



# Thermal fitness costs and benefits of developmental acclimation in fall armyworm

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## ABSTRACT

Global increases in mean temperatures and changes in precipitation patterns due to climate change, coupled with anthropogenic pathways, have intensified biological invasions of pest insects. Continuous exposure to bouts of acute and chronic heat and fasting stresses (during e.g., droughts) might improve pest performance under recurring stresses, therefore enhancing/reducing fitness within- or across- life stages (i.e., 'carry-over' effects). Here, we examined developmental acclimation effects in the invasive fall army worm *Spodoptera frugiperda* – a highly invasive economic insect pest of cereal crops, particularly maize – using standardized heat tolerance metrics. Specifically, we assessed the effects of acute (3h) and chronic (3 days) heat treatments (at 32°C, 35°C, 38°C), as well as fasting (48h), on 3rd instar larvae, and tested fitness traits (critical thermal maxima [CT<sub>max</sub>] and heat knockdown time [HKDT]) at a later life stage (4<sup>th</sup>/5<sup>th</sup> larval instar). Acclimation to heat stress and fasting had significant fitness costs (lower CT<sub>max</sub>) across majority of treatments. However, both heat and fasting acclimation improved HKDT (except for 35 and 38°C [acute acclimation] and 35°C [chronic acclimation]). Our results suggest context-specific developmental acclimation costs and benefits in *S. frugiperda*. In particular, heat and fasting acclimation potentially have fitness costs and benefits for subsequent developmental stages facing high temperature stress. These results are important for estimating the effects of prior stressful events on future survival of invasive insect species and may be significant in predicting pest population dynamics under changing environmental conditions.

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## Introduction

Biological invasions are a growing ecological and economic threat worldwide [1,2]. The success and impact of invasive alien species may interact synergistically with environmental changes, such as increasing temperature for improved

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survival chances of invasive species, but potential synergies between these processes remain largely unknown [3]. Insects are among the most impactful taxa worldwide when they invade, owing to a myriad of introduction pathways and rapid human-mediated dispersal, driving some of the highest economic costs worldwide among invasive species [4,5]. The fall armyworm (FAW) *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) is an economic invasive insect pest of South American origin [6] that attacks cereal crops, particularly maize. It first invaded the African region through west Africa in 2016 [7,8], and by 2017, it had spread to the whole of eastern Africa and parts of southern Africa including Botswana [8,9], before spreading to the Middle East and Asia (India) in 2018 [10,11].

FAW is a highly multivoltine polyphagous pest, feeding on over 350 plant species across different families [12–14], with a high preference for maize. Larvae feed on leaves, stems, and economic parts of plants e.g., maize cobs, thereby causing losses [15]. To reach the adult stage, they go through six instar stages, that may take as little as ~11 days (at 32 °C) [16]. However, FAW larva has striking host plasticity, varying from five to ten instar stages depending on host plant [17,81] reportedly having more 'instars on sub-optimal hosts. This host plasticity facilitates development on less favourable hosts [18] or droughts. Given this host plasticity, African invasion by the FAW represents a substantial biosecurity threat. For example, FAW has threatened maize production across the world, e.g., the pest accounted for ~17.7 million tones of maize losses across 12 African countries to date [19]. Maize remains, nevertheless, a staple food for over 200 million people globally [20] and accounts for 40% of the cereal production in Sub-Saharan Africa [21] with economic, social and political significance. Thus, FAW continental invasion and associated crop losses exacerbate food security crises in Africa (see e.g., [22]).

Bio-physical environmental conditions experienced during early life stages of an organism are significant determinants of many key fitness life history traits [23]. In particular, factors such as individual diet, feeding frequency, temperature and relative humidity (RH) environments during early-life stages have significant effects on subsequent developmental stages [24,25,82]. Determining the effects of within-developmental stage phenotypic plasticity has been the focus of research for decades [23,25,26]. However, the effects across developmental stages within-generation remain scarce (but see [27], [28]), despite their ecological significance. For example, insect developmental stages may be spatially separated, raising questions about how environmental history may differentially shape fitness of subsequent developmental stages within the same generation, but across new environments (e.g., [29]). Indeed, FAW developmental stages may also occupy  $\geq 2$  spatially distinct bio-physical environments [30] resulting in likely different fitness consequences in subsequent instars. Through adult flight migrations [31] and larval silking [32], FAW uses this behavioral adaptation to extend its geographical range into novel areas to circumvent inter- and intra-specific competition. However, it is not known whether prior environment affects fitness of subsequent developmental stages, or aids invasiveness of FAW. Previous studies have nevertheless documented that overcoming environmental barriers, e.g., of temperature and desiccation tolerance, are critical for invasion success [33]. For this reason, invasive insects often have high basal stress tolerance, phenotypic plasticity [34–37] and metabolic flexibility [38].

Other external stressors, such as lack of food, have also been documented to influence insect thermal tolerance in complex, often in unpredictable ways [39]. Fasting can occur when there is a lack of adequate food (due to various environmental perturbations) to meet the energy requirements for biological processes in the insect's body [40]. This food deprivation stress is presumed to result in a trade-off in insect thermal tolerance [41] due to cross talk or cross tolerance [42]. Several studies have supported this notion, as fasting pre-treatment often impairs cold tolerance in insects [43,44]. However, fasting acclimation appears not to have any effects on heat tolerance (see [41,43]). Nevertheless, how stressful traits in one developmental stage interact with the subsequent developmental stages and environments remains unknown in FAW, despite evidence for phenotypic plasticity within and across ontogeny (see e.g., [25,26]) and across different developmental stages and seasons/environments (i.e., 'carry-over' effects) [45–48].

Despite overwhelming evidence of the effects of prior environment on insect fitness [29,45,46], few studies have investigated developmental acclimation effects for invasive insects with a view of making inferences for pest invasiveness. Nevertheless, investigation of the effect of environmental history has large ecological implications for organismal fitness under changing environments. Unravelling developmental acclimation is important in determining how species may react to changes in environment across developmental stages and seasons, and how this may shape their fitness and by extension, their population dynamics. This has downstream implications on designing pest control strategies e.g., through development of early warning systems. Here, we thus examined innate within-generation developmental temperature and fasting acclimation effects on heat tolerance in *S. frugiperda* following high temperature acute and chronic acclimation, as well as fasting. Given its tropical origin, heat tolerance may remain a key trait that facilitates invasion, and more-so in arid and semi-arid environments such as Botswana. We hypothesise that temperature and food deprivation stress in one instar may have heat tolerance fitness costs or benefits across other subsequent non-acclimated developmental stages (developmental acclimation). Confirmation of positive adaptive developmental acclimation effects may have implications on *S. frugiperda* invasiveness under heterogeneous stressful environments associated with changing climate. This knowledge is important in informing spatially-dependant *S. frugiperda* pest management strategies.

## Materials and Methods

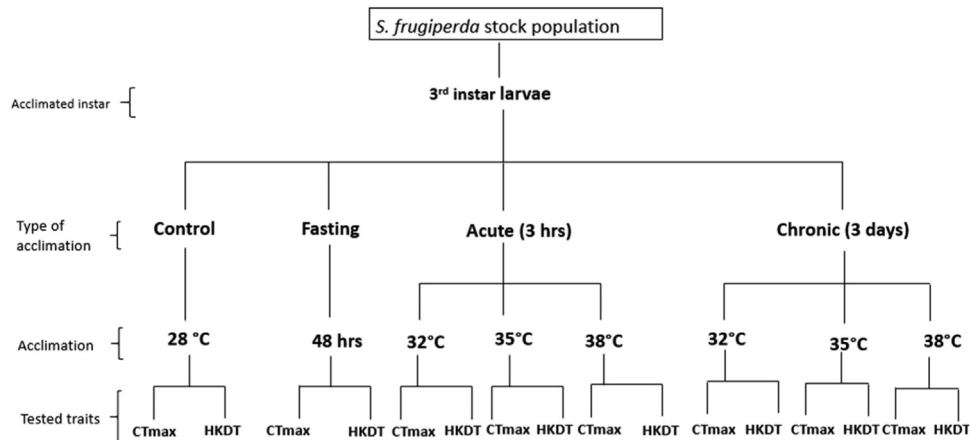
### *Insect rearing and maintenance*

Field populations of *S. frugiperda* were collected as 2<sup>nd</sup>–5<sup>th</sup> instar larvae from infested maize crops from two commercial farms; Talana farms (S22°.13467; E28°.59468) and Motloutse River farm, Bobonong Village, Central district of Botswana,

**Table 1**  
Magnitude and direction of change of critical thermal maxima and heat knockdown time.

Type of acclimation	Acclimation temperature (°C)	*Magnitude of change ( $CT_{max}$ ) (folds)	*Magnitude of change (HKDT) (folds)
Acute	32	0.968	1.175
	35	0.974	0.840
	38	0.995	0.832
Chronic	32	0.991	1.290
	35	0.099	1.240
	38	0.995	1.572
Fasting	28	0.981	1.130

\* Magnitude < 1 indicates deleterious (negative) effects of acclimation, whereas magnitude > 1 indicates beneficial (positive) effects of acclimation.



**Fig. 1.** Schematic flow diagram indicating acclimated developmental stages, type of acclimation (acute versus chronic), acclimation temperatures (28 [control]; 32; 35 and 38 °C) and the traits tested (HKDT and  $CT_{max}$ ). Traits were tested on instar 4 in acute acclimation and instar 5 in chronic acclimation pre-treatments. Heat knockdown temperatures were specific to acclimation treatment temperature, and were derived from average  $CT_{max}$  values, following methods by [55].  $CT_{max}$  = critical thermal maximum; HKDT = heat knockdown time.

and placed in 50 ml vials containing artificial diet, adopted from [49]. Both farms are within the same region and experience similar climatic environments. Specimens were reared in Memmert climate chambers (Memmert GmbH + Co. KG, Schwabach, Germany) in the laboratory at optimal conditions ( $28 \pm 1$  °C,  $65 \pm 10\%$  RH) and fed on the same artificial insect diet (see [49]). Both pupae and moths were kept in Bugdorm cages (Megaview Science Co., Ltd, Taichung, Taiwan) in climate chambers. All moths were fed on 10% sucrose solution *ad libitum*. To obtain the next generation of FAW for experimental use, moths were mated in oviposition cages containing a 4-week-old maize plant (as oviposition substrate). Following oviposition, eggs were allowed to incubate and hatch on the host plant (maize). After hatching, 1<sup>st</sup> instar neonates were subsequently transferred to vials containing the artificial diet [49]. Each vial comprised three larvae, reared up to 3<sup>rd</sup> instar in the laboratory. However, following moulting to the 3<sup>rd</sup> instar stage, all larvae were transferred into individual vials in preparation for the experiments and simultaneously to circumvent larval cannibalism, which is usually more apparent starting from the 3<sup>rd</sup> instar onwards (see [15]). Experiments were run using these lab-reared 3<sup>rd</sup> instar larvae from F<sub>1</sub> to F<sub>4</sub> generations, randomised across the treatments. We assumed that under ambient conditions, laboratory adaptation has insignificant effects on thermal fitness across the three tested generations, as has been observed in similar experiments [50]; but see [51]. Acclimation treatments were done following moulting of 3<sup>rd</sup> instar larvae, and heat tolerance traits (i.e., critical thermal maxima [ $CT_{max}$ ] and heat knockdown time [HKDT]) were tested on 4<sup>th</sup> instar larvae following acute acclimation and 5<sup>th</sup> instar larvae following chronic acclimation (as majority of the larvae moulted twice during the 3-day chronic acclimation plus one day recovery period).

### Acclimation experiments

Experimental treatments (acclimation) comprised acute and chronic sub-lethal high temperature acclimation and fasting. This was undertaken in 3<sup>rd</sup> instar larvae by exposing insects to temperatures of 28.0 (control) 32.0, 35.0 and  $38.0 \pm 1.0$  °C (each under  $65 \pm 10\%$  RH) for 3 hours (acute) and 3 days (chronic) acclimation treatments (see Table 1) in Memmert climate chambers. Temperatures selected for acclimation were ecologically relevant and based on a previous study that showed temperatures across Botswana to reach up to 42 °C during heat waves [52]; see Fig. 1, and considering that the optimal temperature range of *S. frugiperda* is 26–30 °C [16]. From the optimum temperature range, 28 °C was selected as the control temperature and 3–4 °C was added to establish mild high temperatures for acclimation, based on modified protocols from

[24]. Control insects were kept at optimal environmental conditions of  $28\pm 1^\circ\text{C}$  and  $65\pm 10\%$  RH during experimental treatments before measuring thermal fitness traits (Fig. 1). Following both acute and chronic acclimation, insects were allowed to recover at optimal conditions ( $28\pm 1^\circ\text{C}$  and  $65\pm 10\%$  RH) for 24 hours before measuring physiological traits.

To determine the effects of feeding status on the thermal fitness of *S. frugiperda*, 3<sup>rd</sup> instar larvae were deprived of food (fasted) for 48 hours. All fasting acclimations were done using a constant time period (48 hours), and results were directly compared to those of acute and chronic temperature treatments. Larvae were removed from artificial diet at 3<sup>rd</sup> instar and individually placed into empty 50 ml vials without any food, but with a water source (cotton wad, to prevent desiccation associated mortality). The larvae were kept under benign conditions ( $28\pm 1^\circ\text{C}$ ,  $65 \pm 10\%$  RH; 12L:12D) to ensure that food deprivation was the only limiting factor, and effective as a treatment. Post 48 hrs, larvae were returned to individual vials with access to food (artificial diet) and water *ad libitum* for 24 hours to allow recovery. Measurement of thermal traits was conducted 24 hours post-recovery following methods by [43]. Control larvae were provided with artificial diet and kept at optimal temperatures and RH ( $28\pm 1^\circ\text{C}$  and  $65\pm 10\%$ ) throughout, prior to running experiments.

### Heat tolerance metrics

To test the effects of heat and fasting acclimation on heat tolerance, (i)  $CT_{\max}$  – the maximum temperature allowing insect activity, and (ii) HKDT – the time taken to knock down an insect following acute heat stress, were measured [23]. Both traits are ecologically sound heat tolerance indices [53,54] and correlate well with insect biogeographical patterns [80]. For  $CT_{\max}$ , individual 4<sup>th</sup> instar (for acute acclimation) and 5<sup>th</sup> instar (for chronic acclimation) larvae were placed into an insulated double jacketed chamber with ten ‘organ pipes’ connected to a programmable bath filled with 1:1 water: propylene glycol, which regulates the flow of liquid around the chamber (Grant GP200-R4, Grant Instruments, UK) [39]. Critical thermal maxima experiments started at  $28^\circ\text{C}$  (FAW optimum temperature) from which temperature was gradually increased using a ramping rate of  $0.25^\circ\text{C}/\text{min}$  until the larvae reached upper temperature limit of activity ( $CT_{\max}$ ) [39] (Table 1). This ramping rate is ecologically more relevant than other ramping rates used in literature e.g.,  $0.5^\circ\text{C}/\text{minute}$  (reviewed in [23]). A thermocouple (type K, 36 SWG) connected to a digital thermometer (Fluke 54 series II, Fluke Cooperation, China; accuracy:  $0.05^\circ\text{C}$ ) was inserted into the organ pipe to record the chamber temperature. The experimental procedure was repeated 3 times to yield  $n \approx 30$  larvae per treatment (30 replications). In this study,  $CT_{\max}$  was defined as the temperature at which an individual larva lost co-ordinated muscle function (self-righting) and ability to respond to mild prodding using a thermally inert object.

Heat knockdown time was assessed on 4<sup>th</sup> instar larvae (following acute acclimation) and 5<sup>th</sup> instar larvae (following chronic acclimation) using standardized protocols [39]. We used treatment-specific heat knockdown temperatures, derived from each treatment’s  $CT_{\max}$  value plus  $2^\circ\text{C}$ . This heat knockdown temperature is ecologically sufficient to elicit heat knockdown effects in insects (see e.g., [24,55]). Thus, knockdown temperatures of  $53.0$ ,  $50.0$ ,  $51.4$ , and  $50.7^\circ\text{C}$  were used as acute knockdown temperatures for  $28$  (control)  $32$ ,  $35$ , and  $38^\circ\text{C}$  acclimation pre-treatments respectively, whereas  $53.0$ ,  $51.6$ ,  $51.9$  and  $50.8^\circ\text{C}$  were used as chronic knockdown temperatures for  $28$  (control)  $32$ ,  $35$ , and  $38^\circ\text{C}$  acclimation pre-treatments, respectively. Ten individual larvae were placed in  $1.5\text{ ml}$  microcentrifuge tubes and placed in a Memmert climate chamber (HPP 260, Memmert GmbH + Co.KG, Germany) set at various temperatures as indicated above. Temperatures above  $CT_{\max}$  cause heat coma in insects and are often used in HKDT assays (see [56]). A video recording camera (HD Covert Network Camera, DS-2CD6412FWD-20, Hikvision Digital Technology Co., Ltd, China) linked to a computer was connected to the climate chamber and used to monitor knockdown activity and timing. Heat knockdown time was defined as the time (in minutes) at which an individual larva lost activity following acute heat stress.

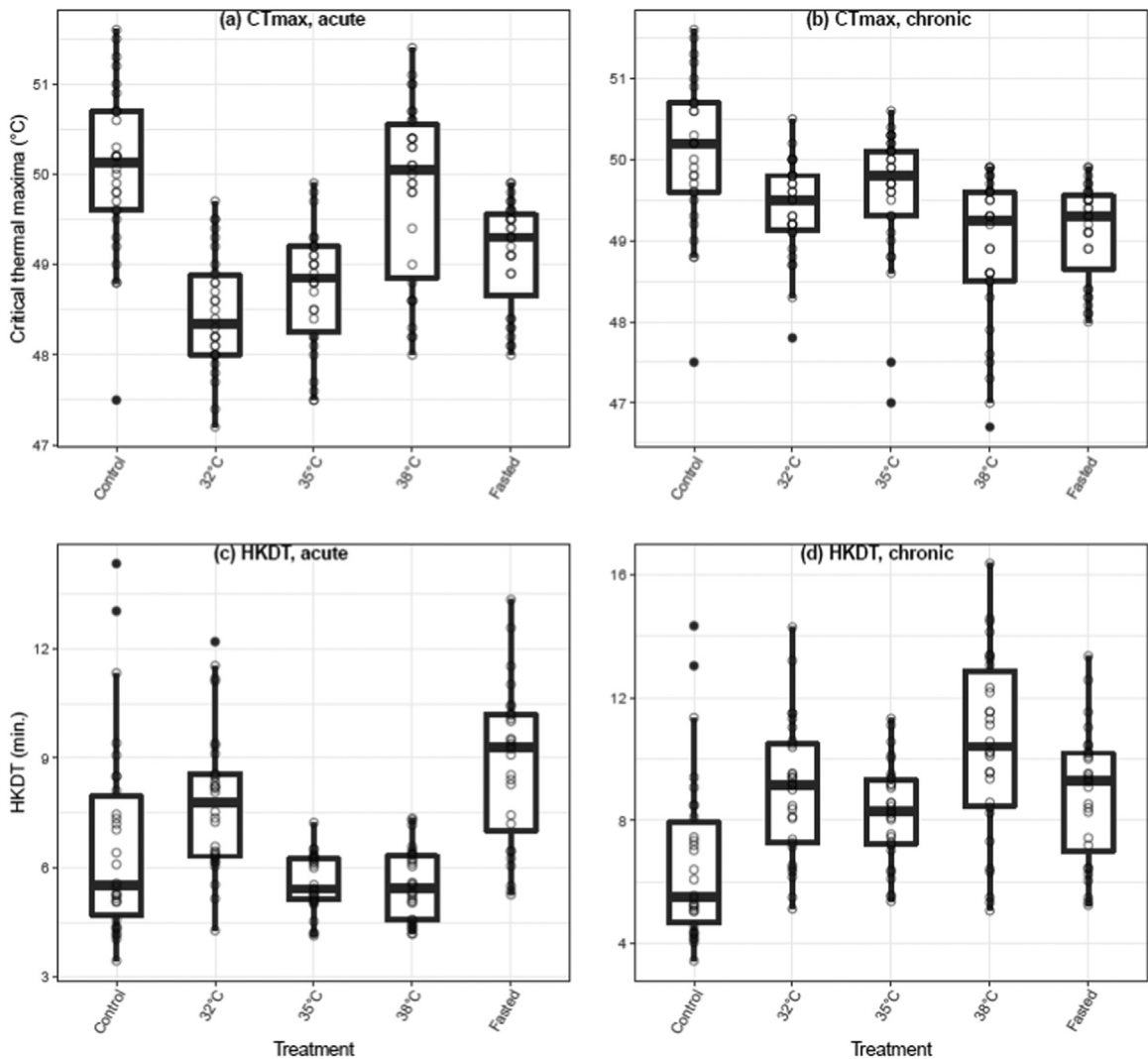
### Data analysis

Data analyses were all performed using R, version 4.1.1 (R Development Core Team, 2021). The residuals were first checked for normality and variance homogeneity using Shapiro–Wilks and Levene’s tests, respectively, and were found to violate normality and homogeneity of variance assumptions. Kruskal–Wallis tests were thus used to examine  $CT_{\max}$  and HKDT as a function of treatment for each respective acute and chronic exposure treatment (i.e., four separate models). Dunn tests were used post-hoc for pairwise comparisons, with p-values adjusted via the Holm method [57].

We summarized the magnitude of both  $CT_{\max}$  and HKDT following acclimation using methods by [58] and [24]. Specifically, we calculated the magnitude of change in thermal fitness conferred by the acclimation treatment using the formula below, where the mean heat tolerance ( $CT_{\max}$  / HKDT) after each treatment was divided by the mean control  $CT_{\max}$  or HKDT results of which were tabulated into Table 1.

$$\text{Magnitude of change} = \frac{\text{Final } CT_{\max} \text{ (or HKDT) for each treatment}}{\text{Control } CT_{\max} \text{ (or HKDT)}}$$

where a value  $> 1$  denotes beneficial acclimation effects, whereas a value  $< 1$  denotes potentially deleterious acclimation effect (see Leori et al., 1994; [59])



**Fig. 2.** Critical thermal maxima (CT<sub>max</sub> [a, b]) and heat knockdown time (HKDT [c, d]) following acute (a, c) and chronic (b, d) temperature treatments. For all fasting pre-treatments, organisms were deprived of food for 48h. In the boxplots, the horizontal bars display the median, the box gives the interquartile ranges, and the whiskers show the largest and smallest values up to  $1.5 \times$  interquartile range. Points are raw data. Acute and chronic represents acute and chronic acclimations

## Results

For acute exposures, CT<sub>max</sub> differed significantly among control group, 32°C, 35°C and fasting acclimation treatments ( $\chi^2 = 58.397$ ,  $df = 4$ ,  $p < 0.001$ ). Control group 4<sup>th</sup> instar CT<sub>max</sub> was significantly higher than 32°C, 35°C and fasting acclimation treatments (all  $p < 0.01$ ), but not 38°C ( $p > 0.05$ ). In turn, 38°C treatment CT<sub>max</sub> was significantly greater than 32°C, 35°C and fasting acclimation groups (all  $p < 0.05$ ). CT<sub>max</sub> following fasting acclimation significantly exceeded the 32 °C treatment ( $p < 0.05$ ) (Fig. 2a). In addition, heat tolerance (CT<sub>max</sub>) for acute treatments was significantly lower than chronic exposure treatments ( $\chi^2 = 35.070$ ,  $df = 4$ ,  $p < 0.001$ ). For chronic acclimation, Control group CT<sub>max</sub> was again highest, and significantly greater than 32 °C, 38 °C and fasting acclimation treatments (all  $p < 0.05$ ), but not 35 °C ( $p > 0.05$ ). CT<sub>max</sub> at the 35 °C treatment was also significantly greater than 38 °C and following fasting acclimation (both  $p < 0.05$ ) (Fig. 2b).

Following acute 3<sup>rd</sup> instar acclimation exposures, HKDT differed significantly among treatment groups ( $\chi^2 = 51.220$ ,  $df = 4$ ,  $p < 0.001$ ). Control HKDT was significantly lower than 32 °C and fasting acclimation groups (both  $p < 0.05$ ), but not 35 °C or 38 °C (both  $p > 0.05$ ). Fasting acclimation and 32 °C treatment groups had the highest HKDT, which significantly exceeded 35 °C and 38 °C (all  $p < 0.001$ ) (Fig. 2c). For chronic exposures, HKDT again significantly differed among treatments ( $\chi^2 = 32.332$ ,  $df = 4$ ,  $p < 0.001$ ). Control group HKDT was significantly lower than 32 °C, 38 °C and fasting acclimation groups (all  $p < 0.01$ ), but not 35 °C ( $p > 0.05$ ), whereas 38 °C significantly exceeded 35 °C ( $p < 0.05$ ) (Fig. 2d).

Chronic and acute acclimation had contrasting results on the direction of both  $CT_{max}$  and HKDT plasticity (Table 1). Both acute and chronic acclimation, as well as fasting, yielded negative deleterious plastic effects (i.e., negative magnitude; see Table 1) for  $CT_{max}$ , whereas positive effects on HKDT were exhibited following chronic exposure and fasting, but not acute exposures beyond 32 °C.

## Discussion

Population dynamics of individuals that may occupy multiple spatially-distinct habitat environments can be highly complex [60]. As such, sub-lethal stressful conditions experienced during early developmental stages e.g., early instars of the larvae, may be important in determining key life history traits, either manifesting as beneficial through e.g., developmental acclimation effects (see [23], or as deleterious (see e.g., [59]. Our results showed that fasting and high temperature acclimation at the 3<sup>rd</sup> instar larval stage had mixed effects on the heat tolerance of subsequent developmental stages (4<sup>th</sup> instar larval stage) in FAW, tested as  $CT_{max}$  and HKDT, and following both acute and chronic acclimation. In particular, fasting, acute and chronic high temperature acclimation of 3<sup>rd</sup> instars reduced  $CT_{max}$  of 4<sup>th</sup> instar larval stage of *S. frugiperda*. This may point to a deleterious effect of developmental acclimation conditions tested here on *S. frugiperda* heat tolerance. Thus, the prior exposure to sub-lethal environmental stressors early in life may have negative consequences for subsequent developmental stages, synonymous to deleterious acclimation [59], and suggest that both the acclimation treatment and  $CT_{max}$  stress test effects are additive (Jorgensen et al., [61]). Although chronic acclimation was lower than control, it generally had higher  $CT_{max}$  than the acute acclimation treatments at the same temperatures. However, HKDT assays yielded contrasting results from those of  $CT_{max}$ , with both fasting and specific high temperature acclimation treatments increasing heat tolerance (HKDT) for both acutely and chronically acclimated 3<sup>rd</sup> instar *S. frugiperda*. Our results, thus, confirm that acclimatory exposure of one developmental stage may have fitness costs and benefits to subsequent developmental stages, and that these costs and benefits depend on the context of the fitness metric being tested (e.g.,  $CT_{max}$  vs HKDT). Thus, exposure to sub-lethal stress during development may have fitness and survival consequences on later life stages [62], and by inference, could affect the propensity of invasive species establishment success in novel environments.

While acclimatory conditions experienced during one life stage of an organism can have fitness costs and benefits within that life stage, acclimatory effects can also manifest across developmental stages. Developmental acclimation effects are adaptive and may presumably facilitate ‘carry-over’ stress resistance under novel stressful environments. *Spodoptera frugiperda* is a highly invasive economic insect pest of cereal crops, particularly maize. Given the mobility of its life stages e.g., larva (through silking) and adults (through flight), it is largely unknown how previous environments may shape fitness of the same and/or subsequent life stages, and by inference, invasion propensity thereof. Our results showed that most acute and chronic heat acclimation treatments, as well as fasting, significantly depressed  $CT_{max}$ . This result means that sub-lethal food deprivation and heat stress at the 3<sup>rd</sup> instar stage larvae may have negative  $CT_{max}$  fitness consequences on 4<sup>th</sup> and 5<sup>th</sup> instar larvae and probably by extension, other subsequent developmental stages. Climate change is often associated with episodes of acute and chronic heat stress, and prolonged droughts that may limit food resources [63,64]. Thus, the deleterious effects of acclimation treatments recorded here may mean that frequent episodes of environmental heat and food deprivation stress faced in nature may offset heat tolerance of subsequent developmental stages, affecting population dynamics of invasive species. The reason for the negative effects of heat acclimation reported here are largely unknown. However, it may point to the notion that the stress faced during acclimation treatment and  $CT_{max}$  assays is additive (see [61]). Moreover, we also speculate that we may have missed certain acclimatory cues or specific treatment combinations that specifically elicits  $CT_{max}$  acclimation responses. Thus, future studies may need to explore differential temperature and time combinations at all higher instar stages of the larvae that may elicit acclimation. One more interesting result observed here is that a treatment to one stress may also have negative effects on a divergent stress. For example, 3<sup>rd</sup> instar acute and chronic fasting acclimation had deleterious consequences on 5<sup>th</sup> instar larval  $CT_{max}$ . This may be indicating that injury associated with diverging environmental stresses may be the same (see e.g., [65,66]), and that divergent stress effects may thus be additive. Nevertheless, the lack of beneficial acclimation effects for heat acclimation reported here is consistent with studies on *Tuta absoluta*, that reported no beneficial acclimation effects following chronic high temperature acclimation [58].

By contrast, both acute and chronic 3<sup>rd</sup> instar larvae acclimation had beneficial effects on subsequent larval HKDT, albeit for specific treatments (32 °C and fasting for acute acclimation, and 32, 38 °C and fasting for chronic acclimation). Conditions eliciting acclimation responses are highly complex and often context-dependent [23–25]. This agrees with our results, that observed positive acclimation responses were specific to certain heat acclimation groups and corroborates with previous reports suggesting that conditions conferring acclimation responses are highly context-dependent (see [24]). Similarly, acute heat acclimation at 35 and 38 °C, and chronic heat acclimation at 35 °C, had no significant effects on HKDT. This result means that heat wave episodes associated with climate change on 3<sup>rd</sup> instar larvae of *S. frugiperda* may have positive or neutral effects on subsequent developmental stages in the context of HKDT but not  $CT_{max}$ . Thus, *S. frugiperda* may have fitness benefits under projected heat stress in terms of enduring long durations of mild to high temperature stress associated with changing climates, potentially translating into greater invasiveness and resilience in high temperature tropical habitats.

Comparisons for HKDT experimental traits have often been investigated using a more constant temperature (see [23]). However, here, we used different heat knockdown temperatures to investigate HKDT across different acute and chronic temperature treatments. Thus, differences in results reported here may also be partly due to the treatment-specific heat knockdown temperature methodology used in our study. Furthermore, the results also showed the positive beneficial effects

of acclimation to a divergent stress trait (fasting) on a different stressor (heat tolerance [HKDT]). Such cross tolerance represents shared co-evolutionary response mechanisms to stress traits involved (see [43]), and represent another facet that may help invasive species survive highly variable stressful environments, e.g., through integrated stress resistance (see discussions in [67]). Cross tolerance results reported here are nevertheless in contrast with reports on *Ceratitis rosa*, where fasting resulted in increased  $CT_{max}$  and reduced HKDT [43]. These results indicate that fasting has dissimilar effects on different traits used to measure heat tolerance, and that elicitation of acclimation responses are trait dependant. Results obtained here thus mean that food deprivation (i.e., temporary absence of host plants) during mid-season droughts, and other plant-damaging natural disasters such as hailstorms, may provide a benefit in periods of rapid heat shock, such as heat waves, through cross tolerance developmental acclimation effects. Increased heat tolerance (HKDT) reported here for certain treatments may represent context-specific expression of heat shock proteins and other hormonal heat stress regulators [55,68]. Heat shock proteins and hormonal activation due to heat stress usually occur over a certain temperature threshold, which are context-dependent but usually range from 39 – 41°C [69]. Similar results were observed in *Drosophila mojavensis* [70], where high temperature acclimation at one developmental stage increased HKDT in subsequent developmental stages [71]. Indeed, sublethal high temperature stress may influence physiological traits in addition to other life history traits e.g., fecundity and longevity [72]. A study on *Plutella xylostella* (L.) showed that high temperature acclimation on larval stages had effects on adult stages, affecting oviposition patterns and adult life span [73]. Our results thus indicate that timing of sublethal high temperature stress such as heat waves may enhance thermal fitness and survival of other life stages of invasive pest insects. Therefore, survival of *S. frugiperda* may increase in hot tropical areas even during high temperature incidences. Inclusion of effects of extreme high temperature incidences in pest management forecasts will increase accuracy of invasive species biogeographical patterns [74]([71]; [80]). Likewise, processes and events at one developmental stage and in a particular season may have far-reaching consequences for other developmental stages in a different season; a phenomenon called 'carry-over' effects [47]. While this phenomenon has largely been explored in migratory birds, little is known on how this affects the fitness of migratory insects in general (but see [75]), and invasive insects in particular. Future work should accordingly examine carry-over effects in *S. frugiperda* and assess how they may shape population dynamics and pest invasiveness. We also observed that acclimation responses were trait-dependant and observed such positive effects only for HKDT; a more acute heat stress metric compared to  $CT_{max}$ . We thus speculate, with caveats, that the differences in chronic exposure to stress during  $CT_{max}$  and HKDT assays may also have affected differential acclimation responses reported here. Future studies should thus look at more acute  $CT_{max}$  ramping methodologies e.g., 0.5 or 1°C/minute (see e.g., [76]) to try and capture potential acclimation cues that we may have missed.

Costs and benefits of plastic acclimation are difficult to predict and are not uniform across species, metrics tested and acclimation treatments. A study done by [77] showed that age, increasing rate of temperature change and duration of heat hardening resulted in a benefit or increase in  $CT_{max}$ . Factors such as body mass have also been shown to have a cost on HKDT [78]. Our results thus show mixed but context (trait)-dependent effects of both acute and chronic developmental acclimation. Specifically, we first show that while both heat and fasting acclimation at one developmental stage negatively affected heat tolerance measured as  $CT_{max}$ , it contrastingly improved another heat tolerance trait (HKDT), suggesting differential trait related acclimation responses. The positive beneficial acclimation responses for HKDT were, however, treatment dependant, suggesting specific cues eliciting acclimation for the HKDT trait. Second, we show that while heat acclimation had negative effects (additive stress effects [see [61]]) for  $CT_{max}$  (same stressor), acclimation to a divergent stress (food deprivation) may also have additive stress effects on a different stress (heat tolerance [ $CT_{max}$ ]). These results support our hypothesis that abiotic stress in one developmental stage may have fitness costs and benefits in the subsequent developmental stages (e.g., [45]). We could, however, not find acclimation responses for  $CT_{max}$  and other treatments for HKDT. We speculate that we may have missed exact treatment combinations that elicit acclimation response for  $CT_{max}$  and these specific treatments for HKDT. Thus, future work should consider more comprehensive acclimation treatment combinations. Forecasting of insect pest invasions are usually done through prediction of how changes in mean temperature affect insect pest population dynamics [73]. Our results provide a step into understanding costs and benefits of developmental acclimation in *S. frugiperda* and how it may affect pest population dynamics. Future pest forecasting models should thus incorporate developmental acclimation responses and by extension, 'carry-over' and integrated stress resistance effects (see e.g., [79,80]) to potentially improve accuracy of model outputs and pest early warning systems.

### Availability of data and material

The raw and analysed datasets of the current study available from the corresponding author on reasonable request.

### Submission declaration and conflict of interest statement

This work has not been previously published. Authors declare no conflict of interests.

### Ethics approval and consent to participate

Not applicable.

## Consent for publication

Not applicable.

## Competing interests

All authors declare no conflict of interests.

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## Authors' contributions

Project conceptualization and management: BS HM CN.  
 Data curation: BS.  
 Formal analysis: RC CN.  
 Investigation: BS HM.  
 Visualization and validation: BS HM RC CN.  
 Writing – original draft: BS HM CN.  
 Writing, review and editing: BS HM RC CN.

## Declaration of Competing Interest

The authors declare no conflict of interest.

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