin model (Fig. 2a, solid line, $Dr = e^{0.13T} - e^{(4.43-(34.09-T)/7.65)}$, $R^2 = 0.877$ for Chinese clones; dashed line, $Dr = e^{0.13T} - e^{(4.28-(32.91-T)/7.65)}$, $R^2 = 0.884$ for west European clones). In contrast to model predictions for both clones based on daily average temperatures (DAT), the nymphal development rate increased rather than decreased with DATs in our experiment (Fig. 2b). On the other hand, upturns were similar between our results and the model predictions based on NTs, although development rates were lower in our temperature regimens (Fig. 2b).

SURVIVAL

The survival of *S. avenae* nymphs was significantly affected by night warming based on the Kaplan–Meier analysis (Fig. S4, $\chi^2 = 52.85$, $df = 5$, $P < 0.001$). The highest survival (75%) was observed at the lowest NT regimen, and this decreased to 37% at the highest NT regimen (Fig. 3, grey diamonds).

Nymphal survival under constant temperatures (Dean 1974; Lykouressis 1984; Acreman & Dixon 1989; Li 1990; Asin & Pons 2001; Yin *et al.* 2003) fitted a nonlinear model (Fig. 3 solid line, $Sur = 1 - T/(345.51 - 0.35T^2)$, $R^2 = 0.925$). Based on this relationship, we did not expect large effects of average NTs on survival, in contrast to the substantial effects of night warming observed in our experiment (Fig. 3).

LONGEVITY

Longevity, was affected by NTs ($F_{5,85} = 7.60$, $P < 0.0001$), being reduced as NT increased (Fig. 4b). When NT_{min}

increased to >20 °C, average adult longevity decreased from around 7 to 3 days (Fig. 4b). The best-fit equation for adult longevity in constant temperatures (Dean 1974; Li 1990; Sengonca, Hoffmann & Kleinhenz 1994; Zhang 1994) was linear (Fig. 4a solid line, $Longevity = 32.73 - 0.91T$, $R^2 = 0.628$). Based on this relationship, longevity was expected to decrease with temperature in our experiment when average daily or NTs were considered, although the longevity we observed were somewhat lower than expected under equivalent constant conditions (Fig. 4b).

FECUNDITY

Fecundity varied across treatments (Fig. 5b, $F_{5,85} = 3.71$, $P = 0.004$), and showed a similar pattern to longevity (c.f.

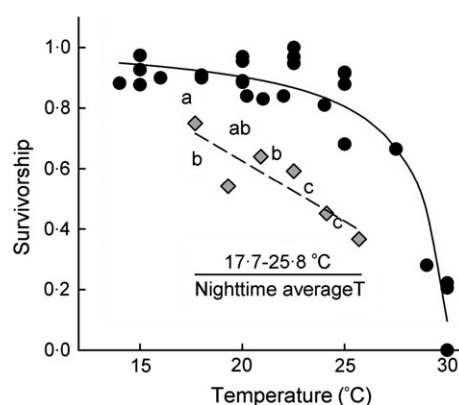


Fig. 3. Comparison of nymphal survivorship in our experiment and under a constant temperature model. Solid dots are data from Dean (1974), Lykouressis (1984), Acreman & Dixon (1989), Li (1990), Asin & Pons (2001) and Yin *et al.* (2003). Grey diamonds represent observed results based on night-time average temperatures; the dashed line represents the regression line and different letters represent significant differences between temperature regimens at $P = 0.05$.

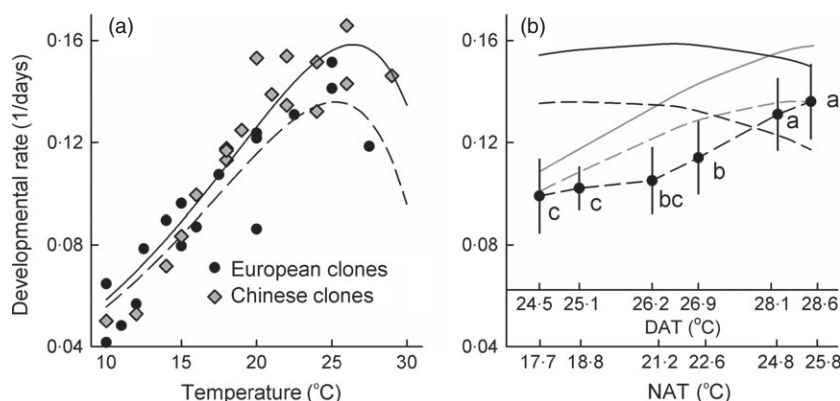


Fig. 2. (a) Nonlinear models describing developmental rates in *Sitobion avenae* nymphs as functions of constant temperatures based on data from Chinese clones (solid line, Li 1990; Liu & Li 1990; Yin *et al.* 2003) and west European clones (dash line, Dean 1974; Lykouressis 1985; Sengonca, Hoffmann & Kleinhenz 1994) respectively. (b) Comparison of development rate between our results (mean developmental rate \pm SD) and constant temperature models. Different letters in the plot represent significantly different temperatures at $P = 0.05$. Solid and dashed lines represent models based on Chinese and European clones respectively. Black and grey lines represent model predictions based on daily average temperature (DAT) and night-time average temperature (NAT) respectively.

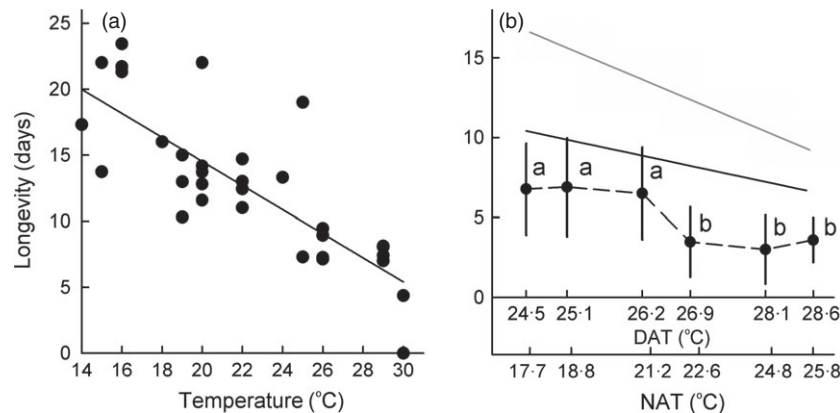


Fig. 4. (a) Linear relationship between adult longevity and constant temperature in *Sitobion avenae* (Dean 1974; Li 1990; Sengonca, Hoffmann & Kleinhenz 1994; Zhang 1994). (b) Comparison of longevity between our results (mean longevity \pm SD) and constant temperature models. Different letters in the plot represent significant differences between temperature regimens at $P = 0.05$. Black and grey lines represent model predictions based on daily average temperature (DAT) and night-time average temperatures (NAT) respectively.

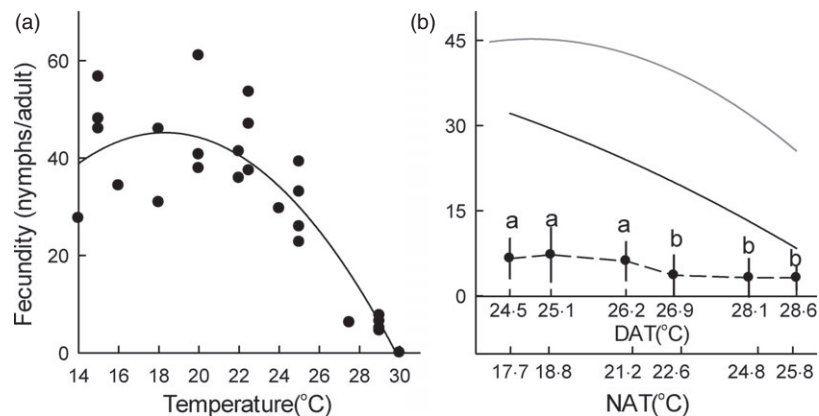


Fig. 5. (a) Nonlinear relationship between adult fecundity and constant temperature in *Sitobion avenae* (Dean 1974; Lykouressis 1984; Acreman & Dixon 1989; Li 1990; Asin & Pons 2001). (b) Comparison of fecundity between experimental results (mean fecundity \pm SD) and constant temperature models. Different letters in the plot represent significant differences between temperature regimens at $P = 0.05$. Black and grey lines represent model predictions based on daily average temperature (DAT) and night-time average temperatures (NAT) respectively.

Fig. 4b). Warmer night conditions ($NT_{\min} > 20^{\circ}\text{C}$) reduced fecundity from six to seven nymphs per adult to around 3 (Fig. 5b). However, fecundity rate was not affected by NTs (Fig. S5b, $F_{5,73} = 0.65$, $P = 0.666$). The best-fit equation for adult fecundity under constant temperatures (Dean 1974; Lykouressis 1984; Acreman & Dixon 1989; Li 1990; Asin & Pons 2001) involved a second-order polynomial model (Fig. 5a $\text{Fecundity} = -69.1 + 12.49T - 0.34T^2$, $R^2 = 0.833$). Fecundity under both constant and NTs (Fig. 5b) varied in a similar way to longevity (c.f. Fig. 4b), except that values in our experiment were markedly lower than expectations based on constant temperatures.

LIFE TABLE PARAMETERS

The summary life table statistics for *S. avenae* (Table S1) show that the intrinsic rate of population increase (r_m) was higher at NT_{\min} treatments of 13–19 °C compared to

21–25 °C (Fig. 6), and a similar trend was apparent for the finite rate of increase (λ). While aphids reared at NT_{\min} values in the range 21–25 °C had a shorter mean generation time (T) and became reproductive adults sooner than those reared at NT_{\min} values of 13–19 °C, their net reproductive rate (R_0) was lower, offsetting the benefits of faster development under warm conditions and resulting in a doubling time (DT) of the population at a NT_{\min} of 25 °C, almost twice as long as under the lowest temperature treatment (NT_{\min} 13 °C).

Discussion

NIGHT WARMING ON HOT DAYS RAISES OPTIMUM TEMPERATURE FOR DEVELOPMENT

Surprisingly, our results did not fit the ‘Kaufmann effect’ (Worner 1992; Ragland & Kingsolver 2008) or the more general ‘Jensen’s inequality’ (Ruel & Ayres 1999), which

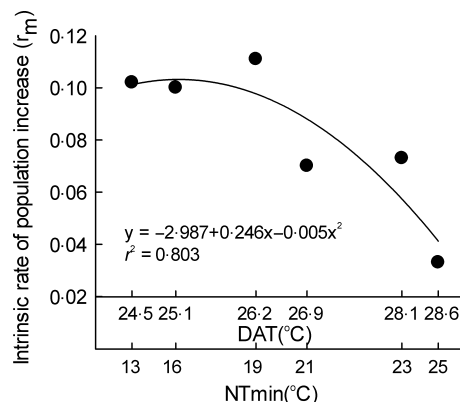


Fig. 6. Intrinsic rate of population increase (r_m) of *Sitobion avenae* at different night-time temperatures regimens.

is used to explain the development differences between constant and fluctuating temperature conditions. According to the Kaufmann effect, when average temperature is close to the optimum temperature for development (T_{opt}), development becomes slower (Worner 1992) and T_{opt} becomes lower (Messenger & Flitters 1959) at fluctuating temperatures than at the corresponding constant conditions. This effect has been demonstrated in many laboratory experiments involving symmetric fluctuating temperature regimes [e.g. tropical butterfly (Brakefield & Kesbeke 1997), corn borer (Fantinou, Perdakis & Chatzoglou 2003), red flour beetle and 16 other species (Hagstrum & Milliken 1991)]. In contrast to these results, the T_{opt} in our temperature regimens was raised to over 28.6 °C – above the T_{opt} at constant conditions (Fig. 2b), although the latter may be somewhat lower for European clones (25 °C) than for Chinese clones (26 °C) reflecting thermal adaptation (Griffiths & Wratten 1979; Hazell *et al.* 2010). Because an asymmetric increase of NTs in hot days is more commonly observed than a parallel increase (Easterling *et al.* 1997; Vose, Easterling & Gleason 2005), our results might be closer to the natural response of small arthropods to hot days than predictions based on the Kaufmann effect.

The discrepancy in developmental performance between symmetric and asymmetric thermal variation seems to be associated with temperature increases. When the mean of symmetric fluctuating temperature rises to T_{opt} , the detrimental impact of any increase in temperature above T_{opt} on development is expected to outweigh the positive effect (Ragland & Kingsolver 2008; Bozinovic *et al.* 2011). This leads to a slower development and lower T_{opt} at symmetric fluctuating temperatures than at a constant temperature. However, if temperature asymmetrically rises to T_{opt} , such as in our temperature regimens where only NTs were increased from 13 to 25 °C (minimum) and 17.7–25.8 °C (average), change occurs within the linear portion of the temperature–development relationship (Fig. 2a). Then any increase of NTs results in a rise of heat units speeding up development (Fig. 2b grey lines) on the assumption that

the effect of NTs on development are partly independent from the inhibitive effect of daytime heat stress.

NIGHT WARMING ON HOT DAYS REDUCES NYMPHAL SURVIVAL LINEARLY

While it is well known that the high-temperature survival depends on the intensity/exposure time (e.g. Denlinger & Yocum 1998; Ma, Hau & Poehling 2004a; Mironidis & Savopoulou-Soultani 2008, 2010) and ramping rate (Chown *et al.* 2009; Hofmann & Todgham 2010; Mitchell & Hoffmann 2010) of heat stress as well as on preconditioning treatments that result in rapid heat hardening or acclimation (Hofmann & Somero 1995; Huang, Chen & Kang 2007; Loeschcke & Hoffmann 2007), the effect of NTs on resistance have not been previously considered. Daytime heat exposures in our experiments were constant, and the decrease in survival (from 75% to 37%) was therefore likely to have been induced by different NTs (Fig. 3 grey diamonds). Survival of aphids declined linearly as NTs increased within a moderate range, unlike inverted U-shaped temperature–survival curves typified by high survival across a wide temperature range and rapid decreases near the upper/lower temperature limits (Amarasekare & Sifuentes 2012). Under constant temperatures, English grain aphids survive well under a wide range of mild temperatures (Fig. 3) – 92–97% (Dean 1974), 88–96% (Acreman & Dixon 1989) at 15–25 °C and 81–90% at 14–25 °C (Li 1990) – but survival declines to zero abruptly at 30 °C (Dean 1974; Asin & Pons 2001).

NIGHT WARMING ON HOT DAYS FURTHER DEPRESSES ADULT PERFORMANCE UNDER DAYTIME HEAT STRESS

Daytime heat stress reduces adult longevity and fecundity and this is exacerbated by increasing NTs. In our experiment, daytime high temperature exceeded 30 °C, the upper temperature limit in *S. avenae* (Kieckhefer, Elliott & Walgenbach 1989; Asin & Pons 2001), shortening adult longevity to 3–7 day, below expectations under constant conditions (Fig. 4b). Fecundity was reduced to three to eight nymphs per adult, much less than expectations based on daily or night-time average temperatures (Fig. 5b), such as observations of 61–33 nymphs between 10 and 25 °C (Dean 1974), 46–39 between 18 and 25 °C (Asin & Pons 2001) and 41–27 between 14 and 25 °C (Li 1990). Although NTs in all treatments (17.7–25.8 °C on average) were not expected to reduce longevity and fecundity so dramatically by themselves (grey lines in Figs 4b and 5b), they did reduce these traits when combined with daytime heat stress (black dots in Figs 4b and 5b). As NT_{min} increased from 13 to 25 °C, longevity was reduced as much as 50% (from 7 to 3 day) and fecundity was decreased from three to eight nymphs per adult. These results suggest that recovery capacity after heat stress may be weakened by increasing NTs.

POSSIBLE MECHANISMS FOR DETRIMENTAL EFFECTS OF NIGHT WARMING ON HOT DAYS

Warm nights might have increased the thermal sensitivity of aphids to daytime heat stress due to the fact that a slower ramping rate can decrease thermal tolerance (Chown *et al.* 2009; Mitchell & Hoffmann 2010). Warmer nights might increase resource and energy consumption for the synthesis of heat tolerance metabolites such as heat shock proteins (hsp), sugars and polyols (Krebs & Loeschcke 1994; Hoffmann, Sørensen & Loeschcke 2003) and/or for heat escape behaviour (Ma & Ma 2012a,b). This in turn could decrease resources available for reproduction and survival. Higher NTs might also slow the degradation of hsp and restoration of normal proteins synthesis (DiDomenico, Bugaisky & Lindquist 1982) that could further negatively impact growth, fertility and survival (Feder *et al.* 1992; Krebs & Loeschcke 1994; Krebs & Feder 1997; Silbermann & Tatar 2000). In addition, any effects of heat stress on aphids may be mediated by symbionts which are sensitive to heat (Burke *et al.* 2010).

FINDINGS ABOUT NIGHT WARMING MAY HELP PREDICT OF POPULATION DYNAMICS

The results could assist in predicting phenological changes in the aphids as well as in predicting pest outbreaks. They suggest that an increase in NTs following daily heat stresses modifies development, survival, longevity and fecundity. The linear degree-day model provides a satisfactory approximation for development under constant or fluctuating temperatures with moderate average and small – amplitude (Eubank, Atmar & Ellington 1973; Liu, Chen & Zalucki 2002), but not with high average and large amplitude temperature change (Hagstrum & Milliken 1991). Timing prediction can be improved by incorporating the nonlinear relationship between development and temperature (Sharpe & DeMichele 1977; Lactin *et al.* 1995), the amplitude of temperature change (Hagstrum & Milliken 1991; Georges *et al.* 2005), and even the daytime temperature (e.g. Sweeney & Schnack 1977; Niehaus *et al.* 2012) into phenology models. However, these approaches still ignore asymmetric effects of night warming which might also help explain discrepancies between field observations and model predictions based on average temperature.

The effect of NTs on survival and reproduction could assist in predicting changes in population numbers. Survival can be predicted typically from constant temperature experiments over a moderate range when temperature fluctuations are assumed to be small (Kieckhefer, Elliott & Walgenbach 1989). However, survival is likely to decrease as temperature fluctuations increase especially with rising DTs (Paaijmans *et al.* 2010; Lambrechts *et al.* 2011). We have now uncovered NT as an additional factor affecting survival which is likely to influence the likelihood of pest outbreaks across regions with similar daytime heat stress but different NTs and to become

increasingly important over time (Fig. S1). We have also found that night warming within a moderate temperature range has a substantial effect on reproductive output particularly through decreasing longevity. Our results and previous studies (Ma, Hau & Poehling 2004b) suggest that reproduction is markedly decreased under high DTs but in addition high NTs will further decrease reproductive output. Therefore both daily maximum and minimum temperatures during hot periods may be important in predicting pest population dynamics.

To what extent will night warming in hot days affect aphid populations within the next few decades? Based on impacts of climate warming on insect herbivores (Bale *et al.* 2002; Menéndez 2007), most models predict pest outbreaks increasing as average temperature rises (Landsberg & Smith 1992; Cannon 1998; Harrington, Fleming & Woitwod 2001). Our results suggest that these forecasts may be tempered by the effects of night warming in hot days. To assess the effect of night warming on populations, we estimated the intrinsic rate of population increase (r_m) (Fig. 6). There was no substantial difference in r_m when NT_{min} increased from 13 to 19 °C (DAT 24.5–26.2 °C), but a marked decline occurred when NT_{min} was over 20 °C (DAT 26.9 °C). Night warming can then exacerbate the negative effect of hot days by more than 30%. These changes could influence pest pressures although further work is required to assess impacts of NT on aphid biomass.

Meteorological data point to an increasing incidence of extremes of hot conditions and increases in NT_{min} in temperate regions (Easterling *et al.* 1997) that are concentrated in middle-latitudes (Stone & Weaver 2003). Aphids and other small arthropods are common in these regions (Dixon 1977) and likely to be particularly affected by changing conditions. Consider the comparison of Wuhan (31°N) and Beijing (40°N) in China as an example; the average number (10–11 days) and daily maxima (about 32 °C) of hot days (daily maximum temperature exceeding 30 °C) differ little between these areas during the winter wheat growing season (Fig. S1). In Wuhan (typical of low latitude regions), daily average NT_{min} is 21 °C during hot periods, and NTs are therefore unfavourable for *S. avenae*. In comparison in Beijing (typical of temperate regions), daily average NT_{min} in hot periods is 17 °C, but this figure is predicted to rise sharply under climate warming. Thus the distribution of *S. avenae* may contract in low latitude regions, and population size may decrease at intermediate latitudes as climate change increases NTs across consecutive hot days.

Acknowledgements

We thank Miss Lin Wang and Li-na Liang for assistance in completing experiments. We also thank Mr. Gang Ma and Chun-ming Bai for beneficial discussions. This research was supported financially by the National Natural Science Foundation of China (grant no. 31170392 and 31272035), Beijing Natural Science Foundation (grant no. 6132029) and Ministry of Agriculture (948 project 2011-G9), China. AAH was supported by a Fellowship from the Australian Research Council.

Data accessibility

Data available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.q2070>.

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Received 9 July 2013; accepted 14 December 2013
Handling Editor: Simon Leather

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Anomalies relative to 1970–2010 average values for the temperature variables of hot days (≥ 30 °C) during decimal wheat growth stages 30–90 in Wuhan and Beijing.

Fig. S2. Relationship between daytime maximum temperatures (DT_{max}) in a winter wheat field and (a) those recorded at a nearby weather station or (b) night-time minimum temperature (NT_{min}) recorded in the same field at Beijing (April–June, 2005).

Fig. S3. Development times of different stages of *S. avenae* under different NTs.

Fig. S4. Survival curves for nymphal stages in *S. avenae* at different NT_{min} regimens.

Fig. S5. Box plots for adult fecundity rate.

Table S1. Life table parameters of *S. avenae* under different NTs regimens.