

ORIGINAL ARTICLE

Thermal performance drifts between the egg parasitoid *Telenomus remus* and the fall armyworm may threaten the efficacy of biological control under climate change

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Abstract

The fall armyworm, *Spodoptera frugiperda* J.E. Smith, is a significant global agricultural pest known for its rapid invasion and devastating impact on crops. While pesticides may be effective for controlling the pest in the short-term, they cause several socio-economic and ecological costs that highlight the need for more sustainable management strategies. *Telenomus remus* (Nixon) is a promising egg parasitoid for its biological control. For the parasitoid to provide effective ecosystem services, it should be able to survive and coexist within the same ecological niches as its host. However, there is limited information regarding the potential responses of *T. remus* to thermal changes. In the context of the changing climate environments, it is key to understand the parasitoid's overall environmental fitness in relation to its host. We investigated the effects of short-term (2 h) and long-term (6 h) acclimation pretreatment of *T. remus* adults and *S. frugiperda* eggs to high and low temperatures (18°C and 32°C, respectively) in comparison with the control (28°C). *Telenomus remus* thermal fitness (critical thermal maxima [CT_{max}], heat knockdown time and critical thermal minima [CT_{min}]), parasitism rates, and adult emergence were determined. Pretreated *S. frugiperda* eggs were assessed for hatchability under the control conditions. Acclimation at low (18°C) and high (32°C) temperatures significantly reduced and increased heat tolerance, respectively. Both temperatures, however, reduced cold tolerance. The parasitoid thermal tolerance polygons following acclimation pretreatment, showed significant heat- but not cold-tolerance gains. Fall armyworm eggs short-term acclimated to 32°C had significantly higher ($p < 0.05$) but comparable hatchability to the control treatment. Similarly, parasitism and adult emergence rates were significantly lower ($p < 0.001$) following long-term acclimation of host eggs and the parasitoid to 32°C. These findings suggest that high temperatures may decouple the *T. remus*-fall armyworm ecological relationship, threatening its success in warming regions. The findings provide valuable insights into the potential environmental resilience and suitability of *T. remus* as a biological control agent across different climates or geographies.

KEYWORDS

acclimation, ecosystem services, host–parasitoid interactions, natural enemies, parasitism, pest management, phenotypic plasticity, *Spodoptera frugiperda*, thermal tolerance

INTRODUCTION

Insects' sensitivity to thermal fluctuations is high, due to their ectothermic nature, and can influence survival and subsequent population dynamics (Colinet et al., 2015; Hance et al., 2007). For interacting host–natural enemy arthropod species, predicting the effects of temperature is important for pest management practitioners as it helps in designing efficacious sustainable strategies for controlling pest species (Machekano et al., 2018). The effects of increasing temperatures with climate change on biological processes may not be unidirectional, making net consequences for climate change highly ambivalent for interacting species, including host–natural enemy interactions (Chidawanyika et al., 2019). Indeed, the success or failure of biological control agents is, thus, dependent on matches or mismatches in their thermal preferences, tolerance and sync in host–natural enemy phenologies. The effects of climate change are increasingly being noticed (IPCC, 2023; Stillman, 2019) with predictions pointing toward more extreme temperatures (Witze, 2024). The consequences of these extreme temperatures are dreadful, especially to biodiversity, ecosystem integrity, function and the provision of insect ecosystem services (Harvey et al., 2023). Insects are essential components of ecosystems, with many of them being natural enemies to many problematic pest species (Hance et al., 2007). As such, climate change presents significant threats to the survival, and success of many natural enemies in biological control programs through direct and indirect effects (Chidawanyika et al., 2019; Nyamukondiwa et al., 2022). Temperature increases indirectly disrupt the synchronous ecological balance among interacting insect species by differentially influencing their biogeography as a result of differences in individual species' thermal preferences and fitness (Chidawanyika et al., 2019; Moore et al., 2021). As a result, the spatial and temporal distribution and synchronization of parasitoids and their hosts face disruptions leading to possible phenological decoupling that increases pest outbreaks (Hance et al., 2007; Tougeron et al., 2020). Although host insect development initially responds positively to increasing temperatures through accelerated development, the success of most parasitoids may be limited under high-temperature environments (Bueno et al., 2008; Kingsolver et al., 2024). Higher trophic levels are expected to be more affected by climate change than their lower trophic-level hosts (Furlong & Zalucki, 2017; Hance et al., 2007; Spahn & Lill, 2022). However, the exact effect of elevated temperatures on parasitoids and their hosts is dependent on species-specific thermal requirements and tolerances (Moore et al., 2021). Heat stress also affects natural enemies' efficacy through their direct effects on developmental time, sex ratios, parasitism windows, and adult longevity (Nguyen et al., 2013; Pomari et al., 2013). For successful ecosystem services provision by natural enemies, they must, thus, be able to adjust their thermal preferences to match those of their hosts (Tougeron et al., 2020). However, several reports suggest likely mismatches in interacting species under temperature stress (Segoli et al., 2024; Tougeron et al., 2020). As such, an

understanding of host–natural enemy specific interactions under changing climate environments can help crop protection scientists and policymakers in designing efficacious pest management programs.

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) is a significant global agricultural pest known for its rapid invasion and devastating impact on crops, particularly maize (Kenis et al., 2023; Mlambo et al., 2024; Timilsena et al., 2022). The pest originated from South and Central America and has invaded Africa, Asia, Oceania, and Europe in the recent past (Cean et al., 2024; Kenis et al., 2023). In Africa, fall armyworm has invaded more than 50 of the 54 countries on the continent and is responsible for maize field losses ranging from 9% to 67% (De Groote et al., 2020; Kassie et al., 2020; Mlambo et al., 2024). Its highly polyphagous and invasive nature has highlighted the need for the development and deployment of sustainable integrated pest management (IPM) options (Kenis et al., 2023). Among the potential IPM techniques, biological control is a strong component of choice due to the global push to reduce over-reliance on synthetic pesticides, which have largely been reported ineffective and environmentally unsustainable (Kenis et al., 2023; Van Den Berg & du Plessis, 2022; Zhang et al., 2021). In addition, biological control is preferable due to advances in insect mass-rearing techniques, environmental and consumer safety advantages, reduced risks of resistance development, sustainability, and cost-effectiveness (Holmes et al., 2016; Kumari et al., 2022). A large number of hymenopteran and dipteran parasitoids are known to attack fall armyworm both in the Americas and Africa (Caniço et al., 2020; Hay-Roe et al., 2016; Kenis et al., 2023), with the majority (~80 species) being found in South America (de Freitas et al., 2019), including *Telenomus remus* (Nixon) (Hymenoptera: Scelionidae). Egg parasitoids that belong to the genera *Telenomus* and *Trichogramma* show great potential (Sithanantham et al., 2001), with the two parasitoid genera showing efficacy of ~64%–100% and up to ~78% under laboratory and field conditions, respectively (Agboyi et al., 2021; Laminou et al., 2020). However, the efficacy of these biological control agents is affected by several environmental factors, chiefly prevailing temperatures and other context-specific biotic interactions (Abd-Elgawad & Askary, 2020; Seehausen et al., 2021). Understanding the effects of environmental factors on natural enemies' fitness is key in explaining their functionality under changing environments and thus determining their suitability in divergent environments.

The use of egg parasitoids for fall armyworm biological control is a relatively more efficient option because they impede egg hatching, hence prevent the development of the economically damaging larval stage (Grande et al., 2021). In addition, egg parasitoids can be reared in large numbers in very small spaces and are effective against a large number of pests (Bueno et al., 2023; Parra & Junior, 2019). *Telenomus remus* is an oligophagous egg parasitoid of lepidopteran pests, primarily of the *Spodoptera* genus (Bueno et al., 2008; Cave, 2000; Kenis

et al., 2019; Wengrat et al., 2021). It is one of the most cosmopolitan and abundant of all fall armyworm egg parasitoids globally (Grande et al., 2021; Navik et al., 2021) with notable field tolerance to most pesticides commonly used in agro-ecosystems (Carmo et al., 2010; Kenis et al., 2023; Mani & Krishnamoorthy, 1986), making it a favorable biological control option in pesticide-laden agro-ecosystems. However, how the distribution and parasitism efficacy of the parasitoid may be shaped by habitat environmental complexities, particularly temperature, is unknown.

Several studies have been conducted on thermal requirements and effects of environmental variables, such as temperature, relative humidity, and photoperiods on *T. remus* development and biological control efficacy as a parasitoid (Bueno et al., 2008; Pomari et al., 2012, 2013). Similarly, much research efforts have targeted fall armyworm climate responses (Chen et al., 2022; Huang et al., 2021; Mbande, Mutamiswa, & Chidawanyika, 2023; Mbande, Mutamiswa, Nyamukondiwa, & Chidawanyika, 2023; Segaiso et al., 2022) and different hosts/diets (Jin et al., 2020; Moraes et al., 2020; Mubayiwa et al., 2023). However, most of this work investigated the pest host or natural enemies separately with no comparative host and natural enemy responses for drawing inferences on the potential influence on biological control. There is, thus, inadequate empirical evidence regarding the possible responses of parasitoids to climate stress, particularly when both parasitoids and hosts are exposed to the same stress simultaneously. Here, we sought to investigate the potential effects of acclimation pretreatment on the physiological limits to activity (plastic responses) of *T. remus* compared with the target life stage of its host. The main objective of the study was to determine the effects of short-term and long-term acclimation pretreatment of *T. remus* adults and fall armyworm eggs to high and low acclimation temperatures on their thermal tolerance limits and other ecological fitness metrics, such as egg hatchability and parasitism efficacy. We hypothesized that long-term acclimation pretreatment to high and low temperatures confers beneficial effects on *T. remus* thermal fitness, and as such improves parasitoid survival, while having deleterious effects on *S. frugiperda* egg hatchability. The results of this study will provide insights on whether *T. remus* will be able to share the same ecological niches with fall armyworm in diverse global agroecosystems as climate change ensues.

MATERIALS AND METHODS

Telenomus remus and *Spodoptera frugiperda* rearing

The *T. remus* population used in these experiments was imported from the National Agricultural Research Organization (NARO) in Uganda (import permit

number—5361/23; issue date—06/03/2023). The parasitoids were reared on eggs of fall armyworm in the Ecophysiological Entomology Laboratory, Department of Biological Sciences and Biotechnology at Botswana International University of Science and Technology. Three batches of approximately 500 fresh fall armyworm eggs (<24 h old) were loosely stuck on egg cards using paper glue (Zhejiang Changchao Stationery Co., Ltd., Yiwu City, Zhejiang Province, China). Each fall armyworm egg batch was then exposed to ~50 unsexed *T. remus* for 24 h for parasitism. Parasitized eggs were kept in 350 mL 'consol' glass jars covered with netted perforated lids to allow for ventilation. These jars were kept in climate chambers (HPP 260; Memmert GmbH + Co.KG, Germany) set at $28 \pm 1^\circ\text{C}$, $60 \pm 5\%$ r.h. until adult emergence. The emerged *T. remus* adults (≤ 12 h old) used for the experiments were sustained on a 10% sucrose solution artificially dyed with yellow food coloring (Robertsons—Libstar Manufacturing Solutions, Gauteng, South Africa). The fall armyworm colony was a laboratory population established from collections from farmers' fields in Palapye ($22^\circ 28' 38''$ S, $27^\circ 14' 01''$ E), Central District Botswana in 2023, and was constantly mated with wild populations (after every five to six generations) to avoid genetic erosion. The host insects were maintained on an artificial diet based on Tefera (2010), at optimal $28 \pm 1^\circ\text{C}$; $60 \pm 5\%$ r.h. in climate chambers.

Short-term and long-term acclimation pretreatment responses to high and low temperatures

The emerged F_1 *T. remus* adults were separately acclimated to low ($18 \pm 1^\circ\text{C}$) and high ($32 \pm 1^\circ\text{C}$) temperatures for 2 h (short-term acclimation) and 6 h (long-term acclimation), while control insects were kept under the optimal conditions ($28 \pm 1^\circ\text{C}$; $60 \pm 5\%$ r.h.) until experimentation. Following acclimation, the parasitoids were returned to the control environment ($28 \pm 1^\circ\text{C}$; $60 \pm 5\%$ r.h.) for 12 h to allow them to recover before experimentation (van der Merwe et al., 1997). The treated adults were then used to assay critical thermal limits (critical thermal maxima [$CT_{\max}$] and critical thermal minima [$CT_{\min}$]) and heat knockdown time (HKDT) against those reared under control environments. These metrics represent a standardized system of thermal tolerance measurement that is easy to record in the laboratory and are essential proxies determining species' biogeography (Andersen et al., 2015; Terblanche et al., 2007, 2011).

Thermal tolerance metrics

Critical thermal maxima ($CT_{\max}$)

Acclimated and control *T. remus* adults were individually placed in each of the 10 transparent glass organ pipes insulated by a double-jacketed chamber connected to a

programmable water bath containing 1:1 water:propylene glycol (Grant GP200-R4; Grant Instruments, UK). The temperature in the water bath was kept at 28°C for an initial 10 min for equilibration before ramping up. The temperature was ramped up from an optimum temperature of 28°C (Wan et al., 2021) using an ecologically relevant rate of 0.25°C per minute (Nyamukondiwa et al., 2013). A thermocouple connected to a digital thermometer (Fluke 54 series II; Fluke Cooperation, China; accuracy: 0.05°C) was inserted into one of the organ pipes to record the temperature inside the pipes. The experimental procedure was repeated twice to have a total of 20 replicates per treatment. The insects were observed continuously, and CT_{max} was recorded as the upper temperature endpoint at which insects lost coordinated muscle functions or the inability to self-right following gentle prodding using a thermally inert camel hair brush (Bennett & Beiting, 1997; Machekano et al., 2018).

Heat knockdown time

Heat knockdown time assays were conducted following procedures outlined by Weldon et al. (2011). Pretreated and control adult *T. remus* were placed inside 0.65-mL Eppendorf microcentrifuge tubes and placed inside a climate chamber set at 45°C and 65% r.h. until they lost coordination. The heat knockdown temperature was determined by rounding up the temperature from the mean CT_{max} of 44.1°C recorded following acclimation to 32°C in the previous experiments. The time taken by individual test insects to lose their self-righting responses was captured in a video by a camera connected to the climate chamber (HD Covert Network Camera, DS-2CD6412FWD20; Hikvision Digital Technology Co., Ltd., China), and was saved automatically to a linked computer. The HKDT for the individual insects was recorded in minutes.

Critical thermal minima (CT_{min})

Adult *T. remus* from each treatment, including the control group, were individually placed inside the 10 organ pipes of the programmable water bath at the set temperature of 28°C for an initial 10 min (for equilibration) before ramping down the temperatures, similar to the CT_{max} experiments. After equilibration, the temperature was gradually decreased at an ecologically relevant rate of 0.25°C per minute (Nyamukondiwa et al., 2013) until each treatment insect's endpoints were recorded. The temperature inside the organ pipes was recorded as previously mentioned. The temperature at which individual insects lost self-righting abilities, as measured by failure to respond to mild stimuli from prodding, as performed under the CT_{max} experiment, was recorded. This experiment was run twice for each treatment to attain 20 replicates.

Effects of short-term and long-term acclimation pretreatment on fall armyworm egg viability and parasitism

In this experiment, 50 freshly laid fall armyworm eggs (≤ 12 h old) were collected from the laboratory colonies and stuck on egg cards (1 cm $\times$ 2.5 cm). The eggs were then placed inside small vials measuring 2.3 cm in diameter and 7 cm in height. These vials were sealed with perforated lids covered with a fine netted clothing to allow for ventilation. The eggs were pretreated at low ($18 \pm 1^\circ\text{C}$) and high ($32 \pm 1^\circ\text{C}$) temperatures for 2 h (short-term acclimation) and 6 h (long-term acclimation). Subsequently, the eggs were transferred for incubation until hatching at $28 \pm 1^\circ\text{C}$ and $60 \pm 5\%$ r.h. The control treatment consisted of eggs kept at $28 \pm 1^\circ\text{C}$ and $60 \pm 5\%$ r.h. throughout the experiment. The experiment was replicated 20 times per treatment. After hatching, the number of emerged neonates was recorded per vial.

To assess the effects of the host's eggs and parasitoid acclimation on parasitism efficacy, 50 fall armyworm eggs on cards and adult *T. remus* were separately acclimated to both experimental temperatures and durations. The insects were allowed to recover for 12 h at control conditions as above. Following the recovery phase (post acclimation), two *T. remus* (one female and one male) were introduced to each vial containing a single egg card for 48 h under control conditions. On the contrary, control individuals were kept at $28 \pm 1^\circ\text{C}$ and $60 \pm 5\%$ r.h. throughout the experiment. The sexing of parasitoids was based on morphology and especially using antennal length. Female *T. remus* have shorter, club-shaped antenna with 11 segments, whereas males have slender, long, geniculate antenna with 12 segments (Priyanka et al., 2023). Percentage parasitism was calculated as the number of emerged adult *T. remus* plus the number of eggs with unviable pupae of the parasitoid (viewed under a microscope) expressed as a percentage of the total number of eggs on the cards. Percentage parasitoid emergence was calculated as a proportion of the total number of emerged adult parasitoids to the total number of parasitized eggs.

Data analyses

All data were tested for normality and homogeneity assumptions using Shapiro–Wilk and Hartley–Bartlett tests, respectively, in Statistica v.14.0 Software (Statsoft, Inc., Tulsa, Oklahoma, USA). All data met the assumptions; hence, they were subjected to two-way analysis of variance in the same software. Mean separation was done using Fisher's Protected LSD test where significant differences existed. To determine the degree of eurythermicity and temperature-dependent survival tactics (see Eme & Bennett, 2009) of *T. remus*, thermal polygons were constructed following methods by Conte et al. (2023), where regression plots for CT_{max} and CT_{min} were superimposed on the same graph, followed by joining their endpoints at 18 and 32°C to form

a quadrilateral for short-term and long-term acclimation. Horizontal lines were inserted at the lowest CT_{min} and lowest CT_{max} to show the magnitude of thermal tolerance, as well as cold and heat tolerance gains or losses following acclimation. In addition, acclimation temperature was regressed against fall armyworm egg hatchability.

RESULTS

Telenomus remus thermal tolerance

Effects of acclimation pretreatment temperature on heat tolerance

Acclimation temperature significantly influenced heat tolerance of adult *T. remus*, measured as the highest temperature to activity leading to heat stupor or CT_{max} ($F_{2, 94} = 27.14$; $p < 0.001$). Individuals pretreated at 18°C had significantly lower CT_{max} ($41.2 \pm 0.27^\circ\text{C}$) compared with the control treatment ($43.0 \pm 0.58^\circ\text{C}$). On the contrary, parasitoids acclimated at 32°C had significantly higher heat tolerance ($CT_{max} = 44.1 \pm 0.11^\circ\text{C}$) than the control. Similarly, acclimation temperature had significant effects on heat knockdown time (HKDT) of *T. remus* adults ($F_{2, 95} = 27.20$; $p < 0.001$). Individuals acclimated at sub-optimal temperatures had significantly lower HKDT than the control. Parasitoids acclimated at 18°C recorded the least HKDT (16.3 ± 0.59 min), followed by those acclimated at 32°C (21.9 ± 1.01 min), whereas the control individuals took longer to be knocked out by the set lethal temperature (23.7 ± 0.47 min) (Figure 1). Acclimation duration (i.e., short-term vs. long-term acclimation pretreatment) had significant effects on HKDT ($F_{1, 76} = 8.01$; $p < 0.05$) but not CT_{max} . Individuals subjected to long-term acclimation took significantly shorter time to be knocked out at heat coma temperature (HKDT = 17.7 ± 0.50 min) than those short-term acclimated (HKDT = 20.4 ± 0.85 min), and these effects were significant at the high-temperature (32°C) acclimation. In addition, there was an overall significant positive correlation between acclimation temperature and heat tolerance (CT_{max} [$r = 0.64$; $p < 0.001$] and HKDT [$r = 0.49$; $p < 0.001$]).

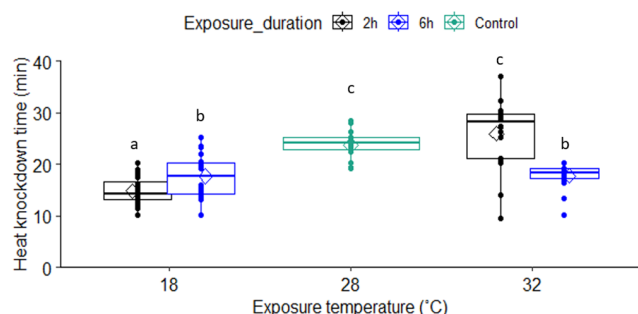


FIGURE 1 Effects of temperature and acclimation pretreatment duration on *Telenomus remus* heat knockdown time (HKDT). Points represent mean $\pm$ SEM ($n = 20$). Plots that do not share the same lowercase letter are significantly different from one another based on Fisher's Protected LSD test at 95% confidence interval.

Acclimation temperature and duration had significant interactive effects on HKDT ($F_{1, 76} = 33.37$; $p < 0.001$), but not CT_{max} . Parasitoid acclimation at 18°C (regardless of duration) and 32°C (long term) significantly reduced HKDT (Figure 1). Although acclimation at low temperature reduced HKDT in relation to the control, short-term acclimated *T. remus* recorded significantly lower heat tolerance than those acclimated at the same temperature for the long term (14.9 ± 0.60 min compared with 17.7 ± 0.93 min) ($F_{1, 76} = 8.01$; $p < 0.05$). On the contrary, *T. remus* pretreated at 32°C for the long term had significantly lower HKDT (17.8 ± 0.54 min) compared with the control ($p < 0.05$), whereas no significant differences existed between the control and those long-term acclimated at the high temperature (Figure 1).

Effects of high- and low-temperature acclimation at different durations on *T. remus* critical thermal minima

Acclimation temperature had significant effects on adult *T. remus* cold tolerance, defined as the lowest temperature to activity measured as CT_{min} ($F_{2, 114} = 4.95$; $p < 0.05$). *Telenomus remus* acclimated at 18 and 32°C had lower cold tolerance ($18^\circ\text{C} = 9.0 \pm 0.39^\circ\text{C}$; and 32°C [long term] = $8.2 \pm 0.41^\circ\text{C}$) than control individuals ($CT_{min} = 7.5 \pm 0.28^\circ\text{C}$) (Figure 2). Duration of acclimation (2 or 6 h) did not have an influence on *T. remus* CT_{min} , but its interactions with temperature were significant ($F_{1, 76} = 12.76$; $p < 0.001$) (Figure 2). Individuals that were acclimated for the short term at 32°C had the highest cold tolerance (lowest CT_{min}) ($6.9 \pm 0.41^\circ\text{C}$) compared with all treatments but were not significantly different from the control group. There were no significant differences between individuals that were acclimated either for the short term or the long term at 18°C ($9.6 \pm 0.42^\circ\text{C}$ and $8.5 \pm 0.63^\circ\text{C}$, respectively) and those acclimated for the long term at 32°C ($9.5 \pm 0.57^\circ\text{C}$). Moreover, correlation analyses showed a significant negative relationship between acclimation temperature and CT_{min} following long-term pretreatment acclimation, whereas no relationship existed following short-term acclimation.

Telenomus remus thermal polygons

Telenomus remus long-term acclimated to high and low temperatures had higher thermal tolerance over short-term acclimated individuals. Parasitoids acclimated for 2 h had a total thermal tolerance polygon measuring 504.8°C^2 , while those acclimated for 6 h had 509.7°C^2 (Figure 3A,B, respectively). Intrinsic tolerance constituted 92.2% (465.2°C^2) and 92.0% (468.7°C^2) of the total tolerance polygon areas following short-term and chronic acclimation, respectively. The lower acquired tolerance was not significant in both instances but was significantly and negatively correlated to acclimation temperature following short-term acclimation (Figure 3A). On the contrary, the upper acquired thermal tolerance zones were significant and almost similar in both instances, measuring

21.1 and 22.7°C², constituting 4.2% and 4.5%, for short-term and long-term acclimated individuals, respectively.

Acclimation temperature effects on *S. frugiperda* egg hatchability and parasitism efficacy

There were significant differences in fall armyworm egg viability tested as hatchability ($F_{4, 95} = 8.82$, $p < 0.001$) as

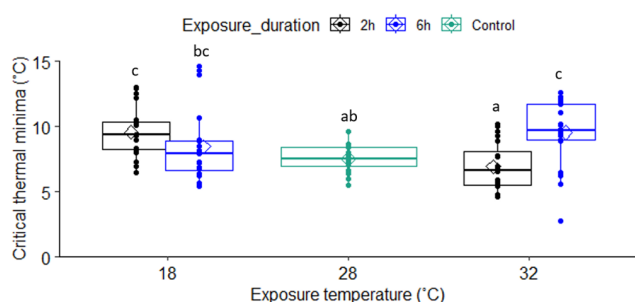


FIGURE 2 Effects of temperature and acclimation pretreatment duration on *Telenomus remus* critical thermal minima (CT_{min}). Points represent mean $\pm$ SEM ($n = 20$). Plots that does not share the same lowercase letter are significantly different from one another based on Fishers Protected LSD test at 95% confidence interval.

shown by differences in hatching percentage. Eggs acclimated for the short term to 32°C recorded a significantly higher hatching percentage (74.0%), but were not statistically different from the control (74.5%). On the contrary, eggs pretreated for the long term at both 18 and 32°C (54%–58%) had significantly lower hatchability than both the control and those short-term acclimated at 32°C (Figure 4).

Temperature and acclimation duration had a significant influence on *T. remus* parasitism rates ($F_{4, 95} = 49.51$; $p < 0.001$) and adult emergence ($F_{5, 95} = 15.26$; $p < 0.001$). Parasitism rates were significantly lower in individuals pretreated at 32°C, with individuals acclimated to this temperature for long-term recording the least parasitism rates (48.9%), followed by those short-term pretreated at the same temperature (67.7%) (Figure 5A). On the contrary, parasitism rates were significantly higher in individuals acclimated at low temperature (18°C, regardless of acclimation duration). These were comparable to the control (74.8–75.7) (Figure 5A). Furthermore, long-term pretreatment at 32°C significantly reduced parasitoid emergence (81.2%) ($F_{1, 76} = 12.39$; $p < 0.01$), followed by long-term acclimation at 18°C. In addition, no significant differences were recorded between the control treatment and those exposed for a short term to 18 and 32°C (Figure 5B).

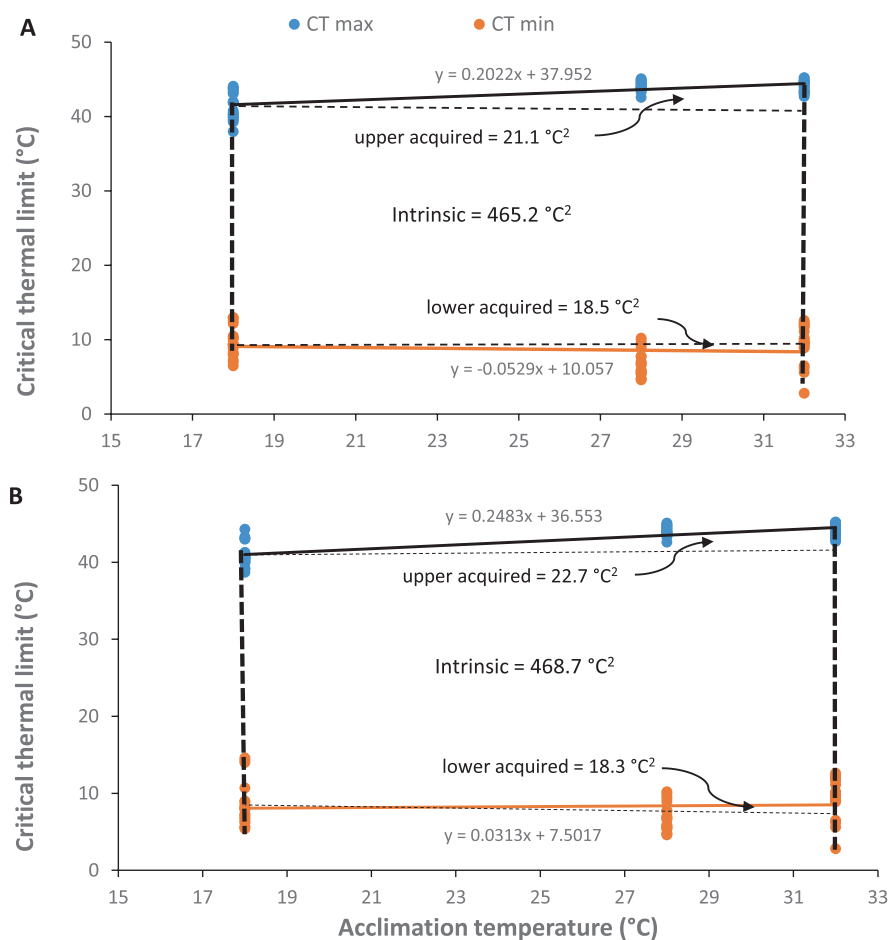


FIGURE 3 *Telenomus remus* thermal polygons following: (A) short-term and (B) long-term acclimation pretreatment. CT_{max} , critical thermal maxima; CT_{min} , critical thermal minima. Measured in °C², thermal polygons show the degree of eurythermicity of a given species as intrinsic (tolerance zone independent of acclimation) and upper and lower zones (acclimation-dependent gains or losses in tolerance).

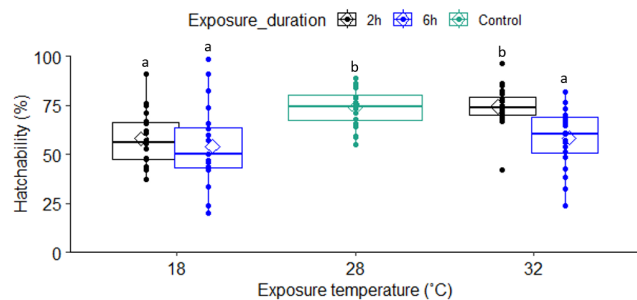


FIGURE 4 Effects of temperature and acclimation pretreatment duration on fall armyworm egg hatching percentage (mean $\pm$ SEM) ($n = 20$). Plots that do not share the same lowercase letter are significantly different from one another based on Fishers Protected LSD test at 95% confidence interval.

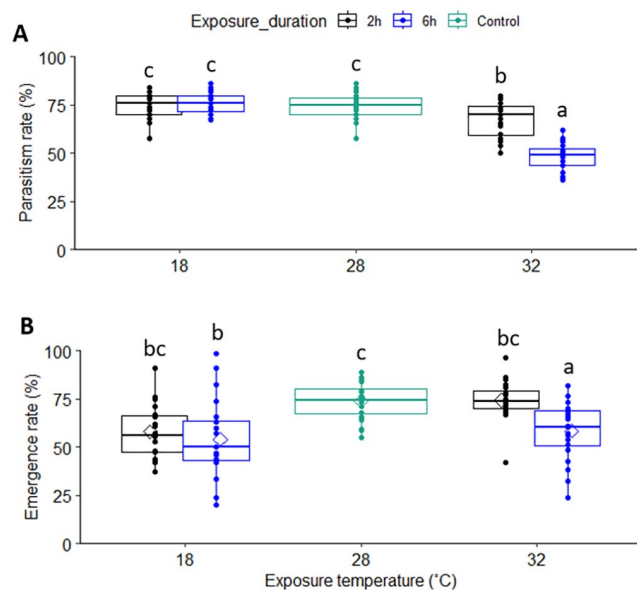


FIGURE 5 Effects of temperature and acclimation pretreatment on *Telenomus remus* parasitism (A) and emergence rates (B) (mean $\pm$ SEM) ($n = 20$). Plots that do not share the same lowercase letter are significantly different from one another based on Fishers Protected LSD test at 95% confidence interval.

DISCUSSION

We set out to determine the comparative responses to thermal stress by *T. remus* and fall armyworm as a proxy to trophic level co-evolution and, thus, potential for geographical co-occurrence. The parasitoids acclimated to high temperature (32°C, both short-term and long-term) recorded higher CT_{max} than those acclimated to low temperature (18°C). These results are in line with the Borget beneficial acclimation theory, which states that when insects are acclimated to novel environments, they experience reversible inter-generational physiological adjustments that aid their survival in similar conditions (Flynn et al., 2015; Marais & Chown, 2008; Wilson & Franklin, 2002). Possible causes for the improved heat tolerance of *T. remus* exposed to 32°C may be reduced metabolic

rates, which result in reduced rates of respiratory water loss, as was the case in findings by Lann et al. (2011) in two related hymenopteran parasitoid species. When poikilothermic organisms are exposed to extremely high temperatures, they respond by initiating compensatory physiological adaptations in the short-term (Hochachka & Somero, 1971). These include alterations in enzyme activities through the actions of inhibitors or activators, modification of intracellular pH, changes in serum and tissue ion concentrations, as well as hormonal and cuticular permeability changes (Neven, 2000; Sheikh et al., 2017; Somero & Hochachka, 1971). In addition, insects may up-regulate heat shock proteins, whose expression may have been present, albeit low, under optimum temperatures (Hochachka & Somero, 1971; King & Macrae, 2015; Li et al., 2009; Sheikh et al., 2017). On the contrary, the reduction of the parasitoid's HKDT following long-term pretreatment at high temperature could be a result of prolonged stress, which could have resulted in cumulative cell damage (Jørgensen et al., 2021). These findings suggest that the survival of *T. remus* may be threatened under global warming due to climate change, as record-high temperatures continue to be experienced.

Similar to fall armyworm, the optimum developmental temperature for *T. remus* is 28°C. The parasitoid had a basal CT_{max} and HKDT of $43.0 \pm 0.58^\circ\text{C}$ and 23.72 ± 0.47 min, respectively. These tolerance levels are generally comparable to those of fall armyworm adults ($\sim 45^\circ\text{C}$) (Mbande, Mutamiswa, & Chidawanyika, 2023), but are lower than those found in other studies on the fourth/fifth instar larvae (Segaiso et al., 2022). Although these basal tolerance levels indicate a high potential for co-existence between the parasitoid and its host, the generally low heat tolerance of the adult parasitoid compared with the fall armyworm larval stages indicates risks of the parasitoid's population decimation under high-temperature environments (Stillman, 2019). This, therefore, may offset the balance between the parasitoid and its host under global change, and in austral arid and semi-arid summers, where temperatures often exceed the recorded *T. remus* CT_{max} values (Davies-Reddy & Vincent, 2017; Nogrady, 2023; Witze, 2024). Tolerance to high temperatures is the main determinant of individual species survival in warming environments (Colinet et al., 2015; Nyamukondiwa et al., 2022). The effects of *T. remus* acclimation to high and low temperatures on other life-history traits need to be ascertained for a wide scale understanding of the implications. Our current results imply that the parasitoid has low activity thermal limits in relation to its host and thus may not be active under projected sub-optimal thermal environments typical in some parts of Africa, and in future in the context of projected climate change (Davies-Reddy & Vincent, 2017; Nogrady, 2023; Witze, 2024) where fall armyworm and its economic effects are most profound (Kenis et al., 2023). The possibility of the parasitoid's inability to perform its ecosystem services all year round in most parts of Africa may be important for crop protection practitioners in modeling pest management strategies.

Record-shattering high temperatures have been recorded during recent summers globally, with projections pointing toward the occurrence of more frequent and severe heat waves (Davies-Reddy & Vincent, 2017; Witze, 2024). In our experiment, the thermal tolerance polygons showed heat tolerance gains following an increase in pretreatment temperatures. These results concur with CT_{max} results previously discussed and are in line with findings by Scott et al. (1997) where prior exposure of *Trichogramma carvacea* to high temperatures had survival benefits under high-temperature environments. These findings further provide scope for thermally preconditioning *T. remus* in mass-rearing programs to mitigate poor field performance via **phenotypic plasticity**.

Our results also showed a basal CT_{min} of 7.5°C for *T. remus*. This low cold tolerance level makes it difficult for the parasitoid to be active and indeed survive chilling winters and unpredictable cold waves (common in mid-latitude areas and in the generally warmer regions of Africa) under climate change (Faranda et al., 2022; Jalili et al., 2010). In addition, our results indicating significantly higher cold tolerance (lowest CT_{min}) in parasitoids acclimated to 32°C for the short-term (comparable to control), whereas those acclimated to 18°C (short-term and long-term) and 32°C (long-term) recorded significantly lower cold tolerance, suggest that pre-exposure to sub-optimal temperatures in nature may come at cold tolerance fitness costs for *T. remus*. An improvement in cold tolerance following short-term acclimation to high temperature may be a result of overlap in mechanisms between heat and cold tolerance (Hoffmann, 2010; Hoffmann et al., 2005). This overlap may not have manifested for individuals acclimated for the long-term owing to the prolonged stressful sub-optimal environments that may have caused cumulative damage (Jørgensen et al., 2021). A general negative correlation between CT_{min} and exposure temperature following *T. remus* long-term pretreatment to test temperatures, whereas no relationship existed following short-term pretreatment, can be attributed to cross-protection mechanisms. This may be through the actions of variant biochemical molecules/enzymes that also work in compensatory mechanisms during heat stress (Hochachka & Somero, 1971). *Telenomus remus* is usually stored under low-temperature environments (10±1°C) to extend its shelf-life and provide opportunities to accumulate sufficient numbers before their eventual release into the targeted environments (Rathee & Ram, 2018; Tefera et al., 2019). Our overall thermal tolerance polygons showed insignificant cold tolerance changes following short-term and long-term acclimation pretreatment, meaning that cold storage of the parasitoids may not negatively influence their ecological performance. This suggests that short-term cold storage of *T. remus* may not affect its survival. However, our study tested adults and did not use other parasitoid developmental stages for more accurate inferences, necessitating more studies in this area.

Our egg viability experiments showed that basal egg hatchability for host fall armyworm was 77±3.74%. This

hatchability is within a natural range in the wild and is comparable to that recorded on two-leaf stage maize (78.4%), but is lower than that recorded on four- to five-leaf stage old maize plants (93.5%) (He et al., 2021). Overall, fall armyworm egg viability was lower at sub-optimal temperatures of 18°C (56.2±2.73%) and 32°C (only for chronic acclimation) (58.5±3.45%) than at control temperature (28°C). The low viability at high sub-optimal temperatures was expected because heat causes developmental impairment through dehydration and desiccation, and protein denaturation and immobilization of some crucial proteins (Hochachka & Somero, 1971; Ma et al., 2021; Mbande, Mutamiswa, Nyamukondiwa, & Chidawanyika, 2023). However, the actual cause of low egg hatchability following acclimation at high temperatures was not ascertained in our study and may need further interrogation. These findings are similar to those of Ali et al. (1990), Mbande, Mutamiswa, Nyamukondiwa, and Chidawanyika (2023), and Savadatti and Adoni (2023) who also recorded low fall armyworm egg hatching success at elevated temperatures (with maximum of 32°C). On the contrary, sub-optimal low temperatures cause impaired embryonic development through enzyme inactivation, arrested respiration and protein synthesis, compromised membrane integrity and altered ionic balances of cells, and unavailability of some key nutrients in non-diapausing species (Higaki & Ando, 2002; Howe, 1967; Neven, 2000). Similar to heat stress, cold stress also causes desiccation through dehydration and osmotic stress at the cellular level in insects (Sinclair et al., 2013).

The least parasitism rates by *T. remus*, which underwent long-term pretreatment at 32°C, followed by those pretreated for short-term at the same temperature, indicate that pre-exposure of *T. remus* to sub-optimal high temperatures may reduce their performance. Similarly, parasitoids pretreated at 32°C recorded low parasitoid adult emergence, suggesting that exposure to high temperatures has deleterious effects on *T. remus* successful development, and thus may lower the delivery of ecosystem services by the parasitoid in nature. This could be attributed to a reduction in the success of oviposition attempts or reduced oviposition preference by females due to heat stress (Spahn & Lill, 2022). In addition, some parasitoids may lose oviposition interest following reduced host quality (Spahn & Lill, 2022). However, our study did not assess these aspects. On the contrary, numerous studies indicate that female parasitoids can assess their host's quality, avoiding either those of lower quality or dead hosts. Our study may have underestimated *T. remus* effectiveness by not factoring host natural mortality. When the *T. remus* parasitism results are superimposed on fall armyworm egg hatchability, high temperature reduced both *T. remus* parasitism rates and host egg hatchability. On the contrary, low temperatures did not affect parasitism rates, but reduced host egg hatchability. These findings indicate better pest control by the *T. remus* under low-temperature environments, and suggest that the common practice of low-temperature storage of the parasitoid does not compromise the parasitoid ecosystem service delivery within optimum temperature ranges. To the pest management

practitioner, a compromised *T. remus* fitness may manifest as reduction in numbers, activity, and consequent reduction in fall armyworm control. Thus, the knowledge of how host–natural enemies' differentially respond to changing temperature conditions may help remodel more efficient climate-resilient pest management programs. In addition, a reduced adult emergence rate can be attributed to potential reproductive abnormalities and activated cellular immunity following stressful conditions. Cellular immunity is utilized by hosts as a survival strategy against endoparasitoids that oviposit in their bodies (Spahn & Lill, 2022). Fall armyworm survive threats from these exogenous agents by activating the innate immune system through up-regulating phenoloxidase production. This enzyme is expressed more in advanced developmental stages than in eggs (Huang et al., 2022), making them more susceptible to parasitism. Through this mechanism, the immune system of hosts detects parasitoid eggs as foreign bodies and mobilizes cellular immunity against them through enzymatic action or encapsulation of the eggs or developing larvae (Andrade et al., 2010; Reed et al., 2007). Nevertheless, parasitoids inject venom into the hosts and kill them during oviposition.

In addition to the reduction of parasitoid thermal fitness and reduced adult emergence, heat stress also reduces parasitoid performance through its direct effects on developmental time, parasitism windows, adult longevity, and female host-searching abilities (Cancino et al., 2020; Larios et al., 2002; Pomari et al., 2013). In addition, temperature also affects sex ratios in insects directly by influencing the sperm stock that is acquired by females during copulation (Nguyen et al., 2013). Information concerning offspring's sex ratio from each thermal treatment can provide crucial information to develop a biological control program against the fall armyworm. Investigating these aspects is useful to fully understand the extent of the impact of acclimation pretreatment, and thus provide more crucial information for use in biological control programs.

Comparing the two experiments' results, long-term pretreatment to high temperature increased *T. remus* heat tolerance, while low-temperature pretreatment reduced both cold and heat tolerance of the parasitoid. Similarly, acclimation to high (long term) and low temperatures generally reduced egg hatchability in fall armyworm. Similar to submissions by Furlong and Zalucki (2017), our results show that as insects get exposed to sub-optimal temperatures under the changing climate and in nature, both hosts and parasitoids may be affected. We found the basal CT_{max} and HKDT of *T. remus* to be $43.0 \pm 0.58^\circ C$ and 23.7 ± 0.47 min, respectively. These basal heat tolerance levels are lower than those of its host fall armyworm reported by Mbande, Mutamiswa, and Chidawanyika (2023) ($\sim 45^\circ C$ on adults) and Segaiso et al. (2022) ($\sim 50^\circ C$ on fourth/fifth instar larvae); a finding that complicates biological control using *T. remus*, particularly where extended durations of high temperatures are experienced. The higher developmental stages of fall armyworm (fourth instar larvae upward and adults) show some high tolerance to extreme temperature

environments, making it difficult to effectively suppress its populations during periods of high-temperature anomalies. In addition to low heat tolerance by *T. remus*, its parasitism efficacy and adult emergence are also reduced at elevated temperatures. These findings concur with submissions by Furlong and Zalucki (2017) and Hance et al. (2007) who argued that parasitoid-mediated biological control is likely to be negatively impacted by increasing bouts of high temperatures and heat waves, a common phenomenon under global climate change.

CONCLUSIONS

Acclimation of fall armyworm eggs and *T. remus* to suboptimal temperatures comes at fitness costs, particularly for the parasitoid. Our overall findings suggest that fall armyworm and *T. remus* will be negatively impacted through host egg desiccation for the former and parasitoid activity and field fitness for the latter. Acclimation pretreatment to elevated temperatures boosted *T. remus* CT_{max} , yet its tolerance levels remained lower than the basal tolerance of its host's developmental stages, as documented in literature. In addition, parasitism rates and adult emergence may be reduced by adult parasitoid pretreatment to elevated temperatures. Our findings suggest valuable insights into the environmental resilience and suitability of *T. remus* as a biological control agent across different climates or geographies, particularly in varying seasons as influenced by climatic conditions. Beneficial acclimation responses of the biological control agent reported here also suggest that leveraging insights from evolutionary physiology can enhance the mass rearing of parasitoids intended for release in environments with varying climate conditions.

AUTHOR CONTRIBUTIONS

Macdonald Mubayiwa: Conceptualization; data curation; formal analysis; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Honest Machekano:** Conceptualization; methodology; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing. **Brighton M. Mvumi:** Conceptualization; project administration; supervision; validation; visualization; writing – review and editing. **Winnifred A. Opio:** Investigation; methodology; resources; validation; writing – review and editing. **Bame Segaiso:** Investigation; methodology; writing – review and editing. **Frank Chidawanyika:** Writing – original draft; writing – review and editing; validation. **Casper Nyamukondiwa:** Conceptualization; funding acquisition; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Datasets analyzed for the current study can be obtained from the corresponding author upon reasonable request.

ETHICS STATEMENT

The authors have nothing to report.

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