

Spatial bet hedging, thermal trade-offs and glyphosate: crickets integrate multivariate information during oviposition

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Animals are increasingly exposed to thermal and chemical stressors across spatially heterogeneous landscapes, and adaptive reproductive decisions may mitigate the effects of multiple stressors. Yet, the combined effects of temperature and glyphosate (a broad-spectrum herbicide that is potentially the most commonly used pesticide worldwide) on maternal decision making and terrestrial embryos are unknown. Here, we integrate the effects of temperature, glyphosate (alone and in its commercial formulation, Roundup®) and spatial heterogeneity on oviposition (egg-laying) behaviour, which affects the fitness of females and their offspring. We used the variable field cricket, *Gryllus lineaticeps*, to test several hypotheses explaining oviposition site selection, specifically the roles of embryo survival, offspring phenotype and maternal survival in oviposition decisions. Temperature (but not glyphosate) affected oviposition and offspring success, with higher performance at intermediate temperatures and lower performance at the extremes, and oviposition increased with the availability of oviposition sites, particularly at warmer temperatures. Environmental context influenced support for oviposition site selection hypotheses. For example, spatial bet hedging (putatively related to maternal survival) was temperature sensitive and it modulated support for the 'offspring phenotype' and 'embryo survival' hypotheses. Specifically, an increased availability of oviposition sites prompted females to oviposit at warmer temperatures, thereby favouring offspring phenotype (increased developmental rate) at an expense to embryo survival (reduced hatching success). In summary, the interconnectedness of spatial and thermal heterogeneity (but not a common pesticide) played large roles in decision making that affects transgenerational fitness.

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Temperature affects all levels of biological organization, and the rising frequency of more thermally variable environments across spatially heterogeneous landscapes continues to threaten animals globally (Sears & Angilletta, 2015; Sears et al., 2016; reviewed in Angilletta, 2009; Vasseur et al., 2014). Animals are also increasingly exposed to nonthermal stressors exhibiting spatial heterogeneity. For example, the use of glyphosate (GLY) has increased nearly 15-fold since the late 1990s, and this broad-spectrum herbicide is now the most commonly used pesticide in the U.S. and, potentially, worldwide (reviewed in Benbrook, 2016). Glyphosate-based herbicides (GBHs) can be toxic to animals, likely due to their inclusion of proprietary surfactants designed to improve the absorption of GLY by plants (Folmar et al., 1979; Gill et al., 2018; Howe et al., 2004; Seok et al., 2011; Vincent & Davidson, 2015). Suboptimal temperatures and GLY/GBH exposure may impose additive costs to

animals, but recent studies indicate the combined costs of these two stressors are nonadditive. For example, temperature can interact with the physiological and behavioural effects of GLY/GBH in aquatic animals (Baier et al., 2016; Fadhlouli & Lavoie, 2021; Gandhi & Cecala, 2016; Parlapiano et al., 2021; Silva et al., 2020) – yet, the combined effects of these two potential stressors on terrestrial animals are unknown.

Multiple stressors are increasingly common (McRae et al., 2008; Nelson et al., 2009; Rohr & Palmer, 2013), but adaptive reproductive decisions can mitigate their effects (Potticary & Duckworth, 2020). Maternal decision making affects the fitness of females and their offspring, and oviposition site selection is a widespread parental behaviour incorporating spatial information (reviewed in Refsnider & Janzen, 2010; Royle et al., 2012). One of the major ecological and evolutionary hypotheses for the nonrandom choice of oviposition sites is that it serves to maximize embryo survival (reviewed in Refsnider & Janzen, 2010). The 'embryo survival' hypothesis predicts that females will prefer ovipositing at sites with thermal or GLY/GBH characteristics that enhance embryo survival (e.g. the

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optimal temperature, T_{opt} , for oviposition matches the T_{opt} for hatching success), and they may also oviposit eggs across multiple sites to improve offspring success (i.e. spatial bet hedging; [Erich et al., 2015](#); [McLaughlin & Wasserberg, 2021](#)), particularly if conditions are suboptimal for offspring survival. A second hypothesis is that oviposition decisions function to modify offspring phenotype (reviewed in [Refsnider & Janzen, 2010](#)). For example, choosing warmer oviposition sites can accelerate embryonic development (reviewed in [Angilletta, 2009](#)), and the 'offspring phenotype' hypothesis predicts that females will select warmer oviposition sites to limit the time that offspring spend in a vulnerable life stage, which may be particularly important if oviposition sites are contaminated with GLY or GBH. Because oviposition can increase females' predation risk, maximizing maternal survival is a third hypothesis for oviposition site selection (reviewed in [Refsnider & Janzen, 2010](#)). The 'maternal survival' hypothesis predicts that females will avoid ovipositing at sites that expose them to stressful conditions, including the risk of predation ([Burger, 1993](#); [Spencer, 2002](#); [Warner & Dill, 2000](#)), and they may also reduce their exploratory behaviour and risk of predation by exhibiting clumped oviposition (i.e. rather than ovipositing evenly across multiple sites). Despite their growing relevance, GLY/GBH exposure, thermal heterogeneity and spatial heterogeneity have not been integrated to understand fitness-related decisions, such as oviposition site selection.

Therefore, we manipulated temperature, GLY/GBH exposure and the availability of oviposition sites to address two related aims. First, we sought to determine the effects of GLY and GBH on the temperature sensitivities of oviposition and offspring success. Second, we examined whether support for oviposition site selection hypotheses (i.e. the 'embryo survival', 'offspring phenotype' and 'maternal survival' hypotheses; [Refsnider & Janzen, 2010](#); see predictions above) varies due to environmental context (e.g. temperature or oviposition site availability). We used the variable field cricket, *Gryllus lineaticeps*, in a series of experiments because oviposition in *Gryllus* crickets is sensitive to a range of factors, including temperature, energetic state, predation risk, immune status and mate quality ([Stahlschmidt & Adamo, 2013](#); [Stahlschmidt, Chu et al., 2020](#); [Stahlschmidt, Jeong et al., 2020](#); [Stahlschmidt et al., 2013, 2014](#)). Furthermore, *G. lineaticeps* is found predominately in California, U.S.A. ([Weissman & Gray, 2019](#)), where GLY is applied to more land area than any other active pesticide ingredient ([California Department of Pesticide Regulation, 2017](#)). The exposure levels of *G. lineaticeps* to GLY in the field, as well as the sensitivity of *G. lineaticeps* to GLY/GBH, are unknown. Thus, we used a concentration of GLY that has shown to negatively affect insect behaviour and physiology when administered via drinking water and is based on field-relevant concentrations (5 mg of GLY/litre of H_2O ; reviewed in [Herbert et al., 2014](#); [Motta et al., 2018](#)). In other taxa, the role of temperature in oviposition has been extensively investigated, and oviposition can also be affected by GLY, GBHs and surfactants contained in GBHs ([de Saraiva et al., 2016](#); [Kibuthu et al., 2016](#); [Prosser et al., 2017](#); [Takahashi, 2007](#); reviewed in [Refsnider & Janzen, 2010](#)). Yet, we are the first to integrate the effects of temperature, GLY/GBH and spatial heterogeneity on oviposition. In summary, our study clarifies the independent and interactive roles of increasingly common environmental factors on maternal decision making and terrestrial embryos.

METHODS

Study Species

Like other *Gryllus* crickets, *G. lineaticeps* is wing dimorphic – adults are either long-winged and often flight capable, or they are

short-winged and flightless ([Weissman & Gray, 2019](#)). Only short-winged crickets were used in the study. They were acquired from a long-term colony that was subsidized annually by progeny from females collected from a natural population (Sedgwick Reserve, Santa Ynez, CA, U.S.A.) that predominately expresses the short-winged phenotype (Z. R. Stahlschmidt, personal observation; L. A. Treidel, personal communication). Throughout ontogeny, these GLY/GBH-naïve crickets were reared in standard conditions: $28 \pm 1^\circ\text{C}$ and 14:10 h light:dark cycle with ad libitum access to water (water-filled shell vials plugged with cotton), commercial dry cat food and shelter (cardboard egg cartons). Adult female crickets were isolated from the colony 6–10 days after final ecdysis to allow time for mating because both sexes are typically sexually receptive at 3–4 days of adult age in *G. lineaticeps* (Z. R. Stahlschmidt, personal observation) and in other *Gryllus* crickets ([Cade & Wyatt, 1984](#); [Solyman & Cade, 1990](#)). Females were then each assigned to one of the experiments described below with ad libitum access to water, food and shelter.

Choice Oviposition Experiment

Females ($N = 174$) were weighed, and each was then transferred to a 1.9-litre translucent plastic container with ad libitum access to food for its choice oviposition trial. Each trial occurred at one of five temperatures (20°C ($N = 36$), 24°C ($N = 33$), 28°C ($N = 35$), 32°C ($N = 36$) or 36°C ($N = 34$)) that reflect the range of thermal microclimates in which eggs are likely laid in the field ([Sun et al., 2020](#)). Three cotton-plugged 30 ml water bottles served as oviposition sites, and they were positioned side by side in each container. An opaque plastic cylindrical sleeve was positioned around each otherwise exposed water-soaked cotton plug, which created a secure, sheltered position for each ovipositing female. Only sheltered sites were used because preliminary trials with 60 *G. lineaticeps* indicated that females would not oviposit in otherwise exposed sites (likely due to increased risk of predation) similar to other *Gryllus* ([Stahlschmidt & Adamo, 2013](#); [Stahlschmidt et al., 2014](#)). Each water bottle was filled with one of three solutions: tap water only (control, CON), glyphosate (GLY; 5 mg/litre 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 GLY-based herbicide (GBH; Roundup® Super Concentrate diluted to 5 mg GLY/litre of H_2O). Both GLY and GBH were included to disentangle the effects of GLY and non-GLY components (i.e. proprietary surfactants) on oviposition and offspring success (see below). Females were allowed to freely oviposit into any of the three substrate treatments. After 24 h, water bottles were removed and the eggs in each cotton plug were counted to determine total oviposition and oviposition specialization (see below). Females were euthanized by freezing at -20°C and then also stored at -20°C . Each female was later dissected and the presence of a sperm-filled spermatheca was recorded. Data from nonmated females ($N = 5$) were not analysed because nonmated crickets generally do not oviposit and nearly 95% of oviposited eggs are fertilized in mated *Gryllus* ([Shoemaker & Adamo, 2007](#)).

Oviposition specialization (coefficient of variation (%)) of oviposited eggs; $100 \times (\sigma/\mu)$ was used to estimate the trade-off between maternal predation risk avoidance and offspring fitness for each female that oviposited. Crickets avoid open, exposed environments and their perceived predation risk strongly influences their oviposition decisions ([Stahlschmidt & Adamo, 2013](#); [Stahlschmidt et al., 2014](#)). A high oviposition specialization value reflected the tendency for a given female to reduce behavioural activity and limit exposure to the open (i.e. exposed, nonsheltered) environment, thereby exhibiting spatially clumped oviposition (i.e. potentially favouring maternal safety over offspring fitness:

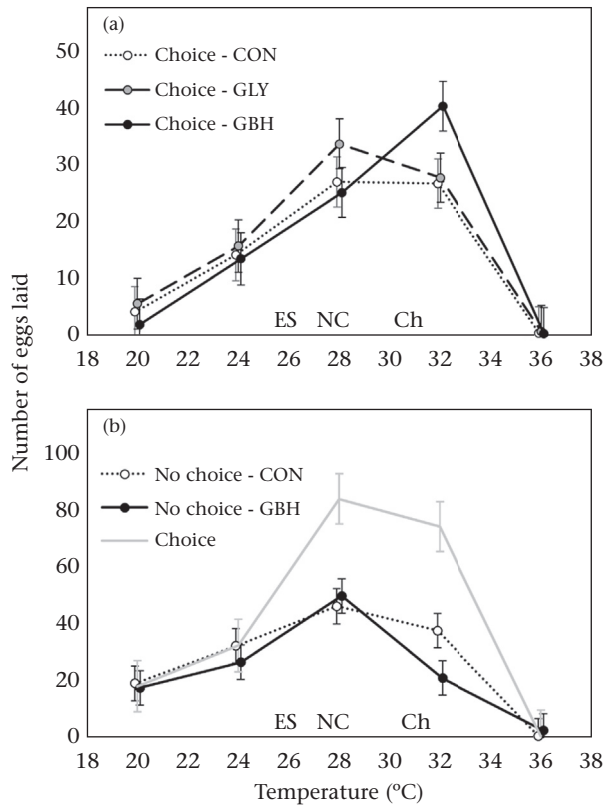


Figure 1. Effects of temperature and oviposition substrate (CON, control; GLY, 5 mg acid equivalent (a.e.) of glyphosate/ml; GBH, glyphosate-based herbicide, 5 mg a.e. of glyphosate/ml) on 24 h egg laying in *G. lineaticeps* where females (a) could choose to oviposit into any of the three substrates (i.e. each female's oviposition is spread among the three plotted series), or (b) were constrained to oviposit into a single site (CON or GBH; i.e. each black series represents the sum total of eggs laid by females). To compare the total number of eggs laid by each female in the choice and no-choice experiments, the grey series in (b) represents the total number of eggs laid by each female pooled across substrate treatments from (a). Along the X axes, the estimated T_{opt} for egg survival (ES), no-choice oviposition (NC) and choice oviposition (Ch) are displayed, and T_{opt} estimates were determined by fitting the data to thermal performance curves (see text for details). Values are displayed as estimated marginal means \pm SEM because maternal body mass was included as a covariate.

reviewed in Refsnider & Janzen, 2010). In contrast, a female with a low oviposition specialization value was one that exhibited oviposition diversification or spatial bet hedging wherein she oviposited eggs more equally across the three sites, thereby potentially improving offspring fitness while increasing her own predation risk. Thus, this experiment allowed us to estimate whether temperature influenced the trade-off between maternal survival and offspring success.

No-choice Oviposition Experiment

Females ($N = 259$) were weighed and generally experienced the same experimental design as in the choice experiment (see above; $N = 51$ – 53 per temperature treatment). However, each female was given access to only one (not three) oviposition sites – either CON or GBH because GLY did not affect oviposition in the choice experiment (see Results). After 24 h, water bottles were removed and the eggs in each cotton plug were counted. Females were euthanized by freezing at -20°C and then also stored at -20°C . Each female was later dissected and the presence of a sperm-filled

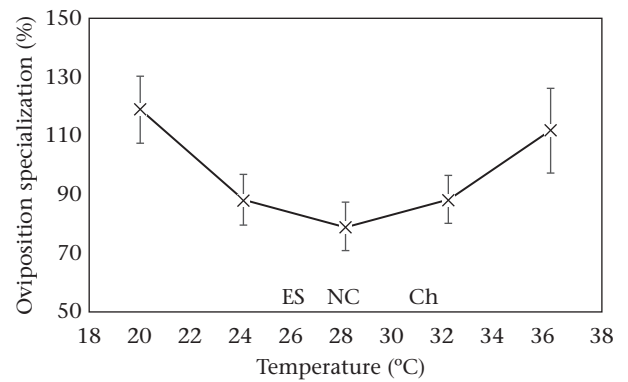


Figure 2. Effects of temperature on oviposition specialization in *G. lineaticeps* where females could choose to oviposit into any of three oviposition sites of varying substrate treatments. A high oviposition specialization value reflected the tendency for a given female to reduce behavioural activity and limit exposure to the open (i.e. exposed, nonsheltered) environment, thereby exhibiting spatially clumped oviposition. A low oviposition specialization value reflected oviposition diversification or spatial bet hedging, wherein eggs were oviposited more equally across the three sites. Along the X axis, the estimated T_{opt} for egg survival (ES), no-choice oviposition (NC) and choice oviposition (Ch) are displayed, and T_{opt} estimates were determined by fitting the data to thermal performance curves (see text for details). Values are displayed as estimated marginal means \pm SEM because maternal body mass was included as a covariate.

spermatheca was recorded. All females were mated and, thus, included in data analyses.

Egg and Hatchling Experiment

Females ($N = 28$) were weighed and experienced the same oviposition substrate options as in the choice experiment (see above). After 24 h at 28°C , water bottles were removed and eggs ($N = 682$ total; mean: 24 eggs per female; range 9–45 eggs per female, depending on the number of eggs laid) were individually incubated in the same substrate treatment in which they were oviposited. Each female's eggs were evenly distributed among the three substrate solutions (CON, GLY or GBH; see above) and three incubators, each of which was maintained at one of the temperatures described above (i.e. 20°C , 24°C , 28°C , 32°C or 36°C) that were chosen at random. Eggs were each incubated in a 1.5 ml microcentrifuge tube that had a small hole poked in its cap with a 1 mm diameter pin to facilitate gas exchange. To maintain egg water balance, each tube contained a small cotton ball (ca. 240 mg) soaked with 0.5 ml of CON, GLY or GBH solution (see above). Glyphosate has a variable half-life in natural water sources exposed to ultraviolet (UV) radiation (49–87 days; reviewed in Mercurio et al., 2014), and it exhibits very low rates of degradation or dissipation in tap water in the absence of UV light exposure (e.g. at least 90% of glyphosate remains after 120 days; Yadev et al., 2017). In natural systems, glyphosate degradation is minimally affected by temperature and is instead largely driven by microbes (Mercurio et al., 2014; Roberts, 1998; Tomlin, 2006). Because there was limited microbial activity and UV radiation in our study, GLY- and GBH-treated eggs likely experienced significant exposure to these chemicals during incubation (8–33 days, depending on temperature). Tubes were placed inside 15-litre plastic containers that were humidified by containing open deli cups filled with water. Eggs in tubes were checked daily to determine egg survival (hatching success) and incubation duration. All females produced viable offspring. Hatchlings were monitored daily until they died to determine hatchling starvation resistance, which is a proxy for

hatchling body size and developmental success in other *Gryllus* (Stahlschmidt & Adamo, 2015; Stahlschmidt et al., 2013).

Statistical Analyses

Data were tested for normality, ln- or square-root-transformed, when necessary (specifically, for the number of eggs laid in the no-choice and choice experiments, respectively), and analysed using SPSS (v.26, IBM Corp., Armonk, NY, U.S.A.). Two-tailed significance was determined at $\alpha = 0.05$. To examine the independent and interactive effects of treatments (substrate and temperature), linear model analyses were performed on the number of eggs laid, oviposition specialization (only for the choice experiment), egg survival, egg incubation duration and hatchling starvation

resistance. A binary logistic generalized linear model was performed on the categorical egg survival data (0: did not survive; 1: survived).

For each model, treatments were included as main effects and maternal body mass was included as a covariate. Maternal identity was included as a random effect for all of the models with the exception of those analysing data from the no-choice experiment. All models tested for interactions between treatments.

To estimate the T_{opt} for oviposition and egg survival, thermal performance curves (TPCs) were tested with several curve estimation regression models (e.g. quadratic, cubic, power, exponential, Gaussian and sigmoidal). All models that significantly fitted the effects of temperature on oviposition and egg survival are reported below, and full results can be found in the Appendix, Table A1.

RESULTS

Choice Oviposition Experiment

The number of eggs laid was greatest at intermediate temperatures ($F_{3,163} = 26.7$, $P < 0.001$) and influenced by a substrate*temperature interaction ($F_{8,328} = 2.2$, $P = 0.030$; Fig. 1a). Only a cubic model significantly fitted the TPC for the number of eggs laid in CON ($R^2 = 0.93$, $F_{2,2} = 13.3$, $P = 0.041$), where estimated $T_{opt} = 29.9$ °C. Similarly, only a cubic model significantly fitted the TPC for the number of eggs laid in GLY ($R^2 = 0.92$, $F_{2,2} = 13.1$, $P = 0.044$), where estimated $T_{opt} = 30.2$ °C. None of the models significantly fitted the TPC for the number of eggs laid in GBH, so estimated $T_{opt} = 32$ °C based on the highest value in our study (Fig. 1a). The number of eggs laid was greater in heavier females ($F_{1,163} = 49.4$, $P < 0.001$), but it was not influenced by substrate treatment ($F_{2,328} = 1.6$, $P = 0.20$; Fig. 1a). Oviposition specialization was greatest at temperature extremes ($F_{4,109} = 2.7$, $P = 0.029$; Fig. 2) and in lighter females ($F_{1,109} = 9.0$, $P = 0.003$).

No-choice Oviposition Experiment

The number of eggs laid was greatest at intermediate temperatures ($F_{4,248} = 33.1$, $P < 0.001$) and in heavier females ($F_{1,248} = 14.6$, $P < 0.001$), but it was not influenced by substrate treatment ($F_{1,248} = 2.6$, $P = 0.11$) or by a substrate*temperature interaction ($F_{4,248} = 0.63$, $P = 0.65$; Fig. 1b). Therefore, data were pooled across substrate treatments to estimate T_{opt} . A quadratic model significantly fitted the TPC for the number of eggs laid ($R^2 = 0.97$, $F_{2,2} = 35.5$, $P = 0.027$), where estimated $T_{opt} = 27.1$ °C. A cubic model also significantly fitted the TPC for the number of eggs laid ($R^2 = 0.99$, $F_{2,2} = 149.4$, $P = 0.007$), where estimated $T_{opt} = 28.3$ °C.

Egg and Hatchling Experiment

Eggs had greater survival at low to intermediate temperatures ($\chi^2_4 = 28.1$, $P < 0.001$) and when laid by lighter females ($\chi^2_1 = 18.8$, $P < 0.001$), but egg survival was not influenced by substrate treatment ($\chi^2_2 = 0.1$, $P = 0.99$) or by a substrate*temperature interaction ($\chi^2_8 = 2.1$, $P = 0.98$; Fig. 3a). Therefore, data were pooled across substrate treatments to estimate T_{opt} . A quadratic model significantly fitted the TPC for egg survival ($R^2 = 0.98$, $F_{2,2} = 53.8$, $P = 0.018$), where estimated $T_{opt} = 24.7$ °C. A cubic model also significantly fitted the TPC for egg survival ($R^2 = 0.99$, $F_{2,2} = 132.7$, $P = 0.007$), where estimated $T_{opt} = 25.9$ °C. Incubation duration was shortest at higher temperatures ($F_{3,304} = 8055.7$, $P < 0.001$) and in eggs laid by lighter females ($F_{1,24} = 10.0$, $P = 0.004$), but it was not influenced by substrate treatment ($F_{2,408} = 0.2$, $P = 0.90$) or by a substrate*temperature interaction ($F_{6,406} = 0.6$, $P = 0.73$;

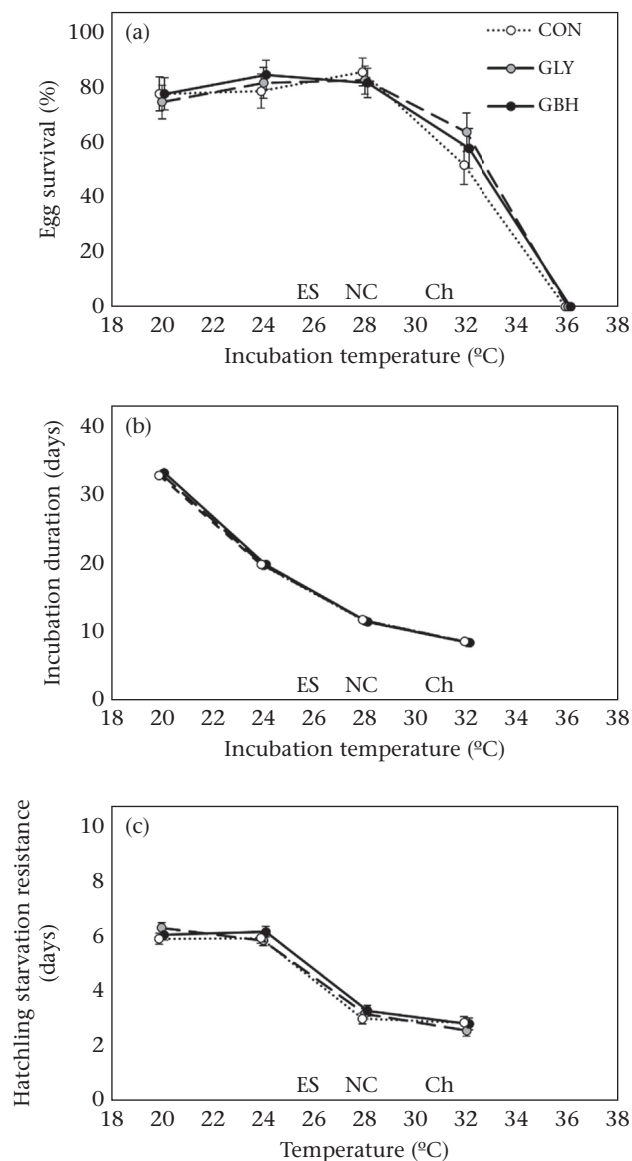


Figure 3. Effects of temperature and incubation substrate (CON, control; GLY, 5 mg acid equivalent (a.e.) of glyphosate/ml; GBH, glyphosate-based herbicide, 5 mg a.e. glyphosate/ml) on (a) egg survival or hatching success, (b) egg incubation duration and (c) hatchling starvation resistance or vigour in *G. lineaticeps*. Along the X axes, the estimated T_{opt} for egg survival (ES), no-choice oviposition (NC) and choice oviposition (Ch) are displayed, and T_{opt} estimates were determined by fitting the data to thermal performance curves (see text for details). Values are displayed as estimated marginal means \pm SEM because maternal body mass was included as a covariate.

Fig. 3b). Starvation resistance was lowest at higher temperatures ($F_{3,210} = 294.1$, $P < 0.001$), but it was not influenced by substrate treatment ($F_{2,413} = 0.8$, $P = 0.45$), a substrate*temperature interaction ($F_{6,408} = 0.9$, $P = 0.47$) or maternal body mass ($F_{1,21} = 0.3$, $P = 0.58$; Fig. 3b).

DISCUSSION

Animals are increasingly exposed to thermal variation and GLY/GBH (reviewed in Benbrook, 2016; Vasseur et al., 2014), but the combined effects of these potential stressors on maternal decision making and terrestrial embryos are unknown. Here, we manipulated temperature, GLY/GBH exposure and the availability of oviposition sites in a field cricket. Our results in *G. lineaticeps* indicate that temperature strongly affected oviposition and offspring success, typical of a thermal reaction norm or TPC (Figs 1, 3). Oviposition was also influenced by the availability of oviposition sites because females laid 65% more eggs when three sites were available relative to only a single site, particularly at warmer temperatures (Fig. 1b; after accounting for maternal body mass as a covariate, effect of experiment (choice versus no-choice) on the total number of eggs laid: $F_{1,422} = 16.3$, $P < 0.001$; interactive effect of experiment and temperature: $F_{4,422} = 6.2$, $P < 0.001$). Yet, GLY and GBH had nominal effects on oviposition and offspring success (Figs 1, 3). We found varied support for three common hypotheses explaining oviposition site selection (i.e. embryo survival, offspring phenotype and maternal survival hypotheses). For example, spatial bet hedging shifted support for the offspring phenotype and embryo survival hypotheses because an increased availability of oviposition sites increased oviposition and promoted thermal decisions favouring developmental rate at an expense to hatching success (Figs 1, 3). In summary, spatial and thermal heterogeneity (but not a common pesticide) played large roles in decision making that affects transgenerational fitness.

Maximizing embryo survival is often considered the most important driver of nonrandom oviposition choice (reviewed in Refsnider & Janzen, 2010), and we found some support for the embryo survival hypothesis in *G. lineaticeps* because females avoided ovipositing at the temperature that was highly lethal to their embryos (i.e. 36 °C; Figs 1, 3a). Yet, the estimated T_{opt} for oviposition was 2.4–7.3 °C higher than the estimated T_{opt} for egg survival, resulting in up to a 72% reduction in hatching success (i.e. from 88% hatching success at 24.7 °C to 51% at 32 °C; Fig. 3a). A similar result has been demonstrated in *Gryllus texensis* (Stahlschmidt & Adamo, 2013), indicating that the thermal mismatch between oviposition and embryonic survival may be common in field crickets. This discrepancy could be due to the importance of embryonic water balance outweighing that of embryonic temperature. Insects sense temperature and moisture via the sensilla of their ovipositors and/or antenna, and thermal reception and hygroreception are often linked (Montell, 2008; Sayeed & Benzer, 1996; Shah, 2012). Therefore, female crickets could interpret suboptimally warm temperatures as favourable for egg survival because these temperatures may signal greater moisture given thermoreception and hygroreception share sensilla on the ovipositors of other insects (Shah, 2012).

The microhabitat in which an egg develops can profoundly affect the phenotype of the embryo, hatchling and/or adult, which can influence higher levels of biological organization (e.g. temperature-dependent sex determination affects population level sex ratios) (Janzen, 1994; reviewed in Refsnider & Janzen, 2010). Some of our results in *G. lineaticeps* support the offspring

phenotype hypothesis because females tended to avoid ovipositing in thermal conditions that were suboptimal for embryonic developmental rate (i.e. 20 °C, 24 °C and 36 °C; Figs 1, 3b). Yet, traits within a given individual can vary in their thermal optima (e.g. warmer temperatures increase developmental rate at an expense to hatchling body size; reviewed in Angilletta, 2009), and the T_{opt} for developmental rate contrasted with the T_{opt} for egg survival and hatchling starvation resistance in our study (Fig. 3). Therefore, our support for the offspring phenotype hypothesis was mixed, and this hypothesis directly conflicted with the embryo survival hypothesis in our study. Thus, the thermal mismatch between oviposition and embryonic survival (see above) may be partly due to females' attempts to balance several fitness-related traits of their offspring.

Predation risk strongly deters oviposition in *G. lineaticeps* and other *Gryllus* (see preliminary results above; Stahlschmidt & Adamo, 2013; Stahlschmidt et al., 2014) in support of the maternal survival hypothesis. Yet, spatial bet hedging during oviposition may balance the costs of predation risks related to movement among several sites (i.e. increased exposure to predators) with the benefits of oviposition diversification (i.e. reducing risk of reproductive failure due to spatially stochastic egg losses). Spatial bet hedging or risk spreading is an adaptive oviposition strategy when future environments are poor or unpredictable in some taxa (Erich et al., 2015; McLaughlin & Wasserberg, 2021; Morrongiello et al., 2012; reviewed in Hopper, 1999). However, *G. lineaticeps* hedged less (not more) in conditions that were thermally unfavourable for their offspring (i.e. high levels of oviposition specialization or 'egg clumping' at 20 °C and 36 °C; Fig. 2). Thus, the cost–benefit analyses for ovipositing *G. lineaticeps* may change with temperature – the benefits of hedging may be lower at temperature extremes where few eggs are likely to succeed (i.e. due to reduced survival or delayed development) whereas the costs of hedging in these conditions are less affected (i.e. predation risks persist). This strategy is influenced by whether a female's lifetime reproduction is more constrained by time or by her supply of eggs (Rosenheim et al., 2008), and our results indicate that oviposition in *G. lineaticeps* may be more constrained by egg supply. Yet, the outcome may be altered by extending oviposition trials from 1 day to 7 days (the natural life span of most adult *Gryllus* is 2–3 weeks: Murray & Cade, 1995; Zera et al., 2007; Zuk, 1987), or by reducing food availability (egg production is strongly tied to food availability in *Gryllus*: e.g. Stahlschmidt & Adamo, 2015; Stahlschmidt, Chu et al., 2020; Stahlschmidt, Jeong et al., 2020). In addition, extreme temperatures may represent stressful conditions that initiate a reduction in risky behaviour because stress can reduce behavioural activity and increase refuge use in many animals (Garcia et al., 2009; Jachowski et al., 2012; Mameri et al., 2020; Morellet et al., 2009). Spatial dynamics also appeared to mediate the decision-making conflict between embryo survival and offspring phenotype (see above) because an increased availability of oviposition sites promoted thermal decisions favouring offspring phenotype (30–32 °C) while a reduced availability of sites promoted decisions favouring egg survival (27–28 °C) (Figs 1, 3). In summary, spatial bet hedging during oviposition can be temperature sensitive and it can mediate parent–offspring and intra-offspring trade-offs.

Many behaviours (e.g. activity, exploration, alarm responses and drinking) are affected by GLY and/or GBH (Bridi et al., 2017; Delkash-Roudsari et al., 2020; Lanzarin et al., 2020; Ren et al., 2018; Tapkir et al., 2019), and GBH and its non-GLY ingredients have even been shown to inhibit oviposition (Prosser et al., 2017; Takahashi, 2007) and negatively affect embryos or larvae of ovipositing insects (Baglan et al., 2018; Rainio et al., 2019). However, *G. lineaticeps*

did not discriminate against ovipositing into GLY- or GBH-exposed sites (Fig. 1), for which we offer two explanations. First, females detected GLY/GBH, but they did not discriminate against these chemicals because they were not costly to embryos (i.e. neither GLY nor GBH affected embryo survival, developmental rate or hatchling starvation resistance; Fig. 3). In which case, *G. lineaticeps* made adaptive oviposition decisions regarding GLY/GBH. Second, females were not capable of detecting GLY/GBH (perhaps because they are not under sufficient selection to do so due to its novelty in their environment or its limited effect on offspring), which did not matter because offspring were unaffected by these chemicals. Here, neither GLY nor GBH induced an oviposition decision in *G. lineaticeps* because they were unable to incorporate this chemical information. Insect chemosensory systems rely on multigene families of chemoreceptors (e.g. olfactory receptors and co-receptors and odorant-binding proteins (OBPs)), and OBPs are the first chemosensory components to encounter odorants, which can be important for oviposition site selection and adaptively evolve to create individual variation in chemosensation (Harada et al., 2012; Jiang et al., 2017; Wang et al., 2010; Xu et al., 2009; Yi et al., 2014). Insecticide exposure increases the expression of OBPs and other chemosensory proteins (Lin et al., 2018), but their sensitivities to GLY or GBH are unknown and require investigation because some insects are adversely affected by these herbicides (e.g. Motta et al., 2018).

In summary, we demonstrate that oviposition in *G. lineaticeps* could not optimize multiple fitness-related traits of offspring. For example, ovipositing at the T_{opt} for egg survival came at costs to T_{opt} for developmental rate and hatchling starvation resistance (Fig. 3). This impossible dilemma (1) indicates that several ecological and evolutionary hypotheses explaining oviposition site selection may be mutually exclusive of one another and (2) facilitates the use of bet hedging to balance trade-offs. Researchers have long recognized that reproductive bet-hedging strategies related to resource allocation are responsive to environmental variation (e.g. the trade-off between the number of eggs and the size or quality of eggs: Fischer et al., 2011; Lack, 1947; Monro et al., 2010; Smith & Fretwell, 1974; Stahlschmidt & Adamo, 2015). We expand on these concepts by highlighting the interconnectedness of spatial dynamics in oviposition and important trade-offs within and between generations – that is, oviposition site availability influenced the thermal trade-off between egg survival and developmental rate, and temperature influenced spatial bet hedging (Figs 1–3). In the absence of predators, perceived predation risk strongly influences reproductive decision making in crickets (Atwell & Wagner, 2015; Hedrick, 2000; Hedrick & Dill, 1993; Stahlschmidt & Adamo, 2013; Stahlschmidt et al., 2014). Yet, the effects of actual predation risk (i.e. via the presence of predators) on reproductive decisions in crickets are less understood and warrant further study. Our results further indicate that GLY and GBH exposure may not be costly to some insect embryos or hatchlings, regardless of temperature (Fig. 3), but work is needed in other taxa. Future studies should also examine the combined effects of GLY/GBH and temperature on other life stages and traits, and it should also seek to fill the knowledge gaps regarding the thermal, hygric and chemical sensitivities of *Gryllus* sensory systems to fully understand the information crickets integrate when making important decisions.

Author Contributions

C.V. and Z.R.S. designed experiment and collected data. Z.R.S. analysed data and led writing of manuscript, and C.V. contributed to writing of manuscript.

Declaration of Interest

None.

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Appendix

Table A1

Regression models testing for thermal performance curves on oviposition in the choice experiment, oviposition in the no-choice experiments and egg survival (note: due to 0% egg survival at 36 °C, functions requiring positive values could not be fitted to the data)

Function	R^2	F	P
Oviposition in the choice experiment			
<i>Control treatment</i>			
Linear	<0.01	0.01	0.92
Logarithmic	0.02	0.06	0.82
Inverse	0.05	0.14	0.73
Quadratic	0.86	6.33	0.14
Cubic	0.93	13.30	0.04
Compound	0.13	0.46	0.55
Power	0.09	0.28	0.63
Sigmoidal	0.05	0.15	0.72
Growth	0.13	0.46	0.55
Exponential	0.13	0.46	0.55
Logistic	0.13	0.46	0.55
<i>Glyphosate treatment</i>			
Linear	<0.01	0.01	0.92
Logarithmic	0.02	0.06	0.82
Inverse	0.05	0.14	0.73
Quadratic	0.86	6.33	0.14
Cubic	0.93	13.30	0.04
Compound	0.13	0.46	0.55
Power	0.09	0.28	0.63
Sigmoidal	0.05	0.15	0.72
Growth	0.13	0.46	0.55
Exponential	0.13	0.46	0.55
Logistic	0.13	0.46	0.55
<i>Glyphosate-based herbicide treatment</i>			
Linear	0.56	5.12	0.09
Logarithmic	0.55	5.00	0.09
Inverse	0.45	3.26	0.15
Quadratic	0.57	1.99	0.28
Cubic	0.90	6.28	0.14
Compound	0.42	2.94	0.16
Power	0.47	3.57	0.13
Sigmoidal	0.47	3.60	0.13
Growth	0.42	2.94	0.16
Exponential	0.42	2.94	0.16
Logistic	0.42	2.94	0.16
Oviposition in the no-choice experiment¹			
Linear	0.13	0.44	0.56
Logarithmic	0.08	0.25	0.65
Inverse	0.04	0.12	0.75
Quadratic	0.97	35.54	0.03
Cubic	0.99	149.35	0.01
Compound	0.30	1.28	0.34
Power	0.23	0.89	0.41
Sigmoidal	0.17	0.61	0.49
Growth	0.30	1.28	0.34
Exponential	0.30	1.28	0.34
Logistic	0.30	1.28	0.34
Egg survival¹			
Linear	0.64	5.33	0.10
Logarithmic	0.56	3.80	0.15
Inverse	0.48	2.75	0.20
Quadratic	0.98	53.79	0.02
Cubic	0.99	132.72	0.01
Compound	—	—	—
Power	—	—	—
Sigmoidal	—	—	—
Growth	—	—	—
Exponential	—	—	—
Logistic	—	—	—

¹ Data from oviposition substrate treatments were pooled when there was no main or interactive effect of substrate treatment.