


Exposure to high temperatures is fatal for eggs and suppresses growth in a false widow spider, *Steatoda grossa*

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ABSTRACT

Ectothermic organisms are highly sensitive to ambient temperature, and exposure to extreme heat can induce a range of lethal and sublethal effects. Spiders are abundant and ubiquitous arthropod predators in most terrestrial ecosystems and studying their responses to different temperature regimes provides valuable insights into effects of temperature on this important group of organisms. Here, we exposed the false widow spider (*Steatoda grossa*), either as eggs or spiderlings to different temperature regimes and monitored their survival and development. The regimes were set at 22/12 °C (day/night), 27/17 °C, 32/22 °C, or were simulated as heatwaves in which the days at 32/22 °C were restricted. Egg and spiderling survival decreased with higher temperature exposure. The growth trajectories of female spiderlings exposed to thermal stress after hatching were stronger affected by the various regimes than those of males. Only the males, which develop much faster than females, reached adulthood and those reared at lower temperatures grew slower but attained significantly more adult body mass. Male spiderlings and, to a lesser extent, eggs and female spiderlings, were able to withstand transient exposure to 32 °C during simulated heatwaves. Our study shows that eggs and young spiderlings are highly sensitive to high temperatures and that female spiderlings are more sensitive than males. Female spiders of this species are mostly sedentary and spend their entire lives in relatively small webs, whereas adult males wander in search of females. Given the higher sensitivity of females and eggs to high temperatures, we argue that females are under strong selection to build webs and place egg sacs at sites where temperatures exceeding 30 °C are avoided.

1. Introduction

Among a suite of anthropogenic factors threatening biodiversity, climate change is increasingly being seen as one of the most serious (Bellard et al., 2012; Malcolm et al., 2006). Climate change occurs over different spatial and temporal scales. Long-term ‘incipient’ warming is characterized by a gradual rise in surface temperature occurring over decades and across most of the biosphere. By contrast, at shorter time-scales (days, weeks) and in smaller geographical regions, climatic extremes, such as heatwaves, droughts, fire and extreme precipitation events are increasing in frequency, duration and intensity (Christidis et al., 2015; Jones et al., 2015). Both facets of climate change generate different kinds of responses in organisms. Long-term warming has led to changes in seasonal phenology and increased numbers of generations per year (Forrest, 2016; Macgregor et al., 2019), as well as in

distributional shifts pole-wards and to higher elevations (Chen et al., 2011; Kelly and Goulden, 2008). Climatic extremes, on the other hand, represent virtually instantaneous threats to survival and fitness and require organisms to endure or ‘ride out’ harsh conditions, such as by seeking cooler microclimates or suspending development via aestivation (Gols et al., 2021; Harvey et al., 2020, 2023; Kiritani, 2013). Given that the range of temperatures that organisms can physiologically tolerate plays a critical role in their distributions across space and time (Chown et al., 2004; Sunday et al., 2012), increasing temperatures and extreme heatwave events pose a significant threat to the persistence of natural populations.

Ectothermic organisms, such as insects and other arthropods, are constrained in their ability to regulate body temperature, which is strongly influenced by ambient temperature. Exposure to high temperatures can induce a range of physiological effects in these organisms

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(Colinet et al., 2015; González-Tokman et al., 2020). All species have upper and lower critical thermal limits (CTL) for survival, whereby if they are exposed to temperatures beyond these critical thresholds for even a short duration, they will perish (Abarca et al., 2024; Hoffmann et al., 2013; Kingsolver and Buckley, 2020). The upper CTL of organisms is species-specific and plays an important role in determining the geographic distribution and (micro)-habitat occupancy of a species. Species found in warmer climates may have lower thermal tolerances than temperate species due to much lower seasonal and diel temperature variability in these biomes (Dewenter et al., 2024; i.e., the climate variability hypothesis, Gutiérrez-Pesquera et al., 2016), although temperate species that are only active for a brief period each season may display similar thermal sensitivity patterns as species at lower latitudes (Johansson et al., 2020).

Different life-stages of arthropods, e.g., eggs, juveniles, pupae or adults vary in their sensitivity to high temperature exposure (Barnes et al., 2019; Klockmann et al., 2017; Mahroof et al., 2003; Radchuk et al., 2013). In addition, temperature experienced during early life stages can also influence later stages by affecting size and fecundity. For example, in *Plutella xylostella*, heat stress, i.e., exposure to 40 °C for 4–8 h, during developmental stages closer to the adult stage (third instar larvae, pupae) caused greater detrimental effects on reproduction than heat stress experienced during earlier life (eggs, first instar larvae) (Zhang et al., 2015). A similar result was found when different life stages of the flour beetle, *Tribolium castaneum*, were exposed to heat stress (Sales et al., 2021). Higher temperatures experienced during early life stages (larvae, nymphs) generally accelerate development but reduce body size (the ‘temperature size rule’, Atkinson, 1994; Ghosh et al., 2013). Other studies have reported that the growth and development of insects is negatively affected by exposure to high, sub-lethal temperatures (Colinet et al., 2015; González-Tokman et al., 2020; Horne et al., 2019). In addition to the stage or age of the organism when exposed to heat, the rate of temperature change and the duration of exposure to high temperatures also strongly influences physiological responses to heat stress (Terblanche et al., 2011; Zhang et al., 2015).

In this study we investigated the effect of temperature regimes on development and survival of eggs and spiderlings in the false black widow spider *Steatoda grossa* Koch (Araneae, Theridiidae, Latrodectinae). This is a cosmopolitan, synanthropic spider species that is found in many temperate and tropical regions but is probably native to Eurasia (Nentwig et al., 2025). It is closely related to true widow spiders, also producing medically significant venom (Isbister and Gray, 2003). Spiderlings and adult *S. grossa* females build relatively small, tangled webs in generally dark, cooler microclimates such as cupboards, sheds, basements and under objects. This suggests that they avoid habitats that are exposed to high temperatures. Males, on the other hand, develop as spiderlings in webs where they catch prey, whereas mature adult males abandon webs to search for females.

Specifically, we exposed the two early *S. grossa* spider life stages (eggs, spiderlings) to (1) different day/night temperature regimes, and (2) simulated heatwaves in which the number of hot days was limited to five days. Survival and development of eggs and spiderlings were monitored under temperatures reflecting ‘average’ (=normal), ‘warm’, and ‘hot’ summer days in the Netherlands. In addition, we exposed egg sacs and spiderlings under simulated heatwave conditions that were varied temporally. Exposure to fluctuating temperatures can render ectothermic organisms more tolerant to temperature stress (Colinet et al., 2015). We hypothesized that exposure to high temperatures (here, 32 °C) negatively affects survival and development of early life stages relative to warm or normal conditions. Moreover, transient exposure to high temperatures during heatwaves is predicted to have less pronounced effects on survival and development compared to prolonged exposure to constant high temperature conditions. We discuss our results in the context of temperature-mediated web-site location and egg sac placement by adult female spiders and microhabitat selection by spiderlings.

2. Methods

2.1. Spider rearing and maintenance

Egg sacs, spiderlings and adults of *S. grossa* originated from a laboratory population maintained at 22±2 °C. This population was established from several hundred individuals collected in various parts of the Netherlands in 2019 and 2020. Spiders were collected in sites such as greenhouses, bike sheds and other manmade structures near houses. The spider had been reared in the lab for four to five generations when this experiment was conducted. The population was maintained under controlled conditions of 22 °C, 50 ± 5 % RH, and a 16 L:8 D photoperiod. Egg sacs laid by females were placed in Petri dishes (8 cm diam.) until hatching, after which spiderlings were placed individually in Petri dishes. Spiderlings were progressively fed on larger prey, beginning with fruit flies (*Drosophila melanogaster* and *D. hydei*) for young spiderlings and house crickets (*Acheta domestica*) for later spiderling instars. Prey used in these experiments was obtained from commercial retailers. At adulthood, males remained in Petri dishes and were fed 2–4 fruit flies (*Drosophila* sp.) every 2–3 weeks, while females were transferred to individual plastic boxes (11 × 11 × 6 cm) and provided with house crickets weekly thereafter. Spider sex can only be distinguished after several molts (c. 5–7 in males, 8–9 in females).

2.2. Temperature regimes

In the first experiment, we investigated survival of egg sacs and spiderlings when exposed to one of three fixed temperature regimes, 22/12 (day/night), 27/17 or 32/22 °C with a 16 L:8 D photoperiod. These temperatures are based on summer maximum and minimum temperatures in De Bilt, a centrally located town in the Netherlands where the KNMI (Royal, Dutch Meteorological Institute) is based. Twenty-two °C is the average maximum daily temperature in July. Days with a maximum daily temperature between 25 °C and 30 °C are considered as ‘summer days’, and those exceeding 30 °C as ‘tropical days’. In addition to these three temperature regimes, egg sacs and spiderling cohorts were exposed to heatwave conditions. The KNMI defines a heatwave as a period of at least five consecutive days with a maximum temperature of 25 °C or higher, of which at least three days must exceed 30 °C (KNMI, 2025). The median duration of the 32 heatwaves in the Netherlands since 1901 has been 8 days and the median high temperature during these heatwaves has been 32.8 °C (range 31.1–37.5 °C) (KNMI, 2025). The simulated heatwave in our experiments covered 8 days, with 3 days at 27/17 °C (day/night temperature) followed by 5 days at 32/22 °C and is referred to as a short simulated heatwave. Three days before and after exposure to heatwave conditions, spiders were maintained at 22/12 °C. Spiderlings were exposed to three additional heatwave settings: extended heatwaves or long heatwaves with 10 day at 30 °C during the day, and consecutive heatwave exposure with a ten-day recovery period at 22/12 °C for both short and long simulated heatwaves (Fig. 1). All experimental temperature treatments were applied using incubators from Sanyo, model MLR-350 and Panasonic model MIR-154 and day/night temperature changed the with photoperiod (16 L:8D).

2.3. Experiment 1. effect of temperature on egg hatching

Thirty virgin female spiders from the rearing population were mated and their egg sacs were collected to be used in experiments. Females can produce more than one egg sac from a single mating event. From each female, we collected the first up to the fourth egg sac (within 16 h after laying) and placed these individually in Petri dishes. Egg sacs produced by each female were randomly assigned to one of the three fixed temperature regimes (Fig. 1A): 22/12 °C (n = 21), 27/17 °C (n = 21), 32/22 °C (n = 19), or short heatwave conditions (n = 20). Egg sacs were exposed to their respective regimes until the eggs died or the spiderlings hatched. Eggs were recorded as ‘dead’ based on their colour and

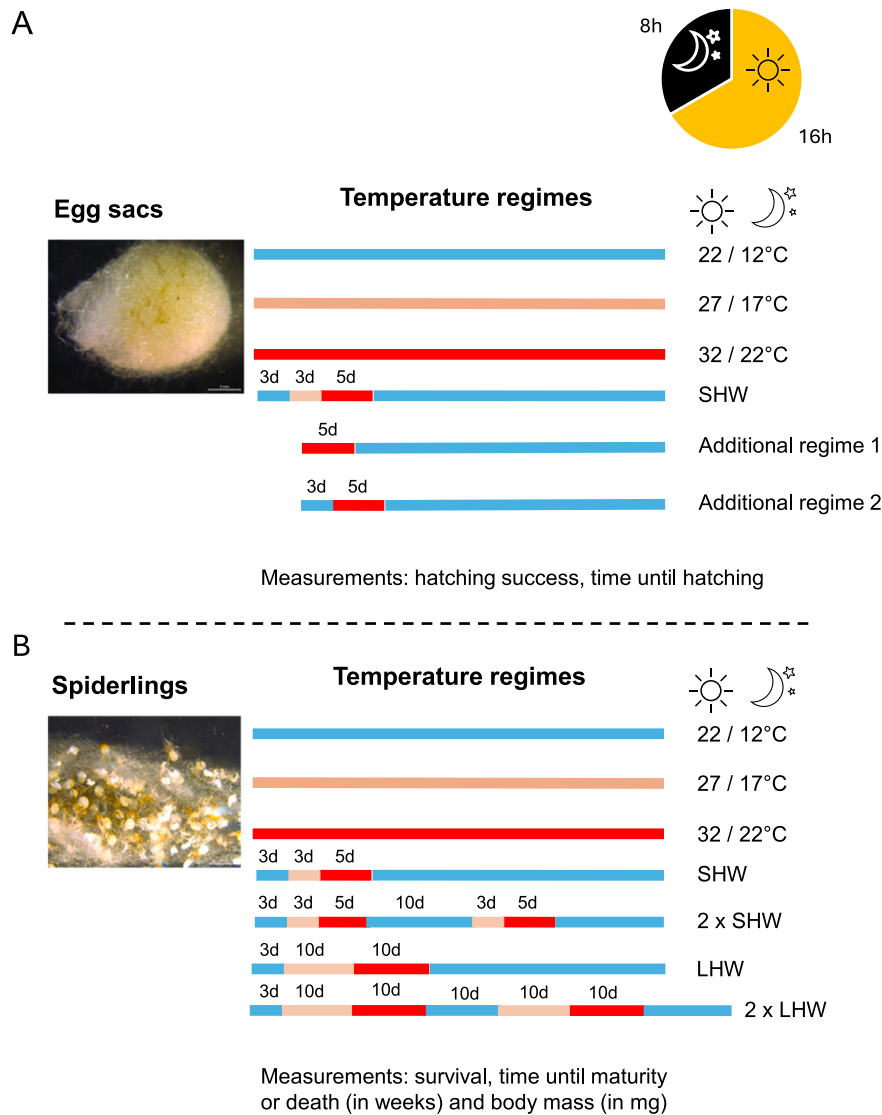


Fig. 1. Overview of the temperature regimes applied to eggs (A) and spiderlings (B) of *Steotoda grossa*. Two types of thermal exposure were applied: fixed thermal stress and simulated heatwave conditions. Temperature regimes are based on summer temperatures in the Netherlands (KNMI): 22 °C (blue lines) is the average maximum temperature, 27 °C (orange) during the day is classified as a ‘summer’ day and 32 °C (red) as ‘tropical’. The standard simulated heatwave consisted of 3 days exposure to 27 °C, followed by 5 days at 32 °C. Spiderling (B) were also exposed to extended heatwave conditions (i.e., 10 days at 27 °C and 10 days at 32 °C), as well as repeated standard and extended heatwaves both with 10 days interval between heatwaves. All treatments shown represent day temperatures. Night temperatures were 10 °C lower.

appearance; dead eggs appear shrunken and are yellow in colour, whereas healthy eggs are white and round (Fig. S1). Neonate spiderlings were killed by freezing at -20 °C, counted and their combined body mass per egg sac was measured using a Mettler Toledo Microbalance MT5 (Columbus, OH, U.S.A., accuracy ±1 µg). To estimate the mean body mass of individual spiderlings, the combined body mass was divided by the total number of spiderlings. In addition, we quantified latency to hatch (number of days until hatching) and hatching success (number of hatched spiderlings/total number of eggs laid) for each egg sac for each temperature regime.

Results revealed 100 % mortality of eggs that were exposed to 32/22 °C continuously, whereas approximately 25 % of the eggs exposed to short heatwave conditions with only 5 days at 32/22 °C successfully hatched. Based on this, two additional temperature regimes were added: (1) 5 days at 32/22 °C and back to 22/12 °C (n = 15), and (2) 3 days at 22/12 °C, followed by 5 days at 32/22 °C and then back to 22/12 °C (n = 16). For this experiment, only the first egg sacs produced by females were used, and hatching success was measured as described above. By

comparing the results of this additional experiment to those obtained from the short heatwave experiment, we aimed to better understand how timing of exposure to high temperature affects hatching of spiderlings.

2.4. Experiment 2. the effect of temperature on survival and growth of spiderlings

In this experiment all egg sacs were maintained at 22/12 °C until hatching and only spiderling stages were exposed to the various temperature regimes. Thirty virgin female spiders from the rearing population were mated. Their first egg sacs were collected and maintained individually in Petri dishes at 22/12 °C until hatching. Twenty-five newly hatched spiderlings from each egg sac were placed individually in Petri dishes with a moist cotton ball, and were randomly assigned to one of the following fixed temperature regimes: 22/12 °C (n = 150), 27/17 °C (n = 150), 32/17 °C (n = 150), or one of four simulated heat wave conditions described earlier (Fig. 1B). The number of replicates was 80

for the short heatwaves (single and double) and 70 for the extended heatwaves (single and double). Spiderlings assigned to simulated heatwave conditions were maintained at 22/12 °C for the first 10 days following hatching and were returned to 22/12 °C afterwards.

Throughout the experiment, spiderlings were fed two freshly killed (by freezing) fruit flies (*D. hydei*) once a week for the first 6 weeks, then four live fruit flies from weeks 7–12, and six live fruit flies from week

$$\text{Growth rate} = \text{Ln}(\text{biomass}_{(\text{end})} - \text{biomass}_{(\text{neonate})}) / \text{period exponential growth}$$

13–21. From week 21 onwards, spiders were provided with one late-instar cricket nymph weekly. Female spiders were maintained under these conditions for a maximum period of 17 months, whereas males, which develop more rapidly, were monitored until maturity (typically 6–8 months). Survival and body mass of spiderlings were recorded every three weeks. Spiders were anaesthetized using CO₂ before weighing on a microbalance.

2.5. Statistical analysis

All analyses were conducted in R 4.3.1 (R Core Team, 2024). Most variables were analyzed using general linear models. When any of the main effects was significant, group means were compared using Tukey HSD tests (“emmeans” package, Lenth et al., 2024). Non-significant interaction terms were removed from the final models (Zuur et al., 2009) and model assumptions were checked using the DHARMA package (Hartig and Lohse, 2022). All tests were two-tailed and considered significant at $p < 0.05$. Means are presented ± 1 S.E. Although we used multiple offspring (eggs or spiderlings) produced by the same mother, we decided not to account for this in the statistical analysis. Preliminary analyses including mother ID as a random factor resulted in poorly fitted models and this is most likely caused by the fact that the number of multiple data entries per mother was low (for some of the regimes there were only single data entries per mother).

To compare the effects of temperature regimes on egg sac performance (hatching success, latency to hatch, and body mass of neonate hatchlings, respectively), we used general linear models. None of the egg sacs hatched when exposed to the 32/22 °C regime generating only zero values for hatching success and no values for hatching latency and spiderling biomass. We excluded the 32/22 °C regime from the statistical analyses due to absence of data or zero variance. Temperature regime (22/12, 27/17 °C or single short heatwave) and egg sac number (i.e., first to fourth egg sac), were included as explanatory variables. Temperature was entered as a fixed factor and egg sac number as a covariate.

Survival of spiderlings exposed to various temperature regimes was compared using Kaplan Meier survival analysis (“survminer” package, Kassambara et al., 2024; “survival” package, Therneau et al., 2024). Individuals that reached maturity were censored, i.e. their survival time was included in the analysis until this point. The effects of fixed day/night temperature regimes (22/12 °C, 27/17 °C or 32/22 °C) and heatwave conditions (short and long heatwaves, both single and double) were analyzed separately. In the second analysis, the 22/12 °C fixed daytime temperature was included as a reference group (i.e., five levels in total). Differences among temperature treatments were tested using Log-Rank tests followed by pairwise Log-Rank tests with a Holm’s correction for inflated type I errors if the effect of temperature regime was significant.

Spiderlings that grew large enough for their sex to be determined, were subjected to additional analyses. Body mass of male and female *S. grossa* spiderlings were plotted over time and growth curves were fitted using the geom_smooth function in the ggplot2 package. The

curves were fitted using Loess regression (Wickham, 2016). Growth rate was estimated as the change in body mass from the first time it was measured (biomass_(neonate)) until the last time point at which growth was still considered exponential (biomass_(end)) (Morin and Dumont, 1994). It is defined as the period during which the relationship between time and the natural logarithm of biomass is linear:

This last timepoint was determined by visual inspection of the individual growth curves. For females the exponential growth phase lasted on average 35 weeks and for males 25 weeks. Growth rates were compared using linear models with temperature regime, sex, and their interaction as explanatory variables.

Males reached maturity within the experimental period and additional variables (age of the spiders when reaching maturity and biomass at maturity) were compared using linear models. Welch’s analysis of variance was used when assumptions of equal variance were violated. Separate analyses were done for fixed temperature regimes and variable heatwave conditions (with 22 °C included for comparison), respectively. The analysis comparing the effect of fixed temperature included only two levels (22 and 27 °C because only few males ($n = 4$) reached maturity at 32 °C.

3. Results

3.1. Experiment 1. effect of temperature on egg hatching

None of the eggs hatched when they were exposed to the 32/22 °C temperature regime. Although hatching tended to be highest in the 22/12 °C regime and lowest under short heatwave conditions (Fig. 2 A), the statistical model without the 32/22 °C regime was not significant (Table 1). Furthermore, hatching success was affected by the order in which the eggs were produced (Table 1). Independent of temperature regime (Table 1), hatching success increased with successive egg sac production from $31 \pm 8\%$ in the first egg sac to $71 \pm 12\%$ in the fourth one.

Hatching success of eggs under short heatwave conditions showed that eggs can survive a brief period of exposure to 32/22 °C. To explore this further, we conducted two additional experiments. In the first

Table 1

GLM results on egg sac hatching success, latency to hatch and spiderling biomass.

Explanatory variable	Hatching success		Latency to hatch		Spiderling biomass	
	F-value (dfs) ^a	P-value	F-value (dfs)	P-value	F-value (dfs)	P-value
Temperature regime	0.42 (2, 56)	0.65	11.5 (2, 46)	<0.001	0.53 (2, 40)	0.59
Order of egg sacs	5.18 (1, 56)	0.026	1.04 (1, 46)	0.31	2.28 (3, 40)	0.09
Interaction	0.75 (2, 56)	0.47	1.41 (2, 46)	0.25	1.33 (6, 40)	0.26
Interaction term excluded						
Temperature regime	3.06 (2, 58)	0.054	30.1 (2, 48)	<0.001	1.85 (2, 46)	0.16
Order of egg sacs	5.54 (1, 58)	0.021	0.46 (1, 48)	0.49	2.99 (3, 46)	0.04

^a Df’s, degrees of freedom of numerator and denominator.

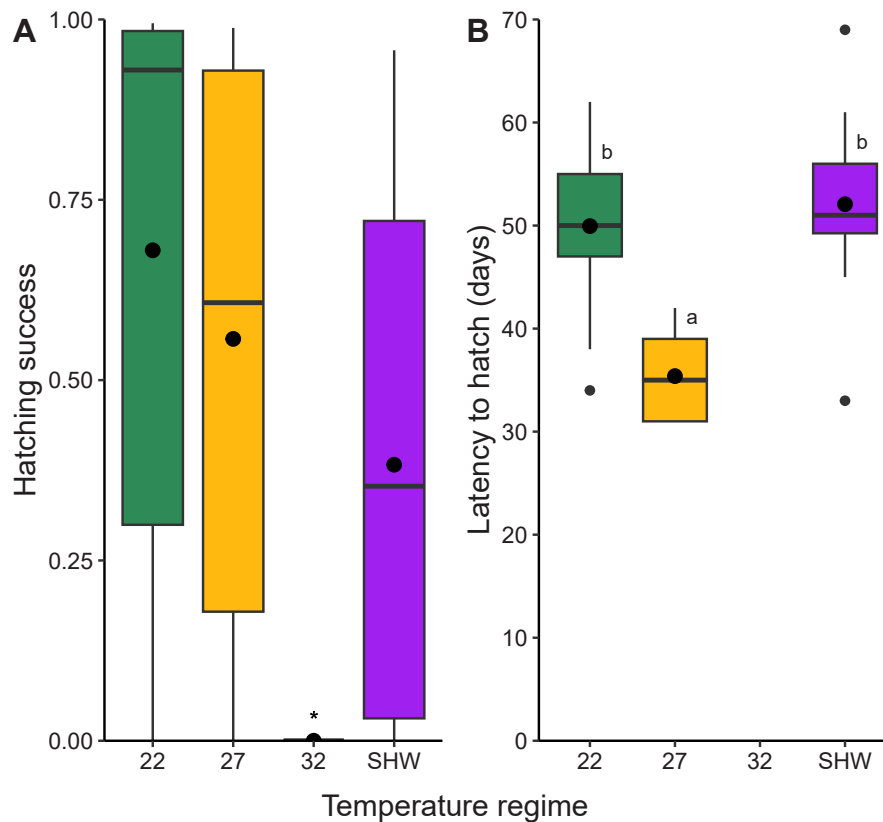


Fig. 2. Effect of temperature on spiderling hatching success (A) and latency to hatch (B). Egg sacs of *Steotoda grossa* were exposed to different regimes within 16 h following their production. Temperatures were set at 22, 27, or 32 °C during the day and 10 °C lower at night. In addition, egg sacs were exposed to a simulated heatwave (SHW, see Materials and Methods). Since egg mortality at 32 °C was 100 %, data on hatching latency is lacking in panel B. Data are presented in boxplots. The horizontal line inside the boxes represents the median, and the box shows the interquartile range (IQR). The whiskers extend from the minimum and maximum values, and outliers are depicted by the dots beyond the whiskers. The black closed circles depict the means. Letters above boxes denote statistical differences (Tukey tests, $P < 0.05$) between treatments. See text for full statistical results. Number of replicates, 21 at 22 °C and 27 °C, 19 at 32 °C and SHW.

additional experiment, eggs sacs were exposed to 32/22 °C for 5 days immediately after their production (window of 14 h). No spiderlings hatched from 15 egg sacs exposed to this temperature regime. In the second additional experiment, egg sacs were first exposed to 22/12 °C for 3 days, followed by 5 days at 32/22 °C and then returned to 22/12 °C. Under these conditions, 10 out of 16 egg sacs failed to hatch. Hatching success of the 6 remaining egg sacs was low (mean \pm SE: 8 ± 2 %, range: 2.4–14.0 %).

Temperature also had a significant effect on the latency of eggs to hatch (Table 1, Fig. 2B). Spiderlings from egg sacs exposed to 27/17 °C hatched significantly faster than those exposed to either 22/12 °C (ca. 14 days earlier, Tukey test, $P < 0.001$) or short heatwave conditions (ca. 17 days earlier, $P < 0.001$). The time it took for spiderlings to hatch did not differ at 22/12 °C and under short heatwave conditions (Tukey test, $P = 0.51$). The order of egg sac production had no effect on hatching latency (Table 1).

The mean body mass of the hatched spiderlings was not influenced by the temperature regime to which the egg sacs had been exposed (Table 1). However, the order of egg sac production affected the mass of neonate spiderlings hatching from it (Table 1). Biomass of spiderlings hatching from the first egg sac (0.309 ± 0.012 mg, mean \pm se) tended to be smaller than biomass of spiderlings emerging from successive egg sacs (2nd egg sac: 0.351 ± 0.011 ; 3rd egg sac: 0.342 ± 0.013 ; 4th egg sac: 0.348 ± 0.014). However, pairwise comparisons of spiderling biomasses were only significant for the first and second egg sac ($t_{46} = 2.73$, $P = 0.042$, all other comparisons $P > 0.10$).

3.2. Effect of temperature regime on spiderling survival and growth

Different fixed day/night temperature regimes significantly affected spiderling survival (Log rank test, $\chi^2_2 = 177$, $P < 0.001$, Fig. 3). Median survival, i.e., the timepoint at which 50 % of the individuals were still alive, decreased from 52 weeks at 22 °C to only 4 weeks at 32 °C (Fig. 3A). Mortality at 27 and 32 °C predominantly occurred early during spiderling development, i.e., within the first 8 weeks after hatching, especially during molting. Also, heatwave conditions had a significant, negative effect on spiderling survival $\chi^2_4 = 27$, $P < 0.001$, Fig. 3B), but only when these conditions were extended (1xLHW and 2xLHW) survival curves differed significantly from spiderling survival at 22 °C (Fig. 3B).

For spiderlings that lived long and large enough for their sex to be determined, growth trajectories were plotted (Fig. 4). Male and female spiderlings exhibited variation in growth patterns when exposed to different fixed day/night temperature regimes. Irrespective of regime type, males matured faster and were lighter at this point than conspecific females. In contrast, none of the female spiderlings reached adulthood within the experimental period of ≈ 500 days.

During the exponential growth phase, male and female spiderlings continuously exposed to the fixed day/night temperature regimes gained biomass along the same trajectories, i.e. their growth rates were similar (Tables 2 and 3). The effect of fixed day/night temperature regimes on growth rate was also not significant (Tables 2 and 3, Fig. 4A and B). However, when spiderlings experienced heatwave conditions (Fig. 4C and D, Table 2), only growth rates of females were affected (Table 3). More specifically, females grew slower (by almost 20 %) when exposed to single and dual SHWs than females reared at 22 °C (both

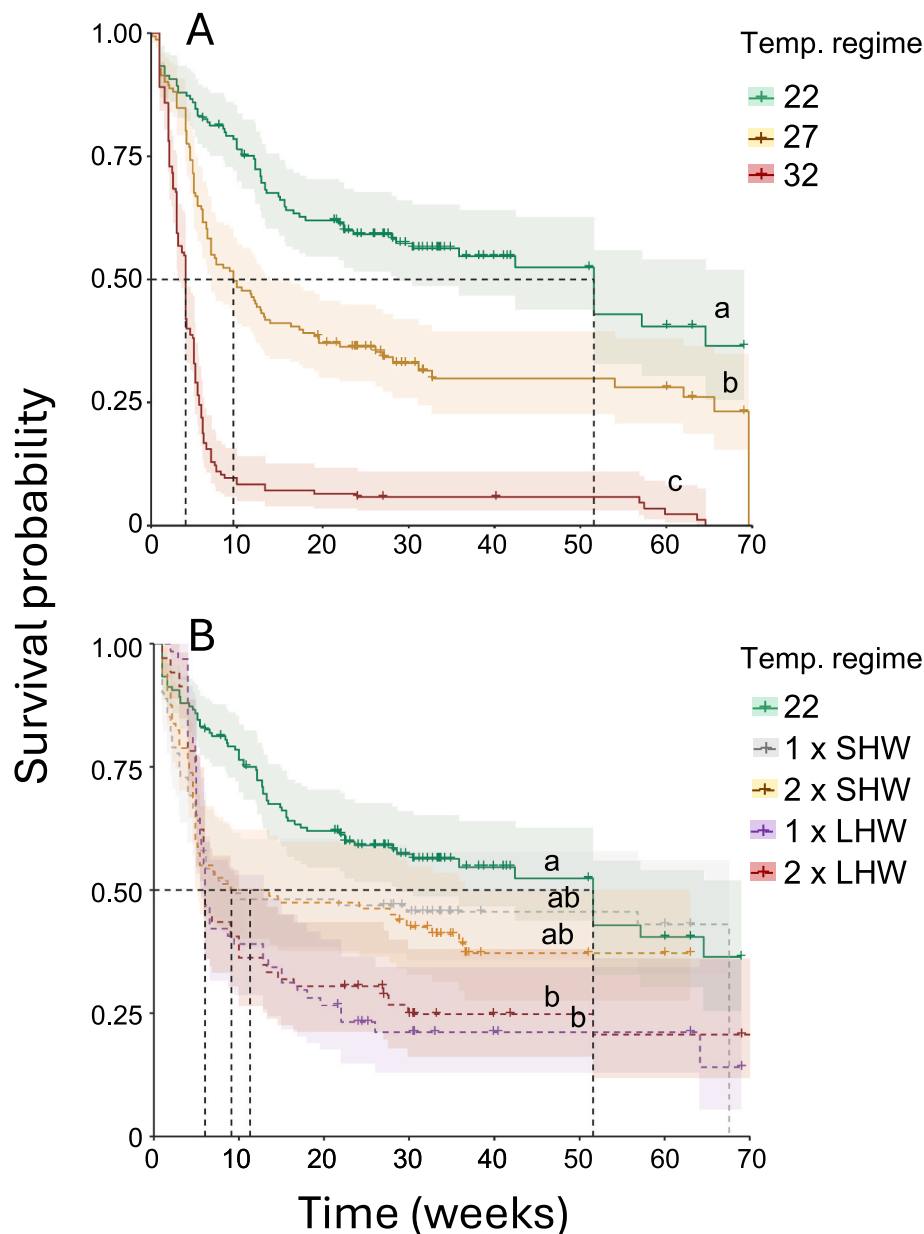


Fig. 3. Survival probabilities of *Steatoda grossa* spiderlings exposed to (A) different fixed daytime temperatures (22, 27, or 32 °C) or (B) single or double simulated heatwave conditions (SHW = standard heatwave, LHW = extended heatwave). For comparison, the 22 °C survival curve is shown in both panels. Temperatures during the night were 10 °C lower than during the day. The black dotted lines denote median survival, i.e. the timepoint at which 50 % of the spiderlings were still alive, the lighter colored areas denote 95 % confidence intervals. Survival curves with different letters differ significantly (Log Rank tests). The number of replicates varied between 149 and 155 for constant daytime regimes and between 64 and 81 for heatwave regimes.

Tukey tests, $P < 0.001$). Growth rates of females exposed to 22 °C and extended heatwaves were not significantly different from each other (Tukey tests, $P > 0.40$).

Beyond the exponential phase, growth trajectories of female spiderlings were severely depressed at the 32/22 °C regime (Fig. 4A). Biomass of the five females that were still alive after 12 months leveled off at this point, then decreased, and spiderlings eventually died. Males reached maturity within the experimental period. When they were exposed to the 22/12 °C regime, males matured later (by approximately 4.5 weeks) but gained more biomass (factor 1.5 to 1.7) than at the other two regimes (Table 4, age at maturity: $F_{1,89,9} = 18.0$, $P < 0.001$; biomass $F_{1,91,8} = 66.5$, $P < 0.001$). None of the heatwave conditions affected male biomass at maturity (overall mean 20.1 ± 0.5 mg, $F_{4,111} = 1.95$, $P = 0.10$). Males tended to reach maturity later when exposed to short heatwave conditions ($F_{4,28,4} = 66.4$, $P = 0.015$), but the difference in

maturity age was only statistically significant for males reared at 22 °C and those exposed to a double short heatwave ($P < 0.01$).

4. Discussion

The results of this study reveal that daily exposure to high temperatures (32 °C) strongly affected early developmental stages, i.e., eggs and spiderlings of *S. grossa*. Concurring with our hypothesis, the duration of heat exposure played an important role in determining the impact on egg and spiderling survival; mortality was significantly reduced when these life stages were exposed to simulated short heatwave conditions in which the number of days with a maximum temperature of 32 °C was reduced. Survival patterns did not change in spiderling cohorts that were exposed to a second short or long heatwave. In addition to the duration of heat exposure, the timing of exposure

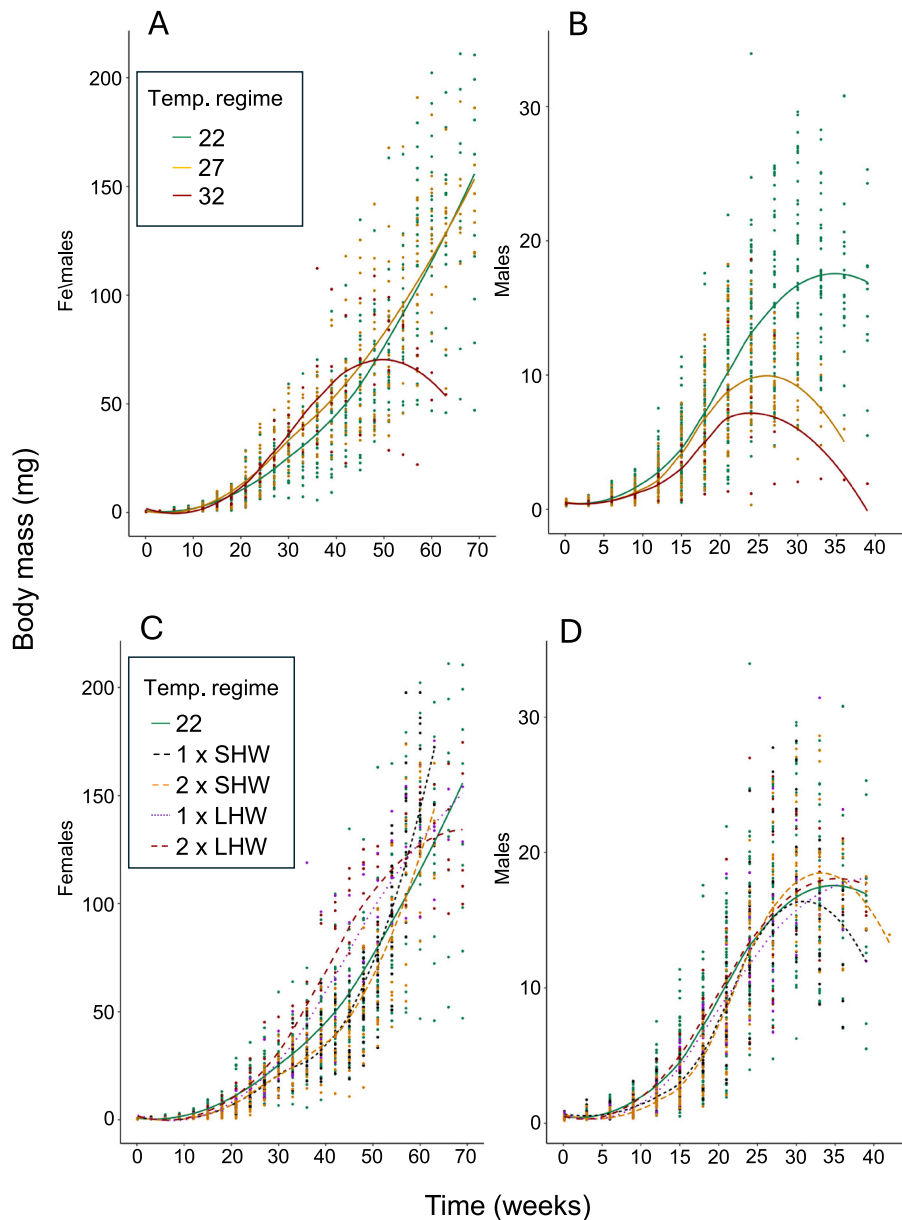


Fig. 4. Growth trajectories of female (A and C) and male *Steatoda grossa* spiderlings (B and D) under different fixed temperature regimes (A and B) and under simulated heatwave conditions (C and D). Within 16 h of hatching, spiderlings were exposed to fixed day temperatures (22, 27, or 32 °C) or different simulated heatwave scenarios (a single SHW, two successive SHW, a single extended heatwave (LHW) or two LHW). Night temperature in all regimes was 10 °C lower in accordance with photoperiod (16 L:8D). Successive heatwaves were separated by a 10-day period at 22 °C. Note: x- and y-axes of the graphs differ for males and females.

(only measured in eggs) also determined to what extent mortality was affected. Exponential growth of male and female spiderlings followed the same trajectories, when spiderlings were exposed to fixed day/night temperature regimes, irrespective of the temperature settings of the regimes. However, when spiderlings were exposed to heatwave conditions, only the exponential growth rates of female spiderlings were affected. Under single and double short heatwave conditions, female growth rates were significantly reduced.

Most female spiders deposit eggs in silken sacs of varying complexity (Turnbull, 1973). Egg sacs provide protection against various threats such as predators, parasitoids, desiccation and thermal variation (Chiavazzo et al., 2015; Ewunkem and Agee, 2022; Hieber, 1992; Schaefer, 1976). Despite this protection, in *S. grossa*, none of the eggs developed into spiderlings when they were exposed daily to 32 °C and hatching success increased significantly when the daytime temperature

was lowered to 27 °C. This shows that the critical thermal limit (CTL) for egg development in *S. grossa* is between these two temperatures. The CTL for spider egg survival is species specific. In some spider species a critical threshold for survival was found to lay between 30 and 35 °C, whereas for other species egg survival was not affected within this range (Li, 2002). However, we found that when exposure to 32 °C was restricted to five days, some offspring survived and hatched. Moreover, we found that daily exposure to 32 °C had the greatest impact on egg survival when eggs were exposed to heat within 24 h after their production. These results suggest that embryos in freshly laid egg sacs may not have developed the 'machinery' to cope with thermal stress, and that only more advanced embryo stages can endure heat stress to some extent when exposure duration is limited.

Spiderling growth and survival were also affected by fixed and variable heatwave temperature regimes, although the effects were less

Table 2

Growth rates of female and male *Steatoda grossa* spiderlings exposed to different fixed temperature regimes and simulated heatwaves. Rates are given for the period during which growth is exponential (i.e., the period during which the relationship between time (in weeks) and the natural logarithm of biomass (in mg) is linear. SE is the standard error of the mean and n gives the number of spiderlings.

Temp. regime	Females			Males		
	Mean	SE	n	Mean	SE	n
22/12 °C	0.117	0.004	25	0.114	0.002	61
27/17 °C	0.110	0.003	17	0.112	0.003	33
32/22 °C	0.114	0.005	5	0.105	0.008	3
Single Short heatwave	0.095	0.002	18	0.108	0.003	18
Double short heatwave	0.094	0.004	15	0.108	0.003	18
Single long heatwave	0.111	0.005	6	0.114	0.004	10
Double long heatwave	0.103	0.010	4	0.112	0.004	9

Table 3

GLM results on spiderling exponential growth rates.

Explanatory variable	Fixed day/night regimes		Heatwave conditions	
	F- value (df s) ^a	P-vale	F- value (df s)	P-vale
Temperature regime	0.80 (2, 138)	0.44	8.59 (4, 174)	<0.001
Sex	0.46 (1, 138)	0.49	0.13 (1, 174)	0.71
Interaction	0.43 (2, 138)	0.64	2.70 (4, 174)	0.03

^a Df s, degrees of freedom of numerator and denominator.

Table 4

Body mass and development time until maturity of male *Steatoda grossa* spiderlings when exposed to various fixed temperature regimes and simulated heatwaves. SE is the standard error of the mean and n gives the number of spiderlings.

Temp. regime	Body mass (mg)			Age at maturity (weeks)		
	Mean	SE	n	Mean	SE	n
22/12	20.1	0.7	61	30.1	0.9	60
27/17	13.6	0.6	33	25.5	0.6	32
32/22	11.9	3.3	3	25.0	1.0	3
Single Short heatwave	20.2	1.1	18	32.5	0.6	18
Double short heatwave	22.5	1.0	18	34.0	0.7	17
Single long heatwave	19.2	1.7	10	30.2	2.1	10
Double long heatwave	16.6	2.1	9	29.7	2.3	9

pronounced compared to those found for eggs. Other studies have also shown that the negative effects of exposure to high temperatures on survival and development of arthropods, including spiders, often decline with progressing life stages (Barnes et al., 2019; Bowler and Terblanche, 2008; Klockmann et al., 2017; Mahroof et al., 2003; Radchuk et al., 2013). For example, in widow spiders, *Latrodectus hesperus* and *L. mactans*, *L. geometricus*, exposure to heat affected eggs of the three species more severely than young conspecific spiderlings (Barnes et al., 2019). As was found for eggs, differences in thermotolerance have also been reported within life stages (Bowler and Terblanche, 2008). In adult holometabolous insects, it is highest at adult eclosion, then rapidly declines before it stabilizes. Within developing stages such as eggs and larval stages, this relationship may be reversed (this study, Zhang et al., 2015) and these opposing effects could be the results of progressing development within early life stages in contrast to senescing in the adult stage.

Acclimation, hardening and heat shock are three mechanism that help organisms to tolerate exposure to environmental stresses such as low and high temperatures (Loeschke and Sørensen, 2005). Acclimation

is the most likely process that explains recovery to heat exposure in this study as it refers to physiological responses to longer periods of moderate, not immediately lethal, temperature stress (Bowler, 2005; Loeschke and Sørensen, 2005). The production of heat shock proteins (HSPs) plays an important role in providing protection against extreme temperature exposure at both ends of the temperature spectrum. For instance, many insect species can withstand brief periods (up to 2 h) of extreme heat (39–42 °C) to some extent and this tolerance has been attributed to the protective activity of HSPs, hormone regulation and other endocrinological factors (González-Tokman et al., 2020). The physiological sequence of responses to thermal stress at temperatures that are only lethal after extended exposure, such as the temperatures applied in this experiment, are not well studied in arthropods (Verberk et al., 2016). Increased metabolic rates (González-Tokman et al., 2020; Li, 2002) and their associated costs (Verberk et al., 2016) may lead to the shutdown of vital physiological processes, eventually causing death if these adverse conditions are not reversed. Interestingly, when spiderlings were exposed to a second heatwave of the same type (i.e., short or long) after a recovery period of 10 days during which temperature did not exceed 22 °C, survival was similar for spiderlings that were exposed to single heatwaves. Fluctuating temperatures can increase heat tolerance (Colinet et al., 2015) allowing individuals to recover from thermal stress. Daily temperature fluctuations combined with the prolonged period in which spiderlings were maintained at 22/12 °C may have acclimated spiderling to tolerate a second heatwave irrespective of their duration.

In addition to survival, exposure to the various regimes differentially affected growth trajectories of male and female spiderlings. When exposed to the fixed temperature regimes, the two sexes grew along the same trajectories during the exponential growth phase, bearing in mind that the exponential growth phase is shorter for males than for females. This was also the case for male and female *S. grossa* reared under different feeding regimes (Harvey, 2022). Only when females were exposed to various heatwave conditions differences in exponential growth rates became apparent. Females grew slower when exposed to short single and double heatwaves but not when the duration of heatwaves was extended (single and double). This result is difficult to explain. Perhaps the duration of the short heatwave regimes with only 5 days over 32 °C was not long enough for female spiderling to recover and to adapt physiologically. *Steatoda grossa* male growth trajectories deviate from female trajectories by reaching maturity earlier at a lower maximum body size (Harvey, 2022). Only males reached maturity within the experimental period of the study. Ectotherms usually grow and mature faster at higher temperatures but attain reduced adult body sizes (the temperature size rule, Atkinson, 1994; Ghosh et al., 2013), which was also the case in this study. Differences between male and female growth patterns became more pronounced when growth progressed beyond the exponential growth phase, especially under the 32/22 °C regime in which growth trajectories of females were severely depressed and all females died. The various heatwave conditions did not affect maximum body sizes of males and only marginally affected the age at which spiders reached maturity. The sex-specific responses to the fixed temperature regimes can be partially explained by the fact that female spiderlings are exposed to these conditions for a longer time period. Nevertheless, male *S. grossa* appeared more tolerant to the various heatwave conditions than female spiderlings, suggesting that physiological demands and or sensitivities differ between the two sexes. If one sex is more strongly affected by heat stress than the other, this can affect population demographics and sizes through e.g., changes in sex-ratios, reproduction and population growth rates (Harvey and Dong, 2023; Petry et al., 2016) and this should be investigated further.

In optimizing fitness, web-building spiders, such as *S. grossa*, are under strong selection pressure when choosing sites in which to construct their webs (Glover, 2013). Females of many web-building spiders (and males in some species) choose sites to construct webs that are based on multiple criteria (reviewed by Glover, 2013). These include prey availability and the risk of exposure to natural enemies (Enders, 1977), intra- and inter-specific competition with other spiders (Vetter and Rust, 2010), vegetational complexity (Halaj et al., 1998; McNett and Rypstra, 2000), and exposure to climatic factors such as wind, rain and temperature variability (Riechert and Tracy, 1975; Samu et al., 1999). In many web-building spiders such as *S. grossa*, males tend to wander widely in search of females and therefore may have more flexibility in choosing preferable microclimates to 'ride out' extreme conditions (Harvey and Dong, 2023). The higher sensitivity to heat stress of female *S. grossa* may explain why this synanthropic spider is often found in sheds and other man-made constructions which may buffer the females and her eggs that are deposited in the web against extreme temperatures (Pincebourde et al., 2016; Cabon et al., 2024a,b).

In this study we used spiders that were collected in the Netherlands. *Steotoda grossa* has a cosmopolitan distribution, including tropical and sub-tropical regions, but is native in temperate Eurasia (Nentwig et al., 2025). Populations from different geographical origins are under selection to adapt to local environmental conditions resulting in genotypic and phenotypic variation (Lasky et al., 2012; Marshall et al., 2020; Sinclair et al., 2012; Schilthuizen and Kellermann, 2014). To what extent the spiders used in this study are adapted to temperate Dutch weather conditions merits further study, as studies have shown that thermal tolerance levels may differ across species' biogeographical ranges and often correlate with environmental attributes (Sinclair et al., 2012; Sørensen et al., 2001; Sorte et al., 2011).

Growing evidence suggests that insects are negatively affected by climate change and climatic extremes such as heatwaves (Halsch et al., 2021; Harvey et al., 2023; Wagner et al., 2021). However, spiders are much less studied than insects, and the 'jury is still out' when it comes to better understanding how a warming climate and concurrent extreme climatic events will affect a wide range of spider taxa (Harvey and Dong, 2023). Most spiders are generalist predators and are important natural enemies in most terrestrial ecosystems, including agricultural systems (Khudr et al., 2020; Michalko et al., 2019; Nyffeler and Birkhofer, 2017). Spiders also act as vital prey for many other species (Cloudsley-Thompson, 1995; Nyffeler and Knörnschild, 2013).

Our study has shown that eggs and spiderlings in a web-building spider, *S. grossa*, are negatively affected by exposure to high temperatures. The timing and duration of heatwaves in relation to *S. grossa* ontogeny are important factors determining impacts on spider survival and development. Moreover, the duration of high temperatures – simulating the intensity of heatwave exposure – is critically important and can have a huge impact on whether the spiders can recover from exposure to heat stress. In the lab, *S. grossa* females can produce up to 17 egg sacs from a single mating (Dong et al., submitted). This could represent a 'bet-hedging' strategy to counter a highly variable thermal exposure range for eggs and spiderlings. Future studies should investigate sex-specific responses of many more spider species across a range of families and habitats to a range of high and low temperatures. This will help to better understand how the duration and frequency of exposure to different temperature extremes affect demographic parameters in this important group of arthropods.

CRedit authorship contribution statement

Yuting Dong: Writing – review & editing, Visualization, Methodology, Investigation, Conceptualization. **Jeffrey A. Harvey:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Melissah Rowe:** Writing – review & editing, Supervision, Conceptualization. **Rieta Gols:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Formal analysis, Conceptualization.

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Declaration of competing interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2025.104323>.

Data availability

Data will be deposited in the DRYAD.

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