Short Communication

Life history strategy dictates thermal preferences across the diel cycle and in response to starvation in variable field crickets, *Gryllus lineaticeps*

Lisa A. Treidel[1,2,*], Christopher Huebner[2], Kevin T. Roberts[3], Caroline M. Williams

University of California, Berkeley, Department of Integrative Biology, Berkeley CA 94720

A B S T R A C T

Insects behaviorally thermoregulate across the diel cycle, and their preferred microhabitats change based on current resources available and the thermal performance optima of traits. Specific combinations of traits being prioritized are set by life history strategies, making life history an important intrinsic determinant of thermal preferences. However, we do not know how life history strategies shape plasticity of behavioral thermoregulation, limiting our ability to predict responses to environmental variability. We compared female variable field crickets (*Gryllus lineaticeps*) that are flight-capable (long-winged) and flightless (short-winged) to test the hypothesis that life history strategy determines plasticity of thermal preferences across the diel cycle and following starvation. Thermal preferences were elevated during the nocturnal activity period, and long-winged crickets preferred warmer temperatures compared to short-winged crickets across the diel cycle when fully fed. However, thermal preferences of starved crickets were reduced compared to fed crickets. The reduction in thermal preferences was greater in long-winged crickets, resulting in similar thermal preferences between starved long- and short-winged individuals and reflecting a more plastic response. Thus, life history does determine plasticity in thermoregulatory behaviors following resource limitations and effects of life history on thermal preferences are context dependent.

1. Introduction

Adaptive plasticity and evolution of organismal thermal preferences may buffer species from performance consequences of changing environments by facilitating energetic savings, reducing exposure to unsuitable microhabitats, and maximizing time spent at physiologically optimal temperatures (Huey et al., 2012; Gilbert and Miles, 2017; Kingsolver and Buckley, 2017; Muñoz and Losos, 2018; Riddell et al., 2021). Thermal preferences often change along with intrinsic (e.g., sex and life history), as well as extrinsic (e.g., climate and resource availability) factors. However, few studies have examined how interactions between intrinsic and extrinsic factors alter plasticity of behavioral thermoregulation, limiting our current ability to predict consequences and potential evolutionary responses to climate change (Buckley and Kingsolver, 2021).

Thermal optima of traits shape temperature preferences (T_{pref}) of ectotherms, defined as the environmental temperature selected in the absence of ecological constraints (Huey and Stevenson, 1979). How-

ever, key physiological traits underpinning life history and fitness, such as growth, locomotion, and egg production rate, have variable thermal optima (Anderson et al., 2011; Kellermann et al., 2019). Consequently, thermal preferences change across the diel (24-hour) cycle (Angilletta et al., 1999; Ellis et al., 2007; Kaneko et al., 2012), through development (Wallman and Bennett, 2006; Dillon et al., 2009), and seasonally (Rismiller and Heldmaier, 1988; Firth and Belan, 1998; Mortensen et al., 2007), allowing the maintenance of a body temperature that is most suitable to meet current performance demands set by life history. Additionally, changes in thermal preferences of ectotherms often arise through phenotypic plasticity to facilitate survival when environmental conditions decline due to stressors such as extreme weather events and reductions in food availability (Brett, 1971; Porter and Tschinkel, 1993; Van Dijk et al., 2002; Sun et al., 2010; Clissold et al., 2013; Gilbert et al., 2016). For instance, locusts prefer warmer temperatures that maximize growth rates when food is abundant, but cooler temperatures that maximize nutrient assimilation efficiency when starved (Miller et al., 2009; Coggan et al., 2011). Life history strategies determine the timing, intensity, and specific combinations of resource allocations among traits, but how these associated priorities shape organismal

thermoregulatory behavior and responses to environmental stressors remains unresolved.

Wing-polymorphisms, characterized by discrete variation in wing-length, are common amongst insects and associated with a life history polymorphism in timing of reproduction, due to a trade-off between flight and oogenesis (Zera and Denno, 1997). Among wing-polymorphic species of field crickets (*Gryllus* spp.), long-winged (LW) individuals are flight-capable allowing them to gain potential fitness benefits of dispersal (e.g., find mates, escape deteriorating habitats, escape predators), but delay onset of reproduction compared to flightless short-winged (SW) individuals (Roff and Fairbairn, 1991). LW and SW crickets differ behaviorally and physiologically because the metabolic demands of flight and reproduction are highly divergent (Zera and Harshman, 2001), providing a powerful system in which we can compare the behavioral thermoregulatory responses of individuals expressing alternative life history strategies to changing environmental conditions.

In the variable field cricket, *Gryllus lineaticeps* , LW individuals prefer higher temperatures resulting in the selection of warmer microhabitats in natural environments than SW individuals, to facilitate reaching high body temperatures necessary to initiate flight (Sun et al., 2020). LW crickets fly at night and have a circadian rhythm in juvenile hormone (JH) expression and titers, while JH expression and titers are acyclic in flightless SW crickets, suggesting that circadian rhythms differ between morphs and may play an important role in regulating morph-specific behavioral patterns (Zera et al., 2018). Here we test the hypothesis that plasticity in thermal preferences either through the diel cycle or in response to food limitation will differ between LW and SW morphs, forming a component of the alternative life history strategies. We first assessed thermal preferences of fully fed crickets across the diel cycle and predicted a larger increase in the thermal preference between morning and night of LW compared to SW crickets. Second, we compared thermal preferences of fully fed and starved crickets. Because flight would be constrained by energy deficits associated with starvation, we predicted LW crickets would exhibit larger reductions in their preferred temperatures compared to SW crickets. The revealed interaction between life history and food availability on behavioral thermoregulation suggests that life history strategies are an important factor altering the strength of organismal responses to environmental stressors.

2. Material and Methods

2.1. Cricket Stocks

A laboratory colony of *G. lineaticeps*, was established at University of California Berkeley in August 2015, from approximately 200 adults collected at Sedgwick Reserve (34°41'34" N, 120°02'26" W), University of California Natural Reserve System (Sun et al., 2020). To maintain an outbred colony and avoid selection on either wing-morph, an equal proportion of randomly selected long- and short-winged reproductively mature adults (*N*= 120, 60 LW and 60 SW) were allowed to mate and lay eggs weekly. Additionally, we collected at least 100 adults fresh from the field and incorporated their offspring into the laboratory colony annually. The experiments described here were performed in 2018-2019 using crickets from approximately the 13-15th generations of this laboratory colony. Throughout development, crickets were maintained under controlled density at 27 °C with a 16-hour light: 8-hour dark photoperiod (lights-off at 21:00), with *ad libitum* access to food and water. To generate experimental crickets, we monitored crickets in their last juvenile life stage daily and removed newly emerged adults. All new adult females were housed separately in age-matched, unmated groups prior to thermal preference measurements.

### 2.2. Thermal Preference Measurements

We assessed the thermal preferences (T$_{pref}$) of female long-winged (LW) and short-winged (SW) crickets across the diel cycle and under fed or starved conditions. We focused on females because the tradeoff between flight and reproduction are more pronounced in females compared to males (Zera and Harshman, 2001). On the fifth day of adulthood, T$_{pref}$ was measured in crickets under fully fed conditions either at the start of the scotophase (21:00 - 22:00) (fed night; *N* = 72, 38 LW and 34 SW) or the start of the photophase (06:00 - 07:00) (fed morning; *N* = 81, 45 LW and 36 SW). The fifth day of adulthood was chosen, because this is the day on which differences in physiological traits and circadian rhythms of LW and SW crickets are most pronounced (Zera et al., 2018). Thermal preferences of a third group of crickets were also measured at nighttime on the fifth day of adulthood, immediately following a three-day (72-hour) starvation during which only water was provided *ad libitum* (starved night; *N* = 50, 26 LW and 24 SW). A pilot experiment revealed that most *G. lineaticeps* adults can survive a ten-day starvation (10 of 12 survived) but lose a significant amount of body mass (on average 18% total mass reduction) (unpublished results). On day-three there was no significant body mass loss or mortality, so we selected a three-day starvation as a mild to moderate stressor.

We quantified T$_{pref}$ of crickets, as previously described in Sun et al. (2020). Briefly, our experimental thermal gradient apparatus was divided into six lanes by steel slats. To form a temperature gradient in each lane that ranged from 15-60 °C, the steel slats were attached to an aluminum heat sink warmed by ceramic heating bulbs and silicon strip heaters on a warm end and a plexiglass wall on the cold end. This temperature gradient included the large breadth of temperatures crickets can access in natural settings throughout the day (Sun et al., 2020). Each cricket was introduced to a randomly selected lane at a randomly assigned starting position within the lane on the experimental thermal gradient apparatus. Random assignments of lanes and starting positions were used to ensure T$_{pref}$ were reached by active behavioral thermoregulation. Following an acclimation period (30 min), the cricket's external body temperature was measured at its midpoint using a thermal camera (E5, FLIR Systems, Wilsonville, OR, USA) at 30, 40 and 50 minutes after release into the gradient. We confirmed that temperatures measured with the thermal camera did not differ from those measured using a K-type thermocouple placed in direct contact with the crickets' cuticle (Paired T-Test: *T=0.73, DF=9, P=0.48)*. Repeated measures were taken to estimate repeatability of T$_{pref}$. However, if the cricket was actively moving at the time of measurement (30, 40, or 50 min), no temperature recording was made. Eight individual crickets (8 out of 198 total) only had one estimate of their T$_{pref}$ and were excluded from statistical analysis.

2.3. Statistical Analysis

All statistical analyses were conducted in R version 4.0.4. We built two separate linear mixed models (LMM) with restricted maximum-likelihood estimation and report *F* tests with Satterthwaite approximation for degrees of freedom for fixed effects (lme4 and lmerTest packages (Bates, 2010; Kuznetsova et al., 2017)). Both LMMs included the T$_{pref}$ of the fed night group, to determine if there was an interaction between wing length (LW or SW), used as a proxy for life history strategy, and either diel rhythms (fed night vs. fed morning) or effects of starvation (fed night vs. starved night) as fixed effects on T$_{pref}$ as the response variable. Cricket identity was included as a random effect, and repeatability of T$_{pref}$ measurements within individuals was moderately high (*r=0.5*). Within individual variation in T$_{pref}$ accounted for an estimated 24.9% of the total variation in T$_{pref}$ in the model testing for effects of diel rhythms and 13.3% of total variation in T$_{pref}$ in the model testing for effects of starvation. Since T$_{pref}$ measures taken at later times in a given trial were slightly lower (on average 0.5-1 °C lower at 50 minutes compared to 30 minutes), models also included measurement time (30, 40, or 50 minutes after introduction of a cricket into the thermal gradient) as a fixed effect. All averages are reported as least squares mean ± standard error.
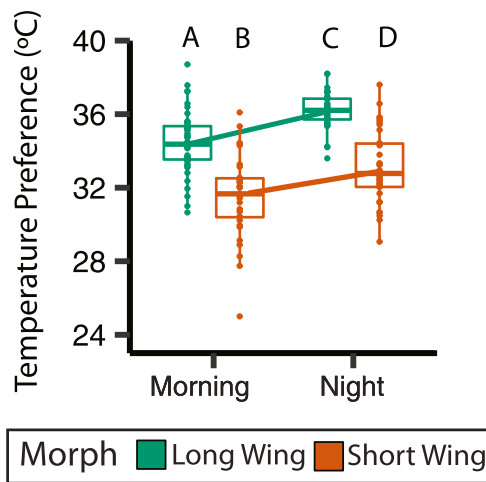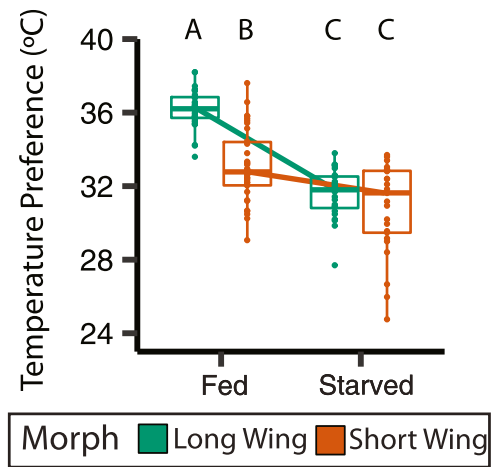
Figure 1. Thermal preference of *Gryllus lineaticeps* field crickets with long (color: green) or short wings (color: orange) at morning (06:00 - 07:00) and night (21:00 - 22:00). Boxplots denote the 25th, median, and 75th quartiles, and solid points show the average thermal preference of individual crickets calculated from repeated measures. Different letters denote significant differences in thermal preferences (Tukey's HSD, *p*<0.05).

Figure 2. Nighttime thermal preferences of *Gryllus lineaticeps* field crickets with long (color: green) and short wings (color: orange) under fed and starved conditions. Boxplots denote the 25th, median, and 75th quartiles, and solid points show the average thermal preference of individual crickets calculated from repeated measures. Different letters denote significant differences in thermal preferences (Tukey's HSD, *p*<0.05).

3. Results and Discussion

3.1. Life history determines diel rhythms in temperature preference when resources are abundant

Crickets selected warmer locations in the experimental thermal gradient at night compared to the morning (Time- $F_{1,134.59}$=24.52, *P*<0.001), reflecting the presence of a diel rhythm in thermal preferences (Figure 1). On average, there was a small increase in preferred temperatures of 1.5 ± 0.3 °C for both long-winged (LW) and short-winged (SW) crickets between the start of the light phase (SW: 31.7 ± 0.3 °C; LW: 34.6 ± 0.3 °C) and the start of the dark phase (SW: 33.0 ± 0.3 °C; LW: 36.2 ± 0.3 °C). *Gryllus* crickets remain relatively inactive in belowground refugia during the daytime but emerge aboveground at sundown and exhibit high rates of locomotor activity throughout the early-evening (Tomioka and Chiba, 1989). Our finding of higher thermal preferences of *G. lineaticeps* at night compared to the morning are thus consistent with prior work reporting elevated thermal preferences during periods of high activity, broadly across ectotherms (Firth and Belan, 1998; Angilletta et al., 1999; Ellis et al., 2007; Hamada et al., 2008). Additionally, diel rhythms in thermal preferences may guide selection of appropriate microhabitats when transitioning between below- and aboveground sites, to support critical life-history-related behaviors including flight, seeking mates, locating oviposition sites, and foraging performed at night. For example, LW crickets rely on behavioral thermoregulation in combination with endogenous heat production to obtain high body temperatures exceeding 30°C, necessary to initiate flight on cool nights, making high thermal preferences at night likely important for dispersal behavior (Sun et al., 2020). For SW crickets, higher thermal preferences at night compared to the morning may facilitate nighttime reproductive behaviors including locating mates and suitable oviposition sites. Consistent with this expectation, the attractiveness of male mating calls is temperature-dependent, and thermal preferences of males enable selection of warm microclimates that improve singing performance (Van Wyk and Ferguson, 1995; Hedrick et al., 2002). Although only females were used in this study, our prior work suggested there were no differences in T_{pref} of male and female *G. lineaticeps* (Sun et al., 2020).

Additionally, at both time points fully fed LW crickets preferred environmental temperatures that were on average 3.1 ± 0.3 °C higher than

SW crickets (Wing Length- $F_{1,134.72}$=108.6, *p*<0.001) and the interaction between wing length and time of day on T_{pref} was not significant (Wing Length × Time- $F_{1,134.46}$=0.50, *P*=0.48) (Figure 1). Higher thermal preferences of LW compared to SW crickets that were observed at night were consistent with our prior findings (Sun et al., 2020). The results here further suggest that differences in thermal preferences associated with alternative life histories in wing-polymorphic insects persist across the diel cycle when resources are unlimited. Selection of higher temperatures by LW crickets compared to SW crickets likely results in elevated metabolic rates, which in turn could support higher energetic costs of dispersal compared to reproduction. Metabolic costs associated with dispersal include not only those incurred during active flight but also throughout the diel cycle to synthesize lipid stores to fuel flight and maintain functional flight muscles (Zera et al., 1997; Crnokrak and Roff, 2002; Nespolo et al., 2008).

In summary, plasticity in diel thermal preferences did not differ between long- and short-winged crickets. Instead, thermal preferences increased to similar extent between night and morning in both morphs and flight-capable long-winged crickets maintained a higher thermal preference compared to flightless short-winged crickets across the diel cycle. Thus, combined these findings suggest that the appropriate diel rhythm of temperature selection by wing-polymorphic variable field crickets have evolved in coordination with nocturnality, and the specific demands of their life history strategy.

3.2. Resource limitation eliminates differences in thermal preferences associated with life history strategies

Crickets preferred cooler environments following an acute starvation, resulting in lower nighttime thermal preferences when starved compared to in a fully fed state (Figure 2). However, thermal preferences declined significantly more for LW than SW crickets (Morph × Food- $F_{1,111.22}$=13.95, *p*<0.001): in LW crickets the observed reduction in average T_{pref} between the fed and starved state was 4.6 ± 0.5 °C, while for SW crickets the observed reduction in average T_{pref} between the fed and starved state was 2.1 ± 0.5 °C. This result reflected a more plastic behavioral thermoregulatory response to starvation in LW compared to SW crickets. As a consequence of these divergent responses, and in contrast to the fed state, thermal preferences of LW and SW crickets were similar at night after short-term starvation (LW: 31.6 ± 0.4 °C; SW: 30.9 ± 0.4 °C; *p*=0.14).

Resource limitations are a ubiquitous environmental stressor faced by organisms in natural settings. When starved, physiological and behavioral plasticity become important for minimizing energetic demands to prolong survival (Wang et al., 2006). The reduction of T_{pref} following starvation observed here, parallels prior work and is consistent with the conclusion that ectotherms seek cooler microhabitats to facilitate energy conservation and nutrient assimilation efficiency during starvation (Brett, 1971; Porter and Tschinkel, 1993; Van Dijk et al., 2002; Sun et al., 2010; Coggan et al., 2011; Gilbert et al., 2016; Umezaki et al., 2018). For *Gryllus* crickets, reductions in body temperatures mediated by behavioral shifts in thermal preferences may be particularly important because they do not actively suppress metabolism during acute starvation (Sinclair et al., 2011). When environmental conditions are outpaced by energy or nutrient demand, LW and SW crickets have both demonstrated reduced investment into costly demands of their life history strategies. For instance, when environmental conditions are stressful, LW crickets forgo flight and degrade their flight muscles via muscle histolysis to reduce metabolic demands (Zera and Tiebel, 1988; Roff, 1990) and rates of oogenesis by SW crickets are reduced when accessibility to dietary protein is limited (Treidel et al., 2021). In this study we have shown that the high thermal preferences in LW crickets compared to SW crickets, are an additional component of their life history sacrificed when resources are limited, suggesting that high thermal preferences are costly to maintain. Therefore, reductions in body temperatures will bolster energy conservation, but reduce the potential for dispersal by flight, and thus the key benefit of the life history strategy adopted by long-winged crickets.

3.3. Summary and Conclusions

Our study provides new insight suggesting that physiological priorities tied to life history are an important factor that interact with nutrient status to set organismal thermal preferences. Under fed conditions, LW crickets prefer warmer temperatures compared to SW crickets throughout the diel cycle. Yet, differences in thermal preferences between LW and SW crickets were absent under starved conditions, when resource allocations to energetically costly life history traits may be curtailed due to energetic constraints. Reductions in thermal preferences accompanied daily periods of inactivity and starvation, consistent with the conclusion that crickets generally rely on behavioral thermoregulation to optimize body temperature in response to acute changes in energy supply or demand on short timescales. However, reductions in thermal preferences following starvation were greater in the flight-capable compared to the flightless morph. Thus, the degree to which thermal preferences were modulated through phenotypic plasticity in response to acute starvation depended on life history. Consequently, our findings demonstrate that plasticity in thermal preferences following exposure to extrinsic stressors will vary based on an individual's current physiological demands, set by life history. Thus, explicit consideration of life history strategy may improve our ability to predict the magnitude of organismal behavioral thermoregulatory responses to environmental stressors.

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Data Accessibility

All data and data analysis scripts are available in the Dryad digital repository (https://doi.org/10.6078/D1440W).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Lisa A. Treidel: Conceptualization, Formal analysis, Resources, Writing – original draft, Writing – review & editing, Visualization. **Christopher Huebner:** Conceptualization, Validation, Investigation, Writing – original draft, Writing – review & editing. **Kevin T. Roberts:** Conceptualization, Resources, Writing – review & editing, Funding acquisition. **Caroline M. Williams:** Conceptualization, Writing – review & editing, Supervision.

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