A simulated heat wave—but not herbicide exposure—alters resource investment strategy in an insect

Z.R. Stahlschmidt [*], J. Choi, B. Choy, P.L. Perez, J. Whitlock

University of the Pacific, 3601 Pacific Ave., Stockton, CA, 95211, USA

A B S T R A C T

Animals are increasingly exposed to potential stressors related to environmental change, and multiple stressors may alter the dynamics by which animals acquire resources and invest those resources into important life-history traits. Stress may lead to the prioritization of current reproduction to maximize lifetime reproduction (i.e., terminal investment [TI]) or, in contrast, prioritize somatic investment over current reproduction to facilitate future reproductive opportunities (i.e., reproductive restraint [RR]). Tests of the TI and RR hypotheses typically use immune challenges as stressors, and have not been explicitly tested in the context of environmental change even though warming influences resource allocation patterns across taxa. Further, the multiple-stressor framework has been a useful construct to clarify the costs of complex environmental shifts to animals, but it has not been leveraged to understand such effects on investment strategy. Thus, we tested the TI and RR hypotheses by manipulating widespread features of environmental change—glyphosate-based herbicide (GBH; Roundup®) exposure and a simulated heat wave—in the variable field cricket (*Gryllus lineaticeps*). A simulated heat wave affected the life-history tradeoff between investment into reproduction and soma. Specifically, heat wave prioritized investment into ovary mass over non-reproductive tissue, even after accounting for food consumption, in support of the TI hypothesis. In contrast, GBH exposure did not affect any measured trait, and crickets did not discriminate between tap water and GBH solution during drinking. Therefore, some—but not all—aspects of environmental change may alter resource investment strategies in animals. We encourage continued integration of the multiple-stressor framework and life-history theory to better understand how animals respond to their rapidly changing environments.

1. Introduction

Investment into life-history traits may be constrained by tradeoffs among traits wherein allocation to one trait obligates a cost to a different trait (van Noordwijk and de Jong, 1986; Roff, 1992; Stearns, 1992; Zera and Harshman, 2001). Investment strategies are flexible and stress can cause organisms to alter investment in two fundamental ways. The "terminal investment" (TI) hypothesis proposes that a mortality threat should lead to the prioritization of current reproduction to maximize lifetime reproduction (Fig. 1; reviewed in Duffield et al., 2017). In contrast, the "reproductive restraint" (RR) hypothesis proposes that such a stressor should prioritize somatic investment over current reproduction, presumably to facilitate future reproductive opportunities (Fig. 1; reviewed in Jehan et al., 2022). Whether an organism adopts a TI or RR strategy may depend on intrinsic and extrinsic factors (e.g., age or nutritional state, and threat level, respectively) (reviewed in Duffield

et al., 2017). Tests of the TI and RR hypotheses have often used immune challenges as stressors (e.g., Adamo, 1999; Bonneaud et al., 2004; Moret and Schmid-Hempel, 2004; Duffield et al., 2017; Jehan et al., 2022; reviewed in Duffield et al., 2017). However, these two mutually exclusive hypotheses have not been explicitly tested in the context of environmental change even though warming influences resource allocation patterns across taxa (Leicht et al., 2013; Ruiz-Vera et al., 2015; Wright et al., 2017; Detto et al., 2018; Carreira et al., 2020; Rosa and Saastamoinen, 2021; Wootton et al., 2022).

Global warming has made heat waves (i.e., 5 d periods where temperatures exceed historical averages) increasingly common for animals (Russo et al., 2016; Dosio et al., 2018; Sun et al., 2018; Shafiei Shiva et al., 2019; IPCC et al., 2021). Yet, heat stress is not the only challenge facing animals. The herbicide glyphosate is the most used pesticide in the U.S., and nearly 1 million tons of glyphosate are used each year globally (Benbrook, 2016; Maggi et al., 2020). Although glyphosate
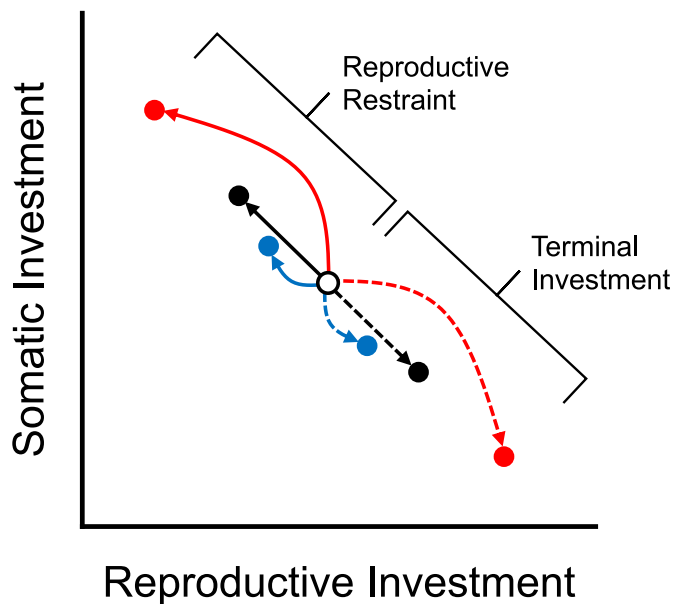

Fig. 1. Conceptual framework for resource allocation during multiple stressors. Animals are expected to navigate a tradeoff during resource allocation wherein investment into reproduction obligates a cost to somatic investment (and *vice versa*). In response to a single stressor, an animal (white circle) may increase prioritization of soma (solid black line) *sensu* "reproductive restraint" or, in contrast, increase prioritization of reproduction (dashed black line) *sensu* "terminal investment". Multiple, covarying stressors may have additive effects on resource allocation decisions (red lines) or non-additive, interactive effects, such as antagonistic effects (blue lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

targets a biochemical pathway unique to plants and some microorganisms, recent work indicates that exposure to glyphosate-based herbicides (GBHs) may impact animals, including humans (Zhang et al., 2019; Battisti et al., 2021; Kabat et al., 2021; reviewed in Gill et al., 2018). Animals can be exposed to chemical and thermal stressors simultaneously, and a multiple-stressor framework may prove useful in understanding the effects of GBH and heat wave exposure on animals' investment strategies *sensu* TI and RR (Fig. 1). Multiple stressors may additively shift allocation (Fig. 1). For example, if heat wave and GBH exposure each increase relative reproductive investment by 10% in isolation, then together they would increase it by 20%. In contrast, these potential stressors may have non-additive, interactive effects, where combined effects are less than (i.e., antagonistic) or greater than (i.e., synergistic) those expected by the additive model (Fig. 1). The multiple-stressor framework has been a useful construct to clarify the costs of complex environmental shifts to animals (Crain et al., 2008; Todgham and Stillman, 2013; Przeslawski et al., 2015; Kaunisto et al., 2016), but it has not been leveraged to understand such effects on investment strategy.

Animals naturally vary in their acquisition of nutritional resources, which, in turn, strongly influences their abilities to invest into life-history traits (van Noordwijk and de Jong, 1986; Roff, 1992; Stearns, 1992; Zera and Harshman, 2001). When food is abundant, the negative correlation or tradeoff between traits can be eliminated (Shoemaker and Adamo, 2007; French et al., 2007; Xu et al., 2012), and large variation in inter-individual resource acquisition can even result in positive correlations between traits (van Noordwijk and de Jong, 1986). Food availability can modulate the effects of temperature or pesticides on investment into life-history traits (Schneider et al., 2010; Johnston et al., 2014; Eder et al., 2018; Glass and Stahlschmidt, 2019; Im et al., 2020). Therefore, it is important to account for resource acquisition (e.g., food intake) when testing for TI or RR related to multiple stressors, such as

heat wave and GBH exposure.

In two experiments, we tested the TI and RR hypotheses using widespread features of environmental change—heat waves and GBH exposure—in the variable field cricket (*Gryllus lineaticeps*). In both experiments, we manipulated thermal environments (simulated heat wave vs. control temperature regimes), and we monitored eating and drinking to account for the role of resource acquisition in resource allocation or investment into reproductive tissue (i.e., ovary mass) and non-reproductive tissues. In the first experiment, we assigned adult females to either GBH solution or tap water as a drinking source to examine the effects of unavoidable exposure to GBH. In the second experiment, we allowed adult females to choose between these two drinking sources to determine whether behavioral (i.e., drinking) decisions can mediate GBH-induced costs and/or shifts in investment strategy. Animals increasingly encounter multiple stressors in their environments (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 multiple-stressor framework and life-history theory to better understand how animals respond to complex environmental change.

2. Materials and methods

2.1. Study system

Gryllus lineaticeps is predominantly found in California, U.S. (Weissman and Gray, 2019) where glyphosate is applied to more land area than any other pesticide (California Department of Pesticide Regulation, 2018). In *G. lineaticeps*, exposure to GBH can reduce growth rate and lifespan (Stahlschmidt et al., 2022). Like other *Gryllus* crickets (Zera and Larsen, 2001; Zera, 2005), *G. lineaticeps* is wing-dimorphic. Adults are either a long-winged and potentially flight-capable morph, or a flightless, short-winged morph. We only used short-winged crickets in the study, and they were acquired from a long-term colony that was subsidized every 1–2 years by progeny from females collected from a natural population (Sedgwick Reserve [SR], Santa Ynez, California, U. S.) that predominantly expresses the short-winged phenotype (authors pers. obs.; L.A. Treidel, pers. comm.). We reared *G. lineaticeps* 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. When they reached adulthood (i.e., within 1 d of adult molt), we weighed each female and individually housed them in 1.9 L transparent plastic enclosures containing pre-weighed food (dry cat food) and a cardboard shelter. We then assigned each cricket to one of two experiments (see below).

2.2. Experiment 1: Heat wave and no-choice manipulation of GBH exposure

We used a 2×2 factorial design to study the independent and interactive effects of temperature (simulated heat wave vs. control conditions) and GBH exposure (GBH drinking source vs. tap water source) on the estimated mass of reproductive and somatic tissues gained, conversion efficiencies for reproductive and somatic tissues, and the amount of drinking solution consumed. We manipulated exposure to GBH by providing crickets (n = 108) with cotton-plugged, 30 ml water bottles filled with one of two solutions: tap water only or GBH solution (Roundup® Super Concentrate diluted to 5 mg glyphosate/L of tap H_2O, the concentration of glyphosate 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). We positioned an opaque plastic cylindrical sleeve around each otherwise exposed water-soaked cotton plug, which created a secure, sheltered position from which females could drink. We also included a second cotton-plugged, 30 ml water bottle in each cricket's enclosure, but crickets were unable to drink from this bottle because we positioned a coarse metal mesh (3.5 mm × 3.5

mm) over the sleeve. We determined the consumption of drinking solution gravimetrically (i.e., comparing mass of water bottles at the onset and conclusion of experiment), and this second water bottle allowed us to account for water lost from each bottle due to evaporation.

We also manipulated crickets' thermal environments (Fig. 2). 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 17 °C to 31 °C each day. This "control" temperature range approximates the average diel temperature variation of the air and soil at SR during the mating season (i.e., adulthood) for *G. lineaticeps* (June–August; https://ucnrs.org/), and it is within the range of thermal microclimates chosen by *G. lineaticeps* at SR during the mating season (Sun et al., 2020; Stahlschmidt et al., 2022). We maintained the remaining crickets in an incubator exhibiting a thermal cycle that changed temperature hourly and ranged from 24 °C to 38 °C each day. This "heat wave" temperature range approximates the average diel temperature variation of the air and soil at SR during a 5 d heat wave in 2020 (https://ucnrs.org/), but was non-lethal in our study. As small ectotherms, short-winged *G. lineaticeps* sourced from SR exhibit minimal thermal inertia or heat retention (i.e., <0.6 °C lag between body and ambient temperatures during shifts in ambient temperature: Sun et al., 2020) compared to the magnitude of difference between our temperature treatments (7 °C). Therefore, we manipulated the body temperature of *G. lineaticeps* in our study by altering thermal environments in our incubators.

Each treatment lasted 5 d because the first 5 d of adulthood are characterized by intense energy demands in *Gryllus* crickets as short-winged females can increase ovary mass by 100-fold or more (Zera and Larsen, 2001; Zera, 2005; Stahlschmidt et al., 2022). At the conclusion of the experiment, we reweighed each cricket, its food, and its water bottles. We then euthanized by freezing (−20 °C) and then stored each cricket at −20 °C. After storage, we removed and weighed each cricket's ovaries to determine investment into reproduction. We used the difference between final body mass and fresh ovary mass to estimate final somatic mass. Somatic mass gained was likely in the form of fat body, which is the major energy storage tissue in insects but is also highly metabolic and important in producing immune molecules, such as antimicrobial peptides (Lemaitre and Hoffmann, 2007; Arrese and Soulages, 2010). At the onset of adulthood, fresh ovary mass comprises 0.98% of total body mass, on average (Stahlschmidt et al., 2022). Thus, we estimated ovary mass and somatic mass at the onset of the experiment, and compared these values to final values to determine how much reproductive and somatic tissue was gained during the experiment. To account for variation in resource acquisition, we estimated food conversion efficiency for ovary mass (estimated ovary mass gained between

Day 1 and Day 6 [mg]/total food ingested [mg]) and for somatic tissue (estimated somatic mass gained between Day 1 and Day 6 [mg]/total food ingested [mg]).

2.3. Experiment 2: Heat wave and choice manipulation of GBH exposure

As in Experiment 1, we determined the effects of a simulated heat wave (Fig. 2) and GBH exposure on the estimated mass of reproductive and somatic tissues gained, and the conversion efficiencies for reproductive and somatic tissues. However, although we manipulated temperature as described above, we positioned three (not two) 30 ml water bottles in each female's enclosure (n = 78): (1) tap water only, (2) GBH solution, and (3) tap water control that was inaccessible for drinking. This allowed each cricket to choose between drinking tap water or GBH solution, while accounting for water lost due to evaporation (see above). At the onset and conclusion of the experiment (i.e., on Day 1 and Day 6 of adulthood, respectively), we weighed each cricket, its food, and its water bottles as in Experiment 1.

2.4. Statistical analyses

We tested data for normality, natural logarithm-transformed when necessary (specifically, for the conversion efficiencies of reproductive and somatic tissues in Expt. 1), and analyzed using SPSS (v.28 IBM Corp., Armonk, NY). We determined two-tailed significance at α = 0.05. To examine the independent and interactive effects of treatments (temperature and drinking solution), we performed linear model analyses on the estimated mass of (1) reproductive and (2) somatic tissues gained, conversion efficiencies for (3) reproductive and (4) somatic tissues, and (5) the amount of food and (6) solution consumed in both experiments (i.e., no-choice [Expt. 1] and choice [Expt. 2]). For the 1st and 2nd models, we included treatments as main effects and initial (Day 1) body mass and the total amount of food consumed as covariates to account for differences in body size and food consumption. For Experiment 2, we included the percentage of solution consumed that was GBH (i.e., relative GBH consumption) as a covariate to test for the effects of GBH consumption on tissue investment. For the 3rd and 4th models, we included the total amount of solution consumed as a covariate to account for differences in water consumption. For Experiment 2, we also included relative GBH consumption as a covariate to test for the effects of GBH exposure on conversion efficiencies. For the 5th models, we included treatments as main effects and initial (Day 1) body mass and the total amount of solution consumed as covariates to account for differences in body size and water consumption. For Experiment 2, we included relative GBH consumption as a covariate to test for the effects of GBH exposure on food consumption. For the 6th models, we included cricket identity in the choice models as a random effect to account for differences in inter-individual variation on solution consumption. For the no-choice experiment, we included initial body mass and the total amount of food consumed as covariates to account for inter-individual differences in body size and food consumption. We report significant results below, and full results can be found in Tables A1-A6.

3. Results

In both experiments, a simulated heat wave increased reproductive investment (Fig. 3A, A1A,B; Table A1) via improving the efficiency by which ingested food was converted into reproductive tissue (Fig. 3B, A1C,D; Table A2). In contrast, heat wave decreased somatic investment (Fig. 3B, A2A,B; Table S3) via reducing the efficiency by which ingested food was converted into somatic tissue (Fig. 3B, A2C,D; Table A4). Larger crickets and those exposed to heat wave consumed more food (Fig. 4A and B; Table A5). Temperature treatment did not affect drinking (Fig. 4C and D; Table A6). Crickets did not discriminate between water and GBH solution during drinking (Fig. 4C and D; Table A6), and GBH solution consumption did not influence investment into tissues,
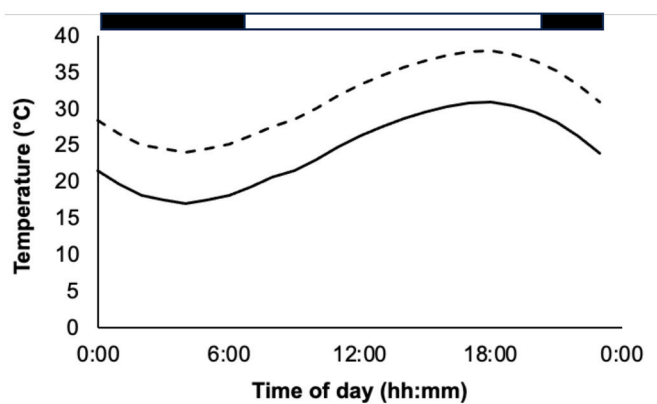

Fig. 2. Temperature treatments based on field-collected data. Adult female *G. lineaticeps* were exposed to either a simulated heat wave (dashed line) or a control temperature (solid line) treatment. The box running horizontally at the top indicates the photophase (white) and scotophase (black).
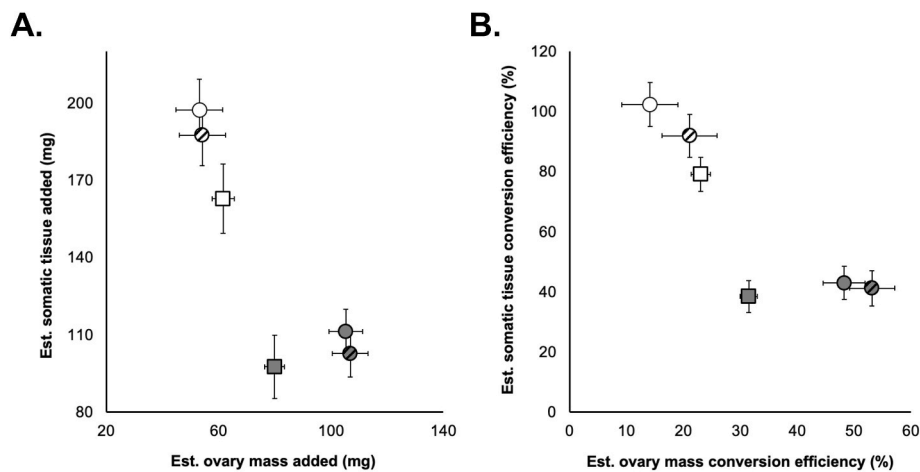
Fig. 3. Heat wave increased prioritization of reproduction over soma. Effects of temperature (control [white symbols] or heat wave [gray symbols]) and water treatment (tap water or glyphosate-based herbicide [GBH]) experienced during adulthood on the estimated (A) amount of reproductive and somatic tissues added, and (B) efficiency by which ingested food was converted to reproductive and somatic tissues in *G. lineaticeps*. Cross-hatching denotes GBH-treated group in Experiment 1, and square symbols denote Experiment 2 groups. Values are displayed as estimated marginal mean ± s.e.m. to account for covariates (e.g., initial body mass; see *2.4* for details).
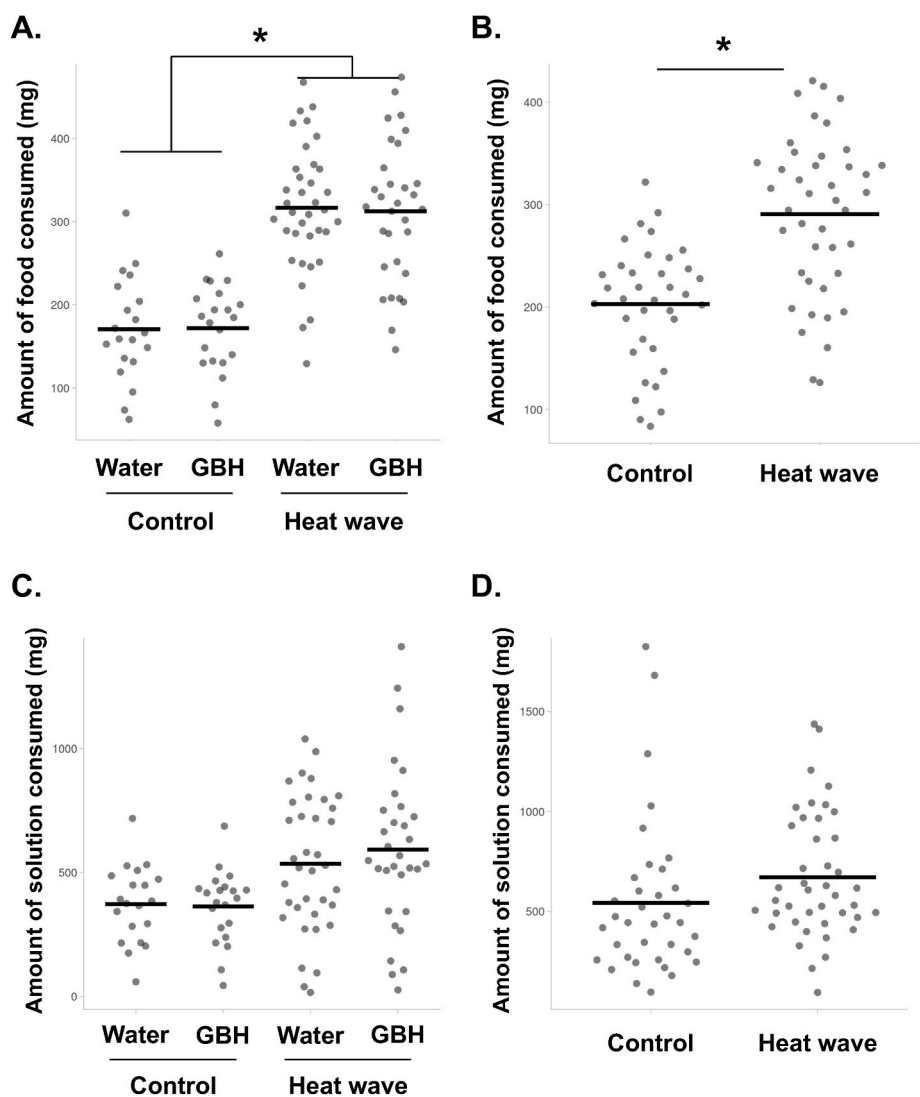

Fig. 4. Heat wave increased feeding, but not drinking. Effects of temperature (control or heat wave) and water treatment (tap water or glyphosate-based herbicide [GBH]) experienced during adulthood on amount of food (dry cat food pellets) in (A) Experiment 1 and (B) Experiment 2, as well as on the amount of drinking solution consumed by *G. lineaticeps* in (C) Experiment 1 and (D) Experiment 2. Raw values are displayed, but analyses accounted for covariates (e.g., initial body mass; see *2.4* for details). Superscripted asterisks denote significant differences.

conversion efficiencies, or food consumption (Tables A1 – A5).

4. Discussion

Features of environmental change influence many organisms'

investment into key life-history traits, such as growth, reproduction, and self-maintenance (Leicht et al., 2013; Ruiz-Vera et al., 2015; Wright et al., 2017; Detto et al., 2018; Carreira et al., 2020; Rosa and Saastamoinen, 2021; Wootton et al., 2022). However, the dynamics by which multiple potential environmental stressors affect tradeoffs between

life-history traits are unclear. Thus, we integrated the multiple-stressor framework and life-history theory to better understand how animals respond to their rapidly changing environments. Our results in a field cricket indicate that a simulated heat wave affects the life-history tradeoff between investment into reproductive and non-reproductive tissues (Fig. 3, A1, and A2). Specifically, heat wave prioritized investment into ovary mass over non-reproductive tissue, even after accounting for food consumption, in support of the TI hypothesis (Fig. 3, A1, and A2). In contrast, GBH exposure did not affect any measured trait, and crickets did not discriminate between tap water and GBH solution during drinking (Figs. 3 and 4, A1, and A2). Therefore, some—but not all—aspects of environmental change may alter resource investment strategies in animals.

A simulated heat wave approximately doubled reproductive investment at the expense of somatic investment in support of the TI hypothesis (Fig. 3, A1, and A2). However, the effects of warming on investment strategy in other taxa are remarkably mixed—plants (TI: Detto et al., 2018; RR: Ruiz-Vera et al., 2015), insects (TI: Rosa and Saastamoinen, 2021; RR: Denis et al., 2013), snails (RR: Carreira et al., 2020; but see [Leicht et al., 2013]: heat wave promoted both growth and reproduction), and fishes (TI: Wootton et al., 2022; RR: Wright et al., 2017). Life-history theory proposes that higher threat levels favor TI over RR (reviewed in Duffield et al., 2017; Jehan et al., 2022). Although heat wave-induced mortality was low in our study (<4% in Expt. 1, and 1% in Expt. 2), warmer temperatures increase mortality in adult *Gryllus* in more natural conditions (i.e., when food is limited: Adamo et al., 2012; Padda et al., 2021). Sublethal threats (e.g., exposure to heat-killed bacteria or LPS) are often used to test for TI and RR because the lethal threat of infection may entail parasitic manipulation that confounds animals' strategic shifts in investment into life-history traits (reviewed in Duffield et al., 2017). Although we used a different type of threat, heat and immune challenge share a commonality—they both have dose-dependent effects where higher temperatures and immune challenge are more stressful. Thus, researchers should continue to use heat exposure to test for TI and RR in the context of climate change, but consideration must be taken when designing experiments and interpreting results.

Warming induces metabolic shifts that may underlie changes in investment strategy. Warmer temperatures typically require increased metabolic rate (reviewed in Angilletta, 2009). However, the ability to reduce energy expenditure during acclimation to warmer temperatures is exhibited by a broad range of organisms– from plants and fungi (Ow et al., 2008a,b; Malcolm et al., 2008) to invertebrates (Powell and Watts, 2006; Lachenicht et al., 2010; Padda et al., 2021) and vertebrates (Geiser et al., 2003; Donelson et al., 2011; Strobel et al., 2012; Abdel-qader and Al-Fataftah, 2014; Seebacher and Grigaltchik, 2014; Stahlschmidt et al., 2015). Although the acclimating effect of hypo-metabolism may be a fundamental feature of thermal plasticity, it is unclear how a shift in investment into life-history traits is associated with a more efficient use of energy (i.e., lower metabolic rate). Yet, our study may provide important clues because food, but not water, consumption increased due to heat wave exposure (Fig. 4). As such, crickets may have increased their production of metabolic water from fat body during heat exposure to reduce net investment into somatic tissue stores and eliminate the need to increase water consumption (Figs. 3 and 4, and A2). In other animals, dry environments and food sources can promote metabolic water production from lipids, which reduces investment into somatic tissue (Frank, 1988; Hadley, 1994; Jindra and Sehnal, 1990; Nicolson, 2009). Water availability can influence this dependence on lipids for water production in free-living insects (Becker and McCluney, 2021), and our results indicate that increased water availability may blunt the reduced investment into somatic tissue. Specifically, crickets in Expt. 2 had more water sources to choose from, drank more water, and had reduced shifts in investment strategy (Figs. 3 and 4, A1, and A2). Future work should continue to incorporate the roles of energy and water balance in investment strategy, particularly given

the increasing prevalence of heat and drought conditions (Sarhadi et al., 2018).

We designed our experiments to determine how investment strategy was affected by multiple stressors. However, we were unable to incorporate the multiple-stressor framework here because GBH exposure was not a detectable stressor (i.e., a factor that disrupts homeostasis, performance, or fitness: Schulte, 2014; Kaunisto et al., 2016). Although the adverse effects of GBH on animals are increasingly well-documented, glyphosate alone and GBH may have subtle or complex effects on animals (Gill et al., 2018; Zhang et al., 2019; Battisti et al., 2021). Work in *G. lineaticeps* has used a field-relevant concentration in a typical formulation (i.e., Roundup® Super Concentrate diluted to 5 mg glyphosate/L of tap H_2O: reviewed in Herbert et al., 2014; Motta et al., 2018), and effects vary considerably– faster development of nymphs and reduced feeding, growth, and lifespan in adults, but no effects on embryonic development or success, or adult body size, flight capacity, or reproduction (Stahlschmidt and Vo, 2022; Stahlschmidt et al., 2022). Had we used higher concentrations of GBH in this study, our results may have been different because glyphosate and GBH have dose-dependent effects on vertebrates (Çavaş and Könen, 2007; Sani and Idris, 2016; Lanzarin et al., 2019) and invertebrates (Hong et al., 2018; Liang et al., 2023), including insects (Baglan et al., 2018; Delkash-Roudsari et al., 2020; Straw et al., 2021; Adamski et al., 2023). Other emerging features of environmental change also exhibit complex dynamics in animal life. For example, a recent meta-analysis demonstrates that animals strongly respond to artificial light at night (a.k.a., ecological light pollution) for some traits (e.g., daily activity patterns and hormone levels), but not others (e.g., stress and immune responses, and biodiversity) (Sanders et al., 2021). Meta-analytical approaches have examined GBH's effects on mortality in bees (Battisti et al., 2021) and on non-Hodgkin lymphoma in humans (Zhang et al., 2019), but we encourage a broader approach to comprehensively understand the role of GBH as a potential stressor across animals.

5. Conclusions

Animals will be increasingly exposed to heat waves and GBHs (Benbrook, 2016; Maggi et al., 2020; IPCC et al., 2021), and the multiple-stressor framework can inform the dynamics by which complex environmental change affects animals' strategic investments into life-history traits. On one hand, we show in separate experiments that a single heat wave event during adulthood can strongly influence the allocation tradeoff between reproductive and somatic tissues indicative of TI (Figs. 3 and 4, A1 and A2). We encourage continued investigations into the links between heat and investment strategy, such as the effects of multiple heat waves across ontogeny because the frequency and developmental timing of heat waves can strongly influence life-history traits in insects (Kingsolver et al., 2021). On the other hand, our results related to GBH exposure highlight our limited understanding of emergent stressors in our changing world. We recommend future work examining other, more stressful features of environmental change combined with thermal stressors, such as exposure to heat waves or gradual warming. Further, the complexity of many environments cannot be captured in one or two variables, and the multiple-stressor framework provides a robust construct to investigate the combined effects of three or more stressors on investment strategy.

CRediT author statement

Stahlschmidt, Z.R. – conceptualization, methodology, formal analysis, resources, visualization, supervision, project administration, writing.

Choi, J. – investigation, writing.

Choy, B. – investigation, writing.

Perez, P.L. – investigation, writing.

Whitlock, J. – investigation, writing.

Funding statement

Declaration of competing interest

We declare no conflicts of interest.

Data availability

Other (please explain: e.g. 'I have shared the link to my data as an attachment').

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2023.103670.

References

Abdelqader, A., Al-Fataftah, A.-., 2014. Thermal acclimation of broiler birds by intermittent heat exposure. J. Therm. Biol. 39 (1), 1–5. https://doi.org/10.1016/j.jtherbio.2013.11.001.

Adamo, S.A., 1999. Evidence for adaptive changes in egg laying in crickets exposed to bacteria and parasites. Anim. Behav. 57 (1), 117–124. https://doi.org/10.1006/anbe.1998.0999.

Adamo, S.A., Baker, J.L., Lovett, M.M.E., Wilson, G., 2012. Climate change and temperate zone insects: the tyranny of thermodynamics meets the world of limited resources. Environ. Entomol. 41 (6), 1644–1652. https://doi.org/10.1603/EN11188.

Adamski, Z., Dzięgelewska, A., Jakubiak, P., Klimaszyk, P., 2023. Lethal and sublethal effects of exposure to Roundup 360 Plus for the *Chaoborus flavicans* larvae (Diptera: Chaoboridae). Turk. J. Zool. 47 (2), 103–110. https://doi.org/10.55730/1300-0179.3120.

Angilletta, M.J., 2009. Thermal Adaptation: A Theoretical and Empirical Synthesis. Oxford University Press, Oxford. https://doi.org/10.1093/acprof:oso/9780198570875.001.1.

Arrese, E.L., Soulages, J.L., 2010. Insect fat body: energy, metabolism, and regulation. Annu. Rev. Entomol. 55, 207–255. https://doi.org/10.1146/annurev-ento-112408-085356.

Baglan, H., Lazzari, C.R., Guerrieri, F.J., 2018. Glyphosate impairs learning in *Aedes aegypti* mosquito larvae at field-realistic doses. J. Exp. Biol. 221 (20) https://doi.org/10.1242/jeb.187518.

Battisti, L., Potrich, M., Sampaio, A.R., de Castilhos Ghisi, N., Costa-Maia, F.M., Abati, R., Sofia, S.H., 2021. Is Glyphosate Toxic to Bees? A Meta-Analytical Review. Science of the Total Environment, p. 767. https://doi.org/10.1016/j.scitotenv.2021.145397.

Becker, J.E., McCluney, K.E., 2021. Urbanization-driven climate change increases invertebrate lipid demand, relative to protein—a response to dehydration. Funct. Ecol. 35 (2), 411–419. https://doi.org/10.1111/1365-2435.13720.

Benbrook, C.M., 2016. Trends in glyphosate herbicide use in the United States and globally. Environ. Sci. Eur. 28 (1), 1–15. https://doi.org/10.1186/s12302-016-0070-0.

Bonneaud, C., Mazuc, J., Chastel, O., Westerdahl, H., Sorci, G., 2004. Terminal investment induced by immune challenge and fitness traits associated with major histocompatibility complex in the house sparrow. Evolution 58 (12), 2823–2830. https://doi.org/10.1111/j.0014-3820.2004.tb01633.x.

Carreira, B.M., Segurado, P., Laurila, A., Rebelo, R., 2020. Heat waves trigger swift changes in the diet and life-history of a freshwater snail. Hydrobiologia 847 (4), 999–1011. https://doi.org/10.1007/s10750-019-04155-3.

Çavaş, T., Könen, S., 2007. Detection of cytogenetic and DNA damage in peripheral erythrocytes of goldfish (*Carassius auratus*) exposed to a glyphosate formulation using the micronucleus test and the comet assay. Mutagenesis 22 (4), 263–268. https://doi.org/10.1093/mutage/gem012.

Crain, C.M., Kroeker, K., Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecol. Lett. 11 (12), 1304–1315. https://doi.org/10.1111/j.1461-0248.2008.01253.x.

Delkash-Roudsari, S., Chicas-Mosier, A.M., Goldansaz, S.H., Talebi-Jahromi, K., Ashouri, A., Abramson, C.I., 2020. Assessment of Lethal and Sublethal Effects of Imidacloprid, Ethion, and Glyphosate on Aversive Conditioning, Motility, and Lifespan in Honey Bees (*Apis mellifera* L.). Ecotoxicology and Environmental Safety, p. 204. https://doi.org/10.1016/j.ecoenv.2020.111108.

Denis, D., Van Baaren, J., Pierre, J.-., Wajnberg, E., 2013. Evolution of a physiological trade-off in a parasitoid wasp: how best to manage lipid reserves in a warming environment. Entomol. Exp. Appl. 148 (1), 27–38. https://doi.org/10.1111/eea.12075.

Detto, M., Wright, S.J., Calderón, O., Muller-Landau, H.C., 2018. Resource acquisition and reproductive strategies of tropical forest in response to the el niño-southern oscillation. Nat. Commun. 9 (1) https://doi.org/10.1038/s41467-018-03306-9.

Donelson, J.M., Munday, P.L., McCormick, M.I., Nilsson, G.E., 2011. Acclimation to predicted ocean warming through developmental plasticity in a tropical reef fish. Global Change Biol. 17 (4), 1712–1719. https://doi.org/10.1111/j.1365-2486.2010.02339.x.

Dosio, A., Mentaschi, L., Fischer, E.M., Wyser, K., 2018. Extreme heat waves under 1.5 °C and 2 °C global warming. Environ. Res. Lett. 13 (5) https://doi.org/10.1088/1748-9326/aab827.

Duffield, K.R., Bowers, E.K., Sakaluk, S.K., Sadd, B.M., 2017. A dynamic threshold model for terminal investment. Behav. Ecol. Sociobiol. 71 (12) https://doi.org/10.1007/s00265-017-2416-z.

Eder, Y., Tschink, D., Gerlach, G., Strahl, J., 2018. Physiology of juvenile hydroids - high food availability mitigates stress responses of *Hydractinia echinata* to increasing seawater temperatures. J. Exp. Mar. Biol. Ecol. 508, 64–72. https://doi.org/10.1016/j.jembe.2018.07.009.

Frank, C.L., 1988. Diet selection by a heteromyid rodent: role of net metabolic water production. Ecology 69 (6), 1943–1951. https://doi.org/10.2307/1941171.

French, S.S., Johnston, G.I.H., Moore, M.C., 2007. Immune activity suppresses reproduction in food-limited female tree lizards *Urosaurus ornatus*. Funct. Ecol. 21 (6), 1115–1122. https://doi.org/10.1111/j.1365-2435.2007.01311.x.

Geiser, F., Drury, R.L., McAllan, B.M., Wang, D.-., 2003. Effects of temperature acclimation on maximum heat production, thermal tolerance, and torpor in a marsupial. J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. 173 (5), 437–442. https://doi.org/10.1007/s00360-003-0352-x.

Gill, J.P.K., Sethi, N., Mohan, A., Datta, S., Girdhar, M., 2018. Glyphosate toxicity for animals. Environ. Chem. Lett. 16 (2), 401–426. https://doi.org/10.1007/s10311-017-0689-0.

Glass, J.R., Stahlschmidt, Z.R., 2019. Should I stay or should I go? Complex environments influence the developmental plasticity of flight capacity and flight-related trade-offs. Biol. J. Linn. Soc. 128 (1), 59–69. https://doi.org/10.1093/biolinnean/blz073.

Hadley, NF., 1994. Water Relations of Terrestrial Arthropods. Academic Press.

Herbert, L.T., Vázquez, D.E., Arenas, A., Farina, W.M., 2014. Effects of field-realistic doses of glyphosate on honeybee appetitive behaviour. J. Exp. Biol. 217 (19), 3457–3464. https://doi.org/10.1242/jeb.109520.

Hong, Y., Yang, X., Huang, Y., Yan, G., Cheng, Y., 2018. Assessment of the oxidative and genotoxic effects of the glyphosate-based herbicide roundup on the freshwater shrimp. Macrobrachium nipponensis. Chemosphere 210, 896–906. https://doi.org/10.1016/j.chemosphere.2018.07.069.

Im, H., Na, J., Jung, J., 2020. The effect of food availability on thermal stress in daphnia magna: trade-offs among oxidative stress, somatic growth, and reproduction. Aquat. Ecol. 54 (4), 1201–1210. https://doi.org/10.1007/s10452-020-09804-7.

IPCC, 2021. In: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.B.R., Maycock, T.K., Waterfield, T., Yelekçi, O., Yu, R., Zhou, B. (Eds.), Climate Change 2021: the Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. https://doi.org/10.1017/9781009157896 (in press).

Jehan, C., Sabarly, C., Rigaud, T., Moret, Y., 2022. Age-specific fecundity under pathogenic threat in an insect: terminal investment versus reproductive restraint. J. Anim. Ecol. 91 (1), 101–111. https://doi.org/10.1111/1365-2656.13604.

Jindra, M., Sehnal, F., 1990. Linkage between diet humidity, metabolic water production and heat dissipation in the larvae of *Galleria mellonella*. Insect Biochem. 20 (4), 389–395. https://doi.org/10.1016/0020-1790(90)90059-4.

Johnston, A.S.A., Hodson, M.E., Thorbek, P., Alvarez, T., Sibly, R.M., 2014. An energy budget agent-based model of earthworm populations and its application to study the effects of pesticides. Ecol. Model. 280, 5–17. https://doi.org/10.1016/j.ecolmodel.2013.09.012.

Kabat, G.C., Price, W.J., Tarone, R.E., 2021. On recent meta-analyses of exposure to glyphosate and risk of non-Hodgkin's lymphoma in humans. Cancer Causes Control 32 (4), 409–414. https://doi.org/10.1007/s10552-020-01387-w.

Kaunisto, S., Ferguson, L.V., Sinclair, B.J., 2016. Can we predict the effects of multiple stressors on insects in a changing climate? Curr. Opin. Insect Sci. 17, 55–61. https://doi.org/10.1016/j.cois.2016.07.001.

Kingsolver, J.G., Moore, M.E., Augustine, K.E., Hill, C.A., 2021. Responses of *Manduca sexta* larvae to heat waves. J. Exp. Biol. 224 (7) https://doi.org/10.1242/jeb.236505.

Lachenicht, M.W., Clusella-Trullas, S., Boardman, L., Le Roux, C., Terblanche, J.S., 2010. Effects of acclimation temperature on thermal tolerance, locomotion performance and respiratory metabolism in *Acheta domesticus* L. (Orthoptera: Gryllidae). J. Insect Physiol. 56 (7), 822–830. https://doi.org/10.1016/j.jinsphys.2010.02.010.

Lanzarin, G.A.B., Félix, L.M., Santos, D., Venâncio, C.A.S., Monteiro, S.M., 2019. Dose-dependent effects of a glyphosate commercial formulation – roundup® UltraMax - on the early zebrafish embryogenesis. Chemosphere 223, 514–522. https://doi.org/10.1016/j.chemosphere.2019.02.071.

Leicht, K., Jokela, J., Seppälä, O., 2013. An experimental heat wave changes immune defense and life history traits in a freshwater snail. Ecol. Evol. 3 (15), 4861–4871. https://doi.org/10.1002/ece3.874.

Lemaitre, B., Hoffmann, J., 2007. The host defense of *Drosophila melanogaster*. Annu. Rev. Immunol. 25, 697–743. https://doi.org/10.1146/annurev.immunol.25.022106.141615.

Liang, D., Li, Y., Li, S., Meng, D., Li, F., Huang, S., et al., 2023. Dose-dependent inhibitory effects of glyphosate on invasive *Pomacea canaliculata* reproductive and developmental growth under oxidative deposition. Ecotoxicol. Environ. Saf. 253. https://doi.org/10.1016/j.ecoenv.2023.114659.

Maggi, F., la Cecilia, D., Tang, F.H.M., McBratney, A., 2020. The Global Environmental Hazard of Glyphosate Use. Science of the Total Environment, p. 717. https://doi.org/10.1016/j.scitotenv.2020.137167.

Malcolm, G.M., López-gutiérrez, J.C., Koide, R.T., Eissenstat, D.M., 2008. Acclimation to temperature and temperature sensitivity of metabolism by ectomycorrhizal fungi. Global Change Biol. 14 (5), 1169–1180. https://doi.org/10.1111/j.1365-2486.2008.01555.x.

McRae, B.H., Schumaker, N.H., McKane, R.B., Busing, R.T., Solomon, A.M., Burdick, C. A., 2008. A multi-model framework for simulating wildlife population response to land-use and climate change. Ecol. Model. 219 (1–2), 77–91. https://doi.org/10.1016/j.ecolmodel.2008.08.001.

Moret, Y., Schmid-Hempel, P., 2004. Social life-history response to individual immune challenge of workers of *Bombus terrestris* L.: a possible new cooperative phenomenon. Ecol. Lett. 7 (2), 146–152. https://doi.org/10.1046/j.1461-0248.2003.00561.x.

Motta, E.V.S., Raymann, K., Moran, N.A., 2018. Glyphosate perturbs the gut microbiota of honey bees. In: Proceedings of the National Academy of Sciences of the United States of America, vol. 115, pp. 10305–10310. https://doi.org/10.1073/pnas.1803880115, 41.

Nelson, K.C., Palmer, M.A., Pizzuto, J.E., Moglen, G.E., Angermeier, P.L., Hilderbrand, R. H., Hayhoe, K., 2009. Forecasting the combined effects of urbanization and climate change on stream ecosystems: from impacts to management options. J. Appl. Ecol. 46 (1), 154–163. https://doi.org/10.1111/j.1365-2664.2008.01599.x.

Nicolson, S.W., 2009. Water homeostasis in bees, with the emphasis on sociality. J. Exp. Biol. 212 (3), 429–434. https://doi.org/10.1242/jeb.022343.

Ow, L.F., Griffin, K.L., Whitehead, D., Walcroft, A.S., Turnbull, M.H., 2008a. Thermal acclimation of leaf respiration but not photosynthesis in *Populus deltoides x nigra*. New Phytol. 178 (1), 123–134. https://doi.org/10.1111/j.1469-8137.2007.02357.x.

Ow, L.F., Whitehead, D., Walcroft, A.S., Turnbull, M.H., 2008b. Thermal acclimation of respiration but not photosynthesis in pinus radiata. Funct. Plant Biol. 35 (6), 448–461. https://doi.org/10.1071/FP08104.

Padda, S.S., Glass, J.R., Stahlschmidt, Z.R., 2021. When it's hot and dry: life-history strategy influences the effects of heat waves and water limitation. J. Exp. Biol. 224 (7) https://doi.org/10.1242/jeb.236398.

Powell, M.L., Watts, S.A., 2006. Effect of temperature acclimation on metabolism and hemocyanin binding affinities in two crayfish, *Procambarus clarkii* and *Procambarus zonangulus*. Compar. Biochem. Physiol. - A Mol. Integ. Physiol. 144 (2), 211–217. https://doi.org/10.1016/j.cbpa.2006.02.032.

Przeslawski, R., Byrne, M., Mellin, C., 2015. A review and meta-analysis of the effects of multiple abiotic stressors on marine embryos and larvae. Global Change Biol. 21 (6), 2122–2140. https://doi.org/10.1111/gcb.12833.

Roff, D.A., 1992. The Evolution of Life Histories: Theory and Analysis. Chapman and Hall, London.

Rohr, J.R., Palmer, B.D., 2013. Climate change, multiple stressors, and the decline of ectotherms. Conserv. Biol. 27 (4), 741–751. https://doi.org/10.1111/cobi.12086.

Rohr, J.R., Sesterhenn, T.M., Stieha, C., 2011. Will climate change reduce the effects of a pesticide on amphibians? Partitioning effects on exposure and susceptibility to contaminants. Global Change Biol. 17 (2), 657–666. https://doi.org/10.1111/j.1365-2486.2010.02301.x.

Rosa, E., Saastamoinen, M., 2021. Warm-night temperature alters paternal allocation strategy in a north temperate-zone butterfly. Ecol. Evol. 11 (23), 16514–16523. https://doi.org/10.1002/ece3.8120.

Ruiz-Vera, U.M., Siebers, M.H., Drag, D.W., Ort, D.R., Bernacchi, C.J., 2015. Canopy warming caused photosynthetic acclimation and reduced seed yield in maize grown at ambient and elevated [CO2]. Global Change Biol. 21 (11), 4237–4249. https://doi.org/10.1111/gcb.13013.

Russo, S., Marchese, A.F., Sillmann, J., Immé, G., 2016. When will unusual heat waves become normal in a warming Africa? Environ. Res. Lett. 11 (5) https://doi.org/10.1088/1748-9326/11/5/054016.

Sanders, D., Frago, E., Kehoe, R., Patterson, C., Gaston, K.J., 2021. A meta-analysis of biological impacts of artificial light at night. Nature Ecol. Evol. 5 (1), 74–81. https://doi.org/10.1038/s41559-020-01322-x.

Sani, A., Idris, M.K., 2016. Acute toxicity of herbicide (glyphosate) in *Clarias gariepinus* juveniles. Toxicol Rep 3, 513–515. https://doi.org/10.1016/j.toxrep.2016.05.004.

Sarhadi, A., Ausín, M.C., Wiper, M.P., Touma, D., Diffenbaugh, N.S., 2018. Multidimensional risk in a nonstationary climate: joint probability of increasingly severe warm and dry conditions. Sci. Adv. 4 (11) https://doi.org/10.1126/sciadv.aau3487.

Schneider, K.R., Van Thiel, L.E., Helmuth, B., 2010. Interactive effects of food availability and aerial body temperature on the survival of two intertidal *Mytilus* species. J. Therm. Biol. 35 (4), 161–166. https://doi.org/10.1016/j.jtherbio.2010.02.003.

Schulte, P.M., 2014. What is environmental stress? insights from fish living in a variable environment. J. Exp. Biol. 217 (1), 23–34. https://doi.org/10.1242/jeb.089722.

Seebacher, F., Grigaltchik, V.S., 2014. Embryonic developmental temperatures modulate thermal acclimation of performance curves in tadpoles of the frog *Limnodynastes peronii*. PLoS One 9 (9). https://doi.org/10.1371/journal.pone.0106492.

Shafiei Shiva, J., Chandler, D.G., Kunkel, K.E., 2019. Localized changes in heat wave properties across the United States. Earth's Future 7 (3), 300–319. https://doi.org/10.1029/2018EF001085.

Shoemaker, K.L., Adamo, S.A., 2007. Adult female crickets, *Gryllus texensis*, maintain reproductive output after repeated immune challenges. Physiol. Entomol. 32 (2), 113–120. https://doi.org/10.1111/j.1365-3032.2006.00552.x.

Stahlschmidt, Z.R., Jodrey, A.D., Luoma, R.L., 2015. Consequences of complex environments: temperature and energy intake interact to influence growth and metabolic rate. Comp. Biochem. Physiol., A : Molecular and Integrative Physiology 187, 1–7. https://doi.org/10.1016/j.cbpa.2015.04.007.

Stahlschmidt, Z.R., Vo, C., 2022. Spatial bet hedging, thermal trade-offs and glyphosate: crickets integrate multivariate information during oviposition. Anim. Behav. 185, 105–112. https://doi.org/10.1016/j.anbehav.2022.01.007.

Stahlschmidt, Z.R., Whitlock, J., Vo, C., Evalen, P., Bui, D., 2022. Pesticides in a warmer world: effects of glyphosate and warming across insect life stages. Environ. Pollut. 307 https://doi.org/10.1016/j.envpol.2022.119508.

Stearns, S.C., 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

Straw, E.A., Carpentier, E.N., Brown, M.J.F., 2021. Roundup causes high levels of mortality following contact exposure in bumble bees. J. Appl. Ecol. 58 (6), 1167–1176. https://doi.org/10.1111/1365-2664.13867.

Strobel, A., Bennecke, S., Leo, E., Mintenbeck, K., Pörtner, H.O., Mark, F.C., 2012. Metabolic shifts in the Antarctic fish *Notothenia rossii* in response to rising temperature and PCO2. Front. Zool. 9 https://doi.org/10.1186/1742-9994-9-28.

Sun, Y., Hu, T., Zhang, X., 2018. Substantial increase in heat wave risks in China in a future warmer world. Earth's Future 6 (11), 1528–1538. https://doi.org/10.1029/2018EF000963.

Sun, B.-J., Huebner, C., Treidel, L.A., et al., 2020. Nocturnal dispersal flight of crickets: behavioural and physiological responses to cool environmental temperatures. Funct. Ecol. 34, 1907–1920. https://doi.org/10.1111/1365-2435.13615.

Todgham, A.E., Stillman, J.H., 2013. Physiological responses to shifts in multiple environmental stressors: relevance in a changing world. Integr. Comp. Biol. 53 (4), 539–544. https://doi.org/10.1093/icb/ict086.

van Noordwijk, A.J., de Jong, G., 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. Am. Nat. 128, 137–142. https://doi.org/10.1086/284547.

Weissman, D.B., Gray, D.A., 2019. Crickets of the genus *Gryllus* in the United States (zrthoptera: Gryllidae: Gryllinae). Zootaxa 4705 (1), 1–277. https://doi.org/10.11646/zootaxa.4705.1.1.

Wootton, H.F., Morrongiello, J.R., Schmitt, T., Audzijonyte, A., 2022. Smaller adult fish size in warmer water is not explained by elevated metabolism. Ecol. Lett. 25 (5), 1177–1188. https://doi.org/10.1111/ele.13989.

Wright, P.J., Orpwood, J.E., Scott, B.E., 2017. Impact of rising temperature on reproductive investment in a capital breeder: the lesser sandeel. J. Exp. Mar. Biol. Ecol. 486, 52–58. https://doi.org/10.1016/j.jembe.2016.09.014.

Xu, Y.-., Yang, D.-., Wang, D.-., 2012. No evidence for a trade-off between reproductive investment and immunity in a rodent. PLoS One 7 (5). https://doi.org/10.1371/journal.pone.0037182.

Zera, A.J., 2005. Intermediary metabolism and life history trade-offs: lipid metabolism in lines of the wing-polymorphic cricket, *Gryllus firmus*, selected for flight capability vs. early age reproduction. Integr. Comp. Biol. 45 (3), 511–524. https://doi.org/10.1093/icb/45.3.511.

Zera, A.J., Harshman, L.G., 2001. The physiology of life history trade-offs in animals. Annu. Rev. Ecol. Systemat. 32, 95–126. https://doi.org/10.1146/annurev.ecolsys.32.081501.114006.

Zera, A.J., Larsen, A., 2001. The metabolic basis of life history variation: genetic and phenotypic differences in lipid reserves among life history morphs of the wing-polymorphic cricket. Gryllus firmus. J. Insect Physiol. 47 (10), 1147–1160. https://doi.org/10.1016/S0022-1910(01)00096-8.

Zhang, L., Rana, I., Shaffer, R.M., Taioli, E., Sheppard, L., 2019. Exposure to glyphosate-based herbicides and risk for non-Hodgkin lymphoma: a meta-analysis and supporting evidence. Mutat. Res., Rev. Mutat. Res. 781, 186–206. https://doi.org/10.1016/j.mrrev.2019.02.001.