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Heat waves affect prey and predators differently via developmental plasticity: who may benefit most from global warming?

Thomas Tscholl, Gösta Nachman, Bernhard Spangl and Andreas Walzer

Abstract

BACKGROUND: Climate warming is considered to affect the characteristics of heat waves by increasing their duration, frequency and intensity, which can have dramatic consequences for ectothermic arthropods. However, arthropods may respond to heat waves via plastic modifications, which could differently affect a predator and its prey. We examined this assumption using prominent counterparts in biological control, the predatory mite *Phytoseiulus persimilis* and its prey, the spider mite *Tetranychus urticae*. Individuals of both species were separately exposed to mild and extreme heat waves during their juvenile development.

RESULTS: Both species developed faster during extreme heat waves, but the proportional increase of the developmental rates was higher in the prey. Independent of sex, *P. persimilis* reached smaller size at maturity under extreme heat waves, whereas the body size modifications were sex-dependent in *T. urticae*: males became smaller, but females were able to maintain their size.

CONCLUSIONS: An accelerated development may result in the reduction of the exposure time of susceptible juvenile stages to heat waves and prey stages to predators. Plastic size adjustments caused a shift in the female predator–prey body size ratio in favor of the prey, which may lead to higher heat resistance and reduced predation risk for prey females under extreme heat waves. In conclusion, our findings indicate that species-specific shifts in age and size at maturity may result in lower suppression efficacy of the predator *P. persimilis* against its prey *T. urticae* with severe consequences for biological control of spider mites, if global warming continues.

Keywords: Climate change; Phytoseiidae; Tetranychidae; Within-generational plasticity; Heat stress; Predator–prey interactions

1 INTRODUCTION

Heat waves are one of the most crucial aspects of climate warming for ectothermic species in relation to juvenile development, fecundity and population growth because heat waves are expected to increase in duration, frequency and intensity in the next decades. Heat waves are different from the long-term increase in mean temperatures because the daily maximum temperatures during heat waves can exceed the upper thermal limits of ectothermic species for several minutes or hours. Such short-term exposure to thermal stress can result in negative effects on fitness relevant traits, even when the daily mean temperatures do not exceed the optimum temperature range for the species in question.

Temperature is also a prominent factor inducing developmental plasticity, which often results in modifications of two essential life history traits: age and size at maturity. Body size is a crucial aspect of arthropod life as it determines fitness-relevant components such as longevity, fecundity and mating success. Age at maturity determines the duration of susceptible juvenile developmental stages and the start of the reproductive phase, impacting directly the intrinsic rate of increase. A general trend in arthropods is the positive correlation between temperature and developmental rates, which may cause smaller body sizes with increasing temperatures, a relationship known as the temperature–size (T–S) rule. Nonetheless, reverse responses with respect to both age and size at maturity are also known for mainly terrestrial arthropods (reviewed in Nylin and Gotthard, Forster et al. and Horne et al.). Evidence for these findings is derived from experiments mainly conducted at constant

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temperatures, which do not reflect natural conditions. Thus, there is only sketchy information about developmental plasticity effects of heat waves on age and size at maturity of terrestrial arthropods. In addition, the few studies addressing such effects yielded diverse results. For example, heat waves increased developmental time and decreased adult size in caterpillars and predatory mites,\textsuperscript{15,16} while the opposite was found in grasshoppers.\textsuperscript{17} Furthermore, heat waves did not influence the body size of flour beetles,\textsuperscript{18} whereas the responses of mosquitoes were in agreement with the T–S rule: fast development at the expense of small body size.\textsuperscript{19} Such species-specific responses will be of particular importance when the two counterparts of a predator–prey interaction respond in opposite directions to heat stress.\textsuperscript{20,21}

We evaluated the thermal responses induced by heat wave conditions on the age and size at maturity of the predatory mite Phytoseius persimilis Astias-Henriot (Acarini: Phytoseiidae) and its prey, the spider mite Tetranychus urticae Koch (Acarina: Tetranychidae). The two species constitute a prominent predator–prey couple in biological control.\textsuperscript{22} T. urticae is a highly polyphagous plant feeding mite affecting global agriculture of over 1000 different plant species.\textsuperscript{23} P. persimilis is a fast-moving, proactive predator that is specialized to prey on spider mites of the genus Tetranychus, thereby contributing to its success as biological control agent against spider mites.\textsuperscript{24} Both mite species develop from egg, through six-legged larva, eight-legged protonymph and deutonymph to the adult stage. Developmental plasticity effects on the juvenile development of both predator and prey are known to be induced primarily by three stressors, namely food (both its quantity and quality), predation risk and temperature. For example, high food quality resulted in increased developmental rates of T. urticae,\textsuperscript{25} while low food availability induced sex-specific effects on age and size at maturity for P. persimilis, reflected in increased developmental time in both sexes and smaller body size of females.\textsuperscript{26} T. urticae also responded to predation risk with sex-specific developmental plasticity: juvenile development under predation risk led to slower development independently of sex, whereas only female size was reduced.\textsuperscript{27} Finally, heat waves as a factor influencing juvenile development are well documented but with diverging effects on both species. The developmental times of T. urticae decreased under heat wave conditions\textsuperscript{28} and fast juvenile development combined with high survival rates was also possible under extreme heat waves with daily maximum temperatures of 40 °C.\textsuperscript{29} In contrast, the predator P. persimilis suffered from high mortality during juvenile development when exposed to heat waves with daily maximum temperatures of 35 °C. Furthermore, the predator was not able to reach adulthood under heat waves with higher maximum temperatures.\textsuperscript{28} For both species, heat wave effects on size at maturity have not yet been documented.

Consequently, both species seemingly respond to changing thermal conditions via plastic developmental modifications, while the prey T. urticae appears to be more resistant against heat waves than its predator P. persimilis.\textsuperscript{28} Based on these considerations, we hypothesized that (i) both species react via plastic responses to heat waves by modifications in age and size at maturity, and (ii) the less heat-sensitive prey gains an advantage over the predator by such heat wave adjustments. To test these hypotheses, the juvenile stages of T. urticae and P. persimilis were exposed to two different climate regimes mimicking mild (daily $T_{\text{max}} = 32$ °C) and extreme (daily $T_{\text{max}} = 38$ °C) heat wave conditions and their effects were assessed by measuring the survival rates, developmental time, food consumption and adult size of the exposed individuals.

## 2 MATERIALS AND METHODS

### 2.1 Mite origin and rearing

Specimens of P. persimilis and T. urticae, used for the establishment of laboratory populations, originated from a commercial producer of natural enemies (Biohelp, Vienna, Austria). The spider mite populations were reared on bean plants (Phaseolus vulgaris L) in a climate chamber at 25 ± 2 °C, 60 ± 15% relative humidity (RH) and a 16 h:8 h (light:dark, L:D) photoperiod. The predator populations were reared on arenas consisting of plastic tiles placed on water-saturated foam cubes in plastic boxes (20 × 20 × 6 cm) half-filled with water.\textsuperscript{30} Bean leaves, infested with spider mites, were provided three times per week. The climatic conditions in the incubators used to rear predators were similar to the rearing conditions of spider mites [25 ± 1 °C, 60 ± 10% RH, 16 h:8 h (L:D)].

### 2.2 Experimental set-up

Cohorts of 15–20 gravid females of either T. urticae or P. persimilis were placed on detached bean leaves and allowed to oviposit for 6 h at a constant temperature of 25 °C. The predatory mites were also provided with spider mite eggs. The deposited eggs were ±3 h old corresponding to 7% (for P. persimilis) and 3.5% (for T. urticae) of the embryonic development, which should limit impairing effects by the thermal environment of the females.\textsuperscript{31} The deposited eggs were subsequently transferred singly onto the experimental units consisting of a small bean leaf (2.5 × 2.5 cm) placed on a water-saturated foam cube in a plastic box. To ensure that the mobile stages of P. persimilis were supplied with ample food during their entire juvenile development, 40 spider mite eggs (the preferred prey of immature predators) were added onto the bean leaves shortly before the larvae emerged. A glue ring (fruit tree grease, Vitax) bordered the arena to prevent mites from escaping. Experimental units for P. persimilis were additionally supplied with a folded plastic piece serving as a refuge.

### 2.3 Heat wave treatments

In Austria most agricultural areas used for growing vegetables and soft fruits are located in the eastern parts, where also P. persimilis is applied to control spider mites. Thus, we evaluated the characteristics of heat waves in Eastern Austria from May through September in the last 10 years (2011 to 2020) using the daily minimum ($T_{\text{min}}$) and maximum ($T_{\text{max}}$) temperature data from the meteorological station of the town Eisenstadt (48.117°N, 16.567°E), capital of Burgenland, Austria (representative for Eastern Austria) provided by the Central Institute for Meteorology and Geodynamics (ZAMG). The definition of heat waves in Central Europe was used, namely that (i) the maximum daily temperature should reach at least 30 °C during at least 3 days, (ii) the mean maximum daily temperature should be at least 30 °C and (iii) the maximum daily temperature should not drop below 25 °C.\textsuperscript{32,33} There were 28 heat waves with a mean duration of 9.9 days (3–29 days) in this decade. The daily $T_{\text{max}}$ and $T_{\text{min}}$ values reached from 30.1 to 39.3 °C (mean 31.5 °C) and 13.3 to 24.3 °C (mean 18.8 °C), respectively. The daily $T_{\text{max}}$ values were <35.0 °C for the majority of heat wave days (159 days, 85.95%), whereas daily $T_{\text{max}}$ of ±35.0 °C was only reached on 26 days (14.05%). Based on these findings we defined heat waves with daily $T_{\text{max}}$ of 32.0 and 38.0 °C as mild heat waves and extreme heat waves,
respectively. Mild heat waves are representative of the present climate change because their frequency was high in the last decade in Eastern Austria. Extreme heat waves, however, might be representative of the prospective climate change, because the daily $T_{\text{max}}$ are considered to increase linearly with the global mean temperatures.\textsuperscript{34}

The experimental individuals were exposed to simulated mild or extreme heat wave conditions during the entire juvenile development using the programmable Panasonic incubator MLR-352H-PE (temperature variation $\pm 0.5 \, ^{\circ}C$, humidity variation $\pm 5\%$ RH). The temperature and humidity regimes were chosen to be representative for Eastern Austria in summer (Table 1). However, it cannot be excluded that the adjusted climatic conditions of ambient air may deviate from the microclimate on the experimental units (detached bean leaves on water-saturated foams). For each species, the total number of experiments was 192, but since experiments where the mite was lost due to drowning were discarded, the actual number of replicates for $T. \text{urticae}$ was 80 for mild and 88 for extreme heat wave conditions. The corresponding values for $P. \text{persimilis}$ were 85 and 96.

2.4 Measured traits

The developmental progress of the mites was observed twice per day (08:00 a.m. and 04:00 p.m.) until they reached adulthood or died. After completing juvenile development, all adults were mounted in a drop of Hoyer’s medium to measure size and determine sex.\textsuperscript{35} The dorsal shield perimeter (predator) or the idiosoma perimeter (prey) was used as an index of size at maturity as these measures integrate information about body length and width. We measured the perimeter of the dorsal shield via the distances of the setae J5, Z5, Z4, Z1, s4 and j1 under a transmitted light microscope (Fig. 1(A) and (B); setae nomenclature as in Takahashi and Chant\textsuperscript{36}). As spider mites do not develop a dorsal shield, we assessed their size by measuring the perimeter of the idiosoma using the distances between the setae f2, e2, c5, Sce and Ve (Fig. 1(C) and (D); setae nomenclature as in Flechtmann and Knihiicki\textsuperscript{37}). The number of spider mite eggs consumed by the first feeding stages of $P. \text{persimilis}$ (proto- and deutonymphs) was also assessed at every observation time. The total feeding damage on the leaves caused by $T. \text{urticae}$ was quantified at the end of the experiment by measuring the area of the feeding scars using transparent mm$^2$ screen.\textsuperscript{38}

2.5 Statistical analyses

Most statistical analyses were performed with R.\textsuperscript{39} Generalized linear models (GLMs) were used to analyze the effects of treatment (two levels: mild or extreme heat wave conditions), species (two levels: $T. \text{urticae}$ or $P. \text{persimilis}$) and their interaction on the survival proportions (binomial distribution, logit link function). The corresponding analysis of deviance was performed using the car package.\textsuperscript{40} Age and size at maturity, and food consumption were analyzed separately for each mite species. We analyzed the effects of treatment, sex and their interaction on these parameters by conducting nonparametric analyses of variance using the General Factorial Design (GFD) package for general factorial designs, even with non-normal error terms and/or heteroscedastic variances.\textsuperscript{41} As recommended, we used the $P$ value for the permuted version of the Wald-type statistic (WTPS). As the two main factors

<table>
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<th>Time of the day</th>
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</table>
(treatment and sex) have only two levels, post hoc tests were not needed unless the interaction term was significant. We then conducted nonparametric multiple comparisons for relative contrast effects using pairwise rankings as an estimation method. Differences between \(T. urticae\) and \(P. persimilis\) were tested by introducing species as an additional explanatory variable in the GFD analyses described above. First, we calculated the proportional increase in developmental rate (1/age at maturity) from mild to extreme heat wave conditions and analyzed the effects of species, sex and their interaction on developmental rate. Second, we calculated the ratio between the predator and the prey with respect to age at maturity and body size index of both sexes and analyzed the effects of treatment and sex on these parameters. As both the numerator and denominator in a ratio are stochastic variables, we estimated the approximate variance of a ratio using

\[
V(m) = m^2 \left( \frac{V(a)}{a^2} + \frac{V(b)}{b^2} \right)
\]

as in Colquhoun, where \(m = \frac{b}{a}\) and \(a\) and \(b\) denote the mean value of body size or age at maturity corresponding to the predator and the prey, respectively. Standard error (SE) for the ratio was calculated as the square root of \(V(m)\). The variances associated with ratios obtained at different heat wave conditions were also used in \(t\)-tests to test whether the two ratios were significantly different. Analyses of ratios were carried out by means of PROC MEANS in SAS on Demand for Academics [SAS Inst. 2021, Cary (USA)]. Survival data are presented in the text as the proportion of surviving individuals with lower and upper 95% confidence interval in parentheses. Otherwise, data are presented as averages ± SE. As sample sizes are fairly large, approximate 95% confidence limits can be obtained as ±2 × SE.

3 RESULTS

3.1 Effects of heat waves on juvenile development and predation rates of the predator

Age at maturity of \(P. persimilis\) was affected by both treatment and sex but not by their interaction. Pooled over treatments, males

![Figure 1. Measurement of the distances between the setae (J5 to J5, J5 to Z5, Z5 to Z4, Z4 to Z1, Z1 to s4, s4 to j1, j1 to j1) on the dorsal shield of \(P. persimilis\) males (A) and females (B) and the distances between the setae (f2 to f2, f2 to e2, e2 to c3, c3 to Sce, Sce to Ve, Ve to Ve) on the idiosoma of \(T. urticae\) males (C) and females (D) used for the calculation of the perimeters of the dorsal shield (\(P. persimilis\)) or idiosoma (\(T. urticae\)).](image-url)
developed faster than females (5.28 ± 0.12 vs 5.35 ± 0.11 days). Pooled over sex, extreme heat wave conditions speeded up juvenile development (4.42 ± 0.03 vs 6.38 ± 0.04 days) (Fig. 2(A) and Table 2). Similarly, only treatment and sex affected size at maturity. Pooled over treatments, female *P. persimilis* were larger than males (802.63 ± 2.08 vs 673.92 ± 2.23 μm), and, pooled over sex, extreme heat wave conditions resulted in smaller adults (737.00 ± 7.07 vs 747.29 ± 7.72 μm) (Fig. 2(C) and Table 2).
3.2 Effects of heat waves on juvenile development and feeding rates of prey

Treatment and sex, but not their interaction, affected the age at maturity of T. urticae. As for predatory mites, males had lower developmental times than females (10.26 ± 0.31 vs 10.55 ± 0.32 days) and juveniles developed faster at extreme heat wave conditions (8.09 ± 0.06 vs 13.17 ± 0.12 days) (Fig. 2(B) and Table 3).

Size at maturity of T. urticae was only influenced by sex and the interaction between treatment and sex. Male mites were consistently smaller than females (634.10 ± 2.96 vs 976.97 ± 7.92 μm), but the treatment effects were dependent on the sex. Male body size declined when exposed to extreme heat waves (pairwise rank test \( P = 0.002 \)), whereas female body size was insensitive to treatment (pairwise rank test \( P = 0.363 \)) (Fig. 2(D) and Table 3).

Feeding by spider mite juveniles (i.e. leaf damage) was affected by treatment and sex, but not by their interaction. Females fed more per day (1.68 ± 0.06 vs 0.95 ± 0.04 mm²/day) than males and juveniles fed 36.04% more (1.51 ± 0.07 vs 1.11 ± 0.06 mm²/day) under extreme heat wave conditions (Fig. 2(F) and Table 3).

3.3 Species comparison: Effects of heat waves on survival, developmental rates and body size ratios

Pooled over species, survival proportions were high (mild heat wave conditions 0.86 (95% confidence interval (CI) 0.80–0.91), extreme heat wave conditions 0.91 (95% CI 0.86–0.94) and not affected by heat wave conditions (GLM \( \chi^2 = 1.880, P = 0.170 \)). Pooled over treatments, P. persimilis showed higher survival proportions than T. urticae (0.92 (95% CI 0.87–0.95) vs 0.85 (95% CI 0.78–0.89); \( \chi^2 = 5.183, P = 0.023 \)). The interaction between treatment and species did not influence the survival (\( \chi^2 = 0.003, P = 0.960 \)).

Independent of sex, the proportional increase in developmental rates due to extreme heat wave conditions was significantly higher in T. urticae than in P. persimilis (63.7% vs 44.9%, test statistic 168.079, \( P < 0.0001 \); Fig. 3). Along the same line, the ratio between predators and prey with respect to age at maturity increased significantly (males \( t_{143} = 5.664, P < 0.0001 \); females \( t_{158} = 6.562, P < 0.0001 \)) when the mites were exposed to extreme heat wave conditions. This applied to both sexes (males 0.495 ± 0.006 vs 0.533 ± 0.008; females 0.473 ± 0.008 vs 0.540 ± 0.006). It also demonstrated that the prey developed relatively faster than the predator when heat wave conditions intensified.

The ratio between predators and prey with respect to body size decreased significantly with intensified heat wave conditions for females (\( t_{158} = 2.481, P = 0.014 \)) but not for males (\( t_{143} = 0.990, P = 0.304 \)) (males 1.057 ± 0.008 vs 1.068 ± 0.008; females 0.840 ± 0.008 vs 0.807 ± 0.006), indicating that only female prey became relatively larger compared with their enemies when exposed to extreme heat wave conditions (Fig. 4).

4 DISCUSSION

Our results provide insights in the ability of the two counterparts in a predator–prey interaction, the predatory mite P. persimilis and its prey T. urticae, to cope with mild and extreme heat waves by means of developmental plasticity. Theoretically, the shifts in age and size at maturity in our experiments could be attributed

<p>| Table 2. Effects of treatment (mild and extreme heat wave conditions) and sex (females, males) on size and age at maturity, and predation of P. persimilis using nonparametric analysis of variance showing the ( P ) value for the permuted version of the Wald-type statistic (WTPS) |
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<p>| Table 3. Effects of treatment (mild and extreme heat wave conditions) and sex (females, males) on size and age at maturity, and feeding of T. urticae using nonparametric analysis of variance showing the ( P ) value for the permuted version of the Wald-type statistic (WTPS) |
|---------------------------------|-----------------|-------------------|-----|-----------------|</p>
<table>
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Heat waves affect prey and predators differently via developmental plasticity

Effects of heat wave conditions during juvenile development

4.1 Heat wave effects on survival, consumption, and age and size at maturity

Survival was high in both species and not affected by heat wave conditions, but generally higher for *P. persimilis* than for *T. urticae*. However, *T. urticae* may compensate for a lower survival rate by having a higher egg production than its predator.\(^{10,11}\)

Most individuals of both species reached adulthood under extreme heat wave conditions despite the daily maximum temperatures (38 °C) clearly above the optimum constant temperature range of *P. persimilis* (24–27 °C\(^{45}\)) and *T. urticae* (30–35 °C\(^{29}\)) allowing fast development and high survival rates. Similar findings have previously been reported for other arthropods.\(^{46,49}\)

Our results show that both mite species can survive short periods of high temperatures that otherwise would be lethal if the mites were exposed to them over extended periods.\(^{50}\) The higher survival rates under fluctuating temperatures could be caused by the activation of physiological adjustments during lower night temperatures.\(^{51}\) Thus, the maximum critical constant temperature (i.e. the temperature at which a population cannot persist) is around 35 °C for *P. persimilis*\(^{46}\) and around 40 °C for *T. urticae*.\(^{52}\)

Food consumption rates were higher for females of both species, which may indicate that female investment in reproduction is more costly compared to males. Additionally, food consumption rates increased in both species at higher temperatures as is also documented in other arthropod predators\(^{53,55}\) and herbivore prey species.\(^{56}\) How should this additional energy gain be converted into age and size at maturity? A general tendency is that arthropods speed up development at the expense of smaller body size at higher temperatures, termed the T–S rule.\(^{12,57}\) Independent of species and sex, mites exposed to extreme heat waves invested in faster development, which could shorten the exposure time of developmental stages susceptible to heat stress. Furthermore, a fast development may enable earlier possibilities of mating.\(^{12}\) In accordance with the T–S rule, males of both species and females of the predator had smaller body sizes at maturity under extreme heat waves. In contrast, the body size of prey females was insensitive to the simulated heat wave conditions. Proximately, extreme heat waves may induce the costly production of heat shock proteins at the expense of body size in males and females of the predator and male prey, but not female prey. Ultimately, being able to obtain a certain adult body size when developing during extreme heat waves may bring several advantages to the prey females because large individuals are reported to be more resistant to heat than smaller individuals\(^{58–60}\); large females usually have increased survival rates or longevity and also have a higher mating success.\(^{8,9,61}\) Finally, large females are able to produce more and/or larger offspring.\(^{5,62,63}\) Consequently, fast development at the cost of smaller body size may allow females to start reproducing earlier\(^{12}\) and can result in more generations per season.\(^{64}\) On the other hand, such modifications could be risky under extreme heat waves as small individuals are highly vulnerable to desiccation and overheating.\(^{39,65,66}\) Therefore, developmental plasticity induced by extreme heat wave conditions is expected to generate large individuals, as documented in a few studies.\(^{17,67,68}\) Based on these aspects, the developmental plasticity effects in age at maturity and the thermal insensitivity of size at maturity exhibited by prey females should be beneficial under extreme heat waves, whereas the trait shifts in the prey males, and predator males and females were only suboptimal (faster development, but at the cost of smaller body sizes). Consequently, our findings indicate that severe heat wave conditions are likely to be more harmful to the predator than to its prey.

Finally, we cannot completely exclude the possibility of diverging genetic adaptations to climatic conditions of our mite laboratory populations relative to natural populations, which may affect our results compared with heat wave responses of natural populations. However, usually only cold-, but not heat-tolerance limits...
of terrestrial ectothermic populations are correlated with their geographic temperature gradients (reviewed in Sunday et al.69). Along the same line, other fitness-related traits such as fecundity, juvenile survival and development varied among 22 Drosophila species, but were not influenced by the climatic variables occurring at their sampling sites.70 Based on these findings, potential differences in genetic adaptations between our laboratory populations and natural populations are expected to have marginal consequences for their thermal performance under heat waves.

4.2 Potential consequences of heat wave-induced developmental plasticity effects on predator–prey interactions

The plastic shifts in the age and size at maturity of the prey induced by extreme heat wave conditions may also reduce their predation risk. First, the extra energy intake achieved at high temperatures was allocated into higher developmental rates, where the spider mites increased their rate by more than 60%, while the increase in the predatory mites was only 45%. Theoretically, this benefit could increase the survival probabilities of prey in a spider mite population under extreme heat wave conditions because an accelerated juvenile development also shortens the exposure time to the predator of the most susceptible developmental stages (eggs, larvae, protonymphs). Additionally, young prey individuals reach the deutonymphal and adult stages faster. Since these stages are rarely overwhelmed by juvenile predators, this may reduce the per capita predation risk of prey during extreme heat wave conditions. Second, arthropod predators, which do not use traps, produce powerful venoms or hunt in groups such as predatory mites, are usually larger than their prey. However, the most voracious predator stage of P. persimilis is the adult female, which is slightly smaller than spider mite females. Thus, T. urticae females are the least preferred prey stage, although they have the highest nutritional value per prey item for the predator P. persimilis. However, only prey females were capable of maintaining large body sizes under extreme heat waves, which decreased the size ratio between female predators and prey. Therefore, when confronted with predators, the prey females may have higher survival probabilities at rising temperatures because the larger prey is able to withstand the attacks of the smaller predator.

Alternatively, the predator can also alter prey age and size at maturity by its mere presence. For example, the developmental rates of T. urticae decreased in both males and females when the juveniles were exposed to contact cues of P. persimilis and female body sizes were smaller, which could be a consequence of reduced feeding activity in the presence of predator cues. Additionally, the predators may also change their predation behavior under extreme heat stress. The higher predation rates on prey eggs under extreme heat wave conditions may indicate that predator individuals become more aggressive against prey to compensate for temperature-caused water loss, increasing their readiness to engage in attempts to overwhelm and kill large prey females.

Finally, the simple extrapolation of our laboratory-based results to the practice of biological control of spider mites under field or greenhouse conditions does not conform to the scientific standard because our experimental design excluded several decisive factors and aspects influencing the predator–prey interactions. First, heat wave effects have to be verified for other fitness-relevant traits of predator and prey, such as mating behavior, fecundity and adult survival, which may provide further shortcomings of the predator under heat stress. For example, the exposure of T. urticae and P. persimilis females to permanent 30 and 35 °C revealed differential effects on their reproductive output: it increased egg number in the prey, but decreased egg number in the predator. Second, heat waves may also change the nutritional value of plants occupied by spider mites, which can result in direct effects on prey and indirect effects on the predator. Additionally, dependent on species and/or variety, plants may create microclimatic niches for both prey and predator used as temporary refuges protecting them from heat stress. Third, spider mite control by means of P. persimilis is applied in both protected and field crops. In particular, the thermal conditions in field crops are similar to ambient temperatures, whereas the daily maximum temperatures in protected crops can be higher or lower than the corresponding ambient air data depending on the state of technology (e.g. walk-in tunnels vs climate-controlled greenhouses).

5 CONCLUSIONS

Our study demonstrates that both the predator P. persimilis and its prey T. urticae are capable of responding to heat waves by plastic developmental modifications of fitness-relevant traits. Such fast plastic responses within a generation may allow individuals to keep pace with the unpredictable occurrence of heat waves and to cope with thermal stress. This ability may be of major importance for ectotherms in the future because climate change will cause heat waves to become more frequent, more intense and longer lasting. Additional investigations will also be required to reveal whether heat waves also induce species-specific parental modifications of offspring traits (i.e. trans-generational effects) in predator and prey. However, our results point at the predator being the species that will suffer most from increasing global temperatures, which may have profound consequences for the suppression efficacy of P. persimilis against spider mites in future decades. Consequently, further experiments are needed to evaluate the combined effects of heat waves, intensified by global warming, and predation risk caused by P. persimilis on its prey T. urticae at both individual and population level.

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CONFLICT OF INTERESTS

The authors declare no competing interests.

AUTHORS’ CONTRIBUTIONS

T.T.: methodology, investigation, data curation, writing – original draft, writing – review and editing, visualization. G.N.: formal analysis, writing – review and editing. B.S.: formal analysis, writing – review and editing. A.W.: conceptualization, methodology, investigation, data curation, writing – review and editing, supervision.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.5497641.
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