

Research

Resolving biological impacts of multiple heat waves: interaction of hot and recovery days

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Heat waves are increasing with global warming and have more dramatic biological effects on organisms in natural and agricultural ecosystems than mean temperature increase. However, predicting the impact of future heat waves on organisms and ecosystems is challenging because we still have a limited understanding of how the different components that characterize heat waves interact. Here we take an experimental approach to examine the individual and combine consequences of two important features that characterize heat waves: duration of successive hot days and recovery days between two hot spells. Specifically we exposed individuals of a global agricultural pest, the aphid *Sitobion avenae* to different heat wave scenarios by factorially manipulating the number of extreme hot days versus normal days and altered which period individuals experienced first in their life cycle. We found that effects of heat waves were driven by a delicate balance of damage during hot periods versus repair during normal periods. Increasing the duration of hot days in heat waves had a negative effect on various demographic rates and life-time fitness of individuals, but magnitude of this effect was typically contingent on the temporal clustering of hot periods. Importantly, this interaction effect indicates that changes in the temporal distribution of extreme hot versus normal days can strongly alter the performance of organisms and dynamics of populations even when the total number of hot days during a given period remains unchanged. Together, these results emphasize the importance of accounting for the temporal distribution and quantitative patterns of extreme temperature events for predicting their consequences of natural and agricultural ecosystems.

Introduction

Climate change has led to an increase in the frequency, intensity and length of heat waves around the globe and this trend is expected to continue both in the short- and in the long-term (Meehl and Tebaldi 2004, Rahmstorf and Coumou 2011, IPCC 2012). For example, daily maximum temperatures of hot days in wheat growing season (May–June) at Wuhan (30°62'N, 114°13'E) in China often exceed 30°C, and

the frequency (Supplementary material Appendix 1 Fig. A1a–b) and duration (Supplementary material Appendix 1 Fig. A1c) of such heat waves has increased in the last 10 years. Heat waves could affect animals and plants in terrestrial and aquatic ecosystem systems (Easterling et al. 2000, Chen and Ma 2010, Wernberg et al. 2013, Leigh et al. 2015). Heat waves have caused catastrophic crop and forest failures (Filewod and Thomas 2014, Bauweraerts et al. 2013, Siebers et al. 2015), and they can reduce population size (Garrabou et al. 2009, Rasmont and Iserbyt 2013, Rubio-Portillo et al. 2016) and alter structure of natural communities (Gillespie et al. 2012, Sentis et al. 2013, Ma et al. 2015b). However, predicting the ecological effects of heat waves is challenging because the characteristics of heat waves can vary considerably across systems, geographic sites and over time (Smith 2011, Kreyling and Beier 2013, Bailey and van de Pol 2016, Buckley and Huey 2016). Thus, identifying how changes in the characteristic of heat waves affect organisms is essential to link global climate change to the dynamics and structures of natural and agricultural ecosystems.

Like many other types of extreme climatic events, ‘heat wave’ is an often poorly defined term (Kreyling and Beier 2013, Bailey and van de Pol 2016). Most definitions focus on a single heat wave based on either the percentile or/and concrete threshold daily maximum or/and minimum temperature which have detrimental effects on organisms (Glickman 2000, Meehl and Tebaldi 2004). However, natural temperatures fluctuate in repeated irregular waves with multiple extraordinary high temperature spells during a given time period (Supplementary material Appendix 1 Fig. A2). As a consequence, organisms in agricultural and natural ecosystems are exposed to such series of heat waves rather than a single heat wave (Bailey and van de Pol 2016). The majority of studies on heat waves are opportunistic, often lacking replication and therefore cannot control for different features of the climate extreme (Smith 2011). Controlled experiment under field conditions (Rouault et al. 2006, Arnone et al. 2011, Jentsch et al. 2011) often simulate a single level of a given climate extreme imposed at a small spatial scale (Smith 2011). As a consequence, we still have a limited understanding of how the timing, duration, and sequence of multiple periods of climate extremity affect biological systems (Gillespie et al. 2012, Sentis et al. 2013, Ma et al. 2015b, Marshall and Sinclair 2015).

Extreme climate events can affect biological systems in various ways, ranging from molecular responses in single organisms to ecosystem structure and functions (Hoffmann et al. 2003, Grimm et al. 2013, Rodriguez-Trelles et al. 2013, Vázquez et al. 2017). Demography is a key factor that links these climatic effects across different levels of organization. Demographic rates determine the temporal and spatial dynamics of a population (Benton et al. 2006, Miller-Rushing et al. 2010, Schurr et al. 2012, Lynch et al. 2014), interspecific interactions (Sentis et al. 2013, Ma et al. 2015b), and even the structure and functioning of ecosystem (Lloret et al. 2012, de Mazancourt et al. 2013). Importantly,

demographic shifts are also the product of complex changes in physiological, biochemical (Hahn and Denlinger 2007, Karl et al. 2008, Zhang et al. 2016) and molecular mechanisms that determine individual growth, development, reproduction, survival and even the stress tolerances (Rinehart et al. 2007, Košťál and Tollarová-Borovanská 2009, Liu et al. 2013). In addition, demographic responses impact the speed and direction of evolutionary trajectories (Lande 1988) and are thus critically important for understanding the evolutionary response of organisms to rapid environmental shifts (Metcalf and Pavard 2007, Richard and David 2009, Hoffmann and Sgrò 2011). Therefore, identifying how extreme climate events affect demography is essential to understanding ecological and evolutionary responses to climate changes (Lande 1988).

Extreme temperatures during hot days can cause various negative effects on organism’s metabolism, protein structure, and other physiological processes (Denlinger and Yocum 1998, Karl et al. 2011, Teves and Henikoff 2011). The majority of organisms have repair mechanisms to counteract these negative effects of high temperatures, but they are generally only effective at ‘normal’ temperature regimes (Bowler and Kashmeery 1979, Malmendal et al. 2006, Rodriguez-Trelles et al. 2013). Extreme hot events often occur multiple times during the life span of an organism (Supplementary material Appendix 1 Fig. A2) (Zhao et al. 2014, Ma et al. 2015b, Zhang et al. 2015b). Thus, the effect of heat waves on organism should depend on the delicate balance of damage versus repair periods (Zhang et al. 2015b). However, we know surprisingly little on how both interact and whether they are independent of each other. For instance, recent studies suggest that the effect of increasing maximum daily temperature depends on the nightly minimum temperature (Zhao et al. 2014). A similar interaction might occur between the successive number of extreme hot versus normal days. Short periods of extreme temperatures separated by sufficiently long periods of normal temperatures may allow organisms to recover before each heat wave and thus may have only minor consequences. In contrast, if hot periods last multiple days without normal days for recovery and repair, the negative effects may rapidly accumulate and result in irreparable damages to the organisms or even death. Such non-independent effects of extreme hot versus normal days would indicate that we could not simply record the days with extreme hot temperatures within a given time period but also need to consider their temporal distribution, i.e. whether and how they are clustered over time or not (e.g. long heat waves without normal days or short but frequent events). Thus, the number of consecutive hot days (i.e. length of heat wave) and the number of normal days between hot days should both be important for biological impacts of multiple heat waves. Understanding the individual and combined effects of these two components will help us to compare the potential implications of changing patterns in extreme temperature events expected with global climate change (Bailey and van de Pol 2016).

Here we examined how multiple heat waves with different alternating patterns affect the demography and fitness of an organism. We exposed individual aphids (a global agricultural pest) to different heat wave scenarios by factorially manipulating the number of extreme hot days versus normal days and altered which period individuals experienced first in their life cycle. This allowed us to answer the following specific questions: 1) how does the number of successive hot days alter life history traits and fitness of organisms? 2) How does the number of normal days between hot days alter the impacts of heat waves? 3) Are the individual effects of hot days and normal days on organism's performance independent? 4) Are the effects contingent on the timing of heat waves relative to the life-cycle of an organism? We found that the effects of days with extreme hot temperatures were dependent on how many normal days individuals have to recover between hot events. Furthermore, effects varied depending on whether individuals experienced hot or normal periods first in their life cycle. Together, these context dependent effects suggest that we need multiple metrics to adequately quantify heat wave patterns over time to accurately predict their effects on natural and agricultural ecosystems.

Material and methods

Study system

To study the impacts of heat waves on population demographics, we used the aphid species, *Sitobion avenae* as a model system. *Sitobion avenae* is often exposed to extreme summer temperatures during the growing season. The nymphal period of *S. avenae* lasts typically only 5–10 days, and adults live on average for 3–20 days depending on temperature regimens (Zhao et al. 2014, Ma et al. 2015a, b). Because of this short life-cycle, *S. avenae* is highly vulnerable to the changes in duration of heat waves and the normal days and its population dynamics and outbreaks in nature are known to be temperature-dependent (Acreman and Dixon 1989, De Barro and Maelzer 1993, Ma 2000). *Sitobion avenae* is an important pest species causing severe yield losses globally (Dean 1974b, Dixon 1977, Qureshi and Michaud 2005). Thus, changes in its population demographics have significant economic consequences.

Experiment design

To test how various heat waves affect demographic traits of aphids, we used a factorial design that independently manipulated the number of successive hot days (1–3 days) and normal interval days (1–3 days). This design allowed us to simulate a range of heat wave regimes (Fig. 1), such as 1) heat waves with different successive hot days but the same normal interval days (columns), 2) heat waves with the same successive hot days but different normal interval days (rows), 3) heat waves with the same proportion of hot days and normal days but differing in absolute hot days and normal days (top-right diagonal). To

reduce the possible variation caused by the starting temperature, we conducted two simultaneous experiments in parallel that either exposed aphids first to hot days or normal days.

To simulate diurnal fluctuation of temperatures in heat waves, we used 35°C and 20°C as the daily maximum and minimum temperatures for hot days, 28°C and 13°C as the daily maximum and minimum temperatures for normal days, respectively (Fig. 2). For all temperature regimens, we applied a sine curve to simulate the diurnal fluctuations with a magnitude of 15°C (Fig. 2b). All these simulated temperature parameters are based on May temperature records in Beijing from 1980–2013 (< <http://data.cma.cn/> >) (Fig. 2a) when our aphids are most abundant in the dominant winter wheat production region in China. In our study regions, heat waves during that period usually last for 1–5 days with an interval of 1–5 days of normal temperatures between heat waves. We designed the hot day as daily maximum 35°C and minimum 20°C based on our previous results that a nighttime temperature 20°C together with a daytime temperature 35°C significantly reduced the fitness of aphids (Zhao et al. 2014, 2017). We chose this temperature range for normal days because the daily maximum temperature (Ma et al. 2015a, b) and minimum temperature (Zhao et al. 2014) have no detrimental effects on fitness of the same species of aphid.

Experimental manipulation

We used life-table experiments to estimate the effect of various types of heat waves on the demographic rates of aphids. For each treatment, 36 newborn aphids (0–6 h old) were placed in a climatic chamber that simulated the diurnal temperature fluctuations of hot days and 36 in a climate chamber that simulated normal days (accuracy: 1°C). Each aphid was placed individually in a 5 ml plastic rearing tube (diameter 15 mm, length 55 mm) covered with a piece of nylon gauze (200 mesh). Each tube contained 0.6% agar solution in one-third of the tube holding a newly-excised wheat leaf for feeding. Wheat leaves in the tubes were renewed every day and the rearing tubes were replaced every third day to keep leaves in fresh mode. Nymphal development and survival were checked twice per day at 08:00 and 20:00 h, respectively. Different instars were identified by their exuvia. Reproduction and survival of adults were observed once a day at 20:00 h, and dead adults and new offspring were removed. After each observation, the focal aphids together with the rearing tubes were returned to the climatic chambers. The experiment ended after all tested individuals had died.

To manipulate the temperature regimes individuals experienced, we moved aphids together with the rearing tubes from the hot day chamber to the normal day chamber or vice versa according to the experimental design. All of these transitions were carried out at 22:00 since the temperature at this time is identical in both chambers (22.5°C). Within each chamber, photoperiod was 16 h (L): 8 h (D), with light from 06:00 to 22:00 and darkness from 22:00 to 06:00. Relative humidity was maintained in the two chambers at the same level (50–70%). All aphids were obtained from stock colonies

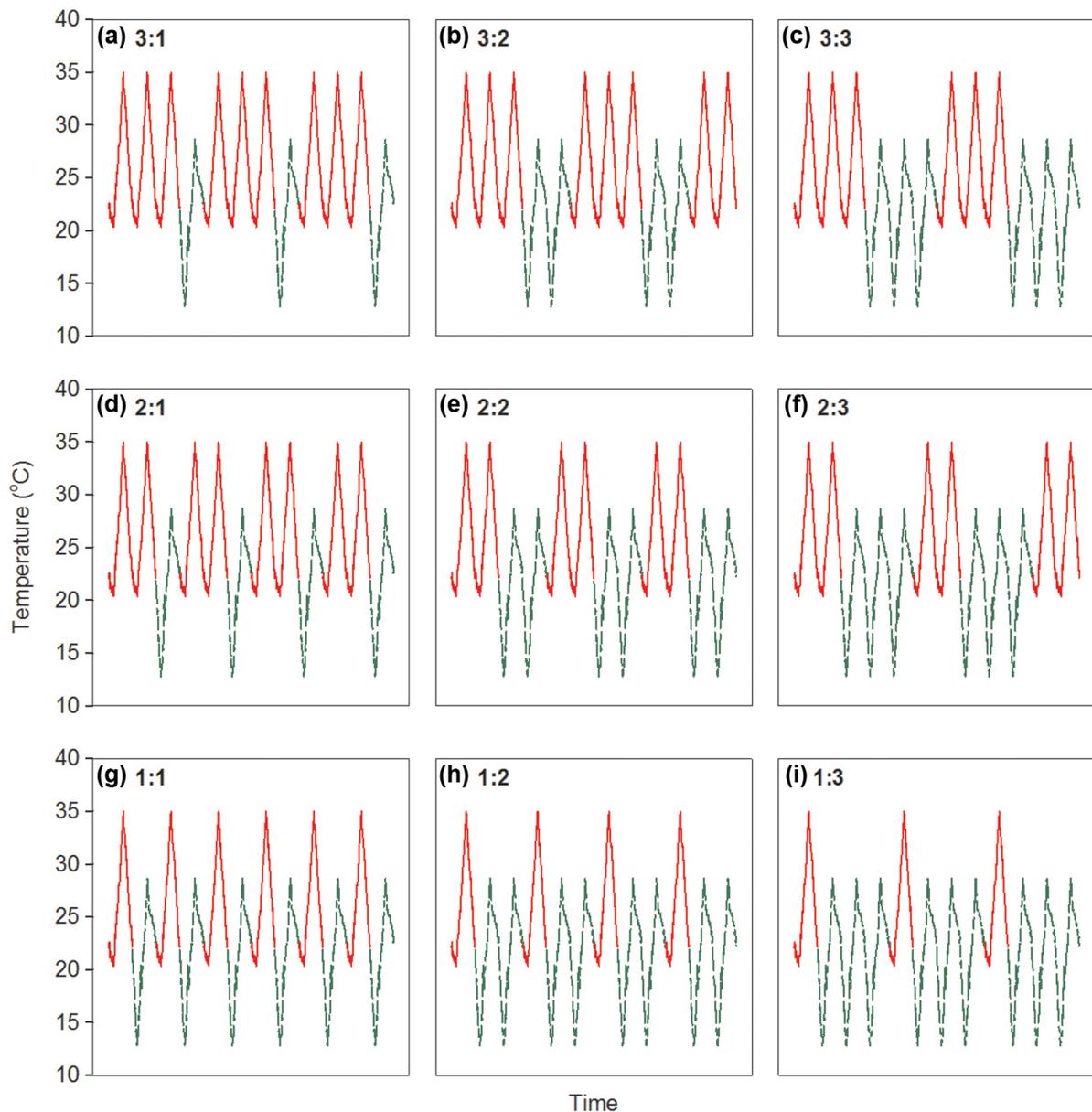


Figure 1. Snapshot of alternation patterns of successive hot days and normal days to simulate different periodic cycles of heat waves. Aphids were exposed under such alternation patterns until they died and only 12 days were shown here for saving space. Red solid lines represent of diurnal fluctuating temperatures of hot days and green dashed lines are the fluctuating temperatures of normal days. Different panels showed different combinations of continuous hot periods (ContH) and continuous normal (ContN) days separating hot periods.

reared on 5–20 cm high winter wheat seedlings (CA0045) in screen cages (60 × 60 × 60 cm) at a constant temperature of 22°C at 50–70% relative humidity and 16 L : 8 D photoperiod. Our pilot experiment demonstrated that the life history performances in such long-term laboratory population are similar to those in the field population reared in the lab for two generations (Ma et al. unpubl.).

Statistical analyses

We used generalized linear models (GLM) with gamma distributed errors to determine how the individual and

interactive effects of hot versus normal days affected fecundity, adult longevity, and duration of the nymphal stage using the ‘glm’ function in R, and the ‘car’ package with type II statistics to test for significant treatment effects. All analyses included the number of continuous hot and number of continuous normal days and whether the cycle (1st day of nymphal stage) started with a hot or normal day as fixed effects, and all possible two and three way interactions among fixed effects. Note that these analyses can only include individuals that survived to the adult stage. We used the package ‘gamlss’ and visual inspection of randomized quantile plots to determine which error distribution provided the best fit

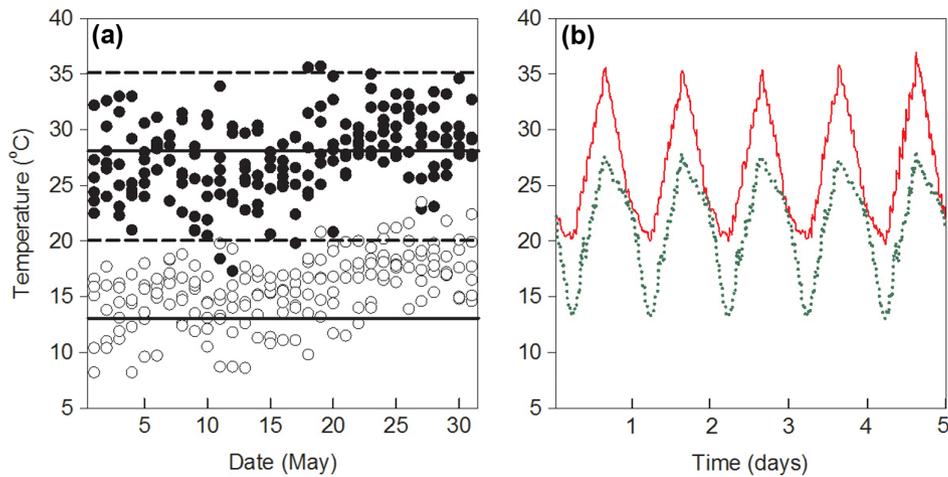


Figure 2. (a) Daily air temperatures recorded in Beijing in May from 2008–2013. Daily maximum (solid circles) and minimum (open circles) air temperatures. Horizontal dashed lines represent maximum and minimum temperatures of hot days and solid lines are the maximum and minimum temperatures of normal days. (b) Diurnal fluctuating temperatures of hot days (red solid lines) and normal days (green dashed lines) in the experiments, as reflected by a 5-day long sample recorded by Hobo data loggers (at 20 min sampling intervals).

to the data but results are robust to specific assumptions. We fit Cox proportional hazard regression models using the ‘survival’ package in R with default settings to determine how treatments affected survival of individuals. This survival analysis complements longevity and development analyses but provides more detailed insights into how the survival curves change throughout the entire life cycle. Differences in treatments and longevity of individuals inherently resulted in differences in the total number of hot days individuals experienced during their lifetime. To account for this potential bias we repeated analyses for adult longevity, survival and fecundity but included the total number of hot days an individual experienced during its life as a covariate. Overall, accounting for differences in total number of hot days did not change main results (Supplementary material Appendix 1 Table A1). The total number of hot days was not related to nymphal development period and thus not included in its analysis.

To get an integrated understanding of how heat treatment effects influenced life-time fitness of individuals and growth rates of populations, we used life-table analysis to calculate the intrinsic rate of increase (r), the net reproductive rate (R_0) and generation time (G) for each treatment. To compare treatments, we used bootstrap procedures to calculate

means and corresponding 95% confidence intervals (2.5th and 97.5th percentile of bootstrap distribution) using 999 randomizations and sampling with replacement.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.5qk4s>> (Ma et al. 2017).

Results

Development

Duration of the nymphal stage (number of days between 1st day of life and adult stage) varied significantly among heat treatments (Table 1), but the significant three-way interaction indicates that the effect of continuous hot days was contingent on how long individuals had to recover between hot events. When the cycle started with a normal day, increasing the number of consecutive hot days increased nymphal period by up to 15% (from 6.7 to 7.7), but only when just one normal day separated hot days (Fig. 3). In contrast,

Table 1. Effect of heat treatments on different demographic rates of individuals. Heat treatments manipulated the length of hot periods (HD) and normal periods (ND) separating hot periods. Cycle start (CS) varied whether individuals first experienced hot or normal day. Values indicate χ^2 statistics of GLMs or Z statistics for Cox proportional hazard models and corresponding p-values with significant values indicated in bold.

Heat treatment	Nymphal period	Adult longevity	Fecundity	Survival curve
Length of hot period (HD)	$\chi^2=4.20$, p=0.041	$\chi^2=10.32$, p=0.001	$\chi^2=24.20$, p < 0.0001	Z=1.48, p=0.138
Length of normal period (ND)	$\chi^2=2.29$, p=0.131	$\chi^2=35.93$, p < 0.0001	$\chi^2=35.24$, p < 0.0001	Z=-2.19 , p=0.029
Cycle start (CS)	$\chi^2=8.72$, p=0.003	$\chi^2=9.66$, p=0.002	$\chi^2=0.17$, p=0.679	Z=1.10, p=0.267
HD: ND	$\chi^2=0.14$, p=0.705	$\chi^2=0.80$, p=0.372	$\chi^2=0.0$, p=0.975	Z=-0.17, p=0.272
CS: HD	$\chi^2=1.00$, p=0.317	$\chi^2=4.44$, p=0.035	$\chi^2=2.85$, p=0.091	Z=-2.06 , p=0.039
CS: ND	$\chi^2=3.51$, p=0.061	$\chi^2=1.20$, p=0.273	$\chi^2=0.85$, p=0.358	Z=-1.10, p=0.272
HD: ND: CS	$\chi^2=13.37$, p < 0.001	$\chi^2=2.01$, p=0.156	$\chi^2=5.99$, p=0.014	Z=1.61, p=0.107

increasing the number of consecutive hot days had no effects when individuals had two or three normal days to recover between hot days (Fig. 3). When the cycle started with a hot day, this pattern changed; here increasing the number consecutive hot days only increased nymphal period when three normal days separated hot days (from 7.3–8.0 days) but had no effects when one or two normal days separated hot periods (Fig. 3).

Adult longevity

The average life span of adults significantly declined with an increase in the number of consecutive hot days and increased with the number of consecutive normal days (Table 1, Fig. 3). While the strongest decrease in adult life span (33% decline from 12.5 days to 8.3 days) occurred when individuals had only one normal day to recover (Fig. 3), the effects of hot and normal days were largely additive. However, the effect of hot days was contingent on whether the cycle started with a hot or normal day. Overall, the negative effect of increasing consecutive hot days on adult life span was much weaker when the cycle started with hot day (average of 23% versus 7% decline respectively, Fig. 3). Accounting for differences in the total number of hot days during the life-time of individuals did not change this general effect of hot and normal days and their interaction (Supplementary material Appendix 1 Table A1).

Fecundity

Just like nymphal development, fecundity significantly varied among temperature treatments (Table 1). While fecundity generally declined on average by 24% with increasing number

of continuous hot days (from 34.9 to 26.6, Fig. 3), the significant three way interaction indicated that this effect was dependent on the number of normal days individuals had to recover from hot days, and whether the cycle started with a hot or normal day. This three-way interaction was largely driven by treatments where only one normal day separated hot days; when the cycle started with a normal day, fecundity dropped by half with increasing number of hot days when only one normal day separated hot periods (Fig. 3), but this negative effect was absent when cycle started with a hot day (Fig. 3). Overall, increasing the number of normal days to recover between hot periods reduced the negative effect of increasing the number of consecutive hot days. This non-independent effect of hot versus recovery periods remained after we accounted for differences in the total number of hot versus normal days individuals experienced during their lifetime (Supplementary material Appendix 1 Table A1).

Survival

Survival patterns differed significantly among heating treatments ($p < 0.0001$) and were strongly influenced by the number of consecutive normal days, and the number of consecutive hot days, although the effect of the latter was contingent on whether the cycle started with a hot or normal day (Table 1). To gain further insight into the patterns, we analyzed survival separately for both types of cycles. While the strong effect of consecutive normal days persisted, this analysis revealed a significant interactions between the number of consecutive normal and hot days ($Z = 2.25, p = 0.024$) when cycles started with a hot day. Overall, the median survival day decreased by ~30% with increasing number of consecutive hot days (Fig. 4). In contrast, increasing the

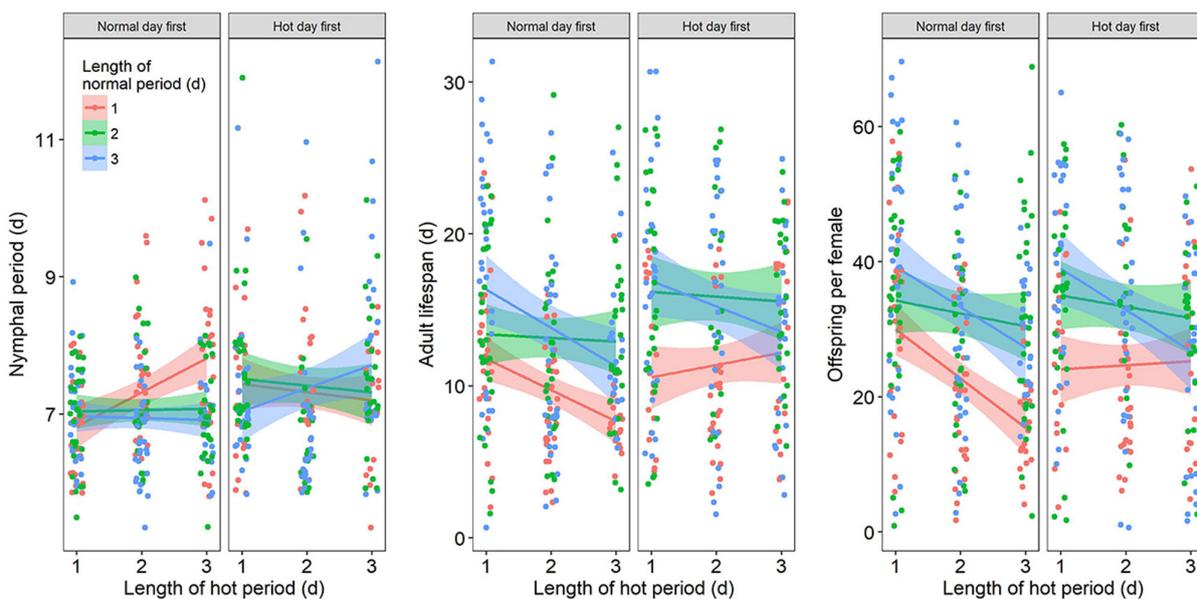


Figure 3. Duration of the nymphal (juvenile) stage, adult lifespan, and fecundity as a function of the number of continuous hot days. Different colors represent different durations of continuous normal days separating hot periods. Panels indicate whether the cycle (1st day of nymphal stage) started with a normal or hot day. Points represent individuals and were offset (jittered) to avoid overlap.

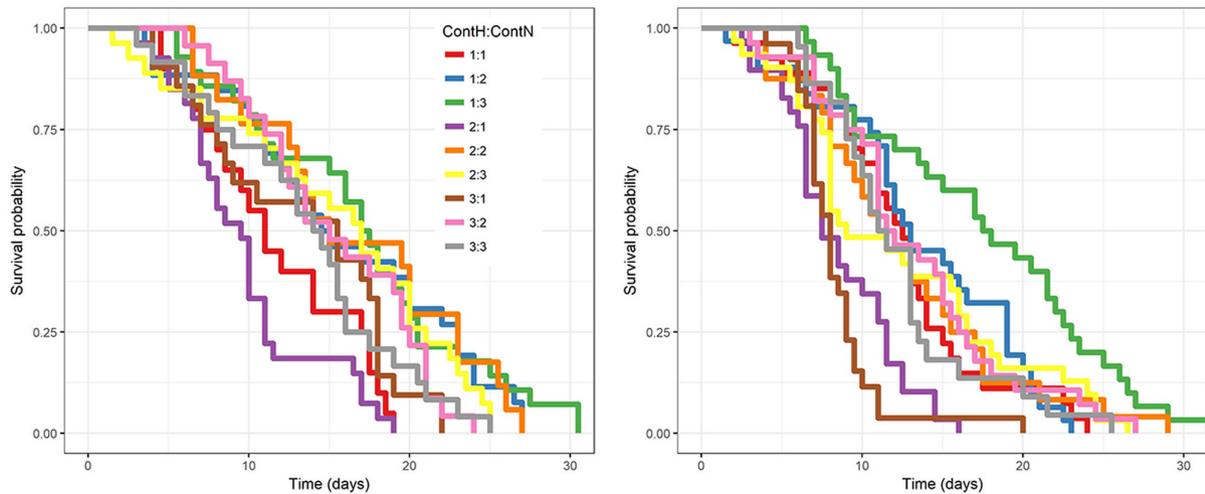


Figure 4. Survival probability of individuals within cohorts over time in different heat treatments. Colors represent different combinations of continuous hot periods (ContH) and continuous normal (ContN) days separating hot periods. Left panel shows treatments where the cycle started with a normal day first, and right pane where cycle started with a hot day first.

number of normal days increased survival, but this positive effect of normal days declined with increasing number of hot days. This effect was particularly strong when cycles started with a hot day explaining the significant interaction for that group of treatments (Fig. 4) and remained after we accounted differences for total number of hot days individuals experienced (Supplementary material Appendix 1 Table A1).

Fitness, population growth rates, and generation time

Several clear patterns emerged when comparing demographic parameters across temperature treatments (Fig. 5). Intrinsic rate of increase, net reproductive rate, and generation time generally decreased with number of consecutive hot days while increasing the number of normal days between hot periods had the opposite effect. However, there was some notable variation among treatment combinations. For instance, increasing the number of consecutive hot days clearly reduced intrinsic rate of increase when only one normal day separated hot periods, but this effect was largely lost when two or three normal days separated hot periods. This is consistent with the frequent interaction effects between consecutive hot and normal days we observed for individual demographic parameters above. Furthermore, treatments also differed depending on whether cycle was started with a normal or hot day. For instance, net R_0 declined with increasing number of consecutive hot days with only one normal day separating hot periods when the cycle started with a normal day, but there was no change when the cycle started with a hot day.

Discussion

Heat waves are increasing with climate change and known to have much more dramatic effects on organisms than changes in mean temperatures (Smith 2011, Thompson et al. 2013,

Vázquez et al. 2017). However, predicting the impact of future heat waves on organisms and ecosystems is challenging because we still have a limited understanding of how the different components that characterize heat waves interact. Here we have focused on two important features that characterize heat waves: duration of successive hot days and normal days between two hot spells. We found that increasing the duration of successive hot days had negative effects on various demographic rates and lifetime fitness of individuals, but these effects were typically contingent on the length of the normal days separating heat waves. These results emphasize that changes in the temporal distribution of extreme hot versus normal days can strongly alter the performance of organisms and dynamics of populations even when the total number of hot days during a given period remains unchanged. Furthermore, we found that individuals that experienced hot or normal days first responded surprisingly different to heat wave patterns, emphasizing the importance of the relative timing of heat events. Together, these results emphasize the importance of accounting for the temporal distribution and quantitative patterns of extreme temperature events for predicting their consequences of natural and agricultural ecosystems.

Context dependent effects of heat waves

An organism often experiences multiple times of extreme hot events during its life (Zhao et al. 2014, Ma et al. 2015b, Zhang et al. 2015b). Our results indicate that effects of heat waves on organisms should depend on the delicate balance of damage during hot days versus repair during normal days. As expected, increasing duration of heat waves had negative effects, while increasing the interval between heat waves had typically positive effects. Increasing the number of successive hot days generally accelerated development, but it reduced fecundity and adult longevity significantly

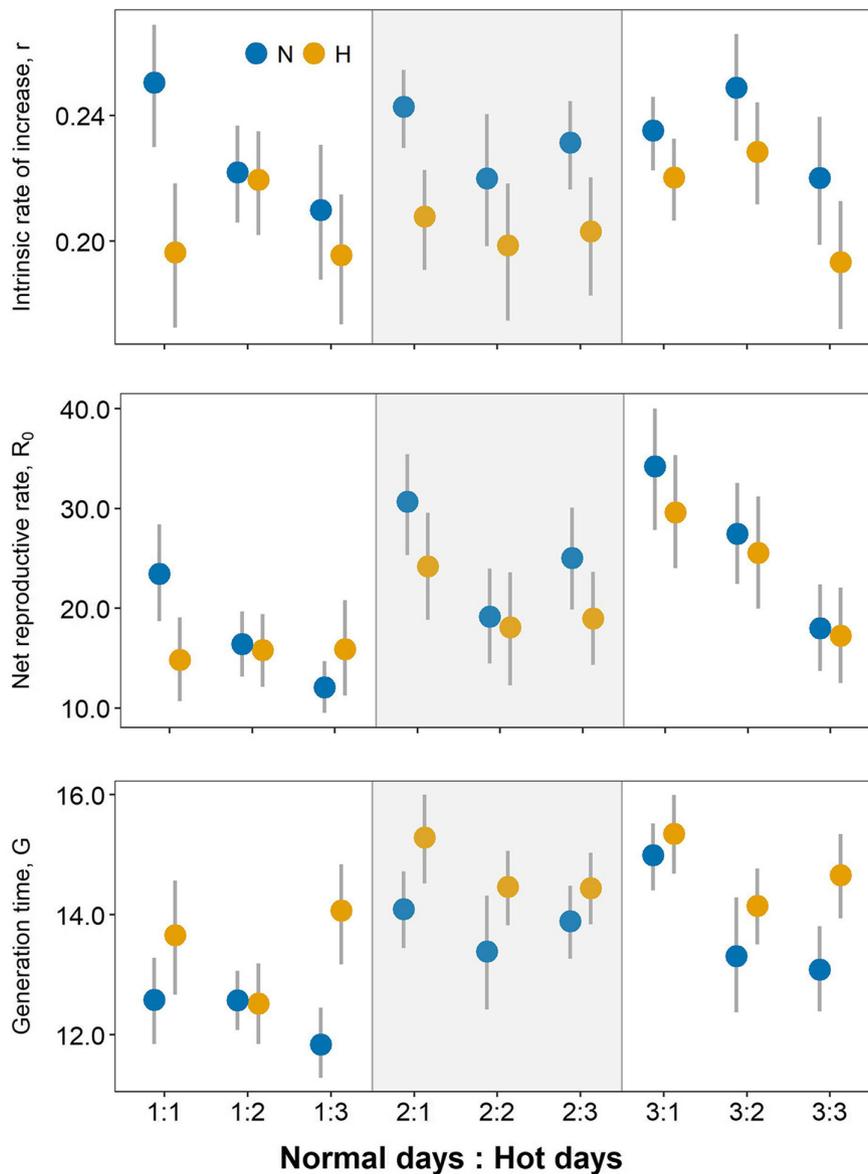


Figure 5. Mean (and 95% CI) intrinsic rate of increase, net reproductive rate and generation time of cohorts exposed to different combination of normal and hot periods. Normal days: Hot days indicates the number of consecutive normal days between consecutive hot days. Colors indicate whether individuals experienced first normal or hot day during the first day of their nymphal stage. Mean and CI were obtained from life-table analysis and estimates via bootstrapping methods based on 999 randomizations.

and did not significantly affect nymphal survival (Fig. 3, 4). Together, this reduced the intrinsic rate of increase and net reproductive rate of individuals (Fig. 5). In contrast, we found that increasing the number of normal days between hot days generally helped to reduce the negative effect of heat waves on lifetime fecundity, longevity and survival (Fig. 3, 4). However, effects of hot and normal days were not independent; increasing the duration of heat waves had less negative effects when hot periods were separated by longer periods with normal temperatures. Together with recent studies demonstrating that lower nighttime temperatures can reduce the negative effects of maximum daily temperature (Zhao et al. 2014), these results emphasize

the importance of normal days in driving the effect of heat waves.

The interactive effects of normal and hot periods are likely driven by a shift in the balance of damage versus repair periods. High temperatures can significantly reduce performance through disturbing metabolism, protein structure, etc. (Denlinger and Yocum 1998, Karl et al. 2011, Teves and Henikoff 2011, Sørensen et al. 2013). However, organisms also have repair mechanisms (Klose et al. 2005, Malmendal et al. 2006, de Nadal et al. 2011). For instance, they can release baseline protein synthesis through dissolving the heat shock proteins (DiDomenico et al. 1982, Dahlgard et al. 1998, Sørensen et al. 2005) that can

operate during normal temperatures to counteract the heat disturbance. Temperature typically fluctuates under natural conditions following diurnal cycles. In our system, the performance of aphids starts to decline at temperatures above 30°C (Dean 1974a). Even on hot days, temperature typically exceeds this threshold only for some hours during daytime and remains in the suitable range for the rest of the day (Zhao et al. 2014). Only sufficient accumulation of heat injury (Krebs and Loeschcke 1994, Denlinger and Yocum 1998) of these sporadic extreme temperatures together with the incomplete recovery during nighttime (Zhao et al. 2014) could result in significant performance inhibition. More successive hot days thus led to accumulation of detrimental heat effects. Previous studies indicate that the average recovery time is proportional to the magnitude of the stress (Rohmer et al. 2004, David et al. 2005). Thus, increasing the number of successive hot days requires a proportional increase in the number of normal days for repair to avoid negative effects, and the longer the recovery period between heat waves the more complete recovery from the heat stress (Zhang et al. 2015a, b). Consistent with this expectation we found that aphid performance varied little when the total number of hot and normal days increased proportionally (Hot: Normal 1:1 versus 2:2 versus 3:3), and increasing normal days for a given number of hot days always had a positive effect.

Timing of heat waves

Heat waves can occur during any point in life, even in short lived organisms like aphids and we found that the timing of heat waves relative to the start of the life-cycle of the individual changed the effects of heat waves. All demographic traits and fitness metrics of aphids were significantly different when individuals experienced normal or hot days first. Temperature treatment starting with hot days generally produced more negative effects on demographics than starting with normal days (Fig. 5). This dramatic effect could be driven by changes in thermal sensitivities with age. Different stages (instars) of insects typically have different thermal sensitivities (Bowler and Terblanche 2008, Kingsolver et al. 2011, Zhang et al. 2015a, Zhao et al. 2017). Many species are more sensitive to extreme climate events during early developmental stages and reproductive periods, including as *Sitobion avenae* (Zhao et al. 2017) and *Plutella xylostella* (Zhang et al. 2015a). For instance, early life stages have much smaller body sizes and thus thermal 'inertia', i.e. their body temperature increases much faster on hot days (Angilletta Jr 2009) and increase rates of temperature-dependent water loss (Gibbs et al. 1998, Klok and Chown 2001). Thus, hot periods during early life stages should have a much stronger negative effect on survival and intrinsic rate of increase which would explain the observed interaction of duration of heat waves and start day of the cycle in our experiment. Regardless of the underlying mechanisms, these results emphasize that the timing of hot events can play an important role in

mitigating the ecological consequences of heat waves in natural systems.

Multiple dimensions of heat waves

We can characterize variation in heat waves by independent components (daily maximum and daily minimum temperature on hot versus normal days, the number of successive hot days and the number of normal days between hot days) that together determine how heat waves influence organisms' demographic rates and population dynamics. Previous studies indicate that the intensity of heat waves can have important consequences. For instance, maximum day temperature of heat waves can alter demographic rates, fitness, and phenology of individuals, population dynamics (Ju et al. 2015, Ma et al. 2015a), and community structure (Gillespie et al. 2012, Sentis et al. 2013, Ma et al. 2015b), even when mean temperatures were below the critical maximum. Similarly, high nighttime temperature exacerbates the detrimental effects of hot days on the demographics and fitness and subsequently decreases risk for pest outbreaks (Zhao et al. 2014). Here we extend these studies by demonstrating that we also need to account for the temporal distribution of hot days. Our results indicate that while the negative effect of high temperatures can increase with the number of successive hot days, long enough periods with normal days between hot days could significantly dampen the negative impacts of hot days. Together with previous studies on the impact of heat intensity, our results indicate that an organism's performances under natural heat waves should depend on the interaction between heat injury level (determined by high temperature intensity and consecutive hot days) and recovery levels (determined by nighttime temperatures and normal interval days).

Given current and future climate change scenarios, predicting the impact of heat waves on organisms is a key challenge of the 21st century (Smith 2011, Kreyling and Beier 2013, Vázquez et al. 2017). The frequency of hot days is often used as an indicator for characterizing heat waves (Gillespie et al. 2012, Sentis et al. 2013, Ma et al. 2015b). However, heat waves in nature are irregular alternations of hot days and normal days and simply counting hot days cannot differentiate between different heat wave patterns. Our study revealed that we can not predict the effect of hot days without accounting for the duration of hot periods and the normal period between them to predict effects of heat waves. This indicates the importance of considering the temporal distribution of hot days and emphasizes the need for multivariate metrics that account for the daily maxima and minima and their temporal distribution to describe how various heat wave scenarios will affect the fitness of individuals and dynamics of natural populations.

Meteorological data indicate that the patterns of heat waves are changing, with increasing hot days and decreasing normal interval days in temperate regions that are concentrated in

middle-latitudes. Heat waves inserted with short normal days may cause more severe biological impact, as they allow less time for systems to recover (Davis et al. 2006, Mironidis and Savopoulou-Soultani 2008, Ghaedi and Andrew 2016). Our findings suggest that an increase in hot days and a decrease in normal days would inhibit the population increase of aphids through reducing survival, longevity and fecundity. Thus, the distribution of *S. avenae* may contract in low latitude regions, and population size may decrease at intermediate latitudes. Similar patterns may arise in other systems, but more studies are needed that examine how the temporal distribution of heat waves affect other animal and plant taxa to determine what general patterns exist across systems and geographic regions.

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Supplementary material (available online as Appendix oik-04699 at <www.oikosjournal.org/appendix/oik-04699>). Appendix 1.