



Artificial heat waves induce species-specific plastic responses on reproduction of two spider mite predators

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Abstract

Climate change models predict that the frequency, intensity and duration of heat waves will increase in the next decades. Heat waves can have profound impact on the reproduction of biocontrol agents ranging from postponing oviposition to manipulating offspring quantity via egg number and quality via egg size. Such species-specific responses of biocontrol agents to heat stress may also affect their success in controlling the target pest. Here, we evaluated the predation and reproductive performance of the two spider mite predators *Phytoseiulus persimilis* and *Neoseiulus womersleyi* exposed to simulated mild, moderate and extreme heat wave conditions over three days. Irrespective of heat wave conditions, all *N. womersleyi* females survived, whereas 12% of the *P. persimilis* females died. Both species responded to heat stress via plastic modifications resulting in increased predation rates and smaller egg sizes. Significantly more *P. persimilis* females postponed oviposition during the experimental phase than *N. womersleyi*. The deposited egg number of *Phytoseiulus persimilis* was not affected by heat wave conditions. On the contrary, the reproductive output of *N. womersleyi* was a function of temperature, i.e., the higher the temperature, the higher the number of deposited eggs. These findings indicate that *P. persimilis* is more heat sensitive in relation to reproduction than *N. womersleyi*. However, further investigations of heat wave effects on other fitness-related traits and their consequences at population level are needed to find out whether *N. womersleyi* is an alternative or supplement to *P. persimilis* as spider mite control agent under heat waves.

Keywords Biological control · Climate warming · Heat stress · Intra-generational plasticity · Reproductive success

Key message

- *Phytoseiulus persimilis* is a successful spider mite predator, but its reproductive performance under short heat waves is still unknown.
- We compared egg number and size, deposited by *P. persimilis* and another spider mite predator, *Neoseiulus womersleyi*, during heat waves.

- Heat stress resulted in smaller egg sizes in both species, but only *N. womersleyi* was able to increase the egg number.
- Our findings may indicate that *N. womersleyi* is a more suitable spider mite biocontrol agent during heat waves than *P. persimilis*.

Introduction

Climate warming is considered to have wide-ranging consequences on arthropods, because nearly all of their vital processes are affected by temperature (Angilletta 2009; Kellermann et al. 2009). Two distinct types of thermal shifts can be provoked by climate warming: the long-term increase in annual mean temperatures and abrupt temperature shifts within hours because of heat waves (Vazquez et al. 2017). Although climate warming scenarios predict that the intensity, duration and frequency of heat waves will dramatically increase in the next decades (Meehl and Tebaldi 2004), most

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previous climate warming studies had evaluated rather the implications of mean temperature increases than heat wave effects on arthropods (Kreyling and Beier 2013). Moreover, the thermal peaks during heat waves, but not the mild increase in the mean temperatures, usually exceed the thermal optima of fitness-relevant traits such as survival, development and fecundity in arthropods. Consequently, the potentially positive effects of the mean temperature increase on the performance of several arthropods (e.g., elongated growing seasons) can be overruled by negative heat wave effects in summer (Kingsolver et al. 2013; Vasseur et al. 2014).

Reproduction is a crucial component of the individual fitness for arthropods and enables their population growth (Walsh et al. 2019), but this essential trait is also temperature sensitive. How should an arthropod respond to heat waves during its reproductive phase? Females are able to shift egg number and size under environmental stress (Roff 1992; Stearns 1992; Fox and Czesak 2000). In relation to offspring quantity, three modifications are documented in literature as response to heat stress. First, heat-stressed females may stop oviposition [fruit flies (Evans et al. 2018); predatory bugs (Okasha 1970)]. Second, females can reduce the number of deposited eggs under heat stress [predatory mites (Zhang et al. 2016); parasitic wasps (Zhang et al. 2019); aphids (Davies et al. 2006; Peng et al. 2020)]. Third, females may act in an opposite manner, reflected in higher oviposition rates under heat stress [aphids (Ma et al. 2015); caterpillars (Mironidis 2014)]. However, offspring quality can also be manipulated by females under heat stress, via egg size (Janowitz and Fischer 2014). The common trend in arthropods is to produce more but smaller eggs at higher temperatures (e.g., Steigenga and Fischer 2000; Geister et al. 2008), which may also depend on the species-specific temperature tolerance of the females. For example, heat-sensitive females may offset energy from current reproduction to their own survival and future reproduction via reducing egg number and egg size (Janowitz and Fischer 2014; Bauerfeind et al. 2018).

Since the last two decades, the predatory mite *Phytoseiulus persimilis* Athias-Léniot (Acari: Phytoseiidae) is well established as natural enemy of the two-spotted spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae) both in European outdoor crops and greenhouses (Schmidt-Jeffris and Croft 2019). *Phytoseiulus persimilis* is a food specialist, which is highly adapted to use *Tetranychus* species as prey (McMurtry and Croft 1997). The predator is able to suppress spider mites very efficiently under conventional summer conditions, which is indicated by the higher intrinsic rate of increase (r_m) in the predator [0.374 at constant 25 °C preying on *T. urticae* (Badii and McMurtry 1984)] compared to the prey [0.286 at constant 26 °C feeding on *Phaseolus vulgaris* (Barati and Hejazi 2015)]. Heat stress, however,

may lower the performance of *P. persimilis* as biocontrol agent against spider mites. First, high temperatures (35 °C) impede the perception of spider mite-induced plant volatiles by the predator, which lowers the prey-searching efficacy of the predator in a plant system with patchily distributed spider mite prey patches (Ozawa et al. 2012). Second, the predator is not able to complete juvenile development and reach adulthood at constant 35 °C (Vanganekunte et al. 2015). Third, the upper heat coma temperature of the predator is significantly lower than the corresponding data of the two-spotted spider mite (41.1 °C versus 47.7 °C) (Coombs and Bale 2012). Taken together, these findings suggest that the predator is heat sensitive, which may result in ineffective spider mite control at extremely high temperatures. Based on its thermal data, the predator mite *Neoseiulus womersleyi* (Schicha) (Acari: Phytoseiidae) might be an ideal candidate for spider mite suppression during heat waves. This predator has a preference for spider mites as prey, and both juvenile development (44.0 days from egg to adult female) and reproduction (2.2 eggs/female/day) are possible at constant high temperatures of 37.5 °C (Sugawara et al., 2017). Additionally, the r_m values at high temperatures (33 °C = 0.402; 35 °C = 0.376; 38 °C = 0.343) clearly exceed the capacity for population increase in the two-spotted spider mite *T. urticae* (Coe and Ahn 2000). However, comparative data in relation to the fecundity performance of these two spider mite predators under heat waves are still lacking.

To close this gap, we compared the reproductive output of *P. persimilis* and *N. womersleyi* exposed to short heat waves by evaluating the following assumptions: (1) mortality of both species is low and not affected by temperature so that all changes in predation, egg number and size are obviously plastic modifications (Walzer et al. 2020); (2) *N. womersleyi* is less heat sensitive than *P. persimilis*, which is reflected in higher reproductive output under heat wave conditions.

Material and methods

Mite origin, rearing cultures and pre-experimental units

The *P. persimilis* population was founded with specimens from a commercial producer of biocontrol agents (Biohelp, Vienna, Austria). Individuals of *N. womersleyi* were collected in Kitashirakawa Oiwake-cho, Sakyo-ku (Kyoto, Japan, 35.0116° N, 135.7681° E), from *Urtica thunbergiana* Siebold. & Zucc. (Rosales: Urticaceae), preying on *Tetranychus kanzawai* Kishida (Acari: Tetranychidae). Around 200 females of *N. womersleyi* were used to found the laboratory population. Both species were reared separately since three years (about 120 generations) on plastic tiles placed on water-saturated foam cubs in plastic containers half-filled

with water. The predators were fed with spider mites (*T. urticae*) in regular intervals (for details see Walzer and Schausberger 2014). To get similarly aged, fecund females of both predatory mite species, 20 females each of *P. persimilis* and *N. womersleyi* from the rearing units were put on separate spider mite-infested bean leaves for oviposition. After 48 h, the females were removed and the progress of juvenile development was observed daily until the predatory mites reached adulthood. The young females of each species (8 to 10 days old) were placed singly in lockable cages (for detailed description of the cages see Schausberger 1997; Walzer et al. 2020) and starved for 24 h. Only females, which were able to deposit eggs during this period, were used as study objects in the experiments. All rearing units and lockable cages were placed in a climate chamber under constant temperatures of 25 ± 2 °C, $60 \pm 10\%$ RH and 16:8 h L:D.

Experimental units and the simulation of heat waves

The experimental units consisted of detached clean bean leaves placed upside-down on wet filter paper at the top of a water-saturated sponge in a plastic box ($10 \times 10 \times 6$ cm) half-filled with water. A sticky paste of fruit tree grease (Vitax Ltd, UK) on tissue stripes (0.5–1 cm width) framed the leaf arenas providing an escape barrier for the predatory mites. Twenty-four h before the experimental start, fertile *T. urticae* females (ten for *N. womersleyi* and twelve for *P. persimilis*) were placed on the bean leaves to produce eggs for 24 h. Then, the *T. urticae* females were removed and the amount of spider mite eggs was adjusted to 80 and 120 for *N. womersleyi* and *P. persimilis*, respectively. The different prey amount for the two species was associated with the species-specific prey need, which is higher for *P. persimilis*. The number of spider mite eggs guaranteed ample prey supply for both predator species over three days. A small plastic tile (0.5×0.5 mm) placed on the detached bean leaf served as shelter and oviposition site for the predatory mite females. The young and gravid females of each species were placed singly on the experimental units and were exposed to daily fluctuating temperature regimes simulating mild ($T_{\max} = 32$ °C, $T_{\min} = 18$ °C, $T_{\text{mean}} = 22.58$ °C), moderate ($T_{\max} = 35$ °C, $T_{\min} = 19$ °C, $T_{\text{mean}} = 25.58$ °C) or extreme heat wave conditions ($T_{\max} = 38$ °C, $T_{\min} = 22$ °C, $T_{\text{mean}} = 28.58$ °C). The chosen temperature regimes are representative for Eastern Austria in summer and correlate with the heat wave definition for Central Europe: (1) the daily $T_{\max}$ is over 30 °C for the first three days, (2) the daily $T_{\max}$ can drop below 30 °C for single days, but not below 25 °C, and (3) the average of the daily $T_{\max}$ should be at least 30 °C for the whole heat wave period (Huth et al. 2000). The relative humidity was set at 60% RH constantly over the whole temperature regime (for

detailed climatic settings see Fig. 1). An experimental period of three days was chosen, which is per definition the shortest heat wave period. This allowed us to evaluate whether short-term heat stress can induce shifts in the reproductive performance of the two predatory mite species. The experimental units were placed in a programmable Panasonic incubator MLR-352H-PE (temperature variation: ± 0.5 °C, humidity variation: $\pm 5\%$ RH), and the three heat wave treatments were replicated 30–33 times for *N. womersleyi* and *P. persimilis*.

Heat wave effects on survival, predation, egg number and egg size

The state of the females (dead, alive), the number of consumed spider mite eggs and deposited predatory mite eggs of the predators were recorded every 24 h over three days at room temperature (22–25 °C). Before the experimental units were placed to the incubator, the deposited predatory mite eggs were placed singly on microscopic slides each day. Then, the semi-major axis (a) and semi-minor axis (b) of the elliptical predator eggs were measured in μm using transmitted light microscope (NIKON, $200\times$ magnification). Subsequently, the egg volume (mm^3) was calculated with the formula of a prolate spheroid: $V = \frac{4}{3}\pi a^2 b$.

The females of both species were singly mounted in drop of Hoyer's medium for body size measurements (length of the dorsal shield) after finishing the experiments (Krantz and Walter 2009).

Statistical analyses

Most statistical analyses were conducted with R (R Developmental Core Team 2020). First, the heat wave effects (mild, moderate, extreme) on the survival functions of the predatory mites (combination of survival time and cumulative survival) were analyzed between and within the species using the Kaplan–Meier procedure and log rank tests (Therneau et al. 2000). Second, female body size can affect prey consumption and the reproductive output in relation to egg number and egg size. Thus, the correlation of female body size and predation (total consumption of spider mite eggs per female), egg number (total deposited egg number per female) and egg size (total egg volume per female) were analyzed for each species separately by linear regressions using IBM SPSS Statistics Version 24.0 (2016, USA). Irrespective of species, female body size did not influence these traits (all P -values ≥ 0.144 , Fig. S11), so that shifts in predation, and egg size and number were exclusively induced by temperature. Third, the effect of the heat wave conditions and species on oviposition ability per day (yes, no) of the females was analyzed using log-linear models, whereas the model with the smallest Akaike information criterion (AIC) was chosen. For this analysis, we considered the

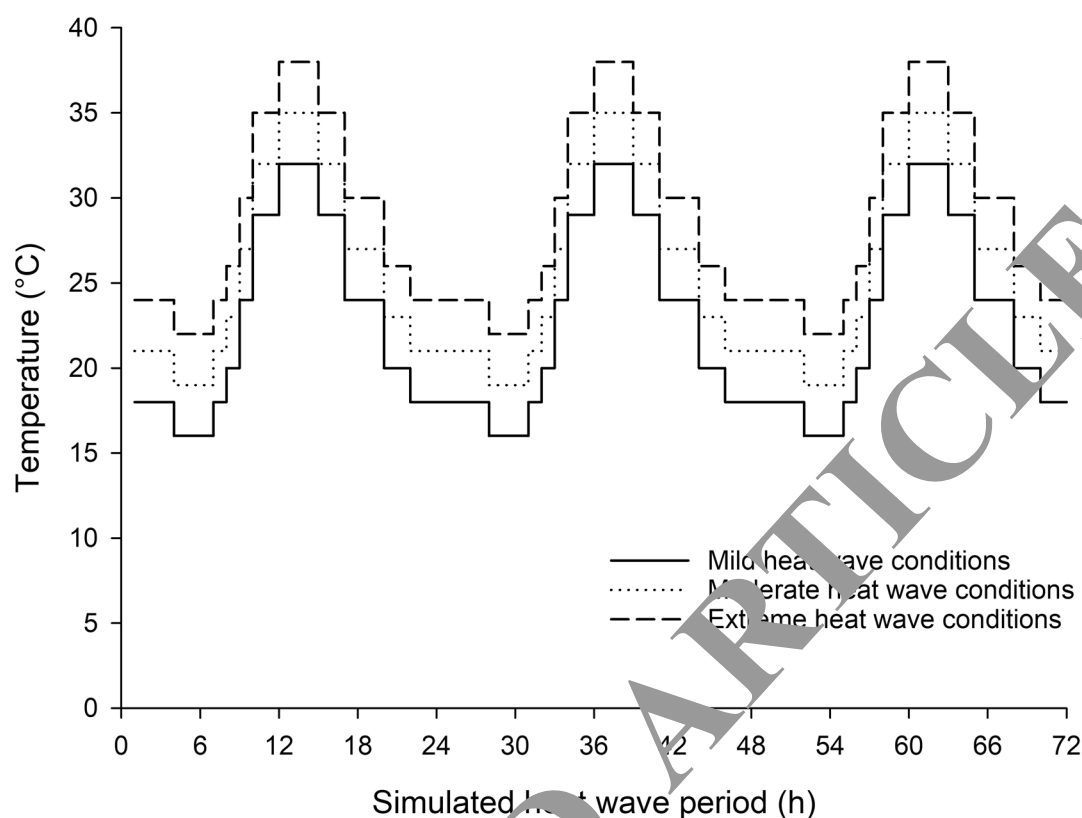


Fig. 1 Thermal conditions for mild, moderate and extreme heat wave conditions. Light conditions corresponded to long-day conditions (L:D=16 h: 8 h). Relative humidity was kept constant at $60 \pm 5\%$

number of females in the following three classes: oviposited on all three days, oviposited on two days and oviposited only on one day. Fourth, the effects of heat waves (mild, moderate, extreme), species (*P. persimilis*, *N. womersleyi*) and their interactions on predation, egg number and time were analyzed by using the package for general factorial designs (GFD) (Friedrich et al. 2017) and the *P*-values generated from the permuted version of the Wald-type statistics (WTS) were used. Only females were considered in this analysis, which survived until the end of the experimental period of three days. To detail heat wave effects within and between the predatory mite species, the data were pairwise compared by Tukey contrast tests, where needed. These tests were performed using the nparcomp package (Lenth et al. 2015). The results are given as mean $\pm$ SE, except for oviposition probability (mean).

Results

Heat wave effects on survival and predation

Pooled over temperatures, the survival functions were affected by species (Kaplan–Meier analysis, log rank test:

$\chi^2_1 = 11.992$, $P = 0.001$). Independent of heat wave conditions, all *N. womersleyi* females ($N = 96$) survived the experimental period of three days, whereas 11 out of 93 *P. persimilis* females died (Fig. 2a). Thus, the statistical analyses of the heat wave effects on the survival functions were only conducted for *P. persimilis*. However, temperature had no influence on the survival of *P. persimilis* females (Kaplan–Meier analysis, log rank test: $\chi^2_2 = 1.357$, $P = 0.507$). Twenty-eight out of 32 females, 28 out of 30 females and 26 out of 31 females survived at mild, moderate and extreme heat wave conditions, respectively (Fig. 2b).

Species and temperature, but not their interaction, affected the predation of the two predatory mite species on spider mite eggs (Table 1). *Phytoseiulus persimilis* females consumed significantly more eggs than *N. womersleyi* females (eggs/female/day: 27.58 ± 0.77 versus 17.48 ± 0.46). Predation was a function of temperature: the higher the heat stress, the higher the consumption rates (mild heat wave conditions, eggs/female/day: 17.34 ± 0.81 , moderate heat wave conditions: 23.58 ± 0.99 , extreme heat wave conditions: 26.75 ± 0.90 , all pairwise Tukey tests: $P \leq 0.006$) (Fig. 3a).

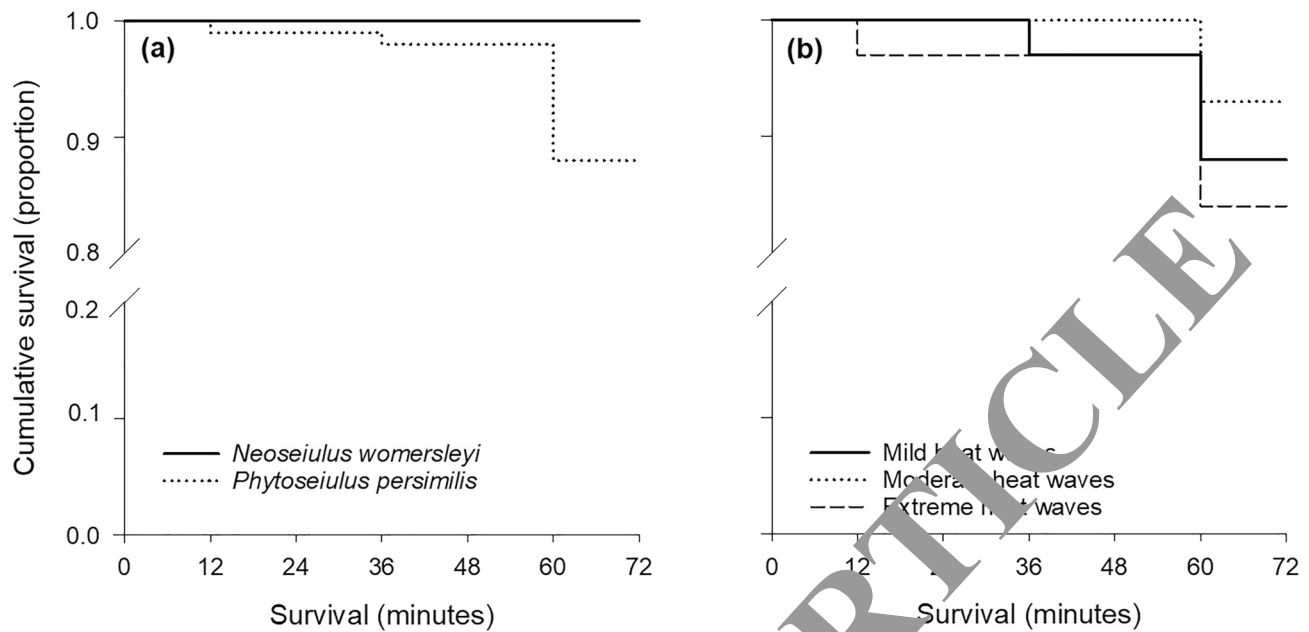


Fig. 2 Survival functions (combination of survival time and cumulative survival) of *Neoseiulus womersleyi* and *Phytoseiulus persimilis* pooled over heat wave conditions (a), and the survival functions of

Phytoseiulus persimilis (b) exposed to mild, moderate and extreme heat wave conditions over three days

Table 1 Heat wave effects (mild, moderate, extreme) on predation (consumed spider mite eggs/female/day), egg number (number of deposited eggs/female/day) and egg size (egg volume in mm^3 /female/day) of the predators *P. persimilis* and *N. womersleyi* using parametric ANOVAs with the permuted version of Wald-type statistics (WTS)

Parameter	Source of variation	F	df	P
Predation	Species	11.757	1	<0.001
	Temperature	16.046	2	<0.001
	Species $\times$ temperature	4.818	2	0.097
Egg number	Species	7.249	1	0.043
	Temperature	32.603	2	<0.001
	Species $\times$ temperature	7.019	2	0.033
Egg size	Species	2355.716	1	<0.001
	Temperature	35.641	2	<0.001
	Species $\times$ temperature	16.609	2	<0.001

Oviposition ability, egg number and size

All *N. womersleyi* females deposited eggs at least on two days, whereas 8 *P. persimilis* females stopped oviposition during the experimental period of three days. These *P. persimilis* females were excluded from the statistical analysis. The best log-linear model (AIC = 79.009, likelihood ratio = 10.11038, $df = 10$, $P = 0.431$) is associated with joint independence of the three-way contingency table (Faraway, 2006) and is given by

oviposition + species + oviposition $\times$ species + temperature with $2 + 1 + 2 + 2 = 7$ degrees of freedom resulting in 10 residual degrees of freedom. It reveals that the species, but not the temperature, affected the oviposition ability of the females. Nearly all *N. womersleyi* females (proportion: 0.95) were able to produce eggs daily compared to *P. persimilis* females (0.78) (Fig. 3b, Table 2).

The number of eggs deposited by the predatory mites was affected by both main factors species and temperature as well as their interaction (Table 1). *Neoseiulus womersleyi* females deposited more eggs than *P. persimilis* females (eggs/female/day: 2.69 ± 0.06 eggs/female/day versus 2.43 ± 0.12). Females laid less eggs under mild heat wave conditions (2.11 ± 0.07) than under moderate (2.71 ± 0.11) and extreme heat wave conditions (2.90 ± 0.12) (pairwise Tukey tests: mild versus moderate and extreme heat wave conditions: $P < 0.001$; moderate versus extreme heat wave conditions: $P = 0.210$), but these heat wave effects were dependent on the species. In *N. womersleyi*, the number of deposited eggs increased with heat stress (all pairwise Tukey tests: $P < 0.001$). In *P. persimilis*, the number of deposited eggs was not affected by the heat wave conditions (all pairwise Tukey tests: $P \geq 0.223$). The reproductive output was not different between *N. womersleyi* and *P. persimilis* females under mild and moderate heat wave conditions (all pairwise Tukey tests: $P \geq 0.980$). Although *N. womersleyi* females deposited more eggs under extreme heat wave conditions

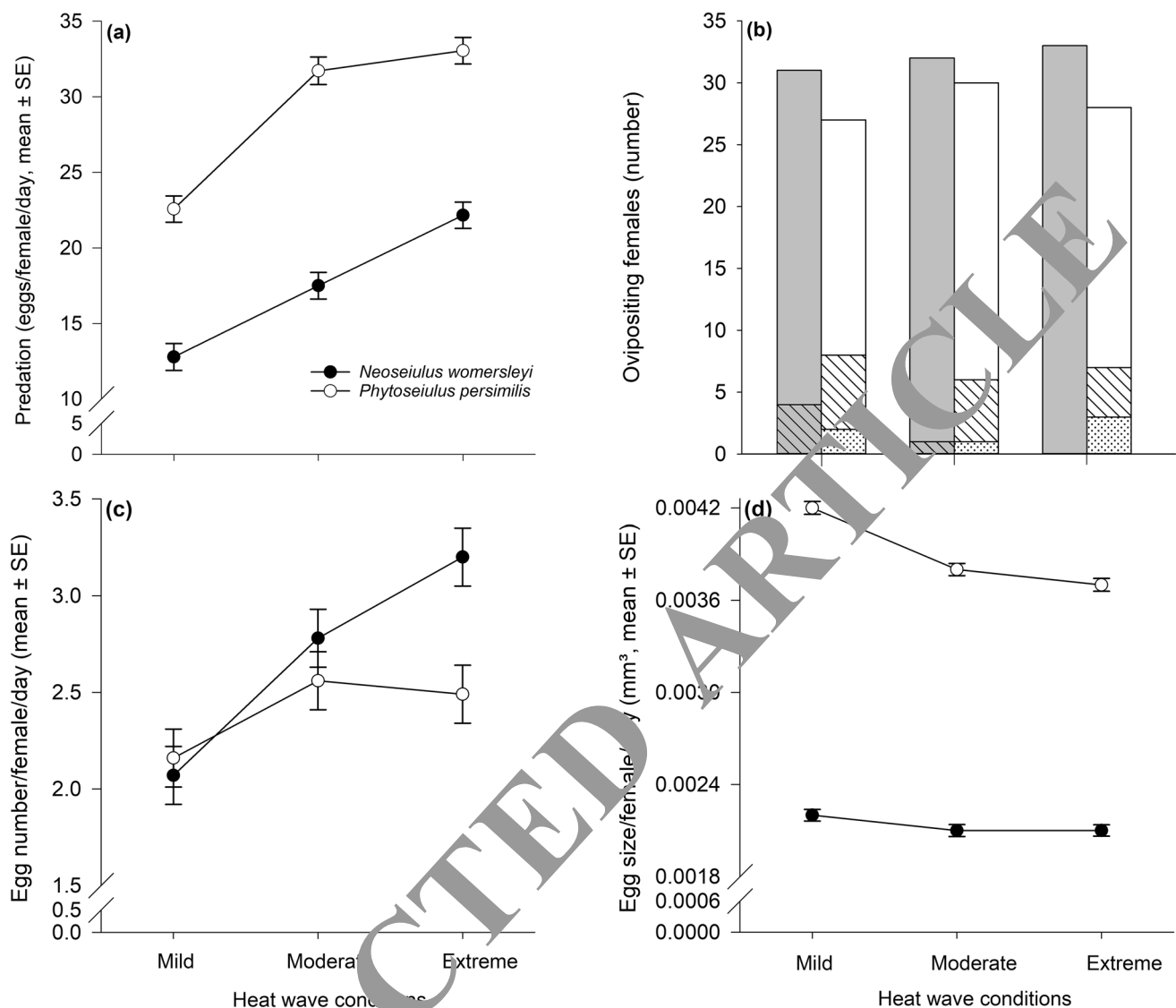


Fig. 3 Predation (a), oviposition abilities [bars without pattern: *N. womersleyi* (□) and *P. persimilis* (□) females oviposited all three days, respectively; bars with line pattern: *N. womersleyi* (▨) and *P. persimilis* (▨) females oviposited on two days, respectively; bars with dot-

ted pattern: *P. persimilis* (▩) females oviposited on one day] (b), egg number (c) and egg size (d) of *Neoseiulus womersleyi* and *Phytoseiulus persimilis*, when exposed to mild, moderate or extreme heat wave conditions over three days.

Table 2 Analysis of deviance table of the best log-linear model analyzing the three-way contingency table formed by heat wave effects (mild, moderate, extreme), species (*Phytoseiulus persimilis*, *Neoseiulus womersleyi*) and oviposition ability (on all three days, on two days, only on one day)

Parameter	Source of variation	LR χ^2	df	P
Counts	Oviposition	217.612	2	<0.001
	Species	1.654	1	0.198
	Temperature	0.080	2	0.961
	Oviposition $\times$ species	16.756	2	<0.001

compared to *P. persimilis*, the differences in egg number were non-significant ($P=0.229$) (Fig. 3c).

Temperature, species and their interaction influenced the egg sizes (volume) of *N. womersleyi* and *P. persimilis* (Table 1). *Phytoseiulus persimilis* eggs were larger than *N. womersleyi* eggs ($0.00393 \text{ mm}^3 \pm 0.000041 \text{ SE}$ versus 0.00212 ± 0.000011). The significant interaction term revealed that the females of both species produced less voluminous eggs under extreme heat wave conditions than under mild heat wave conditions (all pairwise Tukey tests: $P \leq 0.015$) (Fig. 3d).

Discussion

Our results revealed that (1) female mortality was higher in *P. persimilis* compared to *N. womersleyi*; (2) mortality of both species was insensitive to heat waves indicating plastic trait changes as response to heat stress; (3) increasing temperatures resulted in higher predation rates of *N. womersleyi* and *P. persimilis*; (4) independent of heat wave conditions, a small minority of *P. persimilis*, but not *N. womersleyi* females, stopped egg production despite of ample prey supply, (5) the number of deposited eggs in *N. womersleyi* was a function of temperature: the higher the daily maximum temperatures, the higher the reproductive output; (6) the oviposition rates of *P. persimilis* were not affected by heat wave conditions; and finally (7) the egg sizes of both species decreased with increasing temperatures.

Heat wave effects on predator survival and prey consumption

Not surprisingly, none of the heat-tolerant *N. womersleyi* females (Lee and Ahn 2000) died when exposed to heat waves. But also few *P. persimilis* females suffered from heat stress resulting to death, although reaching adulthood is not possible for *P. persimilis* under constant 35 °C (Vangansbeke et al. 2015). These high survival rates of the *P. persimilis* females may be attributed to the recovery from heat injury during phases of lower night temperatures (Zhao et al. 2014). Additionally, high temperatures may induce the production of heat shock proteins in *P. persimilis* females, which protect cells from heat damage (Ozawa et al. 2012; Tian et al. 2011).

An increase in the predation rates caused by higher temperatures is a common phenomenon in arthropods (Vucic-Pestic et al. 2011; Wang et al. 2020). The two predator species responded in a similar manner by consuming more spider mite eggs during increasing heat stress, which might be a compensation for water loss. Since spider mite eggs are non-mobile and defenseless prey stages, prey search success should be a function of predator activity only: the higher the activity, the higher the encounters with spider mite eggs resulting in increased predation rates. Thus, increased activity induced by higher temperatures was likely the cause of increased spider mite egg predation by the two predatory mite species. Such thermal effects on predator activity leading to higher predation rates are also documented for dragonflies, lady beetles and ground beetles (Vucic-Pestic et al. 2011; Ferreira et al. 2020; Wang et al. 2020).

Heat wave effects on egg number and size

Theoretically, the surplus of energy gained by higher consumption rates can be used to invest in (1) reproduction and/or (2) in the survival of the predator. A negligible minority of *N. womersleyi* females, but about one-fifth of *P. persimilis* females, invested in survival only by stopping egg production. These females may postpone reproduction and restart egg production under optimal conditions. Such a strategy is documented for the predatory mite *N. cucumeris*, exposed to transient intense predation risk (Montserrat et al. 2007).

Based on laboratory experiments under constant temperatures, *P. persimilis* usually has a higher fecundity under its optimal thermal conditions than *N. womersleyi* (Walzer and Schausberger 2013; Sugawara et al. 2017). Here, the total number of deposited eggs of *P. persimilis* was lower under heat wave conditions than *N. womersleyi*. These results were mainly attributed to the ability of *N. womersleyi* to increase the reproductive output with increasing heat stress. Contrary, *P. persimilis* females may suffer from direct heat effects by ovarian deformations (Zhao et al. 2016) and blocked vitellogenesis (Audit-Lamour and Busson 1981) and/or indirect heat effects by changed metabolic rates (Acar et al. 2001) and the production of heat shock proteins lowering the resources for reproduction (Gonzalez-Tokman et al. 2020). However, egg sizes of both species decreased under extreme heat wave conditions. Thus, costs may arise for offspring of both species, if small egg size correlates with adult body size irrespective of offspring sex. Small females and males may suffer from dehydration and overheating at high temperatures (Kingsolver et al. 2007; Gardner et al. 2011; Walzer et al. 2020). Inferiority in resource competition and reduced reproductive success are other potential disadvantages of small body size (Blanckenhorn 2000; Walzer and Schausberger 2013, 2014). Alternatively, offspring may compensate for the originally small size by compensatory or catch-up growth under optimal conditions (Hector and Nakagawa 2012; Walzer et al. 2015).

Obviously, the two predatory mite species are subjected to different trade-offs under heat stress. The partially postponing of the oviposition, the non-ability to increase the number of deposited eggs despite higher predation rates, and the smaller egg sizes of *P. persimilis* indicate a trade-off in favour of adult survival at the expense of fecundity (Stearns 1992; Zhang et al. 2018). In contrast, *N. womersleyi* deposited a higher number of eggs at the expense of egg size under increasing heat stress. Such trade-offs between egg number and size are well documented for arthropods under stressed conditions (Stearns 1992), including predatory mites (Walzer and Schausberger 2015). Nonetheless, *N. womersleyi* may have a benefit

against *P. persimilis* in controlling spider mites under heat wave conditions, because *N. womersleyi* invests more in fecundity.

Potential implications on spider mite control

Phytoseiulus persimilis should be superior in suppressing spider mites over *N. womersleyi* under conventional summer conditions mainly because of its higher predation rates and reproductive output (Friesse and Gilstrap 1982; Lee and Ahn 2000; Fathipour et al. 2018; Sugawara et al. 2018). However, spider mites are known to be very heat-resistant (Coombs and Bale 2012; Luedeling et al. 2011; Urbaneja-Bernat et al. 2019), so that they may benefit from extreme temperature events such as heat waves via increasing their capacity for population increase. Consequently, a similar heat-resistant predator is needed for successful spider mite control. Our findings may indicate that *N. womersleyi* reaches higher population densities under heat wave conditions than *P. persimilis* because of the higher reproduction performance of the former. Whether *N. womersleyi* could be a more efficient biocontrol agent against spider mites under heat waves than *P. persimilis* cannot be deduced from our results because of some caveats. (1) Other fitness-related traits such as juvenile and adult survival are also strongly affected by temperature. These traits decreased dramatically in *N. womersleyi* when exposed to constant extreme high temperatures (Lee and Ahn 2000; Sugawara et al. 2017). However, the assessment of heat resistance at constant temperatures does not reflect heat wave conditions with short-term temperature peaks allowing a daily recovery at moderate temperature. Thus, the survival probabilities of *N. womersleyi* are likely higher under heat waves than under constant high temperatures as it is also documented for aphids (Chen et al. 2013), beetles (Chidawanyika et al. 2017), caterpillars (Xing et al. 2015), fruit flies (Petravy et al. 2001) and predatory mites (Walzer et al. 2020). (2) Predatory mite species with a high reproductive potential such as *N. womersleyi* and *P. persimilis* produce female-biased sex-ratios with 70% to 80% females under optimal conditions (Sabelis 1985), but the females are able to change the offspring sex-ratio under environmental stress resulting in a balanced sex-ratio (Sabelis 1985; Walzer and Schausberger 2015). Producing less female eggs can save energy for the survival of the females, because female eggs are larger than male eggs (Toyoshima and Amano 1996; Sabelis et al. 2002; Walzer and Schausberger 2015). Less female offspring also means a lower capacity for population increase. However, whether *N. womersleyi* shifted the offspring sex-ratio under extreme heat wave conditions via producing less female eggs remains an open question. (3) The performance of heat-exposed species may be achieved by within-, trans-generational plasticity and genetic adaptations (Gonzalez-Tokman et al. 2020). However, thermal

within-generational plastic modifications such as acclimation and hardening increased cold-tolerance, but had limited effects on heat-tolerance in ectotherms (Gunderson and Stillman 2015). Furthermore, heat-exposed parents may alter offspring traits and consequently their thermal performance via trans-generational plasticity, as it has been shown in fruit flies and predatory mites (Schiffer et al. 2013; Walzer et al. 2020). Finally, local adaptation to climatic conditions by genetic modifications is a further mechanism affecting heat resistance. For example, the efficacy of *P. persimilis* to suppress spider mites under heat waves in Spain was high compared to another predatory mite, *Neoseiulus californicus* (Urbaneja-Bernat et al. 2019). The authors concluded that the origin of the used predator populations was responsible for their differential performance as biocontrol agents. *Neoseiulus californicus* derived from a commercial producer reared under optimal climatic conditions. On the contrary, *P. persimilis* came from a wild population sampled in the North-Eastern part of Spain, which possibly led to genetic adaptations to extreme hot weather events in *P. persimilis*, but not in *N. californicus* (Urbaneja-Bernat et al. 2019). Along the same line, one predator population used in our experiments came from a commercial producer (*P. persimilis*), the other was a wild population (*N. womersleyi*). Thus, ignoring such adaptive mechanisms may result in over- or underestimating of the reproductive performance and consequently the suppression potential of biocontrol agents on their target pest when exposed to heat stress (Gunderson and Stillman 2015).

In conclusion, our findings provide some evidence that *N. womersleyi* is a heat-resistant species suitable for use as spider mite control agent during heat waves. Further research should be directed at the evaluation of the full potential of *N. womersleyi* as alternative or supplemental predatory mite to *P. persimilis*.

Author contribution statement

AW and EK conceived and designed research. TS and AW conducted the experiments. BS analyzed the data. AW wrote the manuscript. All authors read and approved the manuscript.

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Data Availability Datasets related to the present study are available upon reasonable request from the corresponding author in the case of publication.

Declarations

Conflicts of interest The authors declare no conflicts of interest or competing interests.

Ethics approval This study does not contain any experiments using any animal species that requires ethical approval.

Consent to participate Consent was given by all participants included in the study.

Consent for publication All authors consent to the publication of this manuscript in Journal of Pest Science.

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