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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

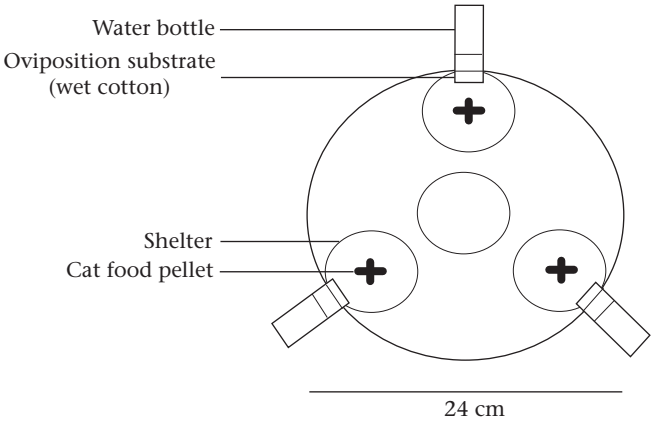

Figure 1. Top view schematic of oviposition site selection arena used for trials. Female *Gryllus texensis* were able to oviposit into the moist cotton substrate of water bottles (2–3 bottles depending on the experiment), which were either sheltered (low predation risk) or not sheltered (high predation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