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Pesticides in a warmer world: Effects of glyphosate and warming across insect life stages☆

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A R T I C L E I N F O

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A B S T R A C T

Glyphosate (GLY) is a broad-spectrum herbicide that is the most commonly applied pesticide in terrestrial ecosystems in the U.S. and, potentially, worldwide. However, the combined effects of warming associated with climate change and exposure to GLY and GLY-based formulations (GBFs) on terrestrial animals are poorly understood. Animals progress through several life stages (e.g., embryonic, larval, and juvenile stages) that may exhibit different sensitivities to stressors. Therefore, we factorially manipulated temperature and GLY/GBF exposure in the variable field cricket (*Gryllus lineaticeps*) during two life stages—nymphal development and adulthood—and examined key animal traits, such as developmental rate, body size, food consumption, reproductive investment, and lifespan. A thermal environment simulating future climate warming obligated several costs to fitness-related traits. For example, warming experienced during nymphal development reduced survival, adult body mass and size, and investment into flight capacity and reproduction. Warming experienced by adults reduced lifespan and growth rate. Alternatively, the effects of GBF exposure were more subtle, often context-dependent (e.g., effects were only detected in one sex or temperature regime), and were stronger during adult exposure relative to exposure during development. There was evidence of additive costs of warming and GBF exposure to rates of feeding and growth in adults. Yet, the negative effect of GBF exposure to adult lifespan did not occur in warming conditions, suggesting that ongoing climate change may obscure some of the costs of GBFs to non-target organisms. The effects of GLY alone (i.e., in the absence of proprietary surfactants found in commercial formulations) were non-existent. Animals will be increasingly exposed to warming and GBFs, and our results indicate that GBF exposure and warming can entail additive costs for an animal taxon (insects) that plays critical roles in terrestrial ecosystems.

1. Introduction

Glyphosate (GLY) is the most used herbicide worldwide, and its application has skyrocketed after being commercialized in the 1970s—globally, GLY use has increased 15-fold since the mid-1990s, and nearly 1 million tons of GLY are now used each year (Benbrook, 2016; Maggi et al., 2019, 2020). An estimated 2 million tons of GLY have been applied to terrestrial ecosystems in the United States alone, and there are growing concerns about the bystander effects of GLY to non-target organisms (Benbrook, 2016). Glyphosate kills plants by inhibiting the shikimate pathway, which biosynthesizes essential aromatic amino acids and is not present in animals (Gill et al., 2017, 2018). Yet, recent work indicates that exposure to GLY-based formulations (GBFs; a. k.a., glyphosate-based herbicides or GBHs) may impact animals, including humans, likely due to adjuvants in GBFs (e.g., proprietary surfactants designed to improve the absorption of GLY by plants) (Gill et al., 2018; Richmond 2018; Battisti et al., 2021; Gandhi et al., 2021; Kabat et al., 2021).

Exposure to chemical pollution is not the only potential stressor animals encounter. Global warming is expected to accelerate, and warming is costly to many facets of animal biology—it may reduce body size, contract geographical ranges, and lead to phenological mismatching (Parmesan, 2006; Yang and Rudolf, 2010; Gardner et al., 2011; Kharouba et al., 2018; IPCC et al., 2021). Animals exposed to both pesticides and warming simultaneously may incur additive costs from these multiple stressors. Alternatively, the costs of multiple stressors may be non-additive or interactive (e.g., antagonistic or synergistic: Crain et al., 2008; Todgham and Stillman, 2013; Kaunisto et al., 2016).

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For example, temperature and insecticide exposure tend to have synergistic effects (i.e., entail interactive, non-additive effects) on insects (Kaunisto et al., 2016). Likewise, warming and GLY/GBFs modulate the effects of one another in the physiological and behavioral responses of aquatic animals (Baier et al., 2016; Gandhi and Cecala, 2016; Silva et al., 2020; Fadhlaoui and Lavoie, 2021; Parlapiano et al., 2021). However, the combined effects of warming and GLY/GBFs on terrestrial animals are less understood (Stahlschmidt and Vo, 2022).

On their journey from birth to death, animals progress through several life stages (e.g., embryonic, larval, and juvenile stages) that may exhibit different sensitivities to stressors (Kingsolver et al., 2011; Tangwancharoen and Burton, 2014; Truebano et al., 2018; Shekh et al., 2019; Leung and McAfee, 2020). Therefore, we factorially manipulated temperature and GLY/GBF exposure in the variable field cricket (*Gryllus lineaticeps*) during two life stages (nymphal development and adulthood) because previous work indicates crickets are sensitive to insecticides (e.g., neonicotinoids, phenylpyrazoles, pyrethroids, and organophosphates: Cummings et al., 2006; Thompson and Brandenburg, 2006; Neuman-Lee et al., 2013; Maliszewska et al., 2018), but crickets' sensitivity to herbicides are not understood. We examined key animal traits, such as developmental rate, body size, food consumption, reproductive investment, and lifespan. We addressed four questions:

(1) Do GLY/GBFs and warming impose additive or non-additive costs? Here, we predict a tendency for non-additive, interactive costs given previous work across taxa (e.g., Crain et al., 2008), as well as in *Gryllus*, in particular (Padda et al., 2021; Padda and Stahlschmidt, 2022).
(2) Do the effects of either potential stressor vary due to life stage? Here, we predict exposure during development will have a greater effect than exposure during adulthood because early life stages tend to be relatively sensitive to abiotic stress (Grosell et al., 2002; Verween et al., 2007; Pineda et al., 2012; Miller et al., 2013; Mohammed, 2013; but see Tangwancharoen and Burton, 2014; Shekh et al., 2019).
(3) Do the effects of either potential stressor vary due to the type of trait (i.e., some traits may be more sensitive to GLY/GBFs than other traits)? Here, we predict warming to reduce developmental duration and body size as in other taxa (reviewed in Angilletta, 2009), but we have no clear *a priori* predictions regarding the trait-specific sensitivity of GLY/GBF exposure given their broad range of effects in animals (reviewed in Gill et al., 2018).
(4) Are the costs of GBFs due to GLY, or to co-formulants? Here, we predict costs of exposure to GBF, but not GLY alone, given the harmful effects of surfactant co-formulants (Tsui and Chu, 2003; Howe et al., 2004; reviewed in Gill et al., 2018).

The threat of multiple stressors is increasing for animals (McRae et al., 2008; Nelson et al., 2009; Rohr et al., 2011; Rohr and Palmer, 2013; Kaunisto et al., 2016), and our study will be the first to integrate the effects of global warming and a common herbicide across the life stages of a terrestrial animal.

2. Materials and methods

2.1. Study system

The variable field cricket, *Gryllus lineaticeps,* is predominately found in California, U.S. (Weissman and Gray, 2019) where GLY is applied to more land area than any other pesticide (California Department of Pesticide Regulation, 2018). We used *G. lineaticeps* from a long-term colony that we subsidized annually with progeny from females collected from a natural population (Sedgwick Reserve, Santa Ynez, CA, U.S.). *Gryllus lineaticeps* is wing-dimorphic, and we maintained the colony at even sex and morph ratios in standard conditions (14:10 light: dark cycle with *ad libitum* access to water, commercial dry cat food, and cardboard egg cartons for shelter) at 28 ± 1 °C. In these conditions, *G. lineaticeps* eggs incubate for ~11 d before hatchling nymphs emerge, and nymphs develop for ~50 d before molting into winged adults that begin mating with ~5 d, and females begin ovipositing immediately thereafter.

We conducted two experiments (see below), and we maintained crickets in standard conditions for both experiments. For Experiment 1, we transferred each cohort of hatchlings (n = 20 per cohort) from the colony to a translucent 15 L plastic container within 2 d of hatching (n = 42 cohorts; n = 820 hatchlings total). For Experiment 2, we transferred each newly emerged adult from the colony to a translucent 1.9 L plastic container within 1 d post-adult molt (n = 276 adults total). We only used short-winged (SW; flight-incapable) morphs for Experiment 2 because the SW morph is the dominant morph at Sedgwick Reserve (L.A. Treidel, pers. comm.).

2.2. Experiment 1: Effects of warming and GLY/GBF during development

We used a 3 × 2 factorial design to study the independent and interactive effects of water treatment and temperature on the success and duration of development, and adult phenotype (e.g., body size, and investment into flight capacity and reproduction). We manipulated exposure to GLY or GBF by providing nymphal crickets with water bottles filled with one of three solutions: tap water only (control, CON), glyphosate (GLY; 5 mg/L of H_2O, the concentration of GLY that has been used in other insect studies and is based on field-relevant concentrations: reviewed in Herbert et al., 2014; Motta et al., 2018), and GBF (Roundup® Super Concentrate diluted to 5 mg GLY/L of H_2O). We changed water bottles weekly, and we included both GLY and GBF to disentangle the effects of GLY and non-GLY components (i.e., proprietary surfactants) on measured variables. Glyphosate exhibits very low rates of degradation in tap water in the absence of UV light exposure (e.g., at least 90% of glyphosate remains after 120 days: Yadav et al., 2017), and its degradation is minimally affected by temperature and is instead largely driven by microbes in natural conditions (Roberts, 1998; Tomlin, 2006; Mercurio et al., 2014). Because there was likely limited microbial activity and UV radiation in our study using chlorinated tap water, GLY- and GBF-treated crickets likely experienced significant exposure to these chemicals. We performed a pilot study in adult *G. lineaticeps* (n = 27) maintained in standard conditions. Based on these crickets' consumption of GBF-treated water (92 ml per day on average), we estimate that each GLY/GBF-treated cricket consumed approximately 0.5 μg of GLY each day.

We also manipulated crickets' thermal environments. We maintained half of the crickets in an incubator (model I-36, Percival Scientific, Inc., Perry, IA, U.S.) exhibiting a thermal cycle that changed temperature hourly and ranged from 18 °C to 38 °C each day (Fig. S1). This control temperature treatment averaged 28 °C (as in standard colony conditions; see above), but its daily variation approximated the thermal fluctuations of microhabitats used by adult *G. lineaticeps* in the field (Sedgwick Reserve, Santa Barbara County, CA, USA: Fig. S1). We maintained the remaining crickets in an incubator exhibiting a thermal cycle that changed temperature hourly and ranged from 23 °C to 42 °C each day (Fig. S1). The maximum temperature in the warming treatment (42 °C) did not exceed the critical thermal maximum of adult *G. lineaticeps* (50 °C; ZRS unpublished). Thus, the warming temperature treatment was acutely sublethal and exhibited the same thermal variation as the control temperature treatment, but it was 4 °C warmer to estimate the predicted increase in temperature at Sedgwick Reserve in 2100 (IPCC et al., 2021).

We checked crickets daily, and we transferred newly emerged adults into individual deli cups and returned crickets to their water and temperature treatment conditions. After 5 d, we determined wing morphology (i.e., SW or long-winged [LW]) and body mass, before killing and storing each cricket at −20 °C. To determine investment into flight capacity, we later dissected crickets to score their flight musculature [dorsolongitudinal muscles (DLM)] from 0 (DLM absent) to 1 (white, histolyzed and non-functional DLM) to 2 (pink and functional DLM) (King et al., 2011; Glass and Stahlschmidt, 2019; Padda et al., 2021). We removed each female's ovaries and dried them to a constant mass to determine reproductive investment because ovary mass at this age strongly correlates with total fecundity in *Gryllus* (Roff, 1994). Last, we determined the length of both femurs for each cricket to determine body size (μ) and bilateral asymmetry (coefficient of variation (%); 100 × (σ/μ)), the latter of which is an indicator of stress (reviewed in Graham et al., 2010).

2.3. Experiment 2: Effects of warming and GLY/GBF during adulthood

To study the independent and interactive effects of water treatment and temperature on adult lifespan, food intake, and food conversion efficiency, we first weighed each cricket and then added pre-weighed dry commercial cat to each cricket's container. We manipulated exposure to GLY/GBF and temperature using the 3 × 2 factorial design described above. Daily, we checked for mortality to determine lifespan. We paired males and females for 24-h periods to facilitate mating encounters at 7, 14, 21, and 28 days of adulthood. We ensured that mating occurred between age-matched pairs of crickets in the same water-temperature treatment groups (e.g., a female in the CON-warming treatment group only mated with CON-warming males). In cases of uneven sex ratios, we matched one male with two females (or *vice versa*). We tried to ensure that each cricket only encountered >1 mating partner during a given mating encounter up to one time in its life, and that each cricket was not mated to the same cricket more than once. We returned each cricket to its individual housing after mating.

Weekly, we weighed each cricket to determine changes in body mass. We also determined food intake between mating events each week because other herbicides can reduce food intake in insects (Ja et al., 2007), and other traits (e.g., sex or lifespan) may also be associated with the rate of food intake. Female *Gryllus* crickets rapidly increase body and gonad mass during the first week of adulthood, and the amount of body mass gained (i.e., growth rate) during early adulthood is strongly correlated with reproductive investment in female *G. lineaticeps* (Stahlschmidt et al. unpublished; reviewed in Zera, 2005). Therefore, we determined whether treatments affected growth rate, as well as the ability of crickets to convert food mass into body tissue (and, thus, reproductive tissue for 1 week old female adults) by estimating ingested food conversion efficiency (body mass gain [mg]/total food ingested [mg] *sensu* Mole and Zera, 1993, 1994).

2.4. Statistical analyses

We tested data for normality, natural logarithm-transformed data when necessary, and analyzed using SPSS (v.26 IBM Corp., Armonk, NY). We determined two-tailed significance at $\alpha = 0.05$. For Experiment 1, we used several general linear mixed models to examine the independent and interactive effects of treatments (water treatment and temperature) and sex on developmental duration, adult body mass and size, bilateral asymmetry, and ovary mass where we included cohort identity ($n = 42$) as a random effect in each model. We also performed an ordinal logistic generalized linear mixed model on the categorical DLM scores (scored from 0 to 2, see above) and treatments. To account for the independent effect of body size, the ovary mass and DLM score models included mean femur length as a covariate. Similarly, we used binary logistic generalized linear models on data from each cricket to determine the effects of treatment on survivorship (0: did not survive treatment; 1: survived treatment) and on wing morphology (SW or LW). For Experiment 2, we used several general linear models to examine the independent and interactive effects of treatments (GLY/GBF and temperature) and sex on adult lifespan, average daily food intake, and the growth rate and the food conversion efficiency during early adulthood. We included initial body mass as a covariate in all Experiment 2 models, with the exception of the conversion efficiency model because initial body mass was used to determine conversion efficiency. We further included body mass gained during early adulthood and average daily food intake as covariates in the lifespan model to examine the sensitivity of longevity to growth rate and feeding rate, respectively, and because these two covariates did not exhibit strong multicollinearity (variance inflation factor = 1.97). All models tested for interactions between and among treatments and sex. Significant results are reported below, and full results are reported in Tables S1-S12. When water treatment independently affected a dependent variable, we used pairwise post-hoc analyses to determine differences between water treatments, and we controlled the Type I error rate associated with multiple comparisons by using the Holm-Bonferroni method.

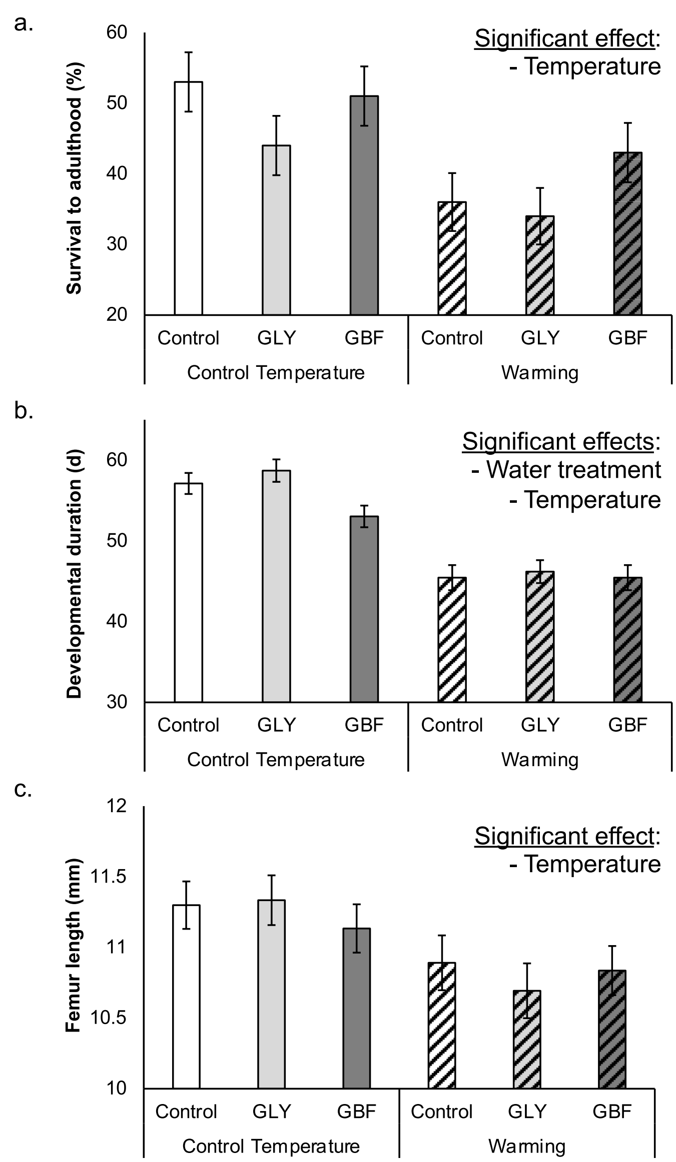

Fig. 1. Effects of water treatment (tap water [control], glyphosate [GLY], or GLY-based formulation [GBF]) and temperature experienced during development on a.) survival to adulthood, b.) developmental duration, and c.) body size (femur length) in *G. lineaticeps*. For full results, see Tables S1, S2, and S4. Values are displayed as mean ± s.e.m.

3. Results

3.1. Experiment 1: Effects of warming and GLY/GBF during development

Warming during development reduced survival to adulthood, and both warming and GBF exposure reduced developmental duration (Fig. 1a and b; Tables S1 and S2). Adult body mass and size were reduced due to warming (Fig. 1c; Table S3). Warming had a greater effect on body mass in females (temperature × sex effect), which were larger and heavier than males (Tables S3 and S4). Neither wing morphology nor bilateral symmetry were affected by any experimental factor (Tables S5 and S6). Flight musculature and ovary mass were reduced due to warming after accounting for variation due to body size (Fig. 2; Tables S7 and S8).

3.2. Experiment 2: Effects of warming and GLY/GBF during adulthood

Adult lifespan was reduced by warming, and GBF exposure in control temperature conditions (temperature × water treatment effect) also reduced lifespan (Table S9; Fig. 3a). Lifespan was further reduced by high feeding rate, small body size (initial body mass), and slow growth rate during early adulthood (Table S9). Feeding rate was reduced in males, small animals, and animals exposed to warming (Fig. 3b; Table S10). Feeding rate was also reduced due to GBF exposure (Fig. 3b), and this effect was greater in females (water treatment × sex effect; Table S10). After accounting for initial body mass, growth rate during early adulthood was reduced in males, in warming conditions, and by GBF exposure (Fig. 4a; Table S11). The efficiency by which ingested food was converted to body mass during early adulthood was reduced in males and by GBF exposure (Fig. 4b; Table S12).

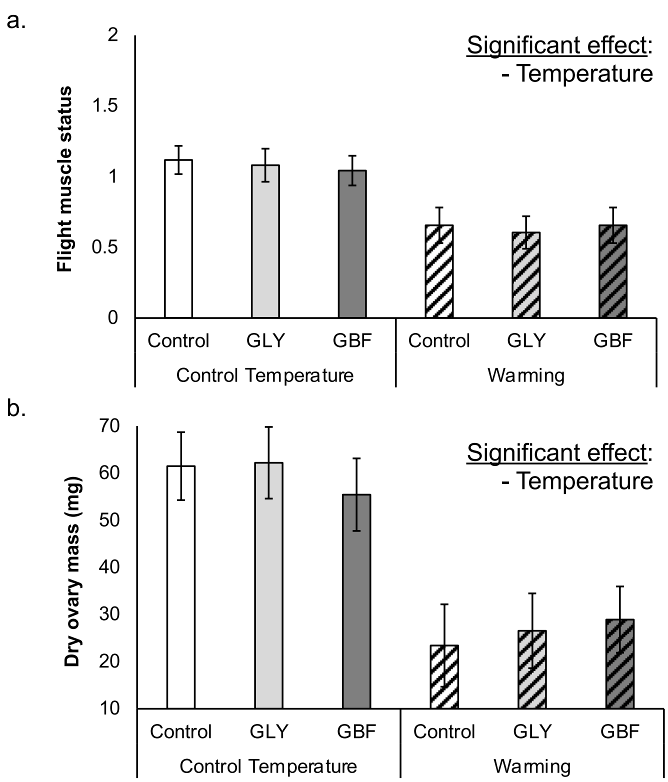

Fig. 2. Effects of water treatment (tap water [control], glyphosate [GLY], or GLY-based formulation [GBF]) and temperature experienced during development on investment into a.) flight musculature (scored from 0 [muscle absent] to 2 [muscle present and functional]), and b.) reproduction (dry ovary mass) in *G. lineaticeps*. For full results, see Tables S7 and S8. Values are displayed as mean ± s.e.m.

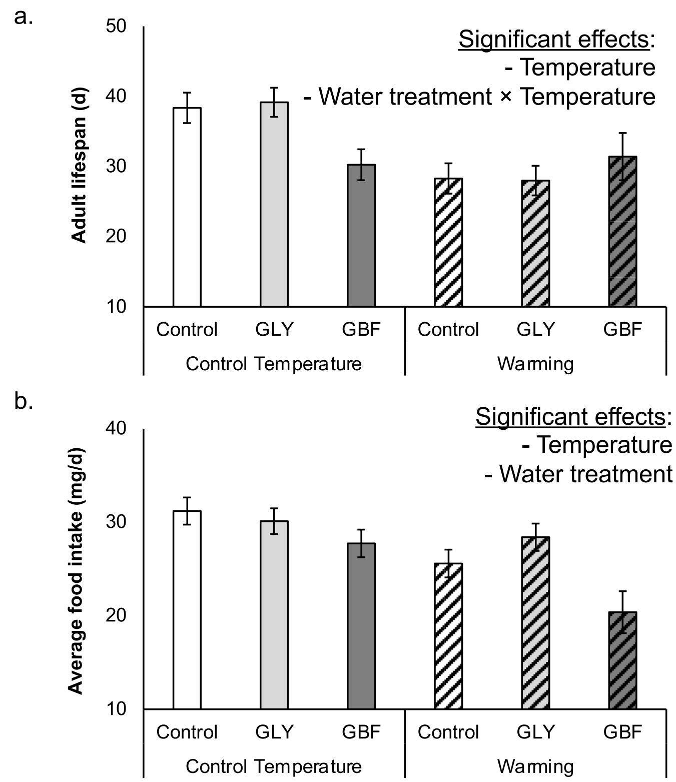

Fig. 3. Effects of water treatment (tap water [control], glyphosate [GLY], or GLY-based formulation [GBF]) and temperature experienced during adulthood on a.) lifespan and b.) feeding rate in *G. lineaticeps*. For full results, see Tables S9 and S10. Values are displayed as estimated marginal mean ± s.e.m. Because initial body mass was included as a covariate.

4. Discussion

The broad-spectrum herbicide, GLY, is the most commonly applied pesticide in terrestrial ecosystems in the U.S. and, potentially, worldwide (reviewed in Benbrook, 2016). However, the combined effects of GLY/GBF exposure and warming on terrestrial animals are poorly understood. Here, we examined how these potential multiple stressors shape a range of phenotypic traits—from growth and survival to reproduction and longevity—across life stages in a field cricket. Our results indicate that a thermal environment simulating future climate warming obligated several costs to fitness-related traits. For example, warming experienced during nymphal development reduced survival, adult body mass and size, and investment into flight capacity and reproduction (Figs. 1 and 2). Warming experienced by adults reduced lifespan and growth rate (Figs. 3 and 4). Alternatively, the effects of GBF exposure were more subtle, often context-dependent (e.g., effects were only detected in one sex or temperature regime), and were stronger during adult exposure relative to exposure during development (Figs. 1–4). The effects of GLY alone (i.e., in the absence of proprietary surfactants found in commercial formulations) were non-existent. In sum, our results indicate that GBF exposure and warming can each entail costs for an animal taxon (insects) that provide critical ecosystem services, including pollination and seed dispersal, nutrient and energy cycling, pest management, and decomposition (reviewed in Cardoso et al., 2020).

4.1. More additive than non-additive costs of warming and GLY/GBF exposure

Multiple stressors are increasingly common for animals (McRae et al., 2008; Nelson et al., 2009; Rohr and Palmer, 2013; Kaunisto et al.,

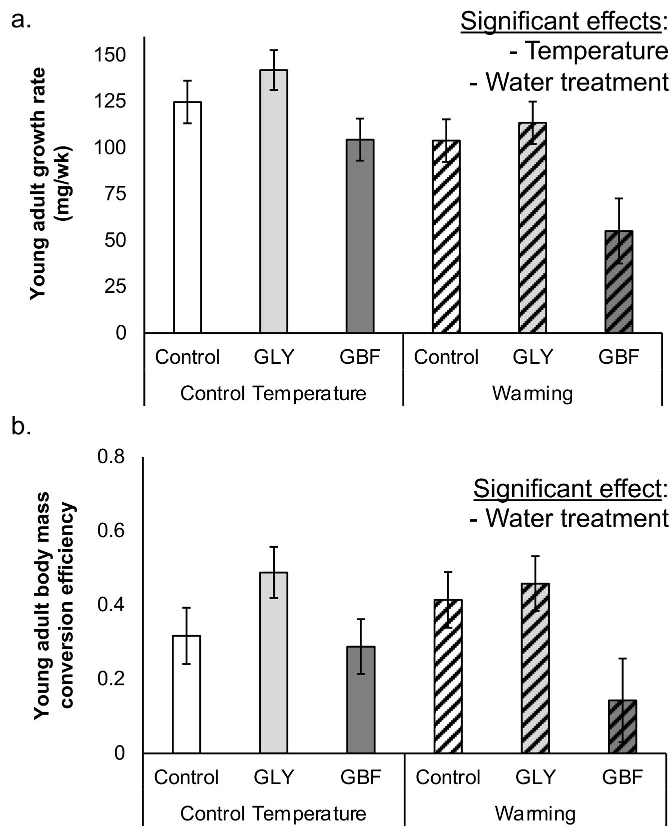

Fig. 4. Effects of water treatment (tap water [control], glyphosate [GLY], or GLY-based formulation [GBF]) and temperature experienced during adulthood on a.) growth rate (body mass gained) and b.) the efficiency by which ingested food was converted into body mass during early adulthood in *G. lineaticeps*. For full results, see Tables S11 and S12. Values are displayed as estimated marginal mean ± s.e.m. for growth rate because initial body mass was included as a covariate and as mean ± s.e.m. for conversion efficiency.

2016), and concurrent stressors may have an additive effect on a given animal trait where the stress due to two factors is simply the sum of either factor alone (Todgham and Stillman, 2013). However, multiple stressors may result in interactive, non-additive effects, such as synergistic or antagonistic effects (Folt et al., 1999; Todgham and Stillman, 2013; Piggott et al., 2015). Our study manipulating GLY/GBF exposure and warming in *G. lineaticeps* revealed that these two factors did not generally constitute multiple stressors—warming was typically costly, but exposure to GLY and (at times) GBF were not costly. For example, water treatment did not affect survival, body size or mass, or investment into flight capacity or reproduction (Figs. 1–2). However, when costs from warming and GBF were detected, they were more likely to be additive costs. Specifically, rates of feeding and growth in adults were reduced by warming and GBF exposure (Figs. 3 and 4). In only one instance were costs non-additive or interactive—the negative effect of GBF exposure to adult lifespan did not occur in warming conditions because both stressors (alone or in combination) appeared to reduce lifespan (Fig. 3a), which suggests that ongoing climate change may obscure the costs of GBFs to non-target organisms. Our study's greater support for additive costs of multiple stressors is in contrast with other multiple-stressor studies in *Gryllus* crickets, including *G. lineaticeps* (Padda et al., 2021; Padda and Stahlschmidt, 2022). Similar studies in other taxa provide a range of support for both additive and non-additive costs of multiple stressors (Løkke et al., 2013; Piggott et al., 2015; Gieswein et al., 2017). Thus, there may not be a universal "rule" for the manner in which concurrent environmental stressors affect animals.

4.2. *Costs of warming and GLY/GBF exposure vary across life stages*

Understanding the effects of complex environmental shifts on animals requires consideration of the entire animal life cycle because life stages may vary in their sensitivities to stressors (reviewed in Kingsolver et al., 2011). Early life stages tend to be more sensitive to abiotic stressors, such as chemical pollutants and heat, putatively due to their smaller body sizes (Grosell et al., 2002; Verween et al., 2007; Klockmann et al., 2017; Pineda et al., 2012; Miller et al., 2013; Mohammed, 2013; but see Tangwancharoen and Burton, 2014; Shekh et al., 2019). However, adult *G. lineaticeps* were more sensitive to GBF exposure relative to nymphs, and both nymphs and adults were strongly affected by warming (Figs. 1–4). Adult crickets contain significant body stores (Stahlschmidt and Chang, 2021), and one explanation for adults' greater GBF sensitivity may be that surfactants contained in GBFs allow for increased accumulation of GBFs during adulthood because GBF co-formulants can rapidly penetrate and accumulate in cells (Vanlaeys et al., 2018). Our pilot data suggest that GLY/GBF-exposed adults consumed approximately 0.5 μg of GLY each day, but future work should examine the amount of GLY consumed by nymphs—as well as whether life stages vary in their bioaccumulation of GLY—to clarify the stage-specific dynamics of GLY/GBF exposure. Another explanation may lie in the interplay between GLY/GBFs and the microbiome. Glyphosate exposure alters gut microbiota in other animals, including in insects (Shehata et al., 2013; Motta et al., 2018; Tang et al., 2020). The richness of the insect gut microbiome is typically greater in earlier life stages (Yun et al., 2014; Juma et al., 2020), which may help nymphs buffer the negative effects of exposure to GLY/GBFs. However, future work is required to determine whether life stages differ in accumulation of GLY/GBF, and whether GLY/GBF exposure has stage-specific effects on the gut microbiome.

4.3. *Warming and GLY/GBF exposure have trait-specific effects*

All traits are not created equal—some traits contribute more directly to fitness than others—so investigating a suite of traits is key to understanding the magnitude of potential stressors to animals. In our study, traits not directly connected to fitness (e.g., bilateral symmetry and wing morphology) were unaffected by warming and GLY/GBF exposure (Tables S5 and S6). Meanwhile, fitness-related traits were highly sensitive to temperature—on average, warming reduced survival by >30% and reproductive investment by >120% (Figs. 1a and 2b). High temperatures can destabilize proteins and membranes, lead to oxygen limitation, and increase energy expenditure and the production of stress-related biomolecules (e.g., heat shock proteins), and these physiological effects can contribute to reduced survival and reproductive investment (reviewed in Angilletta, 2009). Other important traits were affected by both warming *and* GBF exposure in our study (e.g., developmental duration, food intake, and adult growth rate). Together, these three traits determine how quickly an animal can disperse and reproduce, and how many resources an animal has acquired for storage, reproductive investment, and self-maintenance. Therefore, the increasing prevalence of combined warming and GBF exposure is likely to strongly impact cricket populations. We encourage continued examination into the effects of temperature and GLY/GBF on traits linked to fitness, such as lifetime egg production and offspring success (e.g., Stahlschmidt et al., 2020; Stahlschmidt and Vo, 2022).

Several traits in *G. lineaticeps* responded predictably to warming and GBF exposure. For example, warming increased developmental rate (i.e., reduced developmental duration) at the expense of adult body size (Fig. 1b and c) in agreement with results in other animals, including other insects (reviewed in Angilletta, 2009; Régnière et al., 2012). Warming associated with global climate change reduces animal body size (Gardner et al., 2011), and smaller animals tend to exhibit decreased fitness (e.g., reduced investment into reproductive tissue or mating success: reviewed in Peters, 1983). In support, smaller crickets in our study exhibited reduced adult lifespan. Crickets that fed at a higher rate also exhibited reduced lifespan (Table S10), which appears to be a universal feature of animal biology (Fontana et al., 2010; Fontana and Partridge, 2015). Yet, warming and GBF exposure during adulthood reduced feeding but shortened (not prolonged) lifespan (Fig. 3). This discrepancy may be due aspects of experimental design. Work linking dietary restriction with longevity generally involves experimental manipulation of food availability (Fontana et al., 2010; Fontana and Partridge, 2015). However, food availability in our study was unlimited, meaning that reduced food intake was voluntary and potentially due to warming- or GBF exposure-induced stress. GBF exposure not only reduced food intake (similar to the effects of other herbicides: Ja et al., 2007). It also reduced the efficiency by which ingested food was converted to body mass during a period of dramatic reproductive investment (Fig. 4c), which suggests a metabolic cost of GBF exposure. Thus, understanding the fitness-related costs of multiple stressors requires careful consideration for the roles of resource (food) acquisition and allocation, particularly because ongoing climate change is expected to create food scarcity for insects due to range contractions of their food plants (Romo et al., 2014, 2015).

4.4. Costs of GBF exposure are not due to GLY

GBFs typically include surfactants as co-formulants or adjuvants, which facilitate the penetration of GLY into plant cells (Giesy et al., 2000). Polyoxyethyleneamine (POEA) is a surfactant commonly found in GBFs, and POEA alone often mimics or exceeds the effects of GBFs on animals (Tsui and Chu, 2003; Howe et al., 2004; reviewed in Gill et al., 2018). Therefore, costs of GBF exposure to animals are likely due to adjuvants, rather than GLY itself. In agreement, we found no effect of exposure to GLY alone on any measured trait (Figs. 1–4), but the effects of higher doses of GLY should be explored because GLY exposure tends to affect survival and the gut microbiome only at higher concentrations (e.g., >11 mg/L of H_2O) in other insects (Motta and Moran, 2020). However, exposure to a common GBF in our study (i.e., Roundup®: 5 mg GLY/L of H_2O + adjuvants) reduced development time, adult lifespan in control temperature conditions, food intake, adult growth rate, and the rate at which ingested food was converted to body mass (Figs. 1–4). Some of these effects were likely linked. For example, reduced growth rate was probably due to reduced food intake, which may be affected by water consumption. Other animals exhibit avoidance behaviors toward GLY/GBFs (Takahashi, 2007; Tierney et al., 2007; da Rosa et al., 2016; Leeb et al., 2020; but see Santos et al., 2012). *Gryllus lineaticeps* do not discriminate against GLY/GBF when making egg-laying decisions (Stahlschmidt and Vo, 2022), but their ability to avoid drinking water sources containing GLY/GBFs is unknown. Physiologically, surfactants interfere with the inner mitochondrial membrane and reduce the proton gradient required for cellular respiration (Bradberry et al., 2004), and oral exposure to POEA damages the gastrointestinal tract and lungs in mammals (Adam et al., 1997). In invertebrates, POEA exposure upregulates antioxidant defenses and can increase apoptosis (Contardo-Jara et al., 2009; Bednářová et al., 2020). However, it is unclear which specific behavioral or physiological mechanism(s) underlie the suite of effects in crickets that we observed.

5. Conclusions

Animals will be increasingly exposed to warming and GBFs (Benbrook, 2016; Maggi et al., 2019, 2020; IPCC et al., 2021), and the multiple-stressor framework provides a useful construct to better understand their effects on animals. Our results in a cricket indicate that warming tends to have larger effects than GBF exposure, and that the costs of these two stressors is more likely to be additive (Figs. 1–4). However, context is important, and we show that warming can reduce the harmful effects of GBF exposure on a fitness-related trait (i.e., adult lifespan: Fig. 3a). Stress biology can also vary due to sex (Kwan et al., 2008; Gruntenko et al., 2016; Moisan, 2021; Vinterstare et al., 2021), and we found that females were more sensitive to warming and GBF exposure. Specifically, female body size was more influenced by warming during development, and GBF exposure during adulthood affected feeding more in females (Tables S4 and S10). *Gryllus* crickets exhibit sexual variation in body size and other morphological characteristics, physiology, and developmental sensitivity to food availability and immune challenge (Zera et al., 2007; Judge and Bonanno, 2008; Kelly et al., 2014; Tawes and Kelly, 2017; Kirschman et al., 2019), and our results add to this list because stress sensitivity may also be sexually dimorphic. Therefore, we encourage researchers to continue to leverage the multiple-stressor framework to clarify how costs vary across different life stages, traits, and sexes. Future work should also consider the dynamics of sequential stressors given the hormetic responses to pesticide- and temperature-related stress in insects (reviewed in Rix and Cutler, 2022). For example, GBF exposure during development may influence—perhaps even improve— adult heat tolerance. After all, a clear understanding of organismal responses to multiple stressors can inform the population-level effects of environmental stress (Sokolova et al., 2012).

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Author statement

ZRS designed the experiments, analyzed the data, and led writing of the manuscript. JW, CV, PE, and DB collected data and assisted with writing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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