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Reproduction of a field cricket under high-intensity artificial light at night and a simulated heat wave

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Abstract

Animals are increasingly exposed to both artificial light at night (ALAN; a.k.a., ecological light pollution) and heat waves. Traditionally, the effects of ALAN and heat waves have been investigated in isolation, and results indicate mixed support for their costs to important decisions made at specific stages of reproduction (i.e., before, during, and after mating). Therefore, we used a factorial design to manipulate temperature and light conditions during adulthood in female variable field crickets (*Gryllus lineaticeps*) to determine (1) whether ALAN has stage-specific effects on reproductive decisions and (2) if ALAN effects on reproduction interact with a simulated heat wave. We found that ALAN simulating bright urban lighting promoted mating success, and a simulated heat wave resulted in even greater benefits to reproduction, including increased reproductive investment (ovary mass prior to mating), the efficiency by which food was converted into reproductive tissue, and reproductive output (number of eggs laid). Heat wave and ALAN did not modulate the effect of one another because we found no evidence of interactive (e.g., synergistic or antagonistic) effects of temperature and light treatments on any reproductive trait. Our study is the first to examine the combined effects of ALAN and heat waves across reproductive stages, and we found that these two increasingly common environmental factors may generally benefit reproduction in an insect.

Significance statement

Animals are increasingly exposed to artificial light at night (a.k.a., ecological light pollution) and heat waves, but the combined effects of these two potential stressors are unknown. Therefore, we manipulated temperature and light conditions during adulthood in female variable field crickets (*Gryllus lineaticeps*) to examine effects across three important reproductive stages—before, during, and after mating. We found that ALAN simulating bright urban lighting promoted mating success, and a simulated heat wave resulted in even greater benefits to reproduction, including increased reproductive investment (ovary mass prior to mating) and reproductive output (number of eggs laid after mating). Our results indicate that these two increasingly common environmental factors may generally benefit reproduction in an insect.

Introduction

Animals are increasingly exposed to a range of stressors due to anthropogenic disturbance (reviewed in Crain et al. 2008; Holmstrup et al. 2010; Kaunisto et al. 2016; IPCC 2021). For example, approximately one-quarter of Earth's land surface experiences ecological light pollution or artificial light at night (ALAN), and the global area affected by ALAN is increasing 2–6% each year (Hölker et al. 2010; Falchi et al. 2016; Kyba et al. 2017). This unprecedented disturbance to natural light patterns is alarming given the critical role of light in regulating systems across all levels of biological organization (reviewed in Gaston et al. 2015; Sanders et al. 2021), and it is contributing to a global decline in key animal taxa (Owens et al. 2020; van Grunsven et al. 2020). Indeed, a recent meta-analysis indicates effects of ALAN on physiology and some behavioral activity patterns in many animals; yet, ALAN exerts mixed effects across fitness-related traits (Sanders et al. 2021). In most animals,

reproduction involves several discrete stages—gamete production, mating, and oviposition—that can respond differently to chronic exposure to ALAN (e.g., Botha et al. 2017; Durrant et al. 2018). Such discrepancy may be due to the unique role that light plays in each stage of reproduction. For example, even in the short term, ALAN may reduce food consumption that fuels reproductive investment because foraging increases predation risk; yet, ALAN may also improve the efficiency of mating decisions that rely upon visual information (Kempenaers et al. 2010; Botha et al. 2017; Willmott et al. 2018; Chen et al. 2021; but see van Geffen et al. 2015; McLay et al. 2018; Touzot et al. 2020; Van den Broeck et al. 2021). Thus, a comprehensive understanding of the effects of ALAN on reproduction requires examining animals' decisions before, during, and after mating.

Similar to ALAN, heat waves (i.e., multi-day periods where temperatures exceed historical averages) are increasingly common in animals' environments (Russo et al. 2016; Dosio et al. 2018; Sun et al. 2018; Shafiei Shiva et al. 2019). Heat waves increase resource (e.g., energy) expenditure and acquisition, leading to diverse effects on stages of reproduction across animal taxa—including benefits (Adamo and Lovett 2011; Leicht et al. 2013) and costs (Adamo et al. 2012; Hurley et al. 2018; Sales et al. 2018; Shanks et al. 2020; Martinet et al. 2021). Heat wave conditions and ALAN are often linked because ALAN is most prevalent in terrestrial ecosystems (Falchi et al. 2016), which experience greater temperature extremes relative to marine ecosystems (IPCC 2021), and ALAN is expanding with urban areas, which are prone to warming (e.g., the urban heat island effect: Oke 1973; Grimm et al. 2008; Youngsteadt et al. 2015). A multiple-stressor framework is a useful construct to examine the effects of covarying environmental factors (reviewed in Crain et al. 2008; Holmstrup et al. 2010; Kaunisto et al. 2016), such as heat wave and ALAN. Multiple stressors may have an additive effect on a given reproductive trait (e.g., mating) where the stress due to two factors is simply the sum of either factor alone (Todgham and Stillman 2013). Here, ALAN and a heat wave may exert independent, additive effects similar to those found in other multiple-stressor studies (Holliday et al. 2009; Kuehne et al. 2012; Gieswein et al. 2017; but see Jackson et al., 2016; Padda et al. 2021). In particular, both short-term ALAN and heat waves may improve mating efficiency given the effects of visual cues and warmer temperatures on sensory systems (discussed in Nguyen and Stahlschmidt 2019). Alternatively, multiple stressors may result in interactive, non-additive effects, such as synergistic or antagonistic effects (Folt et al. 1999; Todgham and Stillman 2013; Piggott et al. 2015). Short-term exposure to anthropogenic noise and ALAN can interact to influence activity patterns (Dominoni et al. 2020), and heat waves and short-term ALAN exposure may similarly modulate the effects of one another on reproduction.

For example, ALAN may only be costly to reproduction during a heat wave (i.e., a light-temperature interaction sensu the food-dependent effects of heat waves on reproductive output: Adamo et al. 2012). Because elevated body temperature increases energy expenditure, an ALAN-induced reduction in foraging may specifically decrease the resources available for reproductive investment during a heat wave. However, despite the increasing prevalence of ALAN and heat waves, the combined effects of these environmental factors across reproductive stages are unknown.

Therefore, temperature and light conditions were manipulated during adulthood in female variable field crickets (*Gryllus lineaticeps*) to examine effects across three important reproductive stages. First, food consumption, ovary mass, and change in body mass were determined prior to mating to examine the acquisition of resources and their allocation to reproductive tissue. Second, mating trials were performed to determine mating success. Third, the number of eggs oviposited was determined to examine reproductive output. Crickets avoid open, exposed environments, and perceived predation risk strongly influences their oviposition decisions (Stahlschmidt and Adamo 2013; Stahlschmidt et al. 2014; Stahlschmidt and Vo 2022). Therefore, oviposition specialization (i.e., tendency for a female to clump her eggs into a small number of oviposition sites) was also determined. During ALAN exposure or at cooler temperatures, a female may have a high oviposition specialization value characterized by her tendency to reduce behavioral activity and limit exposure to the open (i.e., non-sheltered) environment thereby exhibiting spatially clumped oviposition (i.e., potentially favoring maternal safety over offspring fitness: reviewed in Refsnider and Janzen 2010).

We used three factorial experiments to test several hypotheses. First, we hypothesized that high-intensity ALAN (i.e., reflecting bright urban light environments) and heat wave exposure would have different effects across stages of reproduction. Here, we predicted that ALAN would have its greatest effect on mating given the role of light-mediated visual information in mating decisions in crickets (Simmons 1986; Saleh et al. 2014; Stahlschmidt et al. 2020) while heat wave exposure would have a greater effect on egg laying given the link between reproductive output and temperature in crickets (Stahlschmidt and Adamo 2013; Stahlschmidt and Vo 2022). Second, we hypothesized that the effects of high-intensity ALAN and heat waves would modulate one another with respect to reproduction. Here, we predicted interactive effects of ALAN and heat wave on pre-mating reproductive investment due to a reduction in food acquisition (discussed above). Our study will be the first to examine the effects of ALAN and heat waves across reproductive stages and decisions thereby informing the role of two increasingly ubiquitous environmental factors in animal fitness.

Materials and methods

Study species

The variable field cricket (*Gryllus lineaticeps*) is native to the western USA and is found predominantly in California (Weissman and Gray 2019). Like other *Gryllus* crickets (Zera and Larsen 2001; Zera 2005), *G. lineaticeps* is wing-dimorphic. Adults are either a long-winged and typically flight-capable morph, or a flightless, short-winged morph. Only short-winged crickets were used in the study, and 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, USA) that predominately expresses the short-winged phenotype (authors pers. obs.; L.A. Treidel, pers. comm.). Throughout ontogeny, crickets were reared in standard conditions: 28 ± 1 °C with ad libitum access to water (water-filled shell vials plugged with cotton), commercial dry cat food, and shelter (cardboard egg cartons). During development, crickets experienced a 14:10 light:dark cycle, which approximates the light:dark cycle during the breeding season in the field (i.e., at Sedgwick Reserve; note: crickets in the field may experience a reduced photoperiod [13 h] during development). Crickets were then assigned to one of four light-temperature treatment groups described below with ad libitum access to water, food, and shelter. For the first two experiments, newly molted adults (< 1 day after final ecdysis) were weighed and individually housed in small translucent deli cups (473 ml) containing shelter (overturned 30-ml opaque containers with access holes). For the final experiment, newly molted adults of both sexes (1:1 sex ratio) were group-housed with ad libitum access to water and food in 15-l translucent plastic containers ($n = 8$–12 crickets per container) with two cardboard egg cartons as shelter and a sheet of transparent acrylic sheeting as a lid.

Experimental design

A 2×2 factorial design was used in three experiments (see below) to investigate how a simulated heat wave and ALAN affected investment into somatic and reproductive tissues (i.e., body and ovary mass, respectively), food consumption, mating behavior, and oviposition in female *G. lineaticeps* ($n = 365$). Thus, crickets were exposed to one of four temperature-light treatment combinations—control (normal [control] temperature and dark nights), heat-only (warm temperature and dark nights), ALAN-only (control temperature with ALAN), and heat + ALAN (warm temperature with ALAN). In each experiment (see details

below), several cohorts of crickets experienced one of the four treatment combinations inside one of two incubators (model I-36, Percival Scientific, Inc., Perry, IA, USA)—that is, each incubator contained crickets experiencing the same temperature-light treatment. To reduce any effects of incubator, both incubators were used to perform experiments for the cohorts in all four treatment combinations.

Crickets experienced one of two temperature treatments that approximate thermal microhabitats used by crickets in the field (Sedgwick Reserve: Sun et al. 2020). Half of the crickets experienced a 17–31 °C sinusoidal diel temperature cycle that changed temperature each hour ("control" temperature treatment). This temperature range approximates the average diel temperature variation of the air and soil at Sedgwick Reserve during the mating season for *G. lineaticeps* (June–August; https://ucnrs.org/). The remaining crickets experienced a 23–37 °C sinusoidal diel temperature cycle ("heat wave" temperature treatment). This temperature range approximates the average diel temperature variation of the air and soil at Sedgwick Reserve during a 5-day heat wave (August 2012; https://ucnrs.org/), but was non-lethal in our study.

To match the duration of exposure to the temperature treatments and to approximate to other studies examining short-term ALAN exposure (e.g., Borniger et al. 2014; Welbers et al. 2017; Van den Broeck et al. 2021), crickets also experienced one of two light regimes for 5–6 days in the incubators described above, after which each individual's final body mass was recorded. Half of the crickets were exposed to a 14:10 light:dark cycle, which approximates the photoperiod during the mating season at Sedgwick Reserve ("control" light treatment). Natural sunlight exhibits an illuminance that is difficult to replicate in controlled laboratory settings (e.g., potentially exceeding 100,000 lx), forcing researchers to design experiments with daylight levels of illuminance that are several orders of magnitude less than natural sunlight. However, daylight for this treatment group was supplied by a light bulb emitting light of a similar temperature or warmth (5300 Kelvin) as natural sunlight. In unoccupied deli cups (see above), daylight was 6.0 lx inside of shelters (where crickets most frequently reside) and 268 lx outside of shelters. The remaining crickets experienced the same sunlight-simulating light source during the day (14 h), but they were exposed to a different light source during the 10-h scotophase ("ALAN" treatment: see below).

The night light was warmer (2750 Kelvin) to simulate the temperature of street lighting recommended by the American Medical Association (Kraus 2016). The illuminance and color temperature of light bulbs were measured using a light meter (Lumu Power 2, LUMULABS, Ljubljana, Slovenia). In unoccupied deli cups, night light was 2.3 lx inside of shelters and 97 lx outside of shelters. Although the level of illuminance (up to 100 lx) does not tend to influence the effects

of ALAN on physiology, life history, or activity patterns across animals, there is wide variation in dose-responses of biological traits due to variation in animals' spectral sensitivities (Sanders et al. 2021). In crickets, chronic exposure to ALAN illuminance of 2 or 5 lx results in similar effects on male calling behavior and locomotion patterns (Levy et al. 2021), and exposure to 10 or 100 lx of ALAN similarly affects courtship and mating behavior (Botha et al. 2017). Other crickets exhibit very little behavioral and locomotor activity during the scotophase (Rost and Honegger 1987; Jacot et al. 2008; Levy et al. 2021), and female *G. lineaticeps* spend an estimated 86–93% of the scotophase under shelter (Fig. S1). Thus, although the night light source represented a very high level of ALAN that simulated bright urban lighting, our study animals were exposed to considerably lower levels of ALAN (i.e., approximately 16 lx based on shelter use). Thus, night light in our study was warmer (lower Kelvin) and dimmer (fewer lux) than daylight, and light was dramatically limited inside the shelters that crickets regularly accessed throughout the study.

Pre-mating: food intake and investment into tissue

Food consumption during early adulthood for female crickets ($n = 127$ total; $n_{control} = 35$; $n_{heat-only} = 33$; $n_{ALAN-only} = 28$; $n_{heat+ALAN} = 31$) was determined by subtracting final food (dry cat food pellets) mass from initial food mass. To determine whether treatments influenced the ability of crickets to convert food mass into body tissue, food conversion efficiency for body mass was estimated (body mass gain [mg]/total food ingested [mg]). Crickets were then euthanized and stored at -20 °C. After storage, their ovaries were removed and dried at 55 °C to a constant mass to estimate investment into reproduction (Roff and Fairbairn 1991; Crnokrak and Roff 2002; Glass and Stahlschmidt 2019). Data on a separate group of *G. lineaticeps* ($n = 35$) indicated that newly molted females exhibit very little investment into reproduction (dry ovary mass; mean $\pm$ s.e.m.: 2.0 ± 0.2 mg, which is approx. 6% of that at 5 days of adulthood). Thus, because nearly all ovarian development occurred during the study period (first 5 days of adulthood), food conversion efficiency for ovary mass was also estimated (dry ovary mass [mg]/total food ingested [mg]) for females in this experiment.

Mating

Female *G. lineaticeps* ($n = 109$ total; $n_{control} = 25$; $n_{heat-only} = 28$; $n_{ALAN-only} = 29$; $n_{heat+ALAN} = 27$) underwent mating trials with males after 5 days of treatment (i.e., on day 6 of adulthood; see above) as both sexes are typically sexually receptive at 3–4 days of adult age in *G. lineaticeps* (authors pers. obs.) and in other *Gryllus* crickets (Cade and Wyatt 1984; Solymar and Cade 1990). Males were virgin,

the same age as their female partners, and individually housed throughout adulthood in the same conditions as females (see above) prior to mating trials (e.g., heat + ALAN males were always paired with heat + ALAN females). During the mating season in the field (i.e., at Sedgwick Reserve, see above), the majority of broadcast mating calls by male *G. lineaticeps* occur for 2–3 h starting at dusk (ZRS pers. obs.). Therefore, males and females were each weighed and then randomly paired in a 1.9-l translucent plastic container with an egg carton shelter and a transparent acrylic sheeting lid to facilitate mating beginning at the end of the photophase (19:00). That is, mating trials occurred in darkness for females in the control light treatment, and they occurred in night light conditions for females in the ALAN treatment.

After 2 h, females were separated from males and visually inspected for the presence of the ampulla of a spermatophore, which is the vehicle by which sperm is transferred from a male to a female (reviewed in Sakai et al. 2017). After a female mounts a male, the spermatophore is attached to the genital chamber of the female, and then sperm is moved internally where it is stored in the female's spermatheca (reviewed in Sakai et al. 2017). After inspection, 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. Mating success was determined by the presence of an external spermatophore or sperm-filled spermatheca.

Post-mating: oviposition behavior

After 6 days of treatment (see above), each female ($n = 129$ total; $n_{control} = 34$; $n_{heat-only} = 29$; $n_{ALAN-only} = 32$; $n_{heat+ALAN} = 24$; $n = 10$ non-mated females [see below]) was removed from group-housing, weighed, and placed in a 1.9-l translucent plastic container with ad libitum access to food for its oviposition trial (e.g., a female experiencing heat + ALAN during group-housing in early adulthood also experienced heat + ALAN during its oviposition trial). 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. For a female to oviposit at several sites, she would need to leave the security of the sheltered sleeve at one site and venture out into the open, non-sheltered environment before ovipositing at a different site. As in previous studies of *Gryllus* oviposition (Stahlschmidt and Adamo 2013; Stahlschmidt et al. 2014), water bottles were removed after 24 h, 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 spermatheca was recorded. Non-mated females were not analyzed.

The total number of eggs each female oviposited was used to estimate the effects of treatment on realized fitness because nearly 95% of oviposited eggs are fertilized in *Gryllus* (Shoemaker and Adamo 2007). Oviposition specialization was used to estimate the tradeoff between maternal predation risk avoidance and offspring fitness for females that oviposited. To estimate oviposition specialization, the coefficient of variation (%) of oviposited eggs (100 * [σ/μ]; a standardized measure of data dispersion) in the number of eggs laid across the three available oviposition sites was determined for each ovipositing female. Crickets are thigmotactic and avoid open, exposed environments, and the perception of predation risk strongly influences their oviposition decisions (Stahlschmidt and Adamo 2013; Stahlschmidt et al. 2014). Thus, a high oviposition specialization value reflected the tendency for a given female to reduce behavioral activity and limit exposure to the open environment thereby exhibiting spatially clumped oviposition. In contrast, a female with a low oviposition specialization value was one that exhibited oviposition diversification wherein she oviposited eggs more equally across multiple sites thereby potentially improving offspring fitness while increasing her own predation risk.

Statistical analyses

Data were tested for normality, and they were arcsine, natural logarithm, or square root transformed when necessary to achieve normally distributed residuals. Data were then analyzed using SPSS (v.26 IBM Corp., Armonk, NY), and two-tailed significance was determined at $\alpha = 0.05$. To examine the independent and interactive effects of treatments (light and temperature), linear model analyses were performed on final body mass, dry ovary mass, food intake, conversion rates for body mass and dry ovary mass, total number of eggs oviposited, and oviposition specialization. The use of ratios or percentages (e.g., percentage of body mass added) should be avoided when data vary allometrically with body size (Packard and Boardman 1987), which is the case for body components in crickets (Kelly et al. 2014; Stahlschmidt and Chang 2021). Therefore, to account for body size, initial body mass was included as a covariate for the final body mass, ovary mass, and food intake models, and final body mass was included as covariate for the total eggs oviposited and oviposition specialization models. A binary logistic generalized linear model was used to determine the main and interactive effects of treatments on mating success (0: not mated; 1: mated) after accounting for mate quality (covariate: male partner body mass). All models were tested for the main effects of light and temperature treatments, as well interactive effects of treatments.

Results

Pre-mating: food intake and investment into tissue

Final body mass was greater in heat wave ($F_{1,124} = 8.4$, $P = 0.0045$) and control light conditions ($F_{1,124} = 4.9$, $P = 0.028$) after accounting for initial body mass ($F_{1,124} = 304$, $P < 0.001$) (Fig. 1a; Table 1). Dry ovary mass was also greater in heat wave conditions ($F_{1,122} = 63$, $P < 0.001$) after accounting for initial body mass ($F_{1,122} = 77$, $P < 0.001$) (Fig. 1b; Table 1). Ovary mass was not affected by light treatment ($F_{1,122} = 0.14$, $P = 0.71$) (Fig. 1b; Table 1). Temperature and light treatments did not interact to significantly influence body mass ($F_{1,124} = 0.14$, $P = 0.71$) or dry ovary mass ($F_{1,122} = 0.96$, $P = 0.33$) (Fig. 1a, b; Table 1).

Food consumption was greater in heat wave conditions ($F_{1,127} = 36$, $P < 0.001$) after accounting for initial body mass ($F_{1,127} = 23$, $P < 0.001$), but it was not affected by light treatment ($F_{1,127} = 0.12$, $P = 0.73$) (Fig. 1c; Table 1). Conversion efficiency for body mass was greater in control temperature ($F_{1,122} = 5.1$, $P = 0.026$) and light conditions ($F_{1,122} = 4.1$, $P = 0.047$) (Fig. 1d; Table 1). Yet, conversion efficiency for dry ovary mass was greater in heat wave conditions ($F_{1,121} = 6.6$, $P = 0.012$) (Fig. 1e; Table 1). Ovary conversion efficiency was not affected by light treatment ($F_{1,127} = 0.12$, $P = 0.73$) (Fig. 1e; Table 1). Temperature and light treatments did not interact to significantly influence food consumption ($F_{1,127} = 0.25$, $P = 0.62$) or the conversion efficiencies for body mass ($F_{1,122} = 0.25$, $P = 0.62$) or ovary mass ($F_{1,121} = 0.33$, $P = 0.57$) (Fig. 1c–e; Table 1).

Mating

Mating success was greater in ALAN conditions (Wald $\chi^2 = 4.6$, df = 1, $P = 0.032$; Fig. 2; Table 1) and when male partners were heavier ($\chi^2 = 6.2$, df = 1, $P = 0.013$). Mating success was not affected by temperature treatment alone ($\chi^2 = 0.59$, df = 1, $P = 0.44$) or an interaction between light and temperature treatments ($\chi^2 = 0.40$, df = 1, $P = 0.53$) (Fig. 2; Table 1).

Post-mating: oviposition behavior

The total number of eggs oviposited was greater in heat wave conditions ($F_{1,119} = 19$, $P = 0.002$) after accounting for maternal body mass ($F_{1,119} = 8.4$, $P = 0.005$), but it was not affected by light treatment ($F_{1,119} = 1.1$, $P = 0.30$) or by a temperature × light interaction ($F_{1,119} = 0.24$, $P = 0.63$) (Fig. 3a); Table 1. Oviposition specialization

Fig. 1 Effects of light conditions (control vs. artificial light at night, ALAN) and temperature conditions (control vs. simulated heat wave) during early adulthood on pre-mating traits in female *Gryllus lineaticeps*: **a** body mass, **b** reproductive investment, **c** food intake, **d** body mass conversion efficiency, and **e** ovary mass conversion efficiency. Sample sizes are included atop each column. Values are displayed as estimated marginal mean ± s.e.m. for **a–c** because initial body mass was included in analyses, and as mean ± s.e.m. for **d** and **e** See text for further details
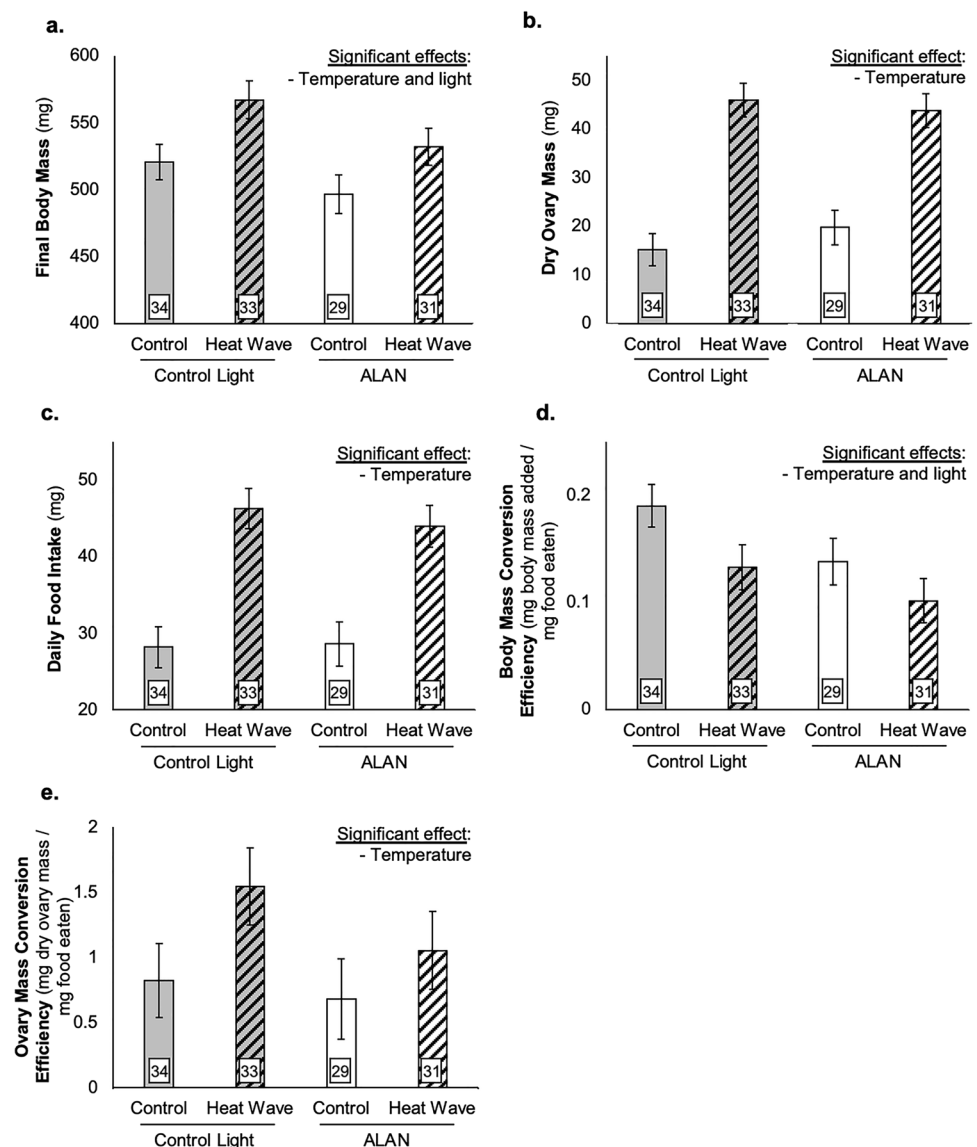
was not affected by temperature ($F_{1,75} = 1.1$, $P = 0.30$), light ($F_{1,75} = 0.51$, $P = 0.48$), a temperature × light interaction ($F_{1,75} = 1.9$, $P = 0.18$), or by maternal body mass ($F_{1,75} = 1.3$, $P = 0.25$) (Fig. 3b; Table 1).

Discussion

Animals are increasingly exposed to ALAN and heat waves (Russo et al. 2016; Kyba et al. 2017; Dosio et al. 2018; Sun et al. 2018; Shafiei Shiva et al. 2019), but the combined effects of these potential stressors on fitness-related traits are unknown. Our results in *G. lineaticeps* indicate that short-term, high-intensity ALAN exposure simulating bright urban lighting during adulthood reduced body mass due to decreased food conversion efficiency (Fig. 1; Table 1). Yet, ALAN did not affect appetite, reproductive investment, or

reproductive output, and it actually promoted mating success in support of our first hypothesis (Figs. 1, 2 and 3; Table 1). A simulated heat wave produced even stronger benefits to reproduction, including increased reproductive investment, conversion efficiency for ovary mass, and reproductive output (Figs. 1 and 3; Table 1). Our second hypothesis was not supported because heat wave and ALAN did not modulate the effect of one another. We found no evidence of interactive (e.g., synergistic or antagonistic) effects of temperature and light treatments on any reproductive trait. In sum, two increasingly common environmental factors—heat wave and, to a lesser extent, ALAN—appeared to generally benefit reproduction in an insect.

Heat wave and ALAN exposure altered resource allocation in *G. lineaticeps* (Fig. 1; Table 1). Crickets exposed to a simulated heat wave ate more food, and they were more efficient at converting food into ovary mass and less efficient
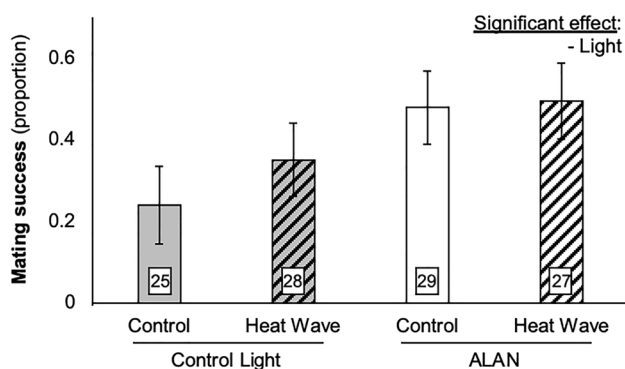
Table 1 Summary results for the effects of light conditions (control vs. artificial light at night, ALAN) and temperature conditions (control vs. simulated heat wave) during early adulthood in female *G. lineaticeps*. Treatments with significantly higher values are displayed as text in the table (e.g., final body mass was greater crickets in exposed to control light conditions and heat wave conditions) and non-significant effects are indicated by dashes. See text for full statistical results, including the effects of covariates (not shown below)

	Light	Temperature	Light×temperature
Final body mass	Control	Heat wave	-
Dry ovary mass	-	Heat wave	-
Food consumption	-	Heat wave	-
Body mass conversion efficiency	Control	Control	-
Ovary mass conversion efficiency	-	Heat wave	-
Mating success	ALAN	-	-
Total number of eggs laid	-	Heat wave	-
Oviposition specialization	-	-	-

Fig. 2 Effects of light conditions (control vs. artificial light at night, ALAN) and temperature conditions (control vs. simulated heat wave) during early adulthood on mating success in *Gryllus lineaticeps*. Sample sizes are included atop each column. Values are displayed as estimated marginal mean ± s.e.m. because mating partner body mass was included as a covariate in the analysis. See text for further details

at converting it into body mass (Fig. 1c–e; Table 1) suggesting that heat waves favor investment into reproduction at the expense of soma. Higher temperatures also reduce body mass conversion efficiency in fish, chickens, and cows (Cahaner and Leenstra 1992; Handeland et al. 2008; reviewed in Johnson 2018). Little is known about the effects of heat stress on resource dynamics in ectotherms. However, it can reduce appetite in livestock (reviewed in Johnson 2018) and may not affect the conversion efficiency of energy allocated to reproduction (i.e., lactation, which can double metabolic demands: reviewed in Nigussie 2018) relative to somatic tissue in cows (Kurihara 1996). Crickets exposed to short-term ALAN exhibited reduced body mass because

decreased body mass conversion efficiency was not offset by increased food consumption (Fig. 1a, c, d; Table 1), and other crickets exposed to longer-term ALAN throughout ontogeny exhibit shifts in circadian patterns of activity and reproductive behavior (Levy et al. 2021). Other animals similarly alter their resource dynamics after exposure to ALAN in the short term (< 2 weeks: Borniger et al. 2014; Welbers et al. 2017) and long term (8 weeks: Fonken et al. 2010). For example, several studies in the common toad elegantly examined the effects of short-term ALAN on activity, as well as on resource acquisition and allocation. Toads exposed to ALAN for 10–20 days do not increase their food consumption; yet, they maintain body mass by reducing their activity and the energy spent on activity (Touzot et al. 2019). Thus, toads appear to alter their activity patterns to maintain energy balance, but their reduced activity may come at a cost to reproduction (Touzot et al. 2020). Therefore, animals may adaptively respond to heat waves and ALAN by exhibiting a suite of behavioral and physiological strategies related to resource acquisition, use, and/or allocation.

Our results indicate that short-term ALAN exposure promoted mating in *G. lineaticeps* in support of our first hypothesis (Fig. 2; Table 1), but the general effects of ALAN on mating are unclear and may be taxon-dependent. Exposure to ALAN impairs mating in some taxa (short term—moths: van Geffen et al. 2015; glow-worm beetles: Van den Broeck et al. 2021; longer term—fruit flies: McLay et al. 2018; toads: Touzot et al. 2020), but it can promote mating in other taxa (short term—moths: Chen et al. 2021; our study; longer term—crickets: Botha et al. 2017; songbirds: Kempenaers et al. 2010). Mating in nocturnal insects appears to be particularly vulnerable to ALAN (reviewed in Owens et al. 2020; Seymoure 2018; Desouhant et al. 2019), and the activity patterns and life history traits of nocturnal rodents and birds appear to be more sensitive to ALAN than their diurnal counterparts (Sanders et al. 2021). In *G. lineaticeps*, advertisement calling by males and above-ground activity largely occurs at dusk and throughout the night (ZRS pers. obs.; Sun et al. 2020). Therefore, exposure to ALAN in the short-term may facilitate mating in field crickets by improving females' ability to discern male quality as predicted by male body size (Simmons 1986; Saleh et al. 2014; Stahlschmidt et al. 2020; our study). Evidently, the interconnected roles of light-mediated signals, quality of light (reviewed in Seymoure 2018), and daily activity patterns may together predict the effects of ALAN on mating across animals.

Even in 1-day trials, crickets exhibit considerable plasticity in oviposition decisions in response to a range of ecological factors (Stahlschmidt and Adamo 2013; Stahlschmidt et al. 2014), and we show that a simulated heat wave (but not ALAN) affects reproductive output in *G. lineaticeps* in support of our first hypothesis (Fig. 3a). This result agrees with other studies demonstrating the positive link between

Fig. 3 Effects of light conditions (control vs. artificial light at night, ALAN) and temperature conditions (control vs. simulated heat wave) during early adulthood on 24-h oviposition in *Gryllus lineaticeps*: **a** total number of eggs laid, and **b** oviposition specialization (coefficient of variation across three available oviposition sites). Sample sizes are included atop each column. Values are displayed as estimated marginal mean ± s.e.m. because maternal body mass was included as a covariate in analyses. See text for further details
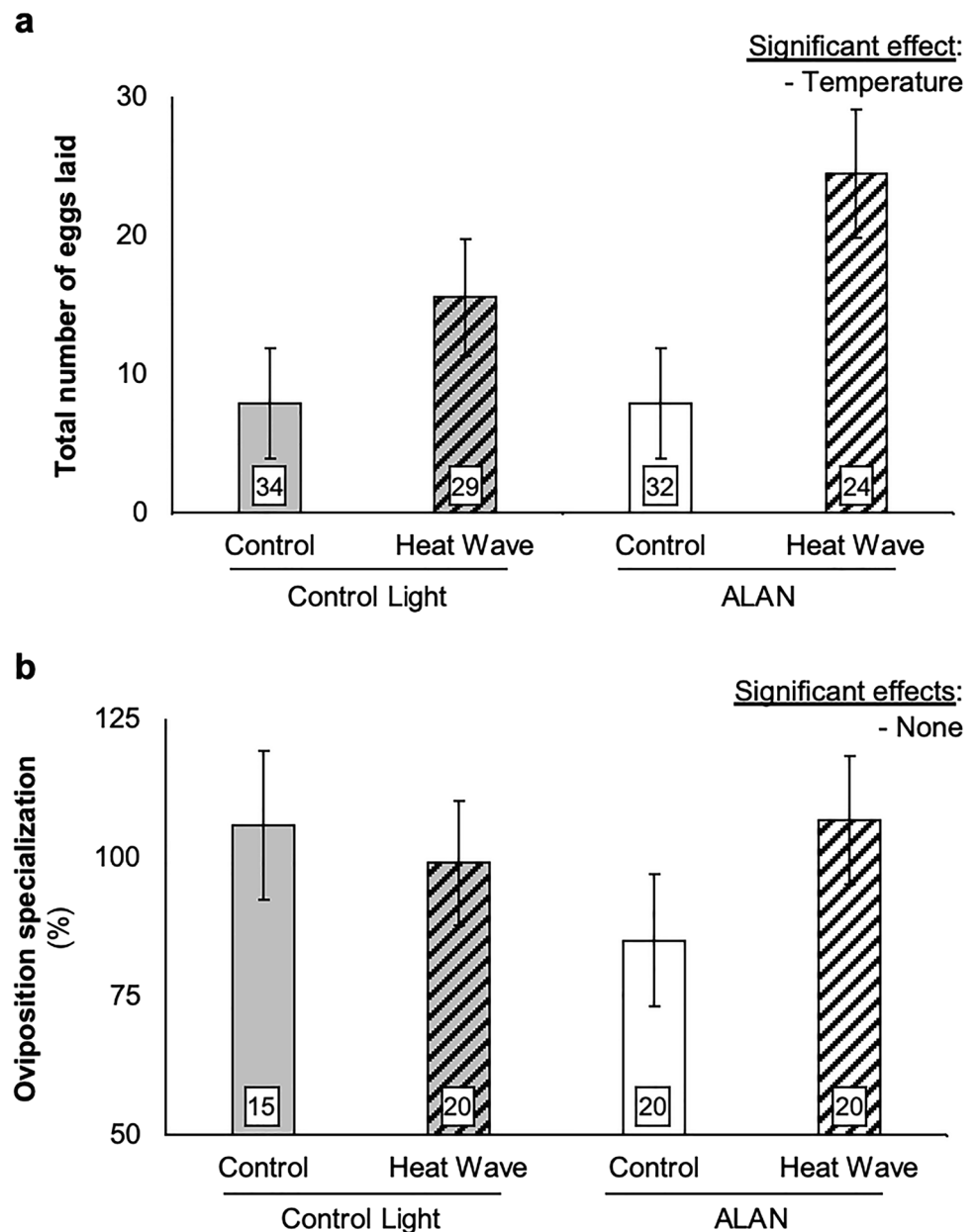
warmer temperatures and egg-laying (reviewed in Angilletta 2009), including in other *Gryllus* (Adamo and Lovett 2011; Stahlschmidt and Adamo 2013; but see Adamo et al. 2012). Like other traits, reproductive output responds non-linearly to temperature (reviewed in Angilletta 2009)—therefore, more drastic heat waves (i.e., those that increase average temperature by > 6 °C) are likely to reduce reproductive output. Further, warmer temperatures typically shift reproductive allocation patterns (i.e., warming increases fecundity at the expense of offspring body size: reviewed in Angilletta 2009), and warming associated with global climate change may drive a general decline in body size (Gardner et al. 2011). Because the occurrence of temperature extremes may pose a greater risk to many animals than gradual warming

(Vasseur et al. 2014), it is critical to understand the thermal plasticity of reproductive allocation in response to heat waves.

Even in the absence of predators, ovipositing *Gryllus* often prioritize predation risk avoidance over their foraging needs and the thermal environment of their developing eggs (Stahlschmidt and Adamo 2013; Stahlschmidt et al. 2014). Yet, we found no evidence that short-term ALAN or heat wave influenced predation risk-related decision-making during oviposition in *G. lineaticeps* (Fig. 3b; Table 1). That is, neither environmental factor influenced the tendency for females to limit exposure to open, non-sheltered environments as indicated by spatially clumped oviposition (i.e., oviposition specialization; Fig. 3b; Table 1), which

is particularly noteworthy given the intensity of ALAN in the non-sheltered environment (97 lx). Together, our results indicate that ALAN did not reduce risky behavioral activity—foraging and oviposition were unaffected, and ALAN increased mating behavior. In other insects, reproductive behavior and predation risk are adversely affected by ALAN, and their predation avoidance tactics (e.g., aposematic coloration and evasive flight behavior) are rendered less effective under ALAN (reviewed in Owens et al. 2020). Therefore, our work in *G. lineaticeps* contributes to a growing body of literature suggesting that this important taxonomic group may be evolutionarily ill-prepared for the rapid expansion of ALAN (Falchi et al. 2016; Kyba et al. 2017; Seymoure 2018; Desouhant et al. 2019; Owens et al. 2020).

Shelters provided respite for ALAN-exposed crickets in our study, but the intensity of night light was quite high in non-sheltered environments (inside shelter: 2.3 lx; outside shelter: 97 lx). Thus, our study tended to simulate a bright urban lighting environment. Yet, many animals experience much lower levels of ALAN than those in our study (Casasole et al. 2017; Aulsebrook et al. 2020). For example, recent studies on crickets used 0.3–5 lx of ALAN (e.g., Crump et al. 2021; Levy et al. 2021). The intensity (or illuminance; lux) does not tend to influence the effects of ALAN on animals (Sanders et al. 2021), including the effects of ALAN on several behaviors in crickets (Fig. S1; Botha et al. 2017; Levy et al. 2021). However, some animals do experience dose–response effects of ALAN (e.g., urban song birds: Dominoni et al. 2014). If an ALAN experiment's night light levels are too high, one would expect inflated the costs of ALAN. However, in our study, we found only modest costs of ALAN, compared with many non-significant effects of ALAN and even one significant benefit if ALAN (summarized in Table 1). We attribute the lack of large effects of ALAN in our study, at least in part, to crickets' circadian patterns of behavior, and to their use of shelters that dramatically reduce ALAN exposure (Fig. S1; Rost and Honegger 1987; Jacot et al. 2008; Levy et al. 2021). Nonetheless, we encourage continued experimental work to explore how ecological consequences vary due to the intensity, spectral qualities, and duration of ALAN exposure.

The perceived stressors of heat wave and high-intensity ALAN were not independently, additively, or interactively costly to reproduction in a field cricket, and they even appeared to provide reproductive benefits (Figs. 1, 2 and 3; Table 1). However, our results should be cautiously interpreted given certain features of our study. First, we manipulated temperature and night-time light only during early adulthood, and both of these environmental factors influence animals during development in other animals (reviewed in Angilletta 2009; Desouhant et al. 2019; Owens et al. 2020). Related, the risks of heat waves and ALAN may be temporally uncoupled in some systems (e.g., a greater risk of ALAN early in the season when the natural scotophase is longer, but a greater risk of heat wave later in the season for summer-breeding animals)—thus, future work should carefully consider the timing of these two potential stressors. Second, effects may vary due to the relative difference between day light intensity and night light intensity. The day light intensity was threefold greater than night light intensity in our study, and a greater day-to-night difference may produce stronger effects of ALAN. Third, several of the positive effects of heat wave that we detected (e.g., increased reproductive investment and output) may be food-dependent as in other *Gryllus* (Adamo et al. 2012). Foraging exposes many animals to predation, and predation risk strongly influences reproductive decision-making in crickets (even in the absence of predators: Hedrick and Dill 1993; Hedrick 2000; Stahlschmidt and Adamo 2013; Stahlschmidt et al. 2014; Atwell and Wagner 2015). Our study accounted for foraging by measuring food consumption (Fig. 1; Table 1)—yet, food was freely available to our study animals, and ongoing climate change is expected to create food insecurity for insects (Romo et al. 2014, 2015). Therefore, researchers should continue to integrate the role of food availability into multiple-stressor experiments (Folt et al. 1999; Sokolova 2013; Gobler et al. 2018; Stahlschmidt and Glass 2020; Padda and Stahlschmidt 2022).

Declarations

Competing interests The authors declare no competing interests.

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