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AIR TEMPERATURE AND DIET ARE NOT ASSOCIATED WITH OXYGEN CONSUMPTION RATE IN BANDED CRICKETS, *GRYLLODES SIGILLATUS*

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Abstract

All living organisms acclimate to their environments, with ectothermic species particularly susceptible to environmental change, specifically temperature. Ectothermic insects like crickets directly alter their physiological processes depending on the environment in which they live. Temperature is vital in regulating processes such as metabolism, respiration, and reproduction, among other things. What remains unclear is how a change in the environment, specifically extreme temperature change and dietary alterations, affects physiological processes. In this study, we performed experiments on ectothermic banded crickets to examine the effects of temperature change and the interaction of temperature and diet on oxygen consumption. For both experiments, we found no effect of temperature change or diet on oxygen consumption, and we were unable to correlate diet or temperature to oxygen consumption rate. We recommend more research to fully understand how temperature change and diet affect oxygen consumption rate.

Keywords: crickets, banded crickets, ectotherms, oxygen consumption, extreme temperature, diet, environment, heat

Introduction

Temperature is an important environmental factor that controls and influences the physiological and biological processes in all living organisms. Temperature is particularly important for ectotherms, as they are dependent on the temperature of the external environment to support their internal temperature (Martin & Huey, 2008). Ectotherms' movement, adult size, reproduction, feeding, digestion, and patterns of daily activity are all affected by temperature (Nespolo et al., 2003). For example, cricket larvae maintained at high temperatures increase food consumption, growth, and oxygen consumption (Roe et al., 1985). There may be a ceiling to this effect, however, as higher temperature initially increased food intake over 9 days in skinks (*Eumeces elegans*), but at higher temperatures, food intake declined over the same time (Du et al., 2000). As

such, there is a link between the temperature of the environment and the organism's metabolic rate.

The increase in global temperature has driven average temperatures up and created unpredictable swings in temperature. Some ectotherms use acclimation as a process to respond to thermal change (Booth, 1998; Randall et al., 2002). In some cases, however, a significant increase in temperature can be too overwhelming for an ectothermic organism to overcome (Martin & Huey, 2008). The continuous increase of average temperature has seemingly shown a response in insects, reflected by changes in their physiological, biochemical, and molecular attributes. These changes can lead to a series of disorders in insects, from protein denaturation to changes in the fluidity of their membranes (Ma et al., 2021). Although it is understood that insects can acclimate to ambient temperatures (Martin & Huey, 2008), it remains unclear how unpredictable or dramatic temperature changes affect insect physiology.

Similarly, other factors such as a lack of or variation in specific nutrients can also alter metabolic and physiological processes. Specifically, a previous study found that variation in nutrients can modulate metabolic rate in mammals (Bozinovic et al., 2007). In addition, endothermic species exposed to low food availability and/or predictability developed low basal metabolic rate, whereas species fed diets consistently high in vertebrates, herbs, nuts, pollen, and nectar developed a high basal metabolic rate (Cruz-Neto & Bozinovic, 2004). In a different study, a decrease in walking stick insects' caloric intake led to a decrease in resting metabolic rate (Roark & Bjorndal, 2009). Likewise, ambient temperature may also interact with diet to modulate metabolic rate in insects (Adamo et al., 2012; Roark & Bjorndal, 2009). Crickets exposed to a six-day heat wave had a lower standard metabolic rate than did those in benign conditions of optimal temperature and ad-lib food, suggesting these conditions promote metabolic activity (Stahlschmidt & Glass, 2020). Taken together, it appears there is a relationship among ambient temperature, food quality/quantity, and metabolism.

Although previous studies have demonstrated that temperature and diet affect metabolic rate in insects (e.g., Adamo et al., 2012; Roark & Bjorndal, 2009; Roe et al., 1985; Stahlschmidt & Glass, 2020), these studies typically have housed animals for at least one week at their treatment temperatures before assessing changes in metabolic processes. As such, the effects of extreme temperature change and diet on oxygen consumption in the short term before acclimation remain unclear. As has been demonstrated in fish (Schulte et al., 2011), acute exposure to increased temperature increases metabolic activity but longer exposure times either stagnate or decrease metabolic activity. Because previous studies in insects have used longer exposure times, it is unclear if the same short-term effect occurs in insects. In this study, we therefore designed two experiments to examine the influence of short-term extreme temperature changes and the interaction of diet and temperature on oxygen consumption rate in adult banded crickets (*Gryllodes sigillatus*). We hypothesized that extreme changes in

temperature would initially increase cricket oxygen consumption rate, before acclimation and downregulation of metabolism. We also hypothesized that a decrease in diet quality would lead to a decrease in oxygen consumption because of the positive relationship between diet and metabolic rate. If crickets are provided with a diet with diverse macromolecules, oxygen consumption should increase, and this may be modulated by variation in temperature, although we did not have a priori predictions regarding directionality of the effect.

Materials and Methods

In this study, male and female ectothermic banded crickets were obtained from a commercial vendor (www.ghanns.com), shipped to the laboratory at Penn State Altoona, and placed into 10-gallon lidded tanks with cardboard egg crates as a hide, ad-lib cat food, and water in a gel form to prevent desiccation and drowning. For the experiments, individual crickets were randomly chosen from the large enclosure and randomly assigned to smaller experimental enclosures. Each enclosure was a clear plastic lidded tank (22 cm x 13 cm x 14.5 cm) with cardboard egg crate material to serve as a hide, a cup of gel water, and ad-lib cat food.

For both experiments, all enclosures were placed in the same animal care room at Penn State Altoona. In this room, the ambient temperature was maintained at 24 °C. A previous study determined that most tropical *Gryllodes* crickets were trapped in the field when the temperatures were between 20 °C and 30 °C (Smith & Thomas, 1988), suggesting that 24 °C is in the middle of the preferred microclimate for tropical crickets. The overhead fluorescent lights were on a 12-hour-on/12-hour-off cycle for all animals. The groups assigned to the control temperature were placed on a table in the room and subjected to 24 °C for the duration of the experiments. The crickets designated for exposure to high temperatures (35 °C) were placed under a 40-watt light source with an 8-hour-on/16-hour-off cycle to raise temperature. Doing so raised the temperature of the enclosures to 36 °C at the peak temperature of the 8-hour cycle; this represented a higher temperature reflective of a heat wave (Adamo & Lovett, 2011). Although the additional light source may have affected metabolism, it is unlikely, as this species is nocturnal and isn't very active during the light portion of the light cycle (Sultana et al., 2021). Finally, for both experiments, every time the oxygen consumption was measured, it was recorded at room temperature, which was roughly 21 °C.

In Experiment 1, we tested the effects of extreme temperature changes on oxygen consumption rate over 4 days. In this experiment, we had three treatment groups, each with three replicates: a control, a control-to-hot, and a hot-to-control treatment (see descriptions below); each enclosure had 10 crickets ($n = 90$ total crickets). Food and water were available ad lib throughout the experiment and were checked every two days to be replenished as needed. For the control group, all individuals were maintained at 24 °C for the 4 days of the experiment. For the control-to-hot treatment, to simulate a dramatic

increase in temperature, the enclosures were placed at the control temperature (24 °C) for two days, then moved to the hot temperature (35 °C) for the next two days. Finally, for the hot-to-control treatment, enclosures were held at the hot temperature (35 °C) for two days, then switched to the control temperature (24 °C) for the final two days. The inclusion of this treatment group was important for assessing if the effects of temperature change are uni- or bidirectional. Oxygen consumption was assessed twice: after two days at the first temperature, then after two days at the second temperature.

In Experiment 2, we tested for the interaction of high temperature and diet on oxygen consumption rate. We tested three diet quality types (control, low quality, and high quality; see below for diet details) at a high temperature (35 °C) to assess if diet and high temperature interact to change the oxygen consumption rate.

Although data on food preferences in the wild is sparse, a previous study found that *Grylloides* are omnivorous, and wild crickets mostly eat organic debris, larvae, flowers, seeds, leaves, and fruits (Gangwere, 1961). Further, captive-bred crickets also increase biomass and demonstrate a preference for foods that vary in nutritional composition, with higher percentages of protein and carbohydrates (Harrison et al., 2014; Morales-Ramos et al., 2020). As such, diet quality was determined by these parameters. The control diet consisted of commercially available cat food, representing most macromolecules and some minerals, but not formulated specifically for insects. The low-quality diet consisted of only apple, which lacks protein and other essential minerals such as calcium. The high-quality diet consisted of apple, kale, and hard-boiled egg. This was determined to be a high-quality diet because of the high diversity of macromolecules, high protein, and minerals. Although this diet did not appear to vary much in terms of macromolecules compared to cat food, it was also fresh and easily digestible in relation to the cat food (Geluso & Hayes, 1999); we therefore classified this diet as the highest quality of the three diet treatments. The high- and low-quality diet foods were chopped in a food processor for 20 seconds to ensure consistent presentation of food size.

We had four treatment groups with three replicates each ($n = 120$ crickets total): control (temperature and diet), high temperature/high-quality diet, high temperature/control diet, and high temperature/low-quality diet. Individuals were subjected to their treatment groups for 48 hours, which has been shown to be enough time for dietary changes to alter physiology (Finke, 2003). Oxygen consumption was assessed immediately before housing in experimental enclosures and at the conclusion of the 48-hour treatments.

For assessment of oxygen consumption in both Experiments 1 and 2, the crickets were removed from their enclosures and oxygen consumption was determined using a respirometer (Carolina Biological Supply); all measurements were taken at room temperature to maintain consistency. Briefly, crickets were placed into the respirometer of the test tube, and oxygen consumption was assessed for 20 minutes. Crickets were

then returned to their enclosures. Average oxygen consumption was calculated, due to some mortality across the days of the experiment.

We used a repeated measures analysis of variance (ANOVA) to compare changes in average oxygen consumption due to treatment, at the two time points in each experiment. To determine if treatment group differentials affected mortality, we ran repeated measures ANOVA on the number of individuals at the beginning and end of the experiment. All analyses were conducted with SPSS for Windows, v. 27 (IBM Corp.), and we considered results to be statistically significant if $p \leq .05$.

Results

For Experiment 1, we found that all data conformed to the assumption of homogeneity of variances (Levene's test, all $p > .285$). We found no differences in oxygen consumption between the two time points of the experiment ($F_{1,6} = 0.612, p = 0.464$), and no statistically significant effect of the interaction of treatment and oxygen consumption ($F_{2,6} = 0.899, p = .455$; Figure 1). Mortality did not differ based on treatment ($F_{2,8} = 3.00, p = .125$).

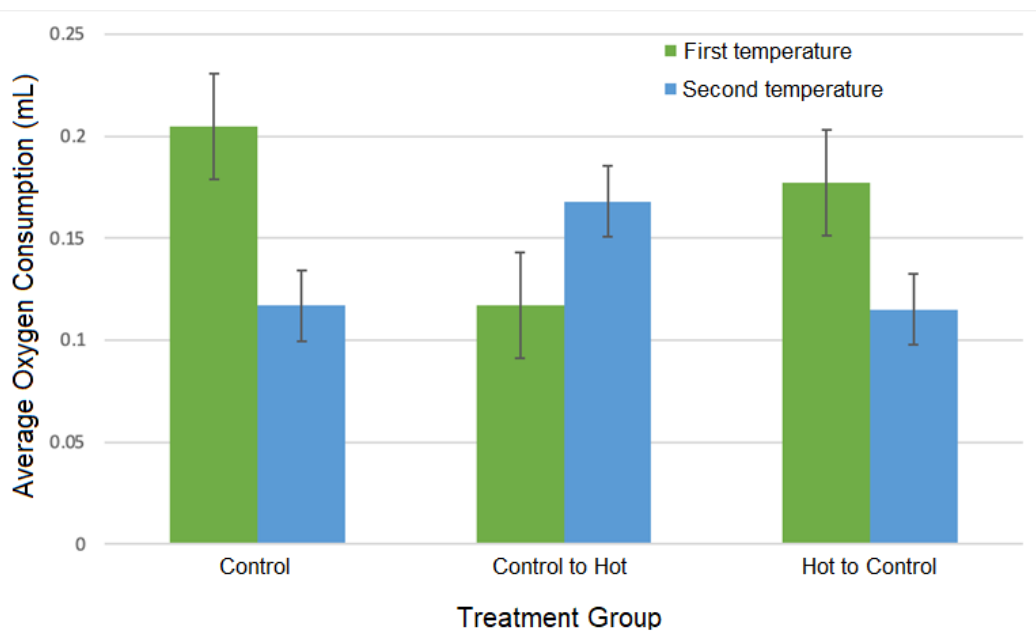


Figure 1. Experiment 1 Oxygen Consumption With Exposure to Short-Term Extreme Temperature Changes

Note. This figure demonstrates the average oxygen consumed (mL) over 20 minutes after 2 days of exposure at the first temperature (either control 24 °C or hot 36 °C) and 2 days after switching to a new temperature (either hot or control). No significant differences were found between the two time points or among the treatment groups, and no interaction between time point and treatment group (all $p > .05$).

In Experiment 2, homogeneity of variances was assessed with Levene’s test and data were square root-transformed to conform to the assumption (all $p > .066$ after transformation). We found no difference in oxygen consumption at the beginning and end of the experiment ($F_{1,8} = 0.569, p = .472$) and no statistically significant effect of the interaction of treatment and oxygen consumption ($F_{3,8} = 2.055, p = .185$; Figure 2). Although we did find a decline in the number of individuals over the time points of the experiment ($F_{1,3} = 189.0, p < .001$), mortality did not differ based on treatment ($F_{1,3} = 0.810, p = .523$).

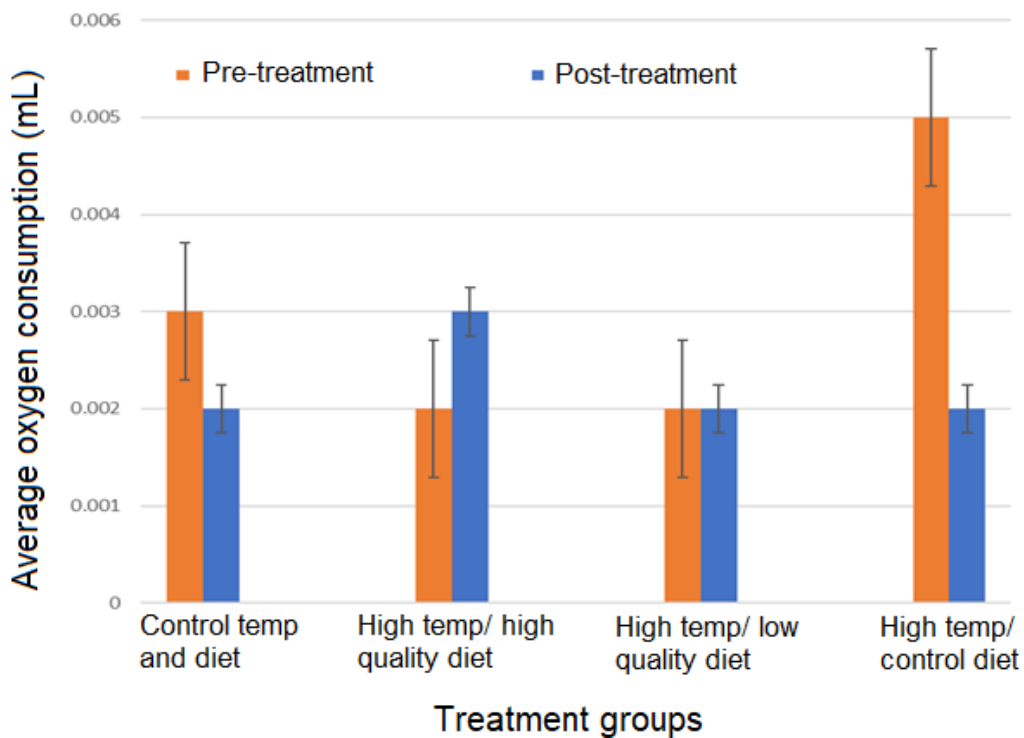


Figure 2. Experiment 2 Oxygen Consumption With Exposure to Either Control (24 °C) or High Temperature (36 °C) and Low-, Normal-, or High-Quality Diet

Note. This figure demonstrates the average oxygen consumed (mL) over 20 minutes immediately before crickets were housed in the treatment groups (pretreatment) and 2 days after being housed in the temperature and diet treatment groups (posttreatment). No significant differences were found between the two time points or among the treatment groups, and no interaction between time point and treatment group (all $p > .05$).

Discussion

For both experiments, when crickets were exposed to high temperatures, we expected extreme short-term temperature changes to affect the metabolism/oxygen consumption rate. Further, we expected diet to interact with temperature to affect oxygen consumption in the second experiment. However, the results from the first experiment indicated no statistically significant differences in oxygen consumption when crickets experienced transitions to different temperatures. Similarly, the results of the second study indicated no significant differences in oxygen consumption based on the interaction between temperature and diet.

In the first experiment, we predicted that extreme changes in temperature, particularly moving from control to high-temperature conditions, would lead to an increase in oxygen consumption. We did not find variation in oxygen consumption when individuals were moved between extreme temperatures, therefore rejecting our hypothesis. These results could potentially be explained by thermal plasticity, in which insects have some degree of thermal tolerance, shown in the field by individuals at range expansion boundaries (e.g., Carbonell et al., 2021). This may suggest that thermosensitivity and thermoregulation can vary as ectotherms acclimate to their environments, leading to a range of suitable living temperatures for such insects (e.g., Angilletta, 2009). The ability to adjust to temperature variation also appears to be species-specific in some insect species, however, such that some species can tolerate temperature variability while others cannot (e.g., Shah et al., 2021). The species in our study may tolerate temperature change fairly well, at least compared to other insects. It may be that factors such as 2 days at the temperature or the degree of the temperature change were able to be tolerated and thus were not sufficient to induce any changes in oxygen consumption. An alternative explanation may be that oxygen consumption did not change but that other trade-offs occurred, such as reproduction and immunity that do trade off with changes in temperature (Adamo & Lovett, 2011) that were not

measured in this study. As such, further research may help to determine if other experimental parameters may affect oxygen consumption rate or other physiological processes.

In the second experiment, we expected that crickets provided a lower-quality diet would have a lower oxygen consumption rate than those in the control group and that when provided a higher-quality diet, they would have a higher oxygen consumption rate. Contrary to our prediction, the increased temperatures and diets had no effect on the oxygen consumption rate of the crickets. Unlike in our study, a previous study found that species fed diets high in vertebrates, herbs, nuts, pollen, and nectar developed a high basal metabolic rate (Cruz-Neto & Bozinovic, 2004), which may suggest that some factor that differed between our study and theirs contributed to our opposing results. Alternatively, a previous study in fish found that diet quality and temperature interact to differentially affect physiology. Specifically, sprint speed and maximum metabolic rate were insensitive to diet and temperature while growth rate was altered with temperature and heart rate was affected by the interaction of diet and temperature (Hardison et al., 2021). The results of this study suggest that diet, temperature, and the interaction of the two do not equally affect physiological outputs and may even demonstrate species-specific differences. Taken together, it may be that diet and temperature may have been affecting metabolism in our study but we did not measure enough physiological variables to demonstrate a link between physiology and temperature and diet.

Although we examined only diet quality in our study, other studies have demonstrated that varying other diet parameters can alter metabolic rate. In some previous studies, species exposed to low food availability and/or predictability developed lower basal metabolic rates (Cruz-Neto & Bozinovic, 2004; Hoogenboom et al., 2013). In a study using walking sticks, *Carausius morosus*, individuals exposed to a decreased caloric intake showed a diminished resting metabolic rate and increased longevity but delayed development (Roark & Bjorndal, 2009). Although we did not see an effect of diet quality on oxygen consumption, it may therefore be that altering a different dietary factor might induce metabolic changes such as oxygen consumption and might be a better reflection of the link between diet and metabolism.

Relating temperature to diet, in a previous study, crickets with access to ad-lib food and exposed to higher temperatures produced more eggs, suggesting that adequate food and increased temperature can be physiologically beneficial (Adamo et al., 2012); however, crickets exposed to a heat wave developed a lower metabolic rate than those in optimal conditions of 24 °C, suggesting that short-term changes in ambient air temperature can also lower metabolic rate, at least in larvae (Stahlschmidt & Glass, 2020). Our study found that exposing crickets to a lower-quality diet did not affect the oxygen consumption rate of crickets in higher temperatures. It also did not align with previous findings that exposing crickets to higher temperatures caused variation in oxygen consumption rate. Our hypotheses were rejected, but further research may help to

determine the influence of temperature and diet on metabolic processes and may relate to some of the factors outlined for Experiment 1.

Future experiments could elucidate why there were differences between our study and others. For example, we did not measure change in mass of either the crickets or the food, which may have yielded more precise results. Similarly, water content in the diet was not assessed but may also affect a cricket's assessment of a "high quality" food item. Additionally, variation in time periods could possibly affect the results. Although we assessed after 48 hours, a shorter (or intermediate) time frame may yield different results. For example, if this species either acclimates very quickly or demonstrates thermal tolerance, we would see effects on a shorter time scale or not at all, respectively. Finally, our experimental enclosures experienced some mortality, which could mean that our postexposure readings included only those individuals who survived the shift in temperature and diet. Future studies could vary any of the aforementioned variables to gain a better understanding of the relationship among temperature, diet, and metabolic processes.

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