

Effects of manipulative prolonged temperature increase on the greater long-tailed hamster (*Tscherskia triton*) in semi-natural enclosures

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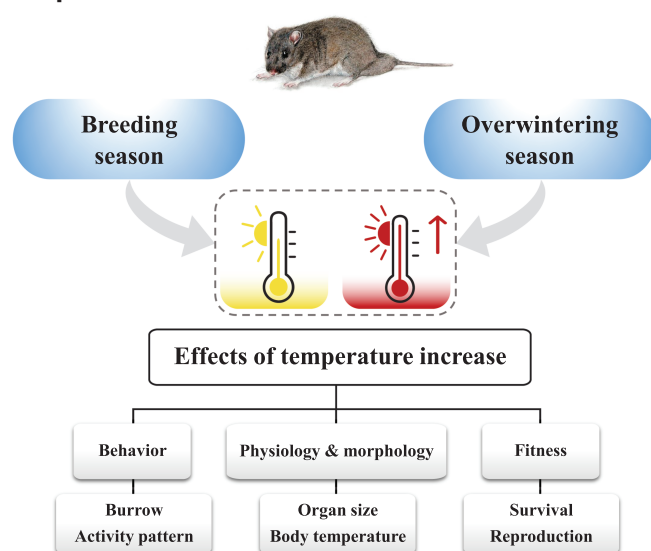
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Abstract

Global climate change has caused range shifts and population declines in various species. However, causal evidence from manipulative studies, particularly for vertebrates, remains scarce. Prolonged temperature increases, a direct consequence of climate change, pose significant challenges to species adaptation and survival. We examined the effects of prolonged temperature increases on reproduction, physiology, and behavior adaption in the greater long-tailed hamster using semi-natural enclosures where temperature was manipulated via plastic roofs and windows, creating a greenhouse effect without affecting rainfall. We analyzed data using grouped enclosures (low temperature, LT; high temperature, HT), which showed that prolonged temperature increases led to reduced reproductivity per capita during the breeding season. In addition, prolonged temperature increases reduced night-time activity in founder hamsters during overwintering, increased burrow depth during the breeding season, and raised testicular weights in founder males during the overwintering season. Our study provides experimental evidence that prolonged temperature increases negatively impact population growth of greater long-tailed hamsters by inducing temperature stress and impairing reproductive performance, highlighting the need to address heat stress in wildlife management under climate warming.

Key words: behavior adaptation, climate warming, heat stress, population decline, small mammals.

Graphical Abstract



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The rapid increase in global temperatures poses a serious threat to ecosystems worldwide, affecting the structure and functioning of natural systems (Hansen et al. 2006; Baker-Austin et al. 2013; Blöschl et al. 2019; Hoegh-Guldberg et al. 2019). Projections indicate that a 2–3 °C increase in average global temperatures could elevate the risk of extinction for 20–30% of plant and animal species. A rise of 4 °C by the end of this century could result in the loss of 15% of marine and terrestrial species (Trisos et al. 2020; IPCC 2022). Climate change is also exacerbating the formation of heatwaves, making them more frequent and intense (Perkins-Kirkpatrick and Lewis 2020). Heatwaves have increased in intensity, frequency and duration in the last decades, with these trends projected to worsen under enhanced global warming.

These prolonged heatwaves are anticipated to significantly affect animal populations, causing declines in their numbers and, if such heatwaves recur over multiple years, potentially leading to eventual extinctions (Fischer and Knutti 2015). For instance, high ambient temperatures during lactation can lead to significant pup losses in golden hamsters, where approximately two-thirds of pups may disappear due to insufficient maternal milk production and energy intake (Ohrnberger et al. 2016). Behavioral adaptations, such as changes in daily activity rhythms and burrowing behaviors, can serve as a first line of defense (Borowik et al. 2020; Teitelbaum et al. 2021; Gunn et al. 2022). For instance, during the summer breeding season, increased ambient temperatures can lead to decreased activity in species such as the grassland lizard (*Tympanocryptis lineata*) (Doucette et al. 2023). Burrowing animals, such as the plateau fence lizard (*Sceloporus tristichus*), may also adjust the depth of their burrows to access cooler, more stable thermal microhabitats, buffering them from the effects of climate change (Telemeco et al. 2017).

Increased temperatures have significant implications for animal fitness, especially affecting survival and reproductive success. Many species display various forms of physiological plasticity to cope with rising temperatures, such as adjustments in organ size and function, but these adaptations may also come with trade-offs. For example, temperature rises can decrease the relative weights of organs such as the heart, kidneys, and liver, potentially compromising physiological function and health (Zhao et al. 1995). In male duroc boars (*Sus scrofa domestica*), increased temperatures can result in testicular shrinkage, reduced semen quality, and decreased sperm production (Suriyasomboon et al. 2005). These physiological changes highlight the energetic demands of thermoregulation, particularly cooling, which require additional energy allocation (Cunningham et al. 2013; Salaberria et al. 2014; Nawaz et al. 2021). Thus, while physiological adaptations are critical for surviving heat stress, they may undermine reproductive performance and population growth. The cumulative impacts of prolonged temperature increases can lead to reductions in population numbers, highlighting a serious risk to species survival under climate change.

Neonates, with their lower energy reserves and higher metabolic demands, are particularly vulnerable to heat stress, as their survival depends not only on their own physiological limitations but also on maternal care and resource provisioning (Rodríguez and Barba 2016; Pontzer et al. 2021; Corregidor-Castro et al. 2023). Elevated temperatures can reduce milk energy output in lactating small mammals, exacerbating neonatal energy deficits and increasing pup mortality, ultimately compromising reproductive success (Ohrnberger

et al. 2016; Zhao et al. 2020b). In addition, heat stress can impair gamete viability and embryonic development, leading to lower offspring quality and survival rates, further diminishing reproductive outcomes in high-temperature environments (Suriyasomboon et al. 2005; Turbill and Prior 2016). The cumulative impacts of prolonged temperature increases can lead to reductions in population numbers, highlighting a serious risk to species survival under climate change.

Building on the challenges posed by heat stress on neonates, other demographic groups, such as juveniles and older individuals, also exhibit varying vulnerabilities to temperature extremes. Physiological factors like metabolic rate, thermoregulatory capacity, and hormonal responses, as well as behavioral differences, influence how individuals cope with elevated temperature (Willisch et al. 2013). For example, juveniles, with their still-developing thermoregulatory mechanisms, may struggle to dissipate excess heat efficiently, making them highly susceptible to hyperthermia during prolonged heatwaves. Similarly, aging individuals often experience a decline in physiological plasticity, reducing their ability to adjust metabolic and cardiovascular responses to extreme temperatures (Varpe et al. 2009; Brodersen et al. 2011). In addition, climate-induced shifts in seasonal patterns, such as altered spring emergence, can cause mismatches between reproductive activities and food availability, further challenging the survival and breeding success of these age groups (Walker et al. 2019).

Beyond physiological and demographic vulnerabilities, climate change also exerts profound impacts on the habitats essential for overwintering survival. Warmer winter temperatures can disrupt seasonal rhythms, including the timing of hibernation and torpor, causing animals to enter and exit these states at atypical times. Furthermore, higher temperatures can lead to changes in soil moisture and vegetation cover, reducing the suitability of burrows or nests that provide critical insulation, particularly against the cold during winter (Deeming 2023). For burrowing animals, such habitats may lose their effectiveness in buffering environmental extremes, exposing them to greater risks of hypothermia or frostbite (Glass et al. 2021).

Associations between rodent population dynamics and climate warming have been widely documented through field surveys (Reed et al. 2007; Kausrud et al. 2008; Cárdenas et al. 2021; Wan et al. 2022). However, experimental manipulations of temperature increases in rodents are rare, in contrast to more common studies in insects, lizards, and birds (Lu et al. 2013; Yan et al. 2017; Andreasson et al. 2018; Sun et al. 2018; Beltran et al. 2020; Han et al. 2020; Corregidor-Castro and Jones 2021). While observational studies struggle to isolate the independent effects of warming, frequently confounded by human disturbances (Maucieri et al. 2023), manipulative studies will offer clearer insights. Understanding the distinct roles and mechanisms driving population dynamics through models or experiments is crucial in the context of ongoing climate warming and human activities (Wan et al. 2019; Bai et al. 2022).

This study investigates the correlative effects of prolonged temperature increases on the population of the greater long-tailed hamster in semi-natural enclosures during the breeding season (April 26–October 9) and the overwintering season (October 23–April 16). The greater long-tailed hamster (*Tscherskia triton*) is a dominant rodent in the agricultural fields across Northern China, the Korean Peninsula, and

near Vladivostok, Russia. Its southern distribution area has been rapidly shrinking in recent decades (Zhang et al. 2023), potentially due to rising temperatures in the North China Plain (He et al. 2018). Our hypotheses are as follows: (1) In terms of behavioral adaptations, we expect that the rodents will try to avoid the increased temperatures by digging deeper burrows and by showing more nocturnal activity. (2) Initially, animals may counter the effects of rising temperatures through behavioral changes, which may help mitigate negative impacts on organ weights and fitness. However, if these behavioral adjustments are insufficient, prolonged temperature increases will result in higher body temperatures and potentially reduced weights of organs involved in thermoregulation and reproduction during the breeding season. (3) As the prolonged heat stress continues, it may negatively impact individual fitness during breeding season, including lower reproduction and survival rates. However, the effects of warming during the overwintering season may vary, highlighting the complex and context-dependent impacts of climate change on animal populations.

Materials and Methods

Study site and species

In this study, we evaluated the effects of prolonged increased temperature on the behavior (activity patterns and burrow characteristics), physiology (body temperature and organ weight), and fitness (survival and reproduction) of the greater long-tailed hamster under semi-natural enclosures (Figure 1E). The experiment was conducted at our research station located in Liucun Town (40°18'N, 116°05'E), Changping District, Beijing. According to weather data from the China Meteorological Administration from 1961 to 2018, the average temperature in the region increased by 1.14 °C. The study site is situated in the temperate zone of Northern China, characterized by a continental semi-humid and semi-arid monsoon climate (annual average temperature: 9–11 °C; annual

precipitation: 500 mm). The average monthly maximum and minimum temperatures are 25.89 and −4 °C, respectively. This site represents a typical habitat for the greater long-tailed hamster, which primarily inhabits agricultural areas, grasslands adjacent to agricultural regions, river valleys, swamps, bushes, and forest margins (Zhang et al. 1998). Common crops in the area include *Zea mays* L., *Triticum aestivum* L., and *Glycine max* (L.) Merr., and the commonly seen rodent species are the greater long-tailed hamster, the striped hamster (*Cricetulus barabensis*), and the striped field mouse (*Apodemus agrarius*).

The greater long-tailed hamster is an aggressive and solitary species. It reaches sexual maturity at 1.5 months, and females reproduce 1–3 times per year, with an average litter size of 9–11 during the breeding season from March to September (Zhang et al. 1998). Dispersal in this species is male-biased, and higher population density can promote genetic diversity by increasing the frequency of dispersal events (Song et al. 2005; Xie and Zhang 2006; Dong et al. 2010). Historically, the distribution of greater long-tailed hamster has been influenced by Quaternary climate changes, with the species expanding into the North China Plain and Northeastern China during warm periods, including the last interglacial (about 130,000 years ago) (Ye et al. 2015). Over the past 10,000 years, the species has been widely distributed in Northern China, likely facilitated by agricultural activities (Ye et al. 2015). Once dominant in farmlands of Northern China, the greater long-tailed hamster's historical range extended to regions near the Yangtze River (28°00'–32°00' N). However, its southern boundary has shown a clear retreat northward, likely due to climate warming and human disturbances.

Experimental design

A total of 12 semi-natural enclosures (3 × 3 m) were constructed, with 6 replicates each for the low-temperature (LT) increase and the high-temperature (HT) increase (Supplementary Figure S1). The LT treatment increased the

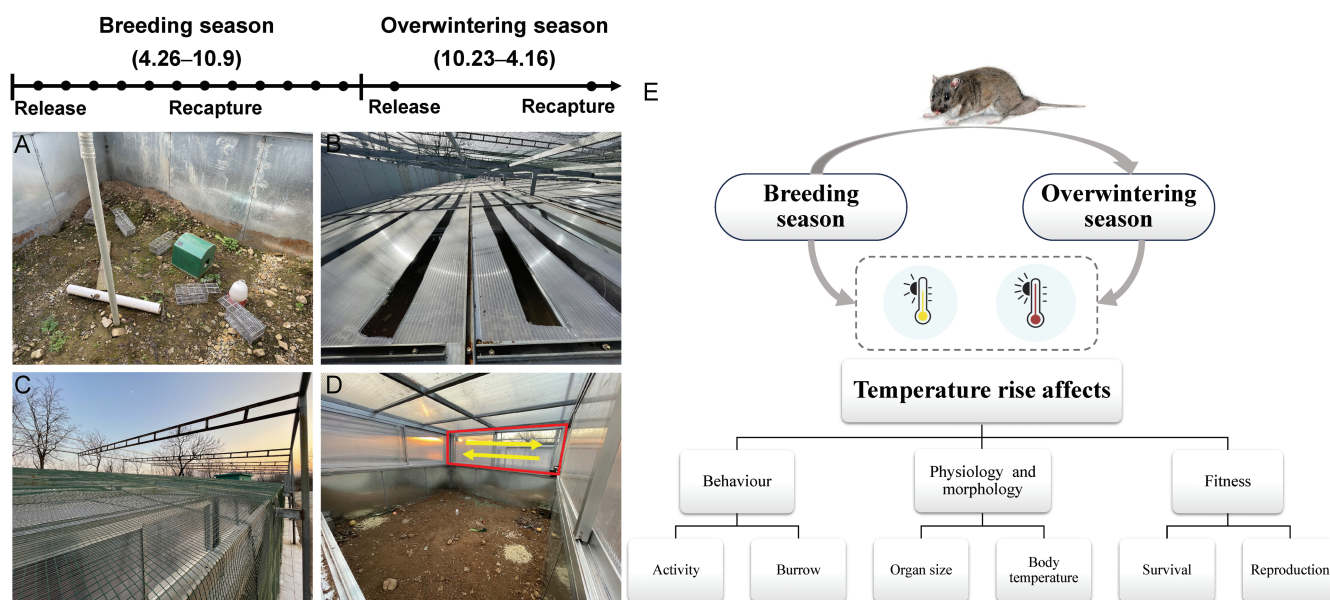


Figure 1. Experimental timeline and enclosure structure. (A) The internal structure of the enclosure; (B) a detailed view of the top of the enclosure, with several sunshine panels slats; (C) details of the galvanized iron mesh outside the enclosure; (D) the temperature can be controlled by opening and closing the windows; and (E) the visual representations of the manuscript. The picture of the greater long-tailed hamster originates from the internet.

average daily maximum temperature by approximately 0.7 °C, while the HT treatment increased it by approximately 2 °C (Supplementary Tables S1 and S2). Each enclosure was constructed with galvanized iron sheets, standing 1 m above the soil surface and extending 1.5 m underground, with the bottom lined with stainless steel wire to prevent hamster escape and predation, while allowing natural water drainage (Figures 1A–D). To simulate prolonged temperature increases, polycarbonate greenhouse strips with 5 cm gaps were placed atop the enclosures, enabling sunlight and precipitation to penetrate naturally (Figure 1B). Eight aluminum alloy windows (each 1.75 × 1 m²) were welded above the galvanized iron sheets in each enclosure. HOBO MX2301A Series Data Loggers (Onset Computer Corporation, Bourne, MA, USA) were used to record temperature and humidity in each enclosure every 30 min. Due to wind and shading effects, observed air temperatures varied across enclosures. Consequently, we reclassified the enclosures into 2 groups based on the maximum observed temperatures: for the breeding season, the LT group had a mean maximum temperature of 28.38 ± 0.35 °C, and the HT group had a mean maximum temperature of 30.4 ± 0.31 °C; for the overwintering season, the LT group had a mean maximum temperature of 11.8 ± 0.33 °C, while the HT group had a mean maximum temperature of 14.01 ± 0.20 °C. This reclassification aimed to simulate prolonged temperature increase conditions (Supplementary Figure S1). The temperature and humidity in all enclosures were monitored throughout both seasons. For the breeding season, data were collected from four enclosures between April 26 and August 7, then extended to all 12 enclosures from August 8 to October 9 (Supplementary Table S1). Continuous monitoring continued during the overwintering season and took place from October 23 to April 16 (Supplementary Table S2).

Exp. 1: breeding season

A total of 72 adult hamsters (3 months old) were obtained from a breeding colony at the Institute of Zoology, Chinese Academy of Sciences for the breeding season (April 26–October 9), and 48 adults for the overwintering season (October 23–May 11). Before release, hamsters were housed individually in polypropylene cages (27 × 16 × 13 cm) with corn cob fragments, and provided with standard rodent chow (63% carbohydrate, 24% protein, and 12% fat by Beijing Keao Xieli Feed Co., Ltd) and water.

After a 2-week acclimation period at the study site, 4 hamsters (2 males, 2 females) were randomly assigned to each enclosure as the founding population. Sufficient rodent chow and water were supplied throughout the experiment. Water was provided via automatic poultry drinkers, which were cleaned weekly to remove debris and algae. All hamsters were dye-marked and tagged with passive integrated transponder (PIT) tags, which were implanted under the dorsal skin. Biweekly recaptures were conducted from April 26 to September 27 to assess body mass (± 0.1 g), body temperature (frontal measurements using a frontal thermometer, ± 0.01 °C), and reproductive status (vaginal condition in females, scrotal condition in males). The procedures for live trapping and population monitoring are described in detail below. New individuals were introduced to replace those that died within the first 4 weeks of the experiment (April 26 to June 29) to maintain a consistent founder population size and sufficiently large sample size (Supplementary Table S9). In the LT group, the first capture of newborn hamsters occurred on July

31 ± 10.5 days, while in the HT group, it was on September 7 ± 7 days, about 38 days later (Supplementary Table S5). At the end of Exp. 1 (September 27–October 9), all hamsters were recaptured and euthanized via abdominal injection of sodium pentobarbital (0.1 mg/10 g body mass) (Zhao et al. 2020a). The weights of kidneys, liver, heart, and gonads (testes or ovaries) were measured (± 0.001 g). The enclosures were then cleaned, and a new set of 48 adult hamsters was introduced for the overwintering season (Exp. 2).

Exp. 2: overwintering season

Exp. 2 commenced after the conclusion of Exp. 1 and involved a new set of 48 adult hamsters, placed in the same enclosures used during Exp. 1. To maintain a consistent founder population size, we replaced any individuals who died at the start of the experiment (October 23–November 25; Supplementary Table S10). In the overwintering season, to avoid the risk of death due to frequent surveys in cold weather, hamsters were released on October 23 and only surveyed once on April 8, and therefore we do not have data on body temperatures during this time. At the end of the experiment (April 8–May 11), all hamsters in the enclosure were captured using live traps for final sampling.

Population census and monitoring

During the breeding season, body mass, reproduction, and survival status of the hamsters were monitored biweekly through live trapping. Traps were set in the evening before the survey day and checked the following morning. The study used sufficient live traps (25 × 12 × 10 cm), which were baited with fresh peanuts. Captured hamsters were first checked for PIT tag presence. Body mass, reproductive status, and survival status were then recorded before they were quickly released. If a PIT tag was lost, the hamster's dorsal side was dyed for identification. Relative growth rate, survival, and reproductive per capita (number of newborns per enclosure divided by the number of founder females) were calculated based on recapture records.

The intelligent monitoring equipment (VIM 4.0, Qingdao Yunzhi Environmental Data Management Co., Ltd.) was used to measure daily rhythms and frequency of hamsters entering the device, with individual recognition through PIT tags (with a sensing distance of about 10 cm). Data on appearance time, PIT ID, air temperature, and humidity were automatically collected every minute and uploaded to the data center (Yang et al. 2022). A total of 7,885 records (LT group = 6,065; HT group = 1,820) from the breeding season and 622 records (LT group = 375; HT group = 247) from the overwintering seasons were analyzed. Burrow depth, oxygen content, temperature, and humidity in the burrows were measured using a portable gas detector (MS400, Shenzhen Eranntex Electronics Co., Ltd.) on the morning of August 24 and October 11 during the breeding season. At the conclusion of the breeding season, all hamsters were euthanized, and tissue samples were collected for further analysis using the same procedures as described above.

Data analysis

We analyzed the data using 2 complementary methods to evaluate the effect of temperature treatments and actual environmental conditions (see Supplementary Information) on all response variables (e.g., body temperature, body weight, and organ weight) during the breeding and overwintering seasons.

Enclosure grouping

Separate linear mixed-effects models (LMMs) were run for the breeding and overwintering seasons to compare whether mean temperature and humidity levels differed between LT and HT enclosures. These models were implemented in the *lme4* library (v. 1.8-15) (Bates et al. 2015), with treatment group as a fixed effect and enclosure as a random effect.

Behavioral modifications due to increased temperature

Activity frequency

Data from the VIM4.0 system during the experiment was used to quantify the total activity frequency for each individual. Duplicate records within a 1-min interval were also removed to prevent bias from repeated movements in a short period. Then, time was categorized into daytime (06:00–17:59) and nighttime (18:00–05:59) to test for activity frequency variations across different times.

We created 3 models using the activity data, with separate models for breeding season (founder and newborn) and overwintering season (founder). All models were constructed using the same fixed and random effects, and the same error distribution. The analysis was conducted using separate GLMMs with a negative binomial distribution and logit link function implemented through the *glmmTMB* library (v. 1.1.4) (Brooks et al. 2017). The response variable was the number of times an individual was recorded during either the day or night. Fixed effects included temperature groups, sex, time of day, and their two-way interactions. ID nested within the enclosure was included as a random effect. Model assumptions were checked using the residual diagnostic plots from the *DHARMa* (v. 0.4.6) library (Hartig 2022).

Burrow characteristics

Four separate GLMMs were constructed to analyze burrow characteristics (depth, oxygen content, temperature, and humidity), as data were only available for the breeding season. Treatment was included as a fixed effect, and enclosure as a random effect. A gamma distribution was applied to oxygen content and humidity, as these variables represent proportion data between 0 and 1.

Physiological traits

Growth rate

The relative growth rate was calculated using recapture data, which it accounts for changes in body mass over time. The formula used was:

$$R = \left[\ln \left(\frac{BM_{t+1}}{BM_t} \right) \right] / T$$

Where R is the relative growth rate; BM_t is the body mass at time t , BM_{t+1} is the body mass at time $t + 1$, and T is the number of days between the 2 captures. Since the response variable values were relatively small and ranged close to zero, we standardized the response variable using $(R - \text{mean}(R)) / \text{SD}(R)$ to enhance the interpretability of the model results. To analyze the data, 3 GLMMs were constructed, with separate models for breeding season (founder and newborn) and overwintering season (founder). Fixed effects included initial body mass, treatment, sex, and the interaction between treatment and sex as fixed effects, with enclosure as a random effect.

Body temperature

Body temperature was measured with a frontal temperature gun, and the variability in body temperature across different treatments was analyzed using GLMMs. Outliers were identified using a z -score threshold of ± 3 (Smiti 2020). The model included fixed effects for treatment, sex, time, and the interaction between treatment and sex for founder hamsters during the breeding season. ID nested within the enclosure was included as a random effect. Due to the small sample size in the HT group (68 in LT vs. 2 in HT), the analysis of newborn hamsters was excluded from the study, focusing only on the founder hamsters.

Organ weight

Absolute organ weights (heart, kidneys, and liver) were analyzed separately using GLMMs, with initial body mass, sex, treatment, and their interactions included as fixed effects, and enclosure as a random effect. Testes and ovaries were analyzed separately by sex, with models including initial body mass and treatment as fixed effects and enclosure as a random effect. Due to the small sample size of male founder hamsters, testicle weight analysis was not conducted.

Fitness

Reproductivity per capita

To test reproductivity per capita in each enclosure under different treatments, we used a Wilcoxon signed-rank test, after assessing the normality of data residuals with Shapiro–Wilks tests.

Survival

Three separate models were created to analyze survival, including models for breeding season (founder and newborn) and overwintering season (founder). Individual mortality was analyzed using a binomial GLMM, with mortality probability (coded as 0 for alive, 1 for dead) as the response variable. Fixed effects included treatment, sex, and their interaction, with enclosure modeled as a random effect.

Pairwise comparisons were made using estimated marginal means method of the *emmeans* library (v. 1.7.0) with a Tukey adjustment of the probabilities ($P < 0.05$) (Lenth et al. 2018). GLMMs were implemented in the *lme4* library (v. 1.8-15) (Bates et al. 2015).

Results

Enclosure conditions

In the breeding season, average daily maximum temperatures were significantly lower in the LT group compared to the HT group (estimate = -2.022 , SE = 0.562 , $t = -3.601$, $P < 0.001$). However, there were no significant differences in mean temperatures or minimum temperatures between treatments (both $P > 0.05$). For humidity, daily maximum and mean humidities were significantly lower in the LT group compared to the HT group (max: estimate = -4.182 , SE = 1.373 , $t = -3.047$, $P = 0.012$; mean: estimate = -3.472 , SE = 1.213 , $t = -2.862$, $P = 0.017$). However, there was no significant difference between groups for minimum humidity ($P = 0.977$).

In the overwintering season, average daily maximum temperatures were significantly lower in the LT group compared to the HT group (estimate = -2.208 , SE = 0.390 , $t = -5.669$, $P < 0.001$). However, no significant differences were found in

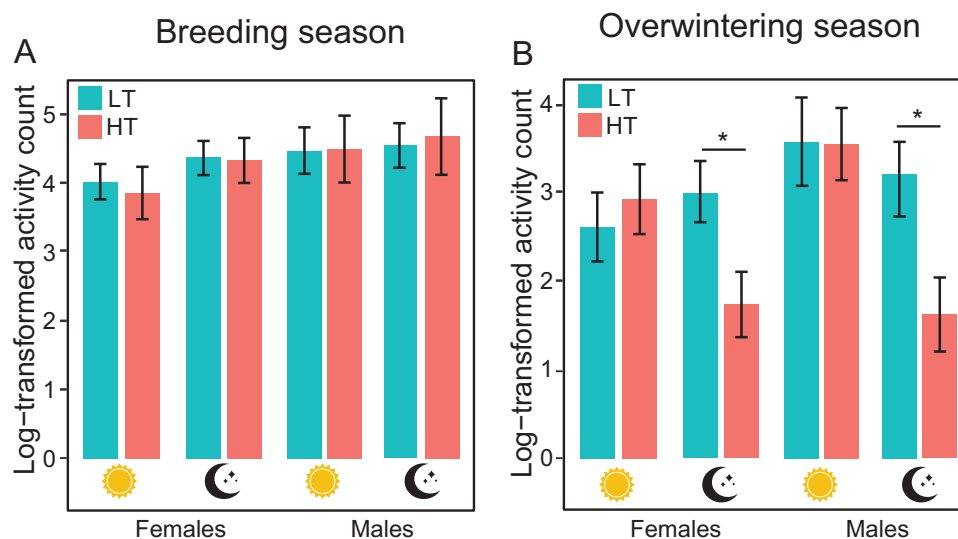


Figure 2. The activity pattern of the founder (A for the breeding season, and B for the breeding season) hamsters at different times (day and night) in prolonged temperature treatments. Error bars indicate the standard error of the mean, *: $P < 0.05$, **: $P < 0.01$.

mean or minimum temperatures between treatments (both $P > 0.05$). Similarly, humidity levels showed no significant differences between treatments (all $P > 0.05$).

Behavioral responses to increased temperature

Activity frequency

A total of 37 founder hamsters were observed for 107 days, and 16 newborn hamsters were observed for 73 days during the breeding season. In addition, 17 founder hamsters were observed for 102 days during the overwintering season using VIM V4.0.

In the breeding season, no significant main effects or interactions for activity frequency were observed in both newborn and founder hamsters (all $P > 0.05$; [Supplementary Table S11](#), [Figure 2A](#), [Supplementary Figure S5](#)).

In the overwintering season, the interaction between treatment and time showed a significant effect on activity frequency ($\chi^2 = 8.775$, $df = 1$, $P = 0.003$). Specifically, during the night, there were significant differences between the LT and HT treatments in both sexes, with the HT group showing a lower activity frequency than the LT group (female: estimate = 1.265, SE = 0.492, $P = 0.018$; male: estimate = 1.606, SE = 0.567, $P = 0.010$; [Supplementary Table S11](#), [Figure 2B](#)).

Burrow characteristics

In the breeding season, the burrow depth in HT group was significantly deeper than in the LT group (estimate = 1.939, $t = -2.271$, SE = 0.854, $P = 0.043$; [Figure 3A](#)). However, there were no significant differences between treatments in burrow oxygen content (estimate = -0.013 , $t = -0.371$, SE = 0.038, $P = 0.711$; [Figure 3B](#)), burrow temperature (estimate = -0.185 , $t = -0.120$, SE = 1.548, $P = 0.907$; [Figure 3C](#)), or humidity (estimate = 0.058, $t = 0.569$, SE = 0.102, $P = 0.570$; [Figure 3D](#)).

Physiological responses to increased temperature

Body growth rate

In the breeding season, the mean number of newborn and founder hamsters per recapture was 20 ± 1.35 and 17.71 ± 4.94 , respectively.

During the breeding season, only initial body mass had a significant negative effect on the relative growth rate of newborn hamsters (estimate = -0.260 , SE = 0.006, $t = -4.595$, $P < 0.001$), whereas treatment, sex, and their interaction showed no significant effects (all $P > 0.05$; [Supplementary Table S12](#), [Supplementary Figure S2A](#)). For founder hamsters, there were no significant effects of initial body mass, treatment, sex, or their interaction on growth rate (all $P > 0.05$; [Supplementary Table S12](#), [Supplementary Figure S2B](#)).

During the overwintering season, initial body mass was the only significant predictor negatively affecting the growth rate of founder hamster (estimate = -0.049 , SE = 0.012, $t = -3.913$, $P = 0.002$). Treatment, sex, and their interaction had no significant effect (all $P > 0.05$; [Supplementary Table S12](#), [Supplementary Figure S2C](#)).

Body temperature

Body temperature in newborn hamsters was not significantly affected by sex or time ([Supplementary Figure S3B](#)). In contrast, founder hamsters showed a significant negative correlation between body temperature and time (estimate = -0.001 , SE < 0.001, $t = -2.131$, $P = 0.035$). No treatment or sex differences were found in founder hamsters (all $P > 0.05$; [Supplementary Table S13](#), [Supplementary Figure S3A](#)).

Organ weight

In newborn hamsters during the breeding season, body mass was significantly positively correlated with organ (liver, kidney, and heart) weights ([Supplementary Table S14](#), all $P < 0.001$). Among these, only sex showed a significant effect on liver weight ($\chi^2 = 4.346$, $df = 1$, $P = 0.04$), with males having higher liver weight than females (estimate = 0.629, SE = 0.302, $t = 2.085$, $P = 0.042$). For gonad weights, body mass was the only significant positive predictor in both sexes (male: estimate = 0.004, SE = 0.001, $t = 3.486$, $P = 0.002$; female: estimate < 0.001, SE < 0.001, $t = 5.868$, $P < 0.001$; [Supplementary Table S14](#), [Figures 4A–B](#), [Supplementary Figures S4A–C](#)).

In founder hamsters during the breeding season, body mass was significantly positively correlated with organ (liver,

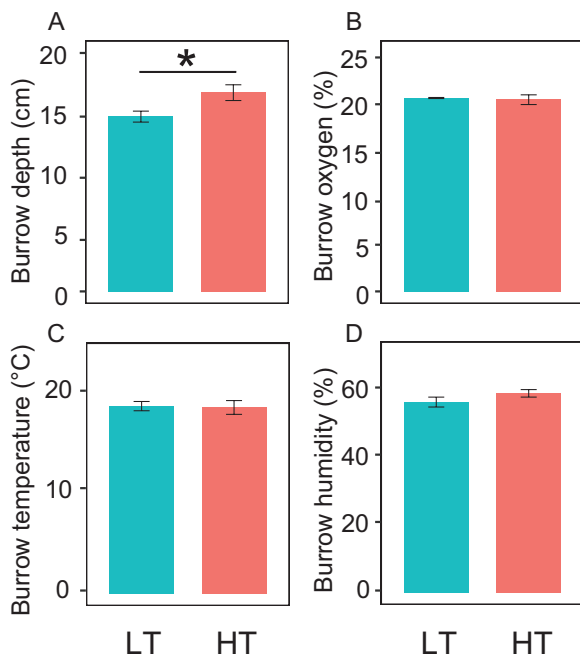


Figure 3. The depth (A), oxygen content (B), temperature (C), and humidity (D) of the burrows in different prolonged temperature treatments. Different colors represent different temperature treatments. The different colors represent the different treatments. Error bars indicate the standard error of the mean, *: $P < 0.05$, **: $P < 0.01$.

kidney, and heart) weights (Supplementary Table S14, all $P < 0.05$). Among these factors, only sex showed a significant effect on heart weight ($\chi^2 = 7.811$, $df = 1$, $P = 0.005$), with females having higher heart weights than males (estimate = -0.139 , $SE = 0.050$, $t = -2.795$, $P = 0.01$). For ovarian weights, female hamsters in the HT group showed marginally higher weights compared to the LT group (estimate = 0.013 , $SE = 0.006$, $t = 2.013$, $P = 0.067$; Supplementary Table S14, Figure 4C, Supplementary Figures S4D–F).

In founder hamsters during the overwintering season, body mass was significantly positively correlated with kidney weights (estimate = 0.006 , $SE = 0.001$, $t = 3.940$, $P = 0.002$). For gonad weights, body mass was significantly positively correlated with gonad weights (male: estimate = 0.018 , $SE = 0.004$, $t = 3.997$, $P = 0.010$; female: estimate = 0.001 , $SE \leq 0.001$, $t = 3.737$, $P = 0.046$). Treatment had a significant effect on gonad weights (male: $\chi^2 = 7.506$, $df = 1$, $P = 0.006$; female: $\chi^2 = 37.830$, $df = 1$, $P < 0.001$), with the HT group having significantly higher gonad weights than the LT group in males (estimate = 0.564 , $SE = 0.206$, $t = 2.740$, $P = 0.040$; Supplementary Table S14, Figure 4F), but significantly lower gonad weights in females (estimate = -0.047 , $SE = 0.001$, $t = -6.150$, $P = 0.004$; Supplementary Table S14, Figure 4E, Supplementary Figures S4G–I).

Fitness responses to increased temperature

Reproductivity per capita

In the breeding season, reproductivity per capita was significantly higher in the LT group (8.4) than in the HT group (0.75) ($W = 35.5$, $P = 0.006$; Supplementary Table S3, Figure 5A). In the overwintering season, although the LT group had a slightly higher reproductivity (7 in LT vs. 3.5 in HT), the difference was not significant ($W = 26$, $P = 0.199$; Supplementary Table S4, Figure 5B).

Survival rate

In the breeding season, male founder hamsters had a significantly higher mortality risk than females (estimate = 1.640 , $SE = 0.825$, $z = 1.988$, $P = 0.047$). There were no differences in survival rates of founder and newborn hamsters between treatment groups, neither in the breeding season nor during overwintering (all $P > 0.05$; see Supplementary Tables S6–S8 and S15).

Discussion

Although prolonged temperatures increase is linked to population decline in small mammals, their specific effects on physiological and reproductive traits remain unclear. In this study, we found that manipulative prolonged temperature increases led to decreased night-time activity in both male and female founder hamsters during the overwintering season and increased burrow depth during the breeding season. Elevated temperatures also increased testicular weight in male founders but decreased ovarian weight in female founders during the overwintering seasons. In addition, both the temperature grouping analysis and the analysis based on actual temperature measurements indicated that prolonged temperature increases during the breeding season reduced per capita reproductive performance. However, we did not find a significant difference in growth rates and survival rates between treatments. Our findings suggest that prolonged temperature increases are associated with negative impacts on the reproductive output of the greater long-tailed hamsters, potentially due to changes in demographic mechanisms, despite their behavioral adaptations to higher temperatures.

Effect of prolonged temperature increases on behavior

It is widely recognized that prolonged increases in temperature can influence the activity patterns of animals (Buchholz et al. 2019). Some species can mitigate the impact of periods with increased temperatures by adjusting their behaviors or activity rhythms (Levy et al. 2019; Mamantov and Sheldon 2021; Riddell et al. 2021). For example, mandarin voles (*Lasiopodomys mandarinus*) exhibit behavioral plasticity by digging deeper burrows in the summer to adapt to higher temperatures under natural conditions (Sun et al. 2019; Wolfe et al. 2020). Similarly, in our study, greater long-tailed hamsters in the HT group also dug deeper burrows during the breeding season, suggesting a comparable behavioral response to prolonged temperature increases. Given this capacity for behavioral adaptation, we examined whether the great long-tailed hamster would similarly shift its behavior under prolonged temperature increases during the overwintering season. The great long-tailed hamster exhibits a distinctive circadian rhythm in its activity patterns, with a fourfold increase in nocturnal activity compared to diurnal activity under normal conditions (Jin et al. 2017). In our study, during the overwintering season, we observed that both male and female founder hamsters in the HT group exhibited reduced night-time activity (from 18:00 to 05:59) compared to the LT group. In contrast, there were no significant differences in day-time activity between the two groups. This reduction in nocturnal activity was not accompanied by an increase in diurnal activity, as diurnal activity remained stable in both groups. While our hypothesis predicted a shift to increased daytime activity, the data indicate that the HT hamsters became less active overall,

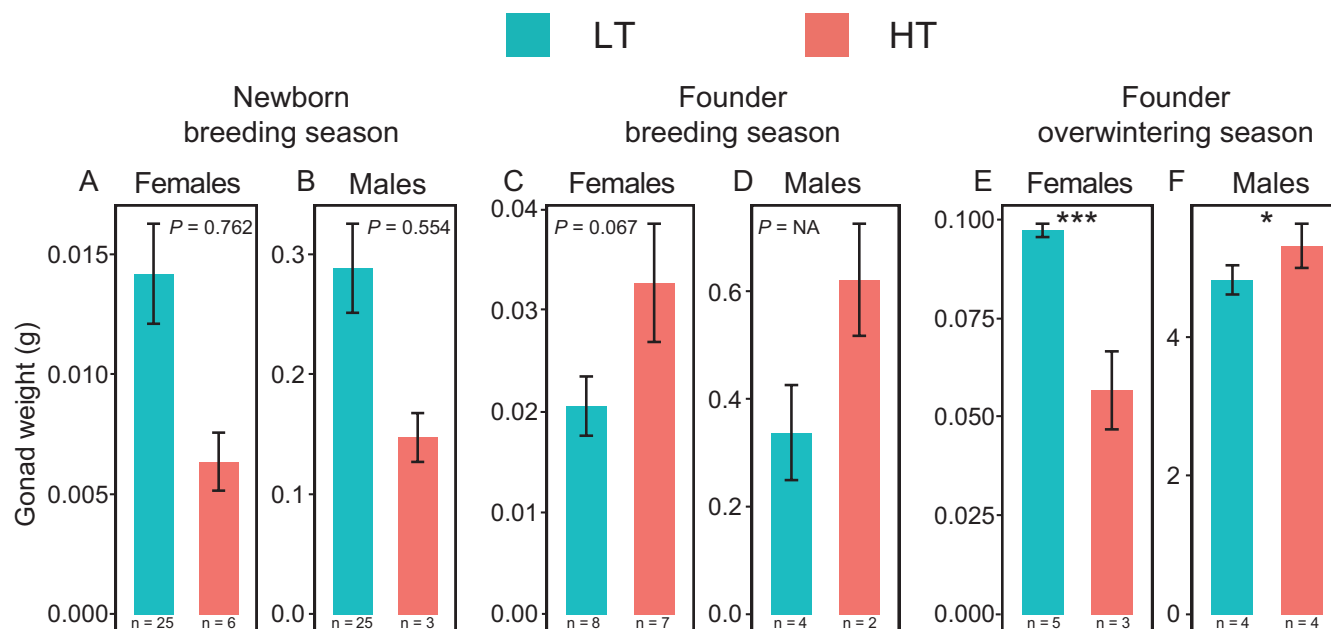


Figure 4. Absolute testis and ovary weights in different treatments during breeding season of newborn hamsters (A and B), and founder hamsters (C and D), and founder hamsters in overwintering season (E and F). The newborn hamsters in overwintering season were not analyzed due to their small size. The different colors represent the different treatments. Error bars indicate the standard error of the mean, *: $P < 0.05$, **: $P < 0.01$.

mainly at night. This suggests that thermal stress may have led to an energy-conserving strategy rather than a shift to daytime activity.

The reduction in night-time activity for the HT group may be attributed to cumulative thermal stress from prolonged exposure to warmer temperatures during the day, leading to an energy-conserving reduction in nocturnal activity. However, while HT hamsters showed more daytime activity than LT hamsters, overall activity remained lower, indicating a general reduction in activity rather than a complete shift to diurnal behavior. Both diurnal and nocturnal activities were similarly affected by thermal stress, resulting in decreased overall activity levels (Telemeco et al. 2017). While our hypothesis is partially supported by the observed reduction in nocturnal activity (Fuller et al. 2010). This indicates that the hamsters' behavioral response to temperature increases may be driven by a need to conserve energy or avoid additional stress (Williams et al. 2017).

The absence of such significant changes during the breeding season may reflect seasonal differences in behavioral and physiological priorities. During the breeding season, energy demands are primarily focused on reproduction, with increased metabolic rates and resource allocation to reproductive efforts that may limit the ability to adjust activity timing in response to thermal stress (Trebatická et al. 2007). However, despite ongoing reproduction during the overwintering season and larger gonad weights in both males and females, energy conservation becomes more critical during this time, making hamsters more sensitive to temperature-induced changes in activity (Guiden and Orrock 2020). This seasonal shift in priorities may explain the observed reduction in nocturnal activity during warmer winters, while reproductive constraints during the breeding season may limit behavioral adjustments.

Rodents are known to adapt to rising temperatures by digging deeper burrows, as observed in laboratory environments

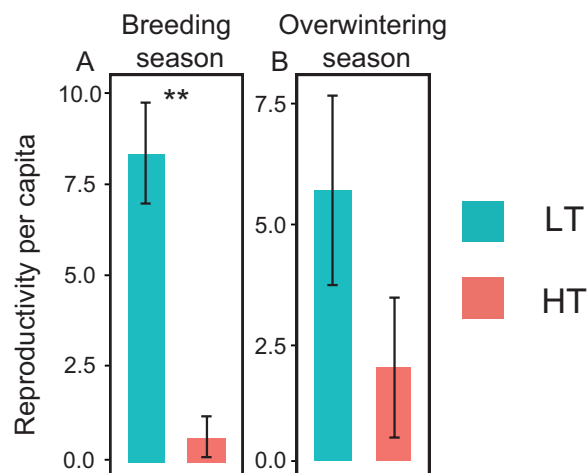


Figure 5. The number of newborns per female founder hamster (per capita reproduction) in different prolonged temperature treatments in the breeding season (A) and the overwintering season (B). The different colors represent the different treatments. Error bars indicate the standard error of the mean, *: $P < 0.05$, **: $P < 0.01$.

(Beltran et al. 2021), and our study supports this observation, finding that burrow depth was significantly greater in the HT group during the breeding season, aligning with our predictions. While we did not measure burrow depth during the overwintering season, previous studies have documented that climate warming can impose heat stress on rodents, prompting such behavioral adaptations (Verzuh et al. 2021). Burrows serve as a thermal refuge for species that predominantly live above ground, helping them avoid high temperatures (Pike and Mitchell 2013; Moore et al. 2018). Deeper burrows in the HT group had similar environmental conditions to those in the LT group. Therefore, to achieve the same cooling effect, hamsters in the HT group needed to dig deeper

(Randall and Thiessen 1980; Bennett et al. 1984; Luna and Antinuchi 2007).

Effect of prolonged temperature increases on physiological and morphological traits

We found that the relative growth rates between the LT and HT groups of founder and newborn hamsters did not differ significantly in either season. This result is consistent with previous studies (Yamauchi et al. 1983), which also observed no significant impact of temperature increases on growth rates. One possible explanation is that an adequate food supply may offset the negative effects of prolonged temperature increases, resulting in no significant difference in relative growth rate. Therefore, while climate warming can influence growth rates in some species, in our study, food availability likely played a key role in preventing such effects from being observed.

Our findings revealed no significant differences in body temperature by sex or time in newborn hamsters from the LT group, suggesting a stable thermal response under these conditions with limited variation due to sex or temporal factors. In contrast, body temperature in founder hamsters significantly declined over time, potentially indicating gradual thermal acclimation or metabolic adjustment. However, no significant effects were observed by treatment or sex, challenging our expectation that LT and HT groups would exhibit divergent thermal responses. This unexpected outcome suggests that founder hamsters may possess adaptive mechanisms that mitigate short-term thermal changes. The decline in body temperature observed in founder hamsters may indicate gradual thermal acclimation or metabolic adjustment. If this trend were solely driven by seasonal cooling, we would expect a similar effect in newborns. However, newborns did not exhibit this pattern, suggesting that additional factors may be involved. One possibility is age-related differences in thermoregulatory capacity, as founders, having undergone prolonged environmental exposure, may possess greater physiological flexibility to adjust body temperature over time. In addition, maternal effects and developmental constraints in newborns could limit their ability to exhibit similar responses. While seasonal cooling may still contribute to this trend, its effects appear to be modulated by age and physiological differences, warranting further investigation.

Contrary to our initial prediction that elevated temperatures would reduce absolute testicular weight during the breeding season and increase it during the overwintering season, we only found that prolonged temperature increases led to an increase in testicle weight in male founder hamsters during the overwintering season. Previous studies on other species, such as deer mice (*Peromyscus maniculatus*), have shown that experimental warming (23 °C vs. 5 °C) leads to a reduction in the mass of most visceral organs (Rezende et al. 2009). However, the observed increase in testicular weight suggests a different adaptive response, indicating that elevated temperatures could drive specific physiological adaptations aimed at enhancing reproductive function. This increase may not indicate a compensatory response to physiological stress; rather, it could be an unintended consequence of heat exposure on reproductive organ development, potentially associated with enhanced spermatogenesis or hormone production. However, females exhibited a reduction in ovarian size, which may indicate a trade-off between thermal tolerance and reproductive investment. Given that female reproductive capacity is often

the primary driver of population growth, this decline in ovarian size could have significant implications for reproductive output and population dynamics.

Effect of prolonged temperature increases on fitness

Despite increased testicular weights in male founder hamsters under elevated temperatures, heat stress may still negatively affect sperm quality by causing structural abnormalities, reducing motility, and impairing fertilization capacity (Yaeram et al. 2006). Moreover, female reproductive investment declined under heat stress, as indicated by reduced ovarian size. Since female reproductive capacity is often the primary determinant of offspring production, this decline could contribute significantly to the observed reduction in offspring number and per capita reproductive output during the breeding season (Figure 4D, E; Supplementary Figures S12 and S13). Previous studies have shown that high temperatures reduce offspring numbers in golden hamsters under laboratory conditions (Ohrnberger et al. 2018), which may be due to a combination of impaired sperm quality, abnormal maternal behavior, or decreased offspring viability due to heat stress (Hearnshaw and Wodzicka-Tomaszewska 1973).

In addition to observing a reduced number of newborn hamsters and lower reproductivity per capita, our study also highlighted how elevated temperatures can affect the timing of reproductive events. Specifically, the first capture of newborn individuals during the breeding season occurred significantly earlier in the LT group compared to the HT group, with a difference of approximately 38 days. This suggests that elevated temperatures in the HT group might delay the onset of reproductive activities or the development of offspring. However, it remains unclear whether this delay reflects a direct response to prolonged thermal stress or a byproduct of disrupted reproductive processes under elevated temperatures. One possible explanation for this finding is that lower temperatures in the LT group provide a more favorable environment for breeding and early development, allowing newborns to be captured sooner. Although both groups reproduced within the normal seasonal timeframe, the higher temperatures experienced by the HT group may have extended the duration of gestation or delayed the initiation of reproductive activities. This delay could reflect a subtle disruption of reproductive timing under heat stress rather than an abnormal shift, suggesting that elevated temperatures can moderately affect the pace of reproductive processes without pushing them outside biologically viable limits. Prolonged exposure to heat has been shown to impact reproductive hormones and reduce the overall rate of reproductive success, which might explain the delayed appearance of newborns in the HT group (Hannan et al. 2024). In addition, the earlier emergence of newborns in the LT group could reflect an adaptive strategy to optimize reproductive timing under cooler conditions, where thermal stress is less pronounced. This suggests that temperature plays a critical role not only in determining reproductive success but also in shaping the timing of key reproductive events, with potential implications for population dynamics and species fitness in response to climate change. These findings underscore the complexity of physiological adaptations to climate change.

While heat stress generally reduces organ size, male founder hamsters exhibited increased testicular weight, contrary to our hypothesis. This finding highlights the need for further

investigation into how reproductive organs respond to thermal stress, particularly in fluctuating environments.

Temperature not only affects reproductive success but also influences survival. For example, temperature inversely affects moose (*Alces alces*) survival in northeastern Minnesota, potentially amplifying cumulative survival effects (Lenarz et al. 2009). Consistent with findings in large-bodied mammals, we observed no significant differences in survival rates for both founder and newborn hamsters between treatment groups (see Supplementary Tables S6–S8 and S15), although numerical differences were present. However, these differences may have been influenced by the constant availability of food in the enclosures, which could have alleviated some of the impacts of temperature stress on survival, potentially mitigating higher mortality rates. This was also associated with lower population growth. While these differences were not statistically significant, they underscore the need for further investigation into species-specific thermal responses, particularly concerning reproduction and survival in fluctuating environments. Climate warming may limit the distribution and availability of thermally suitable habitats at both regional and landscape scales (Davies et al. 2006). In our semi-natural enclosures, the greater long-tailed hamsters had limited options to escape the prolonged temperature increases, as food was always available, and there were no predators present, other than digging deeper burrows. Although our study focused on reproduction and survival separately, the observed reduction in reproductive success may impact population persistence, as fewer offspring could limit recruitment in subsequent generations. A smaller population size may, in turn, reduce genetic diversity and resilience to environmental stressors, which could influence survival. In addition, increased mortality could further constrain reproduction by reducing the number of breeding individuals, creating a cyclical effect. These potential feedback loops highlight the need for further research to assess the long-term effects of prolonged temperature increases on population viability.

Limitations of this study

In our study, to maintain a consistent founder population size and ensure a sufficiently large sample, we replaced dead individuals with new ones during the initial 4 weeks of the experiment. While these replacements did not undergo the same temperature treatments as the original founders, additional analyses showed no significant effect of replacement status on most measured variables, including activity, growth rate, body temperature, organ weights, and survival, except for a minor difference in body temperature during the breeding season, which did not affect the overall conclusions. Nonetheless, future studies should consider tracking original and replacement animals separately to ensure robustness. In addition, the limited enclosure space, due to the expense of constructing temperature simulation infrastructure, constrained population size, and may have increased result uncertainty. Larger greenhouse infrastructures would improve future studies on the prolonged effects of temperature increases on small mammals.

Implications of this study

Currently, the earth is experiencing accelerated climate warming which has caused range contraction or local extinction or disappearance of many species. Our findings underscore

the critical need to address the adverse effects of heat stress on wildlife populations as climate warming accelerates. The observed declines in reproduction and population growth in species like the greater-long-tailed hamsters may provide experimental evidence that climate warming may be attributed to southern boundary contract of the species (Zhang et al. 2023). Our results highlight the urgent need for wildlife management strategies that incorporate climate resilience. Future conservation efforts must not only address the direct impacts of temperature increases but also consider how these changes interact with ecological and physiological factors to safeguard biodiversity and ecosystem health. We recommend that conservation initiatives prioritize habitat preservation in cooler areas, enhance habitat connectivity to facilitate movement towards more suitable climates, and support long-term monitoring of vulnerable populations to track adaptive responses.

Authors' Contributions

Z.B.Z. and X.R.W. designed and conceived the studies. D.Z., X.M.X., Y.N.G., and X.R.W. conducted the experiments. L.L.H. contributed to data collection. D.Z. and X.R.W. analyzed the data, prepared the figures, and drafted the manuscript. Z.B.Z., X.R.W., and D.Z. revised the manuscript. Z.B.Z. and X.R.W. acquired funding and supervised the project. All authors contributed critically to the drafts and gave final approval for publication.

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Data Availability

The data reported in this paper are available in a supplementary information file.

Ethics Statement

The study conforms to the legal requirements of China in which it was carried out, including those relating to conservation and welfare and to the journal's policy on these matters. All animal handling or raising was conducted in line with the guidelines of the Animal Care and Use Committee (ACUC) of the Institute of Zoology, Chinese Academy of Sciences. D.Z., X.R.W., X.M.X., and Y.N.G. owned the diploma of handling laboratory animals issued by ACUC (1120102200102, 1121111000109, 1120102200100, 1121111000107).

Conflict of Interest

The authors declare that they have no competing interests.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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