SHORT COMMUNICATION

Stress tolerance is influenced by artificial light at night during development and life-history strategy

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ABSTRACT

Artificial light at night (ALAN) is increasingly prevalent worldwide, but life-history strategy may mitigate the costs of ALAN for animals. Yet, interactions among ALAN, life-history strategy and tolerance to climate-related stressors are unknown. We determined if developmental ALAN exposure (1) affects development, (2) affects adult phenotype, including heat and desiccation tolerance, and (3) affects and/or interacts with life-history strategy. We used the variable field cricket (*Gryllus lineaticeps*) because its geographic range is increasingly exposed to ALAN, heat, and drought conditions, and it exhibits different life-history strategies (flight-capability versus flight-incapability). ALAN affected adult phenotype, with positive effects on body mass (and size) and female reproductive investment, and a negative effect on heat tolerance. Life-history strategy also affected stress tolerance; flight-incapable females had greater heat tolerance and their desiccation tolerance was improved by ALAN exposure. Key features of environmental change (i.e. exposure to ALAN, heat and drought) may favor some life-history strategies over others.

KEY WORDS: ALAN, Cricket, Desiccation tolerance, Heat tolerance, Light pollution, Life history

INTRODUCTION

Artificial light at night (ALAN), also known as ecological light pollution, is increasingly prevalent in terrestrial environments. Nearly one-quarter of land surfaces worldwide are exposed to ALAN (Falchi et al., 2016), and global ALAN levels have increased >2% each year (Kyba et al., 2017). Exposure to ALAN impacts several features of animal biology, including physiology, phenology, life-history traits, and daily activity (Fyie et al., 2021; reviewed in Sanders et al., 2021). Although ALAN tends to have negative effects, animals may shift their life histories to mitigate costs because life-history strategy can influence their stress responses (Sanders et al., 2021; Stark et al., 2004; Schultner et al., 2013; Padda et al., 2021; but see Tüzün et al., 2020). Furthermore, different strategies may exhibit different sensitivities to ALAN. In which case, ALAN may favor one strategy over another. However, it is unknown if the expression of life-history strategies is affected by ALAN exposure (e.g. whether ALAN increases use of a given strategy) or if ALAN has strategy-specific effects on fitness-related traits (e.g. whether a given strategy proves more costly in ALAN).

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In addition to ALAN, stressors associated with climate change (e.g. heat and drought) are on the rise in many global regions (Sarhadi et al., 2018; IPCC, 2021). Although the effects of ALAN on the stress response have been examined (e.g. McLay et al., 2018; Grunst et al., 2020; Miner et al., 2021; Czarnecka et al., 2022), its role in heat or desiccation tolerance is unknown. Field crickets (*Gryllus* spp.) offer unique insight into the relationships among ALAN, life-history strategies and stress tolerance. *Gryllus* exhibit a wing dimorphism that mediates two distinct life-history strategies during early adulthood: flight-capable females have low reproductive investment while flight-incapable females have high reproductive investment (Roff, 1984; Zera and Mole, 1994; Zera, 2005; Stahlschmidt, 2022). This wing dimorphism in *Gryllus* is a genetic polymorphism and an environmental polyphenism (Zera, 2005). It is genetically determined and responsive to selection (reviewed in Roff and Fairbairn, 2001; Roff et al., 2002; Zera, 2005) but it can also be influenced by environmental factors (Roff and Fairbairn, 2007; Glass and Stahlschmidt, 2019; reviewed in Wu et al., 2014). In other crickets, a similar wing dimorphism is altered by light pulses in the scotophase (night-time) during development (Masaki and Yasuhiko, 1989) and exposure to ALAN affects mating behavior (Botha et al., 2017; Levy et al., 2021). The variable field cricket (*Gryllus lineaticeps*) has a geographic range encompassing areas where ALAN, heat and drought conditions are increasingly prevalent (Bennie et al., 2015; Sarhadi et al., 2018; Weissman and Gray, 2019; IPCC, 2021). Thus, we manipulated ALAN exposure during development in *G. lineaticeps* to test three hypotheses. (1) ALAN exposure is costly to adult phenotype. This hypothesis is based on the tendency for ALAN to impact the daily activity patterns and life-history traits of many animals, including crickets (Levy et al., 2021; reviewed in Sanders et al., 2021). Further, ALAN reduces melatonin levels in crickets (Jones et al., 2015) and melatonin is important for stress tolerance in insects (Subala et al., 2017; Fan et al., 2021). Therefore, we predict that developmental ALAN exposure is costly and thereby increases fluctuating asymmetry (a stress indicator: reviewed in Graham et al., 2010), and reduces body size, reproductive investment and stress (heat and desiccation) tolerance. (2) ALAN exposure promotes expression of the flight-capable life-history strategy, which would allow crickets to disperse to less stressful environments. *Gryllus* maintain or increase flight capacity at the expense of survival and/or reproduction during several types of stress (food: Glass and Stahlschmidt, 2019; heat and water: Padda et al., 2021; food and water: Padda and Stahlschmidt, 2022). Thus, we predict a greater frequency of flight-capable crickets in the ALAN-exposed treatment group. (3) However, ALAN exposure is more costly to individuals expressing the flight-capable life-history strategy because flight-capable *Gryllus* exhibit greater sensitivities to other stressors (e.g. oxidative and immune challenges: Stahlschmidt et al., 2020; our unpublished results), potentially due to greater energetic requirements of the flight-capable strategy (Zera and Mole, 1994;

Zera et al., 1997; Nespolo et al., 2008; Sun et al., 2020; Stahlschmidt, 2022). Here, we predict interactive effects between light treatment and flight morphology whereby ALAN exposure will have disproportionate costs to body size, reproductive investment and stress tolerance for flight-capable crickets.

Our study will be the first to examine the interconnectedness of the responses of animals to three increasingly prevalent features of environmental change: heat, drought and light pollution. Specifically, we will test whether ALAN influences sensitivity to climate-related stressors and determine the role of life-history strategy in mitigating the effects of ALAN.

MATERIALS AND METHODS
Study organism
Gryllus lineaticeps Stål 1861 has a geographic range that extends from southwestern Oregon, through California, and into Baja California, Mexico (Weissman and Gray, 2019). Like several other *Gryllus* spp., *G. lineaticeps* expresses two different wing morphs, short-winged (SW) and long-winged (LW) (Weissman and Gray, 2019). At the onset of adulthood, flight-incapable SW females invest heavily into fecundity (Zera, 2005). During early adulthood, LW crickets can be categorized into the LW(h) (histolyzed, non-functional dorso-longitudinal flight muscle (DLM)] and LW(f) (functional DLM) morphs. Thus, the morphs can be categorized into two different life-history strategies, flight-incapable SW or LW(h) and flight-capable LW(f) morphs, during early adulthood. The LW(h) morph in *Gryllus* has been found to be more physiologically similar to the SW morph than to the LW(f) morph (Zera et al., 1997; Zera and Larsen, 2001; Stahlschmidt, 2022). Yet, LW (both h and f morphs) and SW *Gryllus* generally differ in adult body mass, DLM status, rates of development and growth, and in their sensitivities to oxidative and desiccation challenges (Glass and Stahlschmidt, 2019; Stahlschmidt et al., 2020; Stahlschmidt and Glass, 2020; Padda and Stahlschmidt, 2022). Therefore, the LW morph can be used as a less precise proxy for flight capacity if DLM status is unknown.

Crickets used in this study were from a long-term colony sourced from the progeny of individuals from a natural population at Sedgwick Reserve, Santa Ynez, CA, USA. Every 1–2 years, the colony was interbred with offspring of females captured from Sedgwick Reserve. Breeding adults in the colony were maintained at an even morph (SW:LW) and sex ratio. Cohorts of 20 newly hatched crickets (<2 days post-hatching) were reared at 28°C in 15 liter translucent plastic bins. Each bin was covered with a clear sheet of acrylic plastic and contained *ad libitum* access to food (dry cat food) and water. Crickets spend a significant amount of time under shelter because predation risk strongly influences their decision-making (even in the absence of predators: Hedrick and Dill, 1993; Hedrick, 2000; Stahlschmidt and Adamo, 2013; Stahlschmidt et al., 2014; Atwell and Wagner, 2015). Thus, to mimic natural conditions, each bin also contained shelters (two egg cartons) that could be accessed freely throughout development

Experimental design
Crickets experienced 14 h of simulated sunlight (5300 Kelvin, a similar color temperature or warmth as natural sunlight; 1–500 lx, depending on shelter use) each day and one of two different night light treatments: ALAN or control. Crickets in the ALAN group (*n*=18 cohorts; *n*=360 total crickets) were exposed to 10 h of ALAN (0.3–40 lx, depending on shelter use) that was warmer than day light (2750 Kelvin) to simulate the color temperature of street lighting recommended by the American Medical Association (Kraus, 2016).

Crickets in the dark night (control) group (*n*=18 cohorts; *n*=360 total crickets) were exposed to darkness at night. The illuminance and color temperature of light bulbs were measured using a light meter (range: 0.15–250,000 lx; accuracy: ±3%; Lumu Power 2, LUMULABS, Ljubljana, Slovenia). Night light in our study was warmer (lower Kelvin) and dimmer (fewer lx) than daylight, and light was dramatically limited inside the shelters that crickets regularly accessed throughout the study. Thus, although the night light source represented a relatively high level of ALAN (40 lx), our ALAN-treated animals were likely exposed to considerably lower levels of light thereby blunting the potential effects of ALAN. However, including shelter represents a more ecologically relevant exposure to light than a design in which crickets are forced to continuously experience ambient light conditions (i.e. 500 lx during the photophase for all crickets and 40 lx during the scotophase for ALAN-treated crickets).

Within 1 day of reaching adulthood, each cricket was housed individually in a small translucent deli cup (473 ml) containing shelter (overturned 30 ml opaque container with access holes) and *ad libitum* access to food and water. All crickets were weighed after 5 days, which approximates when the trade-off between investment into flight versus reproduction peaks in *Gryllus* (*Gryllus firmus*: Zera, 2005; *G. lineaticeps*: Z.S., unpublished results). After being weighed, males were euthanized (see below) and females were typically tested for desiccation or heat tolerance. To estimate desiccation tolerance at 28°C, the water source was removed from each cricket's container. Each cricket was then checked daily until death, and the time to death (days) was used as an estimate of desiccation tolerance. Although only LW individuals are capable of flight, all crickets exhibit histolyzed flight muscle after approx. 7 days, which prevented post-mortem determination of flight morphology for desiccation trials.

There are two general experimental protocols to assess heat tolerance: static (duration to knockdown upon exposure to a constant, high temperature) and dynamic (temperature at which knockdown occurs after exposure to a constantly ramping temperature) (reviewed in Jørgensen et al., 2021). These two protocols typically yield consistent results (i.e. a positive correlation between static and dynamic estimates of heat tolerance), but values from the static protocol can be more heritable (Mitchell and Hoffmann, 2010; Jørgensen et al., 2019). Therefore, heat knockdown trials were performed at a field-relevant temperature (45±1°C: Sun et al., 2020; Stahlschmidt et al., 2022a). Each cricket was acclimated in a 50 ml centrifuge tube with access to water (cotton ball soaked with 10 ml of water) for 1 h at room temperature. Then, each cricket was transferred to a 473 ml glass jar submerged in 45°C water bath between 16:00 h and 16:30 h (i.e. 10–10.5 h into the 14 h photophase). Every minute, each cricket was flipped over, and it was considered knocked down when it could no longer right itself. The time to knockdown (min) was used as an estimate of heat tolerance, after which each female was euthanized (see below)

Females not assessed for desiccation tolerance and males were euthanized and stored at −20°C. After storage, the length of hind femurs from each cricket were measured and mean femur length was used as an index of body size (Nguyen and Stahlschmidt, 2019). Functional asymmetry, a stress indicator (Graham et al., 2010), was assessed as the coefficient of variation (mean/s.d.) of femur length for each cricket. To assess reproductive and flight investment, flight muscle score and ovary dry mass were determined. Here, DLMs were scored as 0 (absence of DLM), 1 (histolyzed, non-functional and white DLM) and 2 (functional, pink DLM) (Crnokrak and Roff, 2002; King et al., 2011; Glass and Stahlschmidt, 2019). Therefore,

crickets were determined to be SW (score of 0 or 1), LW(h) (score of 0 or 1), or LW(f) (score of 2). To estimate reproductive investment, gonads from each cricket were removed, dried to a constant mass at 55°C and weighed to determine dry mass. Ovary mass is proportional to fecundity (egg number) in *Gryllus* (*G. firmus*: Roff, 1994; *G. lineaticeps*: Z.S., unpublished results). During dissections, mating status (i.e. presence of sperm-filled spermatheca) was assessed, and all females were 'not mated'.

Statistical analyses

Data were tested for normality, natural logarithm-transformed when necessary and analyzed using SPSS (v.26 IBM Corp., Armonk, NY). Two-tailed significance was determined at α=0.05. Several general linear mixed models were used to examine the independent and interactive effects of light treatment (control and ALAN) and flight morphology [i.e. SW, LW(h) and LW(f)] or wing morphology (i.e. SW vs. LW) on developmental duration, heat tolerance, desiccation tolerance, adult body mass and size, functional asymmetry and gonad mass. Sex was included as a fixed effect when applicable (e.g. only females were assessed for stress tolerance) and cohort identity was included as a random effect in each model. For each model, all interactions between and among fixed effects (e.g. light treatment, sex and flight morphology) were initially included; for example, to determine and account for whether females (that invest more heavily into reproductive tissue) were more sensitive to light treatment relative to males. Sex independently influenced body and gonad mass (i.e. strong female-biased sexual dimorphisms), and sex also interacted with other factors (e.g. light treatment and flight morphology) to influence body and gonad mass. Thus, sexes were analyzed separately for body and gonad mass to better understand the effects of ALAN and life-history strategy on these two traits.

A general linear model was performed on data from each cohort to determine the effects of treatment on survivorship (i.e. proportion of crickets surviving to adulthood in each cohort). An ordinal logistic generalized linear mixed model was performed on flight morphology. To determine effect size, eta squared (η^2) or partial eta squared (η_p^2) were determined for each fixed effect and effect–effect interaction, and effect sizes were considered small, medium, or large at η^2 (or η_p^2)=0.01, 0.06, and 0.14, respectively (Cohen, 1988). Significant results are reported below and all results are shown in Table 1. Pairwise *post hoc* analyses were used to determine differences between the three flight morphs and to interpret interactive effects, and the Type I error rate associated with multiple comparisons was controlled by using the Holm–Bonferroni method.

RESULTS AND DISCUSSION

Survival, functional asymmetry and flight morphology were not affected by any factor (Fig. S1A–C; Table 1). Females developed significantly faster than males (mean±s.e.m.: 51±1.0 days versus 54.2±0.9 days, respectively), and flight-capable crickets [LW(f)] developed faster than either the SW or the LW(h) morph (Fig. S1D; Table 1).

Crickets exposed to ALAN generally had greater body size, and females had greater body mass and reproductive investment (Fig. 1 and Fig. S1F; Table 1). *Gryllus* exhibit sexual size dimorphism (Stahlschmidt and Chang, 2021; Stahlschmidt et al., 2022a), and females in our study were heavier than males and exhibited greater reproductive investment (Fig. 1E,F). Flight-incapable females were heavier than flight-capable females (mean±s.e.m: 788.8±19.4 mg versus 657.1±22.8 mg, respectively) and they had greater ovary mass (23.1±2.2 mg versus 68.8±1.6 mg) (Fig. 1B and Fig. S1f; Table 1). Body size (both sexes) and body mass (females only) were greater in LW crickets relative to SW crickets (Fig. 1A and Fig. S1f; Table 1).

Stress tolerance was only determined in females, and flight-incapable and ALAN-exposed crickets had reduced heat tolerance (Fig. 2A; Table 1). We detected only one significant interactive effect of flight capacity and light treatment, specifically, desiccation tolerance was greatest in SW crickets that were exposed to ALAN, and crickets in all other treatment combinations exhibited similar desiccation tolerances (Fig. 2B; Table 1). The effect of flight morphology on desiccation tolerance was not determined because *Gryllus* do not exhibit functional flight muscle after early adulthood.

Across animal taxa, ALAN tends to entail an array of costs, from reduced cognition and offspring number to increased predation (reviewed in Sanders et al., 2021). However, key features of development (developmental duration and success, and bilateral symmetry) were not affected by ALAN exposure in our study (Fig. S1A–C), and ALAN exposure actually benefited other fitness-related traits (e.g. increased body size in both sexes and greater body mass in females: Fig. 1A,F) in contradiction to our first hypothesis that ALAN exposure is costly to adult phenotype. Developmental stress also has positive effects on fitness-related traits in crickets and other taxa (Durrant et al., 2018; Crino and Breuner, 2015) and it can promote heat tolerance in insects (Willot et al., 2021). As it does for other traits (e.g. reviewed in Sanders et al., 2021), ALAN had a relatively modest effect on body size in our study (i.e. η_p^2=0.051, indicative of small-to-medium effect sizes: Cohen, 1988). Yet, ALAN exposure during development had greater effects on reproductive investment in females (i.e. η_p^2=0.17, indicative of a large effect size: Fig. 1B; Table 1), which is likely due, in part, to larger body size (reviewed in Peters, 1983). ALAN-related increases in body size (Fig. 1A) and ovary mass may be due to a longer daily feeding period (*sensu* changes in activity patterns exhibited by other animals: Sanders et al., 2021). In another cricket (*Acheta domesticus*), sub-adults and adults exhibit circadian patterns of feeding (Nowosielski and Patton, 1963). However, investigation is required to determine whether developmental ALAN alters such patterns in *Gryllus*. Exposure to ALAN does not generally promote body size across animals (Sanders et al., 2021), potentially because of opposing pressures on body size by other aspects of environmental change (e.g. warming: Gardner et al., 2011; Fryxell et al., 2020; but see Siepielski et al., 2019). However, ALAN exposure may offset or even outweigh reductions in body size caused by warming. In addition to food subsidization and non-native species, urban environments are characterized by both warmer temperatures and ALAN exposure and urbanization promotes body size in several animal taxa, including insects (McKinney, 2002; Wilby, 2008; Shochat et al., 2010; Penick et al., 2015; Beasley et al., 2018; Merckx et al., 2018; Putman and Tippie, 2020; IPCC, 2021).

Developmental ALAN exposure and flight (or wing) morphology had substantial effects on stress tolerance (demonstrated by their medium effect sizes: Fig. 2; Table 1). For example, ALAN exposure reduced heat tolerance by approx. 25% and SW crickets exhibited approx. 38% greater desiccation tolerance (i.e. could survive 3 days longer) than LW crickets after ALAN exposure (Fig. 2). In the field, *G. lineaticeps* adults in the founding population emerge during a July breeding season, which is characterized by hot and dry microclimates (e.g. 40°C or higher with 0.25 mm of monthly precipitation on average) (Sun et al., 2020; Stahlschmidt et al., 2022a;

Table 1. Effects of light treatment during development, sex and/or flight morphology on fitness-related traits in *Gryllus lineaticeps*.

	Effect	d.f.	*F*	*P*	Partial eta squared
Survival to adulthood	Light treatment	1,34	0.73	0.40	0.021
Functional asymmetry	Light treatment	1378	0.20	0.66	0.001
	Sex	1378	0.92	0.34	0.002
	Flight morphology	2378	0.91	0.41	0.005
	Light×Sex	1378	2.06	0.15	0.005
	Light×Flight	2378	0.41	0.66	0.002
	Sex×Flight	2378	0.46	0.63	0.002
	Light×Sex×Flight	2378	0.24	0.79	0.001
Flight morphology	Light treatment	1	1.0	0.31	0.003
Developmental duration	Light treatment	1,51	0.74	0.39	0.002
	Sex	**1380**	**8.76**	**<0.01**	**0.023**
	Flight morphology	**2377**	**3.27**	**0.039**	**0.017**
	Light×Sex	1380	1.56	0.21	0.004
	Light×Flight	2377	0.90	0.41	0.004
	Sex×Flight	2379	0.08	0.92	<0.001
	Light×Sex×Flight	2379	0.61	0.55	0.003
Femur length	**Light treatment**	**1,42**	**10.0**	**<0.01**	**0.051**
	Sex	**1374**	**14.2**	**<0.01**	**0.032**
	Flight morphology	**2375**	**6.19**	**<0.01**	**0.033**
	Light×Sex	1374	0.99	0.32	0.002
	Light×Flight	2375	2.49	0.08	0.012
	Sex×Flight	2372	2.63	0.07	0.014
	Light×Sex×Flight	2372	0.19	0.83	0.001
Body mass (males)	Light treatment	1,52	2.4	0.13	0.014
	Flight morphology	2242	0.64	0.53	0.004
	Light×Flight	2242	2.9	0.06	0.025
Body mass (females)	**Light treatment**	**1135**	**6.9**	**0.010**	**0.049**
	Flight morphology	**2135**	**25**	**<0.01**	**0.27**
	Light×Flight	2135	0.98	0.38	0.014
Testes mass	Light treatment	1,53	3.4	0.07	0.017
	Flight morphology	2246	0.37	0.69	0.003
	Light×Flight	2246	0.48	0.62	0.005
Ovary mass	**Light treatment**	**1,16**	**7.2**	**0.016**	**0.17**
	Flight morphology	**2,47**	**46**	**<0.01**	**0.63**
	Light×Flight	2,47	1.8	0.17	0.057
Heat tolerance (females)	**Light treatment**	**1,16**	**5.18**	**0.037**	**0.12**
	Flight morphology	**2,48**	**3.79**	**0.030**	**0.08**
	Light×Flight	2,48	0.42	0.66	0.013
Desiccation tolerance (females)	Light treatment	1,28	5.18	0.67	<0.001
	Wing morphology	**1,48**	**3.79**	**<0.01**	**0.071**
	Light×Wing	**2,48**	**0.42**	**0.025**	**0.032**

Survival to adulthood (*n*=36 cohorts of 20 crickets each across both light treatment conditions); functional asymmetry (coefficient of variation in femur length; *n*=500); flight morphology (*n*=513); developmental duration (*n*=510; females developed faster than males); femur length (body size; *n*=508); adult body mass in males and females (*n*=504); dry gonad mass in males and females (*n*=322); female tolerance to heat and desiccation (*n*=62 for heat tolerance; *n*=99 for desiccation tolerance).
Eta squared or partial eta squared was determined to assess effect sizes, which were considered small, medium, or large at=0.01, 0.06 and 0.14, respectively (Cohen, 1988). Significant effects are bold.

US Climate Data 2022). Therefore, variation in heat and desiccation tolerance is likely to be highly ecologically relevant. That said, future work is required to fully understand the implications of the effect sizes on stress tolerance observed in our study.

We offer three physiological explanations for our results related to stress tolerance. First, in support of our first hypothesis (ALAN exposure is costly to adult phenotype), ALAN-exposed females had reduced heat tolerance (Fig. 2A) because ALAN reduces melatonin levels in other crickets (Jones et al., 2015). Melatonin supplementation increases stress tolerance in insects (Subala et al., 2017; Fan et al., 2021), and it improves heat tolerance in vertebrates (Sahin et al., 2004; Abbas et al., 2007; Sharma et al., 2013). Thus, an ALAN-induced reduction in melatonin levels may have decreased heat tolerance in our study. Second, serotonin is the precursor to melatonin (Vanecek, 1998), and it regulates circadian rhythms in crickets (Saifullah and Tomioka, 2002) and increases water excretion in other insects (Mykles et al., 2010). If developmental ALAN exposure downregulates the serotonin–melatonin system, then water stores may be conserved thereby promoting desiccation tolerance (in contradiction to our first hypothesis). Third, ALAN only benefited the desiccation tolerance of flight-incapable crickets (i.e. SW crickets, because most LW crickets were likely flight-capable: Fig. 2B and Fig. S1C) because flight capacity influences circadian rhythms. For example, flight-capable *Gryllus* females tend to exhibit larger daily fluctuations (i.e. greater circadian rhythmicity) in juvenile hormone levels, global gene expression patterns and metabolic rate (Zhao and Zera, 2004; Zera et al., 2018; Stahlschmidt, 2022). Thus, serotonin–melatonin systems in flight-capable crickets may be less sensitive to ALAN-related perturbations, meaning that only flight-incapable crickets receive the desiccation tolerance benefits of ALAN-induced reductions in serotonin. Melatonin is an ancient antioxidant that is important to circadian rhythms and stress tolerance for plants and animals (reviewed in Zhao et al., 2019); therefore, future efforts
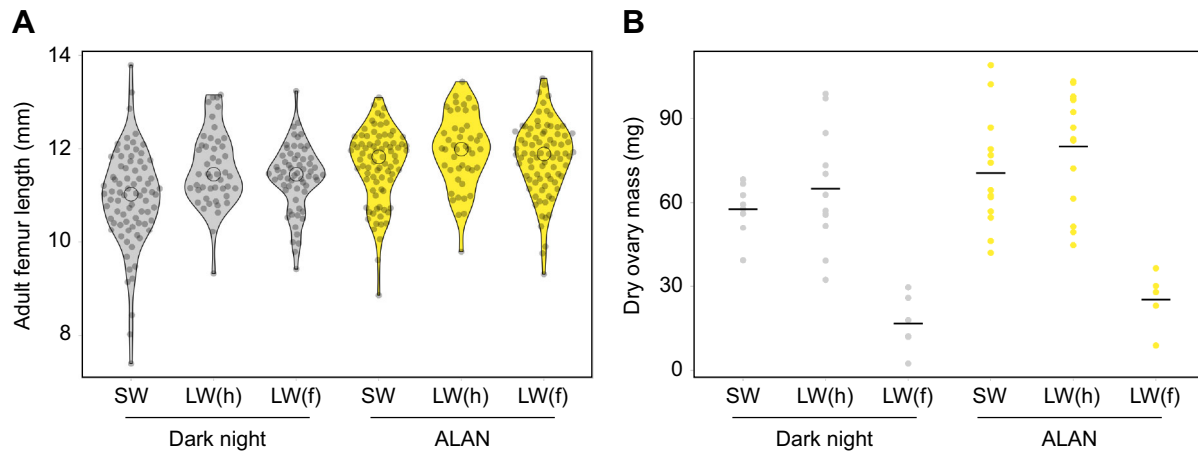
Fig. 1. Effects of light treatment and wing morphology on body size and reproductive investment in crickets (*Gryllus lineaticeps*). Short-winged crickets (SW), long-winged crickets with histolyzed flight muscle [LW(h)] and long-winged crickets with functional flight muscle [LW(f)] were kept in the dark or exposed to artificial light at night (ALAN). Effects of light treatment were examined on (A) body size (*n*=508; mean values indicated by open circles), and (B) female reproductive investment (*n*=58; mean values indicated by bold horizontal lines) in sex effects are described in Results. Significant effects were observed on light treatment, wing morphology and sex (A) and on light treatment and flight morphology (B).

should explore its role in mediating the effects of ALAN on stress tolerance.

Variation in life-history strategies allows animals to adaptively respond to their environments (Ricklefs and Wikelski, 2002). Yet, the expression of life-history strategy (investment into flight versus reproduction) was not developmentally plastic in response to ALAN (Fig. S1C), contradicting our second hypothesis that ALAN exposure will promote the expression of the flight-capable life-history strategy. This hypothesis characterized ALAN as a stressor that would favor the dispersal phenotype (i.e. flight-capable and/or LW morph). In contrast, ALAN appeared to be beneficial as it promoted adult body size and ovary mass (Fig. 1), in agreement with recent work demonstrating positive effects of short-term ALAN exposure on mating behavior in *G. lineaticeps* (Stahlschmidt et al., 2022b). Likewise, our third hypothesis (ALAN exposure will prove more costly to individuals expressing the flight-capable life-

history strategy) was not supported. Life-history strategies in *G. lineaticeps* did influence stress tolerance, which has been shown in other taxa. For example, 'fast-living' organisms, characterized by early reproduction, can be less susceptible to stress relative to their 'slow-living' counterparts characterized by delayed reproduction (Stark et al., 2004; Palacios et al., 2012; Schultner et al., 2013; Padda et al., 2021; but see Tüzün et al., 2020). In agreement, 'fast-living' *G. lineaticeps* (i.e. SW females with greater reproductive investment during early adulthood: Fig. 1B) had greater desiccation tolerance when exposed to ALAN and greater heat tolerance in both light treatments relative to 'slow-living', flight-capable females that delay reproductive investment (Fig. 2). Similarly, SW or flight-incapable *G. firmus* are less sensitive to water limitation and oxidative challenge relative to LW crickets (Stahlschmidt et al., 2020; Padda and Stahlschmidt, 2022). Therefore, continued exposure to ALAN and climate-related
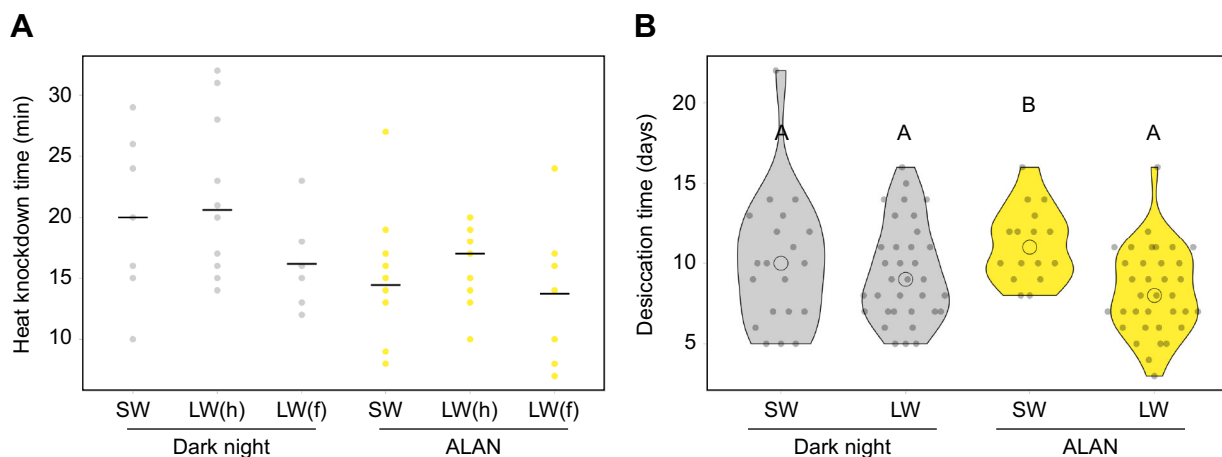

Fig. 2. Effects of light treatment and wing morphology on heat tolerance in female *G. lineaticeps*. Short-winged crickets (SW), long-winged crickets with histolyzed flight muscle [LW(h)] and long-winged crickets with functional flight muscle [LW(f)] were kept in the dark or exposed to artificial light at night (ALAN). (A) Effects on heat tolerance in female crickets (*n*=62; mean values indicated by bold horizontal lines). (B) Effects of light treatment and wing morphology on desiccation tolerance (*n*=99; mean values indicated by open circles) in female crickets. Although only LW individuals are capable of flight, all crickets exhibit histolyzed flight muscle after approx. 7 days, which prevented post-mortem determination of flight morphology for desiccation trials. Different letters denote significant differences in pairwise comparisons. Significant effects were observed on light treatment and flight morphology (A) and on wing morphology and light treatment×wing morphology (B).

stressors (e.g. heat and drought: Sarhadi et al., 2018; IPCC, 2021) may disadvantage the flight-capable morph. Accordingly, *Gryllus* may offer key insight into the dynamic between life-history strategy and stress tolerance in the context of environmental change.

In *Gryllus*, ALAN may disrupt life-history strategy-specific variation in circadian physiology. Flight-capable crickets exhibit greater circadian rhythmicity in hormone levels, patterns of gene expression and whole-animal metabolism (Zhao and Zera, 2004; Zera et al., 2018; Stahlschmidt, 2022). Therefore, future work should continue to characterize circadian biology in *Gryllus*, as well as the effects of ALAN on overall and strategy-specific rhythmicity. For example, ALAN may blunt circadian patterns of physiology and behavior, particularly for individuals expressing the flight-capable life-history strategy. Currently, the connections among ALAN, circadian biology, life-history strategy and stress tolerance are unknown. Furthermore, ALAN may impose other ecological costs (e.g. increased predation: reviewed in Sanders et al., 2021) that may differentially affect particular life-history strategies. For example, temperature shifts have divergent effects on the behavior of the two *G. lineaticeps* wing morphs: heat waves increase boldness in SW crickets and reduce it in LW crickets (Padda et al., 2021). Because ALAN may be an evolutionary trap that is driving global declines of insects (reviewed in Hopkins et al., 2018; Owens et al., 2020), our study represents an important first step in understanding the role of ALAN in shaping two of an animal's most important tools to address ongoing global change: life-history strategy and stress tolerance.

References

Abbas, A. O., Gehad, A. E., Hendricks, G. L., , III, Gharib, H. B. A. and Mashaly, M. M. (2007). The effect of lighting program and melatonin on the alleviation of the negative impact of heat stress on the immune response in broiler chickens. *Int. J. Poul. Sci.* **6**, 651-660. doi:10.3923/ijps.2007.651.66

Atwell, A. and Wagner, W. E. (2015). Along came a spider who sat down beside her: perceived predation risk, but not female age, affects female mate choosiness. *Behav. Process.* **115**, 143-148. doi:10.1016/j.beproc.2015.04.002

Beasley, D. E., Penick, C. A., Boateng, N. S., Menninger, H. L. and Dunn, R. R. (2018). Urbanization disrupts latitude-size rule in 17-year cicadas. *Ecol. Evol.* **8**, 2534-2541. doi:10.1002/ece3.3879

Bennie, J., Duffy, J. P., Davies, T. W., Correa-Cano, M. E. and Gaston, K. J. (2015). Global trends in exposure to light pollution in natural terrestrial ecosystems. *Remote Sens.* **7**, 2715-2730. doi:10.3390/rs70302715

Botha, L. M., Jones, T. M. and Hopkins, G. R. (2017). Effects of lifetime exposure to artificial light at night on cricket (*Teleogryllus commodus*) courtship and mating behaviour. *Anim. Behav.* **129**, 181-188. doi:10.1016/j.anbehav.2017.05.020

Cohen, J. (1988). *Statistical Power Analysis for the Behavioral Sciences.* New York, NY: Routledge Academic.

Crino, O. L. and Breuner, C. W. (2015). Developmental stress: Evidence for positive phenotypic and fitness effects in birds. *J. Ornithol.* **156**, 389-398. doi:10.1007/s10336-015-1236-z

Crnokrak, P. and Roff, D. A. (2002). Trade-offs to flight capability in *Gryllus firmus*: the influence of whole-organism respiration rate on fitness. *J. Evol. Biol.* **15**, 388-398. doi:10.1046/j.1420-9101.2002.00401.x

Czarnecka, M., Jermacz, L., Glazińska, P., Kulasek, M. and Kobak, J. (2022). Artificial light at night (ALAN) affects behaviour, but does not change oxidative status in freshwater shredders. *Environ. Pollut.* **306**, 119476. doi:10.1016/j.envpol.2022.119476

Durrant, J., Botha, L. M., Green, M. P. and Jones, T. M. (2018). Artificial light at night prolongs juvenile development time in the black field cricket, *Teleogryllus commodus*. *J. Exp. Zool. B Mol. Dev. Evol.* **330**, 225-233. doi:10.1002/jez.b.22810

Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C. C. M., Elvidge, C. D., Baugh, K., Portnov, B. A., Rybnikova, N. A. and Furgoni, R. (2016). The new world atlas of artificial night sky brightness. *Sci. Adv.* **2**, e1600377. doi:10.1126/sciadv.1600377.

Fan, W., Li, G., Zhang, X., Wang, Y., Wang, C., Xu, B., Guo, X. and Li, H. (2021). The role of melatonin and tryptophan-5-hydroxylase-1 in different abiotic stressors in *Apis cerana cerana*. *J. Insect Physiol.* **128**, 104180. doi:10.1016/j.jinsphys.2020.104180.

Fryxell, D. C., Hoover, A. N., Alvarez, D. A., Arnesen, F. J., Benavente, J. N., Moffett, E. R., Kinnison, M. T., Simon, K. S. and Palkovacs, E. P. (2020). Recent warming reduces the reproductive advantage of large size and contributes to evolutionary downsizing in nature: Warming leads to evolutionary downsizing. *Proc. R. Soc. B* **287**, 20200608. doi:10.1098/rspb.2020.0608rspb20200608.

Fyie, L. R., Gardiner, M. M. and Meuti, M. E. (2021). Artificial light at night alters the seasonal responses of biting mosquitoes. *J. Insect Physiol.* **129**, 104194. doi:10.1016/j.jinsphys.2021.104194

Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L. and Heinsohn, R. (2011). Declining body size: A third universal response to warming? *Trends Ecol. Evol.* **26**, 285-291. doi:10.1016/j.tree.2011.03.005.

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

Graham, J. H., Raz, S., Hel-Or, H. and Nevo, E. (2010). Fluctuating asymmetry: Methods, theory, and applications. *Symmetry* **2**, 466-540. doi:10.3390/sym2020466

Grunst, M. L., Raap, T., Grunst, A. S., Pinxten, R., Parenteau, C., Angelier, F. and Eens, M. (2020). Early-life exposure to artificial light at night elevates physiological stress in free-living songbirds. *Environ. Pollut.* **259**, 113895. doi:10.1016/j.envpol.2019.113895.

Hedrick, A. V. (2000). Crickets with extravagant mating songs compensate for predation risk with extra caution. *Proc. R. Soc. B* **267**, 671-675. doi:10.1098/rspb.2000.1054

Hedrick, A. V. and Dill, L. M. (1993). Mate choice by female crickets is influenced by predation risk. *Anim. Behav.* **46**, 193-196. doi:10.1006/anbe.1993.1176

Hopkins, G. R., Gaston, K. J., Visser, M. E., Elgar, M. A. and Jones, T. M. (2018). Artificial light at night as a driver of evolution across urban–rural landscapes. *Front. Ecol. Envir.* **16**, 472-479. doi:10.1002/fee.1828

IPCC (2021). Summary for policymakers. In *Climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the Intergovernmental Panel on Climate Change* (ed. V. Masson-Delmotte et al.). Cambridge University Press.

Jørgensen, L. B., Malte, H. Overgaard, J. (2019). How to assess Drosophila heat tolerance: Unifying static and dynamic tolerance assays to predict heat distribution limits. *Funct. Ecol.* **33**, 629-642. Doi: 10.1111/1365-2435.13279

Jørgensen, L. B., Malte, H., Ørsted, M., N. A. Klahn and J. Overgaard (2021). A unifying model to estimate thermal tolerance limits in ectotherms across static, dynamic and fluctuating exposures to thermal stress. *Sci. Rep.* **11**, 12840. doi: 10.1038/s41598-021-92004-6

Jones, T. M., Durrant, J., Michaelides, E. B. and Green, M. P. (2015). Melatonin: a possible link between the presence of artificial light at night and reductions in biological fitness. *Philos. Trans. R. Soc. B Biol. Sci.* **370**, 20140122. doi:10.1098/rstb.2014.0122.

King, E. G., Roff, D. A. and Fairbairn, D. J. (2011). Trade-off acquisition and allocation in *Gryllus firmus*: A test of the Y model. *J. Evol. Biol.* **24**, 256-264. doi:10.1111/j.1420-9101.2010.02160.x

Kraus, L. J. (2016). Human and environmental effects of light emitting diode (LED) community lighting. *Action of the AMA House of Delegates 2016 annual meeting: Council on Science and Public Health report 2-A-16*. American Medical Association.

Kyba, C. C. M., Kuester, T., De Miguel, A. S., Baugh, K., Jechow, A., Hölker, F., Bennie, J., Elvidge, C. D., Gaston, K. J. and Guanter, L. (2017). Artificially lit surface of earth at night increasing in radiance and extent. *Sci. Adv.* **3**, e1701528. doi:10.1126/sciadv.1701528.

Levy, K., Wegrzyn, Y., Efronny, R., Barnea, A. and Ayali, A. (2021). Lifelong exposure to artificial light at night impacts stridulation and locomotion activity patterns in the cricket *Gryllus bimaculatus*. *Proc. R. Soc. B* **288**, 20211626. doi:10.1098/rspb.2021.1626.

Masaki, S. and Yasuhiko, W. (1989). Response to nigh interruption in photoperiodic determination of wing form of the ground cricket *Dianemobius*

fascipes. *Physiol. Entomol.* **14**, 179-186. doi:10.1111/j.1365-3032.1989.tb00950.x

McKinney, M. L. (2002). Urbanization, biodiversity, and conservation. *Bioscience* **52**, 883-890. doi:10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2

McLay, L. K., Nagarajan-Radha, V., Green, M. P. and Jones, T. M. (2018). Dim artificial light at night affects mating, reproductive output, and reactive oxygen species in *Drosophila melanogaster*. *J. Exp. Zool. A Ecol. Integr. Physiol.* **329**, 419-428. doi:10.1002/jez.2164

Merckx, T., Kaiser, A. and Van Dyck, H. (2018). Increased body size along urbanization gradients at both community and intraspecific level in macro-moths. *Glob. Change Biol.* **24**, 3837-3848. doi:10.1111/gcb.14151

Miner, K. A., Huertas, M., Aspbury, A. S. and Gabor, C. R. (2021). Artificial light at night alters the physiology and behavior of western mosquitofish (*Gambusia affinis*). *Front. Ecol. Evol.* **9**, 617063. doi:10.3389/fevo.2021.617063

Mitchell, K. A. and Hoffmann, A. A. (2010). Thermal ramping rate influences evolutionary potential and species differences for upper thermal limits in Drosophila. *Funct. Ecol.* **24**, 694-700. doi: 10.1111/j.1365-2435.2009.01666.x

Mykles, D. L., Adams, M. E., Gäde, G., Lange, A. B., Marco, H. G. and Orchard, I. (2010). Neuropeptide action in insects and crustaceans. *Physiol. Biochem. Zool.* **83**, 836-846. doi:10.1086/648470

Nespolo, R. F., Roff, D. A. and Fairbairn, D. J. (2008). Energetic trade-off between maintenance costs and flight capacity in the sand cricket (*Gryllus firmus*). *Funct. Ecol.* **22**, 624-631. doi:10.1111/j.1365-2435.2008.01394.x

Nguyen, K. and Stahlschmidt, Z. R. (2019). When to fight? disentangling temperature and circadian effects on aggression and agonistic contests. *Anim. Behav.* **148**, 1-8. doi:10.1016/j.anbehav.2018.11.014

Nowosielski, J. W. and Patton, R. L. (1963). Studies on circadian rhythm of the house cricket, *Gryllus domesticus* L. *J. Insect Physiol.* **9**, 401-404, IN1-IN4, 405-410. doi:10.1016/0022-1910(63)90049-0

Owens, A. C. S., Cochard, P., Durrant, J., Farnworth, B., Perkin, E. K. and Seymoure, B. (2020). Light pollution is a driver of insect declines. *Biol. Conserv.* **241**, 108259. doi:10.1016/j.biocon.2019.108259

Padda, S. S. and Stahlschmidt, Z. R. (2022). Evaluating the effects of water and food limitation on the life history of an insect using a multiple-stressor framework. *Oecologia* **198**, 519-530. doi:10.1007/s00442-022-05115-w

Padda, S. S., Glass, J. R. and Stahlschmidt, Z. R. (2021). When it's hot and dry: Life-history strategy influences the effects of heat waves and water limitation. *J. Exp. Biol.* **224**, jeb236398. doi:10.1242/jeb.236398.

Palacios, M. G., Sparkman, A. M. and Bronikowski, A. M. (2012). Corticosterone and pace of life in two life-history ecotypes of the garter snake *Thamnophis elegans*. *Gen. Comp. Endocrinol.* **175**, 443-448. doi:10.1016/j.ygcen.2011.11.042

Penick, C. A., Savage, A. M. and Dunn, R. R. (2015). Stable isotopes reveal links between human food inputs and urban ant diets. *Proc. R. Soc. B* **282**, 20142608. doi:10.1098/rspb.2014.2608

Peters, R. H. (1983). *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.

Putman, B. J. and Tippie, Z. A. (2020). Big city living: a global meta-analysis reveals positive impact of urbanization on body size in lizards. *Front. Ecol. Evol.* **8**, 580745. doi:10.3389/fevo.2020.580745

Ricklefs, R. E. and Wikelski, M. (2002). The physiology/life-history nexus. *Trends Ecol. Evol.* **17**, 462-468. doi:10.1016/S0169-5347(02)02578-8

Roff, D. A. (1984). The cost of being able to fly: A study of wing polymorphism in two species of crickets. *Oecologia* **63**, 30-37. doi:10.1007/BF00379781

Roff, D. A. (1994). Evidence that the magnitude of the trade-off in a dichotomous trait is frequency dependent. *Evolution* **48**, 1650-1656.

Roff, D. A. and Fairbairn, D. J. (2001). The genetic basis of migration and its consequences for the evolution of correlated traits. In *Causes, Consequences and Mechanisms of Dispersal at the Individual, Population and Community Level* (ed. C. Clobert, J. Nichols, J. D. Danchin and A. Dhondt), pp. 191-202. Oxford, UK: Oxford University Press.

Roff, D. A. and Fairbairn, D. J. (2007). Laboratory evolution of the migratory polymorphism in the sand cricket: Combining physiology with quantitative genetics. *Physiol. Biochem. Zool.* **80**, 358-369. doi:10.1086/518012

Roff, D. A., Mostowy, S. and Fairbairn, D. J. (2002). The evolution of trade-offs: Testing predictions on response to selection and environmental variation. *Evolution* **56**, 84-95.

Sahin, K., Onderci, M., Gursu, M. F., Kucuk, O. and Sahin, N. (2004). Effect of melatonin supplementation on biomarkers of oxidative stress and serum vitamin and mineral concentrations in heat-stressed Japanese quail. *JAPR* **13**, 342-348. doi:10.1093/japr/13.2.342

Saifullah, A. S. M. and Tomioka, K. (2002). Serotonin sets the day state in the neurons that control coupling between the optic lobe circadian pacemakers in the cricket *Gryllus bimaculatus*. *J. Exp. Biol.* **205**, 1305-1314. doi:10.1242/jeb.205.9.1305

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

Sarhadi, A., Ausín, M. C., Wiper, M. P., Touma, D. and Diffenbaugh, N. S. (2018). Multidimensional risk in a nonstationary climate: Joint probability of increasingly severe warm and dry conditions. *Sci. Adv.* **4**, eaau3487. doi:10.1126/sciadv.aau3487.

Schultner, J., Kitaysky, A. S., Gabrielsen, G. W., Hatch, S. A. and Bech, C. (2013). Differential reproductive responses to stress reveal the role of life-history strategies within a species. *Proc. R. Soc. B* **280**, 20132090. doi:10.1098/rspb.2013.2090.

Sharma, S., Ramesh, K., Hyder, I., Uniyal, S., Yadav, V. P., Panda, R. P. and Sarkar, M. (2013). Effect of melatonin administration on thyroid hormones, cortisol and expression profile of heat shock proteins in goats (*Capra hircus*) exposed to heat stress. *Small Ruminant Res.* **112**, 216-223. doi:10.1016/j.smallrumres.2012.12.008

Shochat, E., Lerman, S. B., Anderies, J. M., Warren, P. S., Faeth, S. H. and Nilon, C. H. (2010). Invasion, competition, and biodiversity loss in urban ecosystems. *Bioscience* **60**, 199-208. doi:10.1525/bio.2010.60.3.6

Siepielski, A. M., Morrissey, M. B., Carlson, S. M., Francis, C. D., Kingsolver, J. G., Whitney, K. D. and Kruuk, L. E. B. (2019). No evidence that warmer temperatures are associated with selection for smaller body sizes. *Proc. R. Soc. B* **286**, 20191332. doi:10.1098/rspb.2019.1332.

Stahlschmidt, Z. R. (2022). Flight capacity drives circadian patterns of metabolic rate and alters resource dynamics. *J. Exp. Zool. A Ecol. Integr. Physiol.* **337**, 666-674. doi:10.1002/jez.2598.

Stahlschmidt, Z. R. and Adamo, S. A. (2013). Warm and cozy: Temperature and predation risk interactively affect oviposition site selection. *Anim. Behav.* **86**, 553-558. doi:10.1016/j.anbehav.2013.06.009

Stahlschmidt, Z. R. and Glass, J. G. (2020). Life history and immune challenge influence metabolic plasticity to food availability and acclimation temperature. *Physiol. Biochem. Zool.* **93**, 271-281. doi:10.1086/709587

Stahlschmidt, Z. R. and Chang, E. (2021). Body condition indices are better surrogates for lean mass and water content than for body fat content in an insect. *J. Zool.* **315**, 131-137. doi:10.1111/jzo.12909

Stahlschmidt, Z., O'Leary, M. E. and Adamo, S. (2014). Food limitation leads to risky decision making and to tradeoffs with oviposition. *Behav. Ecol.* **25**, 223-227. doi:10.1093/beheco/art110

Stahlschmidt, Z. R., Jeong, N., Johnson, D. and Meckfessel, N. (2020). From phenoloxidase to fecundity: Food availability does not influence the costs of oxidative challenge in a wing-dimorphic cricket. *J. Comp. Physiol. B Biochem. Syst. Envir. Physiol.* **190**, 17-26. doi:10.1007/s00360-019-01244-6

Stahlschmidt, Z. R., Whitlock, J., Vo, C., Evalen, P. and Bui, D. (2022a). Pesticides in a warmer world: Effects of glyphosate and warming across insect life stages. *Environ. Pollut.* **307**, 119508. doi:10.1016/j.envpol.2022.119508.

Stahlschmidt, Z. R., Chun, P., Luc, D., Masuda, G., Rocha, A. and Sandhu, S. (2022b). Reproduction of a field cricket under high-intensity artificial light at night and a simulated heat wave. *Behav. Ecol. Sociobiol.* **76**, 109. doi: 10.1007/s00265-022-03220-7.

Stark, J. D., Banks, J. E. and Vargas, R. (2004). How risky is risk assessment: The role that life history strategies play in susceptibility of species to stress. *Proc. Natl. Acad. Sci. U.S.A.* **101**, 732-736. doi:10.1073/pnas.0304903101

Subala, S. P., Zubero, E. E., Alatorre-Jimenez, M. A. and Shivakumar, M. S. (2017). Pre-treatment with melatonin decreases abamectin induced toxicity in a nocturnal insect *Spodoptera litura* (lepidoptera: Noctuidae). *Environ. Toxicol. Pharmacol.* **56**, 76-85. doi:10.1016/j.etap.2017.08.025

Sun, B. J., Huebner, C., Treidel, L. A., Clark, R. M., Roberts, K. T., Kenagy, G. J. and Williams, C. M. (2020). Nocturnal dispersal flight of crickets: Behavioural and physiological responses to cool environmental temperatures. *Funct. Ecol.* **34**, 1907-1920. doi:10.1111/1365-2435.13615

Tüzün, N., Debecker, S. and Stoks, R. (2020). Strong species differences in life history do not predict oxidative stress physiology or sensitivity to an environmental oxidant. *J. Anim. Ecol.* **89**, 1711-1721. doi:10.1111/1365-2656.13235

Vanecek, J. (1998). Cellular mechanisms of melatonin action. *Physiol. Rev.* **78**, 687-721. doi:10.1152/physrev.1998.78.3.687

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

Wilby, R. L. (2008). Constructing climate change scenarios of urban heat island intensity and air quality. *Environ. Plann. B Plann. Design* **35**, 902-919. doi:10.1068/b33066t

Willot, Q., Loos, B. and Terblanche, J. S. (2021). Interactions between developmental and adult acclimation have distinct consequences for heat tolerance and heat stress recovery. *J. Exp. Biol.* **224**, jeb242479. doi:10.1242/JEB.242479.

Wu, H. J., Zhu, D. H., Zeng, Y., Zhao, L. Q. and Sun, G. X. (2014). Brachypterizing effect of high density and its relationship with body injury in cricket species *Velarifictorus micado* (orthoptera: Gryllidae). *Ann. Entomol. Soc. Am.* **107**, 113-118. doi:10.1603/AN13052

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

Zera, A. J. and Larsen, A. (2001). The metabolic basis of life history variation: Genetic and phenotypic differences in lipid reserves among life history morphs of

the wing-polymorphic cricket, *Gryllus firmus*. *J. Insect Physiol.* **47**, 1147-1160. doi:10.1016/S0022-1910(01)00096-8

Zera, A. J. and Mole, S. (1994). The physiological costs of flight capability in wing-dimorphic crickets. *Res. Popul. Ecol.* **36**, 151-156. doi:10.1007/BF02514930

Zera, A. J., Sall, J. and Grudzinski, K. (1997). Flight-muscle polymorphism in the cricket *Gryllus firmus*: Muscle characteristics and their influence on the evolution of flightlessness. *Physiol. Zool.* **70**, 519-529. doi:10.1086/515865

Zera, A. J., Vellichirammal, N. N. and Brisson, J. A. (2018). Diurnal and developmental differences in gene expression between adult dispersing and

flightless morphs of the wing polymorphic cricket, *Gryllus firmus*: Implications for life-history evolution. *J. Insect Physiol.* **107**, 233-243. doi:10.1016/j.jinsphys.2018.04.003

Zhao, Z. and Zera, A. J. (2004). The hemolymph JH titer exhibits a large-amplitude, morph-dependent, diurnal cycle in the wing-polymorphic cricket, *Gryllus firmus*. *J. Insect Physiol.* **50**, 93-102. doi:10.1016/j.jinsphys.2003.10.003

Zhao, D., Yu, Y., Shen, Y., Liu, Q., Zhao, Z., Sharma, R. and Reiter, R. J. (2019). Melatonin synthesis and function: Evolutionary history in animals and plants. *Front. Endocrinol.* **10**, 249. doi:10.3389/fendo.2019.00249