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Warm and cozy: temperature and predation risk interactively affect oviposition site selection

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Because reproductive decision making affects all taxa, parents often use environmental cues to optimize their decisions. Although prefertilization decisions (e.g. mate choice) are well studied, postfertilization decisions, such as oviposition site selection (OSS), can also have profound effects on parent and offspring fitness. We used the Texas field cricket, *Gryllus texensis*, to examine how OSS was affected by temperature and predation risk. These two factors constrain fitness and may trade off with one another or contribute to parent–offspring conflict (e.g. if ovipositing at offspring's thermal optimum entails increased risk of predation to the parent). Crickets preferred oviposition sites that were warmer and had lower predation risk, but they traded off their preference for temperature with predation risk during OSS. Yet, *G. texensis* preferred to oviposit at sites that were significantly warmer (up to 30.5 °C) than their preferred body temperature and the optimal temperature of offspring (26–27 °C). This thermal mismatch may be due to selection on hygrosensation (not thermosensation). We show that widespread environmental factors can exert complex interactive effects on important reproductive decisions.

Reproductive decision making is important across taxa given its effect on both parent(s) and offspring (Lima 1998, 2009). Thus, animals typically use cues from their environment to optimize their decisions (e.g. forgoing breeding when predation risk is high: reviewed in Lima 2009). Individuals often base mating decisions on multiple, interactive cues that signal costs or benefits, which can result in trade-offs (Fawcett & Johnstone 2003). For example, female crickets make a trade-off between their preference for high-quality mates and low predation risk: they prefer songs from low-quality males when mating with high-quality males entails increased predation risk (Hedrick & Dill 1993; Csada & Neudorf 1995).

Like those made before fertilization, decisions made after fertilization can profoundly influence multiple life-history traits and, thus, may obligate trade-offs. For example, oviposition site selection or nest site selection is widespread, and it affects both egg-laying females (predation risk: Encalada & Peckarsky 2007) and their offspring (body size: Brown & Shine 2004; predation risk and growth rate: Brodin et al. 2006; parasitization: Amano et al. 2008). Although females should prefer to lay eggs in locations that enhance the performance of their offspring (sensu the preference–performance hypothesis: Jaenike 1978; Thompson 1988), recent reviews on the topic yielded equivocal results (Gripenberg et al. 2010; Refsnider & Janzen 2010). Inconsistent support for such adaptive oviposition site selection (OSS) may be the result of insufficient selective pressure for OSS (Potter et al. 2012), females' inability to assess oviposition site quality (Hopper 1999; Gripenberg et al. 2007), or both. Furthermore, trade-offs between aspects of oviposition site suitability may influence OSS. For example, OSS in lepidopteran insects may involve trade-offs between temperature and predation risk to ovipositing females (Eilers et al. 2013) or offspring (Potter et al. 2009, 2012). Thus, like prefertilization decisions, OSS may be affected by interactions between several environmental factors.

Temperature and predation risk are characteristics of oviposition site suitability that are particularly compelling factors to investigate because they constrain fitness across taxa (Lima 1998; Angilletta 2009). They may also contribute to parent–offspring conflict during OSS. Oviposition is time intensive in field crickets (ca. 1 min per egg: Sugawara & Loher 1986) so females may spend a significant amount of time at a given oviposition site. Females and offspring may have different thermal optima leading to oviposition in sites that benefits females at the expense of offspring. Also, some sites may provide an optimal temperature for offspring, but expose females to high risks of predation.

We hypothesize that temperature and predation risk will influence OSS both independently and interactively. We used the Texas field cricket, *Gryllus texensis*, to test four predictions based on

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this hypothesis. First, females will prefer oviposition sites that are sheltered and, thus, considered to exhibit low predation risk (Hedrick & Dill 1993; Csada & Neudorf 1995) over sites that are not sheltered (high predation risk). Second, females will prefer oviposition sites of lower thermal quality when sites of higher thermal quality entail increased predation risk; that is, they trade off their preference for temperature with predation risk during OSS. Third, the thermal optimum for eggs (the incubation temperature that maximizes hatching success and the size and condition of hatchlings) differs from the preferred temperature of females (27 °C: Adamo 1998; Stahlschmidt & Adamo 2013). Fourth, females will predominately oviposit in sites that approximate their preferred temperature (27 °C). Together, our studies elucidate the dynamics by which two widespread environmental factors influence oviposition decisions in a simple model system.

METHODS

We used long-winged adult *G. texensis* that were part of a long-term colony, which has been described previously (Adamo & Lovett 2011). Briefly, we supplied all crickets with water and food (cat food pellets) ad libitum and housed crickets in a room maintained at 26 ± 1 °C and a 12:12 h light:dark cycle except during behavioural trials. We performed several experiments (see below), but no cricket was used in more than one experiment. All studies were approved by the Animal Care Committee of Dalhousie University (no. I9-026) and are in accordance with the Canadian Council on Animal Care.

Experiment 1: Effects of Incubation Temperature on Offspring

To control for maternal effects, we used a split-clutch design to determine the effects of temperature on hatching success, hatchling size (femur length) and hatchling vigour (a proxy for hatchling energy stores: the duration each hatchling could survive without food) using previously described methods (Stahlschmidt et al. 2013). We isolated 12 female crickets 11–13 days postadult moult from group housing in the colony because *G. texensis* are typically mated by 10 days postadult moult (Solymar & Cade 1990). We housed crickets individually in transparent 2000 ml plastic containers in a room maintained at 26 ± 1 °C and allowed them to oviposit eggs into their cotton-filled water bottles overnight.

The following morning, we carefully removed 20 freshly laid eggs from each female's water bottle using clean forceps. We carefully placed each egg inside a 1.5 ml centrifuge tube on substrate, which consisted of approximately one-quarter of a sterile cotton ball moistened with 500 µl of double-distilled water. We individually incubated each egg at one of four randomly assigned temperature treatments: stable 22, 26, 29.5, or 33 °C ($N = 5$ eggs per temperature treatment per female). We checked eggs daily, and we considered an egg to be nonviable if it did not hatch after 40 days, which was nearly twice the incubation duration of eggs in the lowest temperature treatment. All eggs determined to be nonviable exhibited visible signs of decomposition by 40 days. We discarded all nonviable eggs and any eggs that were damaged during the removal–incubation process.

After hatching, we kept food-deprived crickets in a room maintained at 26 ± 1 °C and a 12:12 h light:dark cycle. We determined hatchling vigour as the number of days posthatching at which a hatchling was nonresponsive. On the day each hatchling was nonresponsive, we stored it in its incubation tube at −20 °C for subsequent analyses of femur length. After briefly thawing the carcass of each hatchling, we gently removed one femur and placed it on a glass micrometer to provide scale. We took a digital image of each femur through a dissecting microscope (56× magnification), and we then analysed femur length using digital software (±0.001 mm; v1.46r, ImageJ, National Institutes of Health, Bethesda, MD, U.S.A.) at a later date.

We used principal components analysis to generate an index of offspring fitness using hatching success, hatchling size and hatchling vigour as initial variables. For subsequent analyses, we included the only principal component (PC) with an eigenvalue >1, which loaded positively onto each initial variable; that is, a relatively high PC score reflected higher hatching success and larger, more robust hatchlings.

Experiment 2: Effects of Temperature and Predation Risk on Oviposition Site Selection

We used a suite of related behavioural trials (experiments 2a–d) to characterize the effects of temperature and predation risk on OSS in *G. texensis*. For 3 days prior to behavioural trials, we individually housed crickets 10–15 days postadult moult in translucent 550 ml plastic containers (mean diameter: 10 cm). Two hours prior to trials, we moved crickets into the room in which trials occurred. We conducted all trials overnight and into the next morning between 1700 hours on the first day until 0900 hours the second day (16 h in total) under dark conditions. At each trial's conclusion, we counted the number of eggs laid in each oviposition site (2–3 sites per cricket, depending on the trial; see below).

Each cricket's trial took place in a cylindrical OSS arena (Fig. 1). We constructed each arena out of aluminium sheeting to a height of 30.5 cm, a diameter of 24 cm, and with ports for three cotton-filled water bottles (height: 6.2 cm; width: 2.4 cm) that served as sources of drinking water and as oviposition sites (Fig. 1). We maintained the temperature (±1 °C) of each oviposition site (2–3 sites per arena, depending on the trial; see below) using flexible heating elements that we controlled remotely. We checked substrate temperature immediately before and after each trial. We placed a single cat food pellet 2–3 cm in front of each oviposition site to serve as a food source through the trial (Fig. 1).

We placed a shelter over the oviposition site(s) (1–3 sites, depending on the trial; see below) in each arena (Fig. 1). Each shelter had two ports that allowed crickets access to the oviposition site and to leave/enter the shelter. The shelters were opaque plastic and in the shape of a truncated cone (width of base and height: 7 cm). Crickets are thigmotactic and prefer sheltered areas over nonsheltered areas likely due to higher rates of predation in

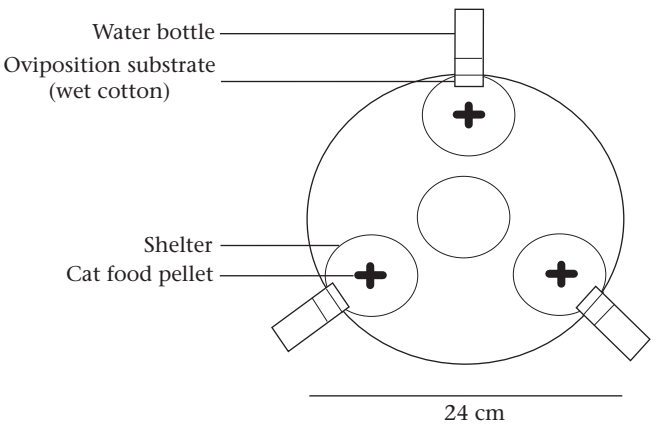

Figure 1. Top view schematic of oviposition site selection arena used for trials. Female *Gryllus texensis* were able to oviposit into the moist cotton substrate of water bottles (2–3 bottles depending on the experiment), which were either sheltered (low predation risk) or not sheltered (high predation risk). See text for details about the specific arrangement of the oviposition sites and shelters for each experiment.

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nonsheltered areas, and shelter-seeking behaviour is even exhibited by laboratory-reared, predator-naïve crickets (Sakaluk & Belwood 1984; Hedrick & Dill 1993; Csada & Neudorf 1995; Hedrick 2000). Thus, we created oviposition sites with low predation risk by providing shelter over water bottles, and we created sites with high predation risk by not providing shelter over water bottles. To reduce the scent of previous crickets, we lined the floor of each arena with clean white paper and wiped the inside surface of each arena with 70% ethanol prior to each trial.

In experiment 2a, we determined females' preferred temperature for oviposition when all three of the oviposition sites either had shelter (low predation risk) or did not have shelter (high predation risk) ($N = 28$). In trials without shelters over the oviposition sites, we provided a single three-ported shelter in the centre of the arena (Fig. 1). We heated two of the water bottles so that the wet cotton substrate was either 26 °C (optimal developmental temperature, see below) or 30.5 °C. We left the remaining bottle at room temperature (21–22 °C). Thus, females could choose to oviposit their eggs into substrate at 21–22 °C, 26 °C and/or 30.5 °C.

Because temperature influences evaporation rate, we also determined the humidity at each oviposition site type by measuring the humidity 2–3 cm from the wet cotton substrate, which approximated the centre of a shelter. Female *G. texensis* are approximately 2–3 cm in total length (Z. R. Stahlschmidt & S. A. Adamo, personal observations), meaning this position provides a reasonable measure of the humidity sensed by females. To measure relative humidity, we used a hygrometer (TR415, Thermor Bios Exactly, Newmarket, ON, Canada), which we calibrated using four different saturated salt solutions at a known temperature (26 °C; $R^2 = 0.99$). We determined the absolute humidity at each oviposition site type because relative humidity is dependent on temperature, which varied among sites. We made conversions to absolute humidity using relative humidity, temperature (recorded at each site using a thermometer, no. 14-648-45, Fisher Scientific) and barometric pressure (recorded from the local weather station) values. Absolute humidity was as follows: 21–22 °C site (sheltered: 10.0 g/m^3; nonsheltered: 9.6 g/m^3), 26 °C site (sheltered: 11.9 g/m^3; nonsheltered: 9.5 g/m^3) and 30.5 °C site (sheltered: 11.8 g/m^3; nonsheltered: 9.6 g/m^3).

In experiment 2b, we determined females' preferred temperature for oviposition when one of the three oviposition sites had shelter (low predation risk) and the other two sites did not have shelter (high predation risk) ($N = 15$–17). Prior to each trial, we randomly determined which oviposition site would have shelter. Again, we heated two of the water bottles so that females could choose to oviposit their eggs into substrate at 21–22 °C, 26 °C and/or 30.5 °C.

We ran two more types of trials (experiment 2c, d) to determine whether females preferred warmer oviposition sites as the indirect consequence of beneficially raising their own body temperature. Because we ran experiments 2a and 2b at room temperature (well below preferred body temperature for *G. texensis*: Adamo 1998; Stahlschmidt & Adamo 2013), female crickets may choose warmer oviposition sites to increase their own body temperature and directly benefit themselves (warmer temperatures increase egg production, immunity and mating frequency in crickets: Kindle et al. 2006; Adamo & Lovett 2011). With this in mind, we designed two related behavioural trials to determine whether females sought warmer temperatures for oviposition simply to beneficially raise their own body temperatures.

In the last two trials, crickets chose between only two oviposition sites, both of which were sheltered (low predation risk) ($N = 20$). In experiment 2c, the room and arena was maintained at 27 °C. We heated one of the water bottles so that the wet cotton substrate was 30.5 °C while the other bottle was left at room temperature. Because the preferred body temperature for adult female *G. texensis* is 27 °C (Stahlschmidt & Adamo 2013), we did not expect females to prefer to oviposit into the 30.5 °C substrate if their decisions were based solely on self-interest; that is, females gained no obvious thermal benefit by associating with the warmer (30.5 °C) oviposition site. Absolute humidity was as follows: 27 °C site (sheltered: 12.7 g/m^3; nonsheltered: 12.7 g/m^3) and 30.5 °C site (sheltered: 13.6 g/m^3; nonsheltered: 11.6 g/m^3). Based on results of experiment 2c (see below), we ran another trial at even higher temperatures. Specifically, we maintained the room and arena at 30.5 °C in experiment 2d. We then heated one of the water bottles so that the wet cotton substrate was 33 °C while the other bottle was left at room temperature. Absolute humidity was as follows: 30.5 °C site (sheltered: 14.0 g/m^3; nonsheltered: 13.9 g/m^3) and 30.5 °C site (sheltered: 15.2 g/m^3; nonsheltered: 13.6 g/m^3). Thus, warmer sheltered sites in our experiments tended to be more humid than cooler sheltered sites, but humidity at nonsheltered sites did not vary with site temperature. Sheltered sites were more humid when they were heated (e.g. 26 °C and 30.5 °C sites in experiment 2a) but not when they were unheated (e.g. 21–22 °C site in experiment 2a).

Statistical Analyses

We performed all analyses with SPSS (v.19, IBM Corp., Armonk, NY, U.S.A.) and we determined two-tailed significance at $\alpha < 0.05$. All data met the assumptions of parametric statistics or were transformed as necessary. To determine the effect of temperature on PC score (index of hatching success and hatchling size and vigour) in experiment 1, we used a repeated measures analysis of variance (rmANOVA) test with maternal identity as the repeated effect. Because the assumption of sphericity was violated, we used a Greenhouse–Geisser epsilon adjustment. We used Bonferroni corrections for pairwise post hoc tests. To determine the effects of temperature and predation risk on OSS in experiments 2a and 2b, we used rmANOVA with substrate temperature as the repeated effect and shelter as a fixed effect. To determine the effects of higher temperatures on OSS in experiments 2c and 2d, we used paired *t* tests.

RESULTS

Experiment 1: Effects of Incubation Temperature on Offspring

The PC score reflecting offspring fitness (index of hatching success and hatchling size and vigour) was significantly affected by incubation temperature ($F_{2,20} = 4.4$, $P = 0.029$; Fig. 2). By fitting these data to a polynomial function ($Y = 0.019X^2 + 0.94X - 11.78$,

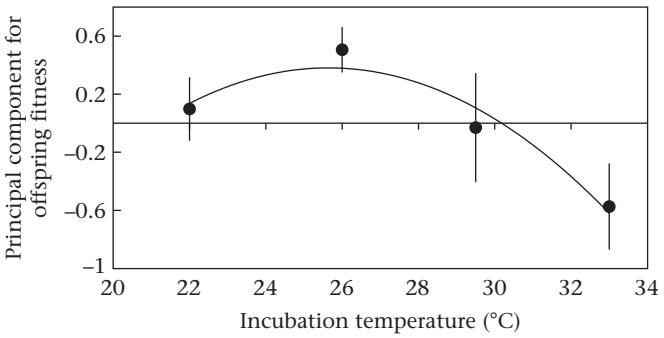

Figure 2. Effects of *Gryllus texensis* egg incubation temperature on the principal component for offspring fitness (index of hatching success, hatchling size and hatchling condition). Values are means ± SE.

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$R^2 = 0.94$), we determined that the optimal temperature for offspring development was 26 °C.

Experiment 2: Effects of Temperature and Predation Risk on Oviposition Site Selection

In experiment 2a, OSS was affected by temperature ($F_{1,36} = 41$, $P < 0.001$), shelter ($F_{1,27} = 25$, $P < 0.001$) and a temperature * shelter interaction ($F_{2,42} = 9.5$, $P < 0.001$) where females overwhelmingly preferred to oviposit into the warmest substrate (30.5 °C) and under shelter (Fig. 3). In fact, females laid more eggs on average during this condition (when arenas were at room temperature and all three oviposition sites were sheltered: 124 eggs) than during any other condition (Figs 3, 4; see below).

In experiment 2b, OSS was affected by temperature ($F_{1,35} = 52$, $P < 0.001$), shelter ($F_{1,26} = 18$, $P < 0.001$) and a temperature * shelter interaction ($F_{2,41} = 8.7$, $P < 0.001$). Females preferred the warmest substrate (30.5 °C) when it was sheltered, but preferred to oviposit into cooler substrate (26 °C) if it was the only sheltered option (Fig. 4). However, there was no temperature-based preference when the only sheltered option was the coolest substrate (21–22 °C) (rmANOVA: $F_{2,28} = 1.7$, $P = 0.20$).

In experiment 2c, females continued to prefer to oviposit into the warmest substrate available (30.5 °C; mean ± SE: 58 ± 10 eggs versus 21 ± 6 eggs) under warm (26 °C) room conditions ($t_{19} = 3.0$, $P = 0.007$).

However, in experiment 2d, females lost their preference for ovipositing into the warmest available substrate (33 °C; mean ± SE: 36 ± 5 eggs versus 33 ± 5 eggs) under warmer (30.5 °C) room conditions ($t_{19} = 0.52$, $P = 0.61$).

DISCUSSION

We used several experiments to demonstrate that, like prefertilization decisions (e.g. mate choice), OSS is influenced by interactions between several environmental factors. Specifically, we found support for our hypothesis that temperature and predation risk independently and interactively influence OSS in *G. texensis*. Females preferred oviposition sites that were warmer (up to 30.5 °C) and sheltered (low predation risk); the latter effect supported our first prediction that females will prefer oviposition sites that are sheltered over sites that are not sheltered. In support of our second prediction that females trade off their preference for temperature with predation risk during OSS, females' preference for warm temperatures changed due to predation risk, and their preference for low predation risk was influenced by temperature (Fig. 4). Together, these results indicate that crickets use multifactorial decision making during OSS.

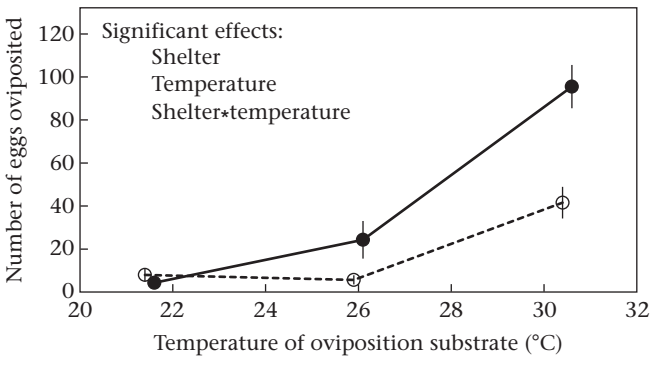

Figure 3. Effects of temperature and predation risk on the number of eggs each female *Gryllus texensis* oviposited when given a choice to oviposit into sites at three different temperatures (21–22 °C, 26 °C and/or 30.5 °C) and all oviposition sites were either sheltered (low predation risk: filled symbols) or not sheltered (high predation risk: open symbols). Values are means ± SE.

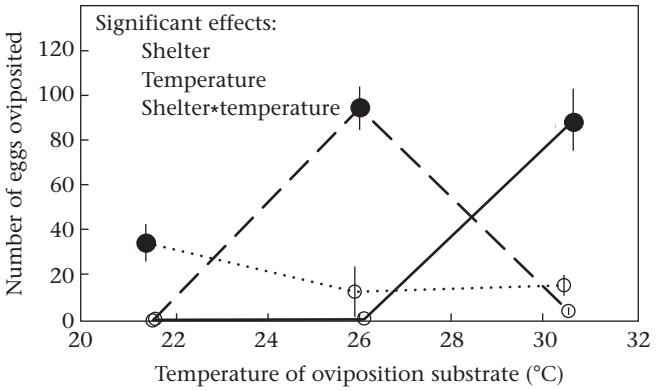

Figure 4. Effects of temperature and predation risk on the number of eggs each female *Gryllus texensis* oviposited when given a choice to oviposit into sites at three different temperatures (21–22 °C, 26 °C and/or 30.5 °C) and only one of the three available oviposition sites was sheltered (low predation risk: filled symbols) while the other two sites were not sheltered (high predation risk: open symbols). For example, the solid line represents females that chose among one sheltered oviposition site (30.5 °C, closed symbol) and two nonsheltered sites (21–22 °C and 26 °C, open symbols). Values are means ± SE.

Yet, the adaptiveness of temperature-based OSS decisions is less clear. Our generally accepted hypothesis was partially based on parent–offspring conflict and supported by our results from manipulation of predation risk; that is, during high predation risk, females reduced oviposition presumably to reduce their own costs at the expense of their offspring. However, we found very little support for parent–offspring thermal conflict in our study system. The preferred temperature of female *G. texensis* (27 °C; Adamo 1998; Stahlschmidt & Adamo 2013) and the temperature that optimizes development of *G. texensis* offspring (26 °C; Fig. 2) were similar, which did not support our third prediction that the thermal optimum for eggs differs from the preferred temperature of females. Furthermore, females preferred oviposition sites that were much warmer than their preferred temperature and the optimal incubation temperature (Figs 2, 3), which did not support our fourth prediction that females predominately oviposit in sites that approximate their preferred temperature. This thermal mismatch may be due to a combination of ultimate and proximate causes (see below).

Females may prefer to oviposit at warm temperatures due to selection on short incubation duration rather than due to selection on other metrics associated with offspring fitness, such as hatching success or hatchling size. Indeed, eggs incubated at 30.5 °C hatched 30% sooner than those incubated at 26 or 27 °C on average (10.5 versus 15.0 days, respectively). Alternatively, there may be very little selection on temperature-based OSS due to an uncertain link between current thermal conditions and future thermal conditions (reviewed in Dillon et al. 2009). That is, if thermal conditions of a given oviposition site vary considerably over the course of incubation (≥10 days), females may gain few (if any) benefits by choosing a site that approximates the optimal temperature for development at the time of oviposition. This rationale, of course, does not explain why female *G. texensis* tended to consistently choose relatively warm oviposition sites (Fig. 3).

In fact, our results regarding temperature-based OSS may be due to ultimate and proximate causes that have little to do with temperature. Given the risk of egg desiccation, there appears to be strong selection on hygrosensation during oviposition in crickets (Hertl et al. 2001; Z. R. Stahlschmidt & S. A. Adamo, unpublished

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data) and other insects (Cherry et al. 1990; Allsopp et al. 1992; Huang et al. 2005; but see Ward & Rogers 2007). In turn, insects possess hygroreceptors on the sensilla of their ovipositors and/or antennae (Sayeed & Benzer 1996; Faucheux 2012; Shah 2012). These hygroreceptors are often located very near thermoreceptors, are structurally indistinct from thermoreceptors and/or use similar sensory mechanisms as thermoreceptors (transient receptor potential or TRP channels); therefore, they are often termed 'thermo-hygroreceptors' (Sayeed & Benzer 1996; Montell 2008; Faucheux 2012; Shah 2012). Furthermore, increased temperatures result in increased neural sensitivity in insects (reviewed in Simmons 2011). Thus, females may choose warmer oviposition sites because they interpret them as moister sites, which they are likely under selection to prefer.

Indeed, humidity is influenced by temperature (warmer air holds more moisture than cooler air) and shelter (shelters increase a site's boundary layer and thereby can reduce convective water flux). For example, warmer sheltered sites in our study tended to be more humid than cooler sheltered sites, meaning females OSS decisions may be facilitated by hygroreception rather than thermoreception. However, humidity at nonsheltered sites did not vary with temperature, yet females still preferred warmer nonsheltered sites over cooler nonsheltered sites (Fig. 3). Sheltered sites were more humid when they were heated, meaning crickets may have responded to site humidity (hygroreception) rather than to the presence or absence of shelter at a given site (thigmoreception). Yet, although humidity at nonheated oviposition sites was not influenced by shelter, females still preferred nonheated, sheltered sites over nonheated, nonsheltered sites in this study (Fig. 3) and in other studies (Z. R. Stahlschmidt & S. A. Adamo, unpublished data). Thus, the temperature and the presence or absence of shelter at sites influenced OSS independent of humidity. Clearly, future research should continue to disentangle the roles of thermoreception, hygroreception and thigmoreception in OSS (e.g. Sayeed & Benzer 1996; Raghu et al. 2004; Dillon et al. 2009).

Although warmer temperatures typically increase reproductive functions in crickets (Kindle et al. 2006; Adamo & Lovett 2011), we did not find that increased environmental temperatures resulted in increased oviposition. Females laid more eggs on average when trials were performed at room temperature (124 eggs, experiment 2a; Fig. 3) than when they were performed at 26 °C (79 eggs, experiment 2c) or 30.5 °C (69 eggs, experiment 2d). Our results also suggest that crickets may be under selection not to put all of their eggs into one basket because females tended to lay more eggs during trials with three oviposition sites (experiments 2a, b) than during trials with only two oviposition sites (experiments 2c, d). Presumably, this OSS strategy reduces the risk that all offspring will suffer due to site-specific traits (e.g. susceptibility to desiccation or pathogen infiltration), but it also increases females' predation risk associated with movement among oviposition sites (Sakaluk & Belwood 1984). However, future investigation is required to more explicitly test this OSS strategy in crickets because three-site trials in our study were performed at room temperature while two-site trials were performed at warmer temperatures (26 or 30.5 °C).

Like the classic study from Hedrick & Dill (1993), we show that predation risk strongly influences a fitness-related decision (OSS) (Fig. 3). We further demonstrate that predation risk interacts with another widespread environmental cue (temperature) to influence OSS in *G. texensis* (Figs 3, 4). In turn, predation risk and temperature affected the number and quality (e.g. hatching success and hatchling size, respectively) of offspring produced in our study. We also demonstrate an unexpected preference for suboptimally warm oviposition sites, suggesting that OSS decisions are driven by a confluence of unique proximate and ultimate causes that require further investigation. In addition, researchers should continue to examine the role of other factors in OSS (e.g. the interaction between food availability and predation risk, and differences between predator-naïve crickets and those exposed to predators), as well as the link between OSS and behavioural syndromes (e.g. the shy–bold continuum: Sih et al. 2004). In summary, we show that widespread environmental factors can exert complex interactive effects on important reproductive decisions.

Acknowledgments

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