METHODS, TOOLS, AND TECHNOLOGIES

The affordable laboratory of climate change: devices to estimate ectotherm vital rates under projected global warming

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Abstract. Determining organisms’ responses to novel temperatures is relevant from ecological, evolutionary, and conservation perspectives. Here, we have validated designs and included biological examples for three affordable devices to estimate thermal responses of ectotherms: (1) a water bath that can be programmed to increase temperatures to estimate an organismal critical thermal maximum (CTmax); (2) a miniature portable refrigerator to estimate an organism’s critical thermal minimum (CTmin); and (3) inexpensive growth chambers that maintain constant temperatures or simulate dynamic environmental temperature patterns. We tested the reliability of the CTmax device at temperature increase rates of 1° and 2°C/min. Observed temperatures deviated 0.01° and 0.02°C from target temperatures, respectively. The CTmin device easily attained target temperatures via manipulation of the input voltage. The maximum deviation from target temperatures in environmental chambers programmed to maintain constant temperatures between 10°C and 30°C was 0.8°C. Environmental chambers programmed to simulate temperature profiles of tropical rain and montane forests deviated from target temperatures by a maximum of –0.5°C to 0.9°C. Examples of applications show that (1) tropical insects at high elevations are less tolerant to high temperatures than insects in lowland forests, (2) nocturnal ants display lower CTmax and CTmin than diurnal ant species, and (3) experiments in growth chambers show high mortality of high-elevation insect species when exposed to temperatures that typify lowland forests, and high mortality of lowland insect species when exposed to temperatures that typify high elevations. The devices described in this study can be mass-produced inexpensively and are currently being used in laboratories in the United States, Mexico, and Costa Rica. The main goal of this project is to encourage the construction of affordable devices and the use of standardized methodologies to create a global network of researchers studying thermal responses in diverse taxa and geographic locations.

Key words: applied ecology; CTmax; CTmin; environmental chamber; global warming; incubator; thermal tolerance.

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INTRODUCTION

Determining organisms’ responses to extreme temperatures is of great ecological and evolutionary relevance (Huey et al. 1992, Folk et al. 2007, Terblanche et al. 2007, Chown et al. 2009, Rezende et al. 2014). Because global warming represents a serious threat to biodiversity on
earth, determining responses of organisms to novel temperatures is also becoming a fundamental conservation issue (Sunday et al. 2014, Scheffers et al. 2016).

Two parameters used in global analyses to determine the tolerances of organisms to extreme temperatures are the critical thermal maximum (CT\textsubscript{max}) and critical thermal minimum (CT\textsubscript{min}; Sunday et al. 2012). Critical thermal temperatures are estimated using quick bioassays where animals are exposed to increasing or decreasing temperatures until individuals lose motor control (Lutterschmidt and Hutchison 1997). These experiments are performed by placing organisms in chambers where temperature can be increased or decreased at constant rates (García-Robledo et al. 2016). Additional experiments to determine the effects of long-term exposure to manipulated temperatures on growth, survival, and reproduction involve experiments where organisms are reared in temperature-controlled environmental chambers (Kingsolver et al. 2011, Greenspan et al. 2016).

One challenge to replicating experiments that assess the temperature tolerance of an organism is the often prohibitively high cost of devices for such physiological and demographic studies. Here, we have developed inexpensive and accurate devices to estimate the critical thermal maximum and minimum temperatures of small ectotherms (i.e., <4 cm in length). We also describe methods for converting readily available commercial 3.2-ft\textsuperscript{3} refrigerators into low-cost, accurate, and reliable environmental chambers. We thoroughly describe the detailed construction of two temperature controllers for environmental chambers using (1) an inexpensive thermostat that can be programmed to maintain constant temperatures and (2) an Arduino-based temperature controller that can be programmed to simulate fluctuating environmental temperatures.

We illustrate applications for these devices using three examples of macroecological and population patterns of thermal tolerance in tropical insects: (1) a study showing that tropical insects at high elevation are less tolerant to high temperatures than insects in lowland forests, (2) a study showing that nocturnal ants display lower thermal tolerance than diurnal ant species, and (3) experiments in growth chambers showing high mortality rates of high-elevation insect species when exposed to temperatures typical of lowland forests, and high mortality of lowland insect species exposed to high-elevation temperatures.

MATERIALS AND METHODS

Critical thermal maximum device

A water heater (Proctor Silex 32oz Hot Pot, Model 45805; NACCO Industries, Cleveland, Ohio, USA) was adapted for use as a water bath to estimate CT\textsubscript{max} of animals (Fig. 1a, A). Arthropods were placed in individual glass vials. Vials were placed horizontally, floating on the surface of the water (Fig 1a, B). The temperature inside the vials was recorded by placing the probe of a digital thermometer (STC-1000; Lerway Tech, Shenzhen, China; accuracy 0.5°C) inside one of the vials (Fig 1a, C). The temperature of the water bath was controlled by a dimmer connected to the heating element (TT-300H-WH; Lutron Electronics, Coopersburg, Pennsylvania, USA; Fig. 1a, D). Temperature increase rates were determined by sliding the switch knob of the dimmer to a level that generated the target-heating rate (Fig. 1a, E). Heating rates can be set from 0.5° to 5°C/min. The critical thermal maximum (CT\textsubscript{max}) was estimated as the temperature at which each arthropod lost motor control (i.e., loss of righting response).

Validation of the CT\textsubscript{max} device.—We evaluated the accuracy of this CT\textsubscript{max} device in achieving two target temperature increase rates, 1° and 2°C/min. We recorded the temperature inside the vials in the water bath every 30 s using a data logger (HOBO U12 4-Channel, precision 0.5°C; Onset Computer, Bourne, Massachusetts, USA). Temperature was recorded until the water reached a temperature of 45°C. After reaching this temperature, we disconnected the dimmer and replenished the water bath with cool water. We recorded heating rates from ambient temperature to 45°C ten times for each heating rate. To determine the accuracy of the device in achieving target temperatures, we performed linear regressions between target and observed temperatures. A description of the construction steps, calibration, and experimental setup is included in Appendix S1.

Example 1: thermal limits of tropical insects along elevational gradients.—To determine whether
high-elevation insect species display lower thermal tolerance than insects in the lowlands, we collected 33 rolled-leaf beetle species (genus *Cephaloleia*, Coleoptera, Chrysomelidae) in tropical rain (60–500 m elevation), premontane (500–1500 m elevation), and montane (1500–2800 m elevation) forests along two tropical elevational gradients in Costa Rica, Central America. Each species included in this experiment occurs in only one life zone (Fig. 2). We estimated CT_max for a total of 759 individuals by increasing temperature in the water bath 1.5°C/min. We tested for differences in CT_max among species from each life zone using generalized linear models (GLMs), with life zone and species as factors. Differences among species were determined using a-posteriori tests (data from Garcia-Robledo et al. 2016).

**Critical thermal minimum device**

To determine the critical thermal minimum (CT_min) of small arthropods (i.e., with length <4 cm), we constructed a miniature cooling chamber (*L* × *W* × *H* = 4 × 4 × 3 cm) that can reach a temperature of 5°C at room temperatures from 20°C to 23°C (Fig. 3). The cooling side of a Peltier element (12 V Peltier Ceramic, TEC1-1270; Hebei IT, Hebei, China) is placed at the base of an expanded polystyrene chamber that contains the organisms for which CT_min will be estimated (Fig. 3a, A). Temperature inside the chamber is recorded by the probe of a digital thermometer attached to the base of the chamber using aluminum tape (STC-1000; accuracy 0.5°C, Fig. 3a, B). During testing, the chamber is closed using a removable clear acrylic lid that allows for the observation of arthropod responses (Fig. 3a, C).

The heating side of the Peltier element is attached to a heat sink with a fan that dissipates heat from the device (Fig. 3a, D). The voltage applied to the Peltier element is regulated by a dimming controller (PWM Dimming Controller, LCC Integral, Shenzhen, China; Fig. 3a, E). Both the dimming controller and the heat sink fan are caps containing arthropods; C, temperature sensor; D, connection between water baths; and E, dimmer. (b) Temperature of a water bath at two temperature increase rates (mean ± standard error). (c) Deviation from target temperatures. Building instructions in Appendix S1.
Fig. 2. $CT_{\text{max}}$ of rolled-leaf beetle species (mean ± standard deviation, minimum–maximum). Barva (a) and
connected to a 12 V power source. Due to the thermoelectric effect, the temperature on the cold side of the Peltier element will vary with the voltage applied. By increasing the voltage input at a constant rate, it is possible to reduce the chamber temperature at a desired rate (e.g., 1.5°C/min). The critical thermal minimum (CT\textsubscript{min}) is estimated as the temperature at which arthropods lose motor control (i.e., loss of righting response). A description of the construction steps, calibration, and experimental setup is included in Appendix S2.

Validation of the CT\textsubscript{min} device.—To determine the temperatures achieved by the cooling chamber at different voltage inputs, we increased the Peltier input voltage stepwise at a rate of 1 V/min to lower chamber temperature from ambient to 5°C. After each cooling cycle, we allowed the device to reach room temperature and repeated our measurements. After repeating this experiment for ten cooling and recovery cycles, we calculated the average temperature reached inside the cooling chamber at each voltage.

Example 2: thermal tolerance in diurnal and nocturnal ants.—This study was performed in the Tehuacán–Cuicatlán Biosphere Reserve, a high-elevation desert in Puebla, Mexico. We estimated CT\textsubscript{max} and CT\textsubscript{min} for two diurnal and two nocturnal ant species for a total of 119 individuals (see sample size in Fig. 4). Temperature was increased or decreased at a rate of 1.5°C/min using a critical thermal maximum device and a critical thermal minimum device, respectively. We tested for differences in upper and lower thermal limits among diurnal and nocturnal species using GLMs, with life zone and species as factors. Differences among species were determined using a-posteriori tests (modified from García-Robledo et al. 2018b).

Environmental chamber
We converted 3.2-ft\textsuperscript{3} refrigerators into temperature-controlled environmental (growth) chambers (Fig. 5). We used 28 × 90 cm of flexible heat tape (Calorique, Wareham, Massachusetts, USA) as the heating element in each chamber.
The 120 V power source of the heating element (Fig. 5B) is connected to either a static or dynamic temperature controller (Fig. 5C). The 120 V power source of the refrigerator is also connected to the temperature controller (Fig. 5C). The temperature sensor is placed in the center of the growth chamber to provide feedback to the controller (Fig. 5D). A detailed description of the construction steps is included in Appendix S3.

**Static temperature controller**

To maintain a constant temperature between 10°C and 30°C inside the environmental chambers, we used static temperature controllers with two built-in 120 V relays (STC-1000; Lerway Tech, Shenzhen, China; accuracy 0.5°C, Fig. 6). Each relay controls one of two outlets (Fig. 6). The temperature controller was programmed to activate each of the outlets when the temperature detected within the environmental chamber was either above or below the set point (Fig. 6). The temperature sensor is placed in the center of the growth chamber to provide feedback to the controller (Fig. 5D). A detailed description of the construction steps is included in Appendix S3.

![Fig. 5A.](image)

**Fig. 4.** Thermal tolerance in two desert ant species. (a) Critical thermal maximum and (b) critical thermal minimum (median ± third quartile, min–max). Letters represent significant differences. AT_ME, *Atta Mexicana*; CA_AT, *Camponotus atriceps*; PO_BA, *Pogonomyrmex barbatus*; PS_MA, *Pseudomyrmex major*.

![Fig. 5.](image)

**Fig. 5.** Converting a 3.2-ft³ refrigerator into an environmental chamber. (A) The heating element (Flexwatt Heat Tape, Calorique, Wareham, Massachusetts, USA) is connected using (B) a 120 V power supply to (C) temperature controller. The unit compressor (cooling element) is also connected to the temperature controller. (D) The temperature controller receives feedback from a thermometer placed in the center of the environmental chamber. Building instructions in Appendix S3.
Dynamic temperature controller

We built a programmable Arduino-based temperature controller to generate fluctuating temperature profiles for the environmental chambers (Fig. 7). We stacked a data logging shield (Adafruit, New York, New York, USA; Fig. 7a) on top of an Arduino UNO board (Fig. 7c). A liquid crystal display (16 × 2 characters) provides information about the system status (Fig. 7b), and a 2-channel relay module connects the 120 V supply to outlets controlling the heater tape and refrigerator unit (Fig. 7d). A description of the construction steps and software installation is included in Appendix S5. The code running on the Arduino-based temperature controller must be compiled and uploaded to the board (Arduino sketch and instructions are also available at https://bitbucket.org/ddierick/climate-chamber).

The temperature profile describing a diurnal cycle in three-minute steps is uploaded from the SD card (see examples of temperature profiles in https://bitbucket.org/ddierick/climate-chamber). The dynamic temperature controller will then switch the heating and cooling elements of the environmental chamber to track the desired diurnal temperature profile (Fig. 7).

Validation of static and dynamic temperature controllers.—To estimate the accuracy of the temperature controller at multiple static temperatures, we programmed thermostats of five environmental chambers to maintain constant temperatures of 10°C, 15°C, 20°C, 25°C, and 30°C. We placed four temperature data loggers (Thermocron iButton DS1921G; Maxim Technology, Chelmsford, Massachusetts, USA) distributed singly among the four shelves with a vertical distance of 20 cm between each iButton. Data loggers measured the temperature inside each environmental chamber every minute for 35 h.

To determine differences between target and observed temperatures using dynamic temperature controllers, we programmed the controllers to simulate temperature cycles for two tropical ecosystems: a tropical rain forest at 130 m elevation (La Selva Biological Station, Costa Rica) and a tropical montane forest at 1900 m elevation (Barva Volcano, Costa Rica). We simulated temperature profiles for the month of January based on a long-term temperature dataset that includes ambient temperatures recorded every 30 min for four years at these two sites (Clark et al. 2015). Temperatures inside the dynamic temperature environmental chambers were monitored following the same protocol as used for the static temperature environmental chambers.

Example 3: survival of high- and low-elevation insects at multiple temperatures.—We performed this study on the La Selva–Barva elevational transect in Costa Rica, Central America. This elevational gradient ranges from sea level to 2700 m elevation (Clark et al. 2015). We collected individuals of two high-elevation and two low-elevation Cephaloleia beetle species (Coleoptera; Chrysomelidae). Individuals were placed in individual containers maintained at 100% humidity. Cohorts of beetles were placed in environmental chambers at

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The text continues with further details on the methodology and observations related to the temperature controllers and their use in ecological studies.
10°C, 15°C, 20°C, 25°C, and 30°C, and fed with leaf tissue from their host plants every 24 h. We recorded survival daily for 40 d. We tested for differences in survival among temperatures using failure-time analyses (Therneau 2015).

RESULTS

Critical thermal maximum and minimum devices

The CT_{max} device generated very consistent temperature increase rates at both 1°C and 2°C/min. Although we found statistically significant differences between target and observed temperatures, the magnitude of this consistent difference ranged from only 0.01°C to 0.02°C (Table 1, Fig. 1b, c).

The performance of the CT_{min} device was consistent over the range of input voltages (Fig. 3b), and target temperatures are easily attained by adjusting the dimming controller during experiments (Fig. 3b). The minimum temperature the cooling chamber could reach was 5°C.

Examples 1 and 2: critical thermal limits of insects in contrasting environments.

— The CT_{max} and CT_{min} devices can accurately detect differences in upper and lower thermal limits of less than 0.5°C. Using the CT_{max} device, we detected significant differences in thermal tolerance among insect species along tropical elevational gradients. High-elevation insect species are less tolerant to high temperatures than species in the lowlands ($F_{20,2} = 64.6, 513.1, P_{\text{life zone}} < 0.0001, P_{\text{species}} < 0.0001$; Fig. 2). When using CT_{max} and CT_{min} devices to estimate upper and lower thermal limits of diurnal and nocturnal ants, nocturnal ants display both lower CT_{max} and lower CT_{min} than diurnal ants (CT_{max}: $F_{3, 114} = 77.0, P < 0.0001$, CT_{min}: $F_{3,50} = 74.7, P < 0.0001$; Fig. 4).

![Fig. 7. Arduino-based temperature profile controller](https://bitbucket.org/ddierick/climate-chamber)
Table 1. Pearson’s product–moment correlations between target and recorded temperatures in CT$_{\text{max}}$ devices at two temperature increase rates.

| Device     | Deviation from target temperature (°C) | Min | Max | Mean  | SE    | DF  | t   | P       |
|------------|----------------------------------------|-----|-----|-------|-------|-----|-----|---------|
| CT$_{\text{max}}$ |                                        |     |     |       |       |     |     |         |
| 1°C/min    |                                        | −0.8| 0.3 | −1 × 10$^{-2}$ | 1 × 10$^{-3}$ | 1488| 89.7| 2.2 × 10$^{-16}$ |
| 2°C/min    |                                        | −1.19| 0.5 | 2 × 10$^{-2}$ | 5 × 10$^{-3}$ | 771 | 105.9| 2.2 × 10$^{-16}$ |

Notes: DF, degrees of freedom; SE, standard error.

Table 2. Paired $t$ test analyses comparing target and recorded temperatures in environmental chambers with attached static or dynamic temperature controller.

| Device                              | Deviation from target temperature (°C) | Min | Max | Mean   | SE    | DF  | t     | P       |
|-------------------------------------|----------------------------------------|-----|-----|--------|-------|-----|-------|---------|
| Static temperature controller       |                                        |     |     |        |       |     |       |         |
| 10°C                                |                                        | 0.4 | 0.8 | 0.6    | 1 × 10$^{-3}$ | 1999| −41.89| <2.2 × 10$^{-16}$ |
| 15°C                                |                                        | 0.2 | 0.7 | 0.1    | 3 × 10$^{-3}$ | 1999| 39.9  | <2.2 × 10$^{-16}$ |
| 20°C                                |                                        | −0.6| 0.1 | −0.3   | 4 × 10$^{-3}$ | 1999| †     | †       |
| 25°C                                |                                        | 0   | 0   | 0      | 0     | 1999| †     | †       |
| 30°C                                |                                        | −0.6| 0   | −0.5   | 1 × 10$^{-3}$ | 1999| −5.6  | 2.5 × 10$^{-10}$ |
| Dynamic temperature controller      |                                        |     |     |        |       |     |       |         |
| Tropical rain forest                |                                        | −0.5| 0.4 | 9 × 10$^{-3}$ | 1 × 10$^{-3}$ | 8639.5| 0.56 | 0.5     |
| Tropical montane forest             |                                        | −0.5| 0.9 | −0.01  | 1 × 10$^{-3}$ | 8639.5| −0.59| 0.5     |

DF, degrees of freedom; SE, standard error.
† Difference between target and recorded temperatures $\approx$ 0.

Fig. 8. Temperature profiles of environmental chambers attached to constant temperature controllers (STC-1000) at target temperatures of 10°C, 15°C, 20°C, 25°C, and 30°C (mean ± standard error). Panels on the right indicate the deviation of observed temperatures from target temperatures (°C).
Environmental chamber and temperature controllers

The environmental chambers maintained constant temperature profiles with a maximum deviation from target temperatures of 0.6°C (Table 2, Fig 8). We recorded statistically significant but minimal differences between target and observed temperatures at 10°C, 15°C, and 30°C (Table 2). These significant differences arise from a combination of using a large dataset, which increases the chance of significance in parametric tests, and a consistent but small difference of 0.1–0.3°C between target and observed temperatures (Fig. 8).

Using the dynamic temperature controllers, we simulated temperature profiles of both tropical rain and montane forests (Fig. 9). There were no significant differences between target and observed temperatures for these two temperature profiles (Table 2). Temperature profiles displayed a maximum average deviation from target temperatures ± 0.01°C (Table 2).

Example 3: survival of high- and low-elevation insects at multiple temperatures.—Experiments using environmental chambers programmed to maintain constant temperatures detected differences in survivorship among high- and low-elevation insect species reared at different temperatures. When measuring survivorship of cohorts of insects exposed to temperatures between 10°C and 30°C, we recorded an increase in mortality in high-elevation insect species with increasing temperatures above 10–20°C (log-L_{eff. belti} = -537.5, X^2 = 130.2, N_{10°C} = 49, N_{15°C} = 49, N_{20°C} = 48, N_{25°C} = 47, N_{30°C} = 48, P < 0.0001; log-L_{kressi} = -172.8, X^2 = 75.9, N_{10°C} = 21, N_{15°C} = 20, N_{20°C} = 12, N_{25°C} = 12, N_{30°C} = 11, P < 0.0001; Fig. 10). Mortality of lowland insect species...
species increases at temperature below 15°C or above 20°C (log-\(L_{fenestrata}\) = -642.5, \(\chi^2 = 255.0\), \(N_{10^\circ C} = 59\), \(N_{15^\circ C} = 60\), \(N_{20^\circ C} = 59\), \(N_{25^\circ C} = 58\), \(N_{30^\circ C} = 57\), \(P < 0.0001\); log-\(L_{heliconiae}\) = -405.1, \(\chi^2 = 211.4\), \(N = 254\), \(N_{10^\circ C} = 50\), \(N_{15^\circ C} = 52\), \(N_{20^\circ C} = 51\), \(N_{25^\circ C} = 51\), \(N_{30^\circ C} = 50\); Fig. 10).

**CONCLUSION**

The critical thermal limit devices described in this study are low cost, portable, accurate, and easily built using materials locally available in most countries. Examples of applications for these devices include estimating changes in thermal tolerances of insects along tropical elevational gradients (García-Robledo et al. 2016), differences in thermal limits of diurnal and nocturnal insects (García-Robledo et al. 2018b), or differences in vital rates such as insect survival. Most studies exploring organismal thermal tolerance use laboratory equipment such as programmable heating water baths or cooling units (Huey et al. 1992, Folk et al. 2007, Terblanche et al. 2007, Chown et al. 2009, Rezende et al. 2014). Two advantages of the devices described in this study are their portability and low cost. For example, transporting a laboratory water bath or a laboratory cooling column to a remote field site is in many cases impractical. Also, the cost of such laboratory equipment ranges between 400 and 1000 U.S. Dollars. This contrasts with the small size of the CT\(_{max}/CT_{min}\) devices described in this study, which can be built with less than 50 U.S. Dollars.

An alternative design of low-cost environmental chambers was previously proposed by Greenspan et al. (2016). This design uses an Arduino UNO controlling Peltier ceramic tiles, which
serve as both heating and cooling elements. This design is an excellent option for experiments that require smaller chambers to track target temperatures with high accuracy.

Because the performance of environmental chambers described in this study may change depending on ambient room temperatures and materials used to build the chambers, users must constantly monitor attained temperatures. At minimum, any new system should be properly validated (as presented here). Reliability can be improved by changing hysteresis parameters (see instructions in Appendix S5). An alternative to increase the reliability of growth chambers is to implement an Arduino sketch that includes active-regulation feedback.

We aimed to use low-cost materials in our designs, so these devices can be mass-produced to replicate studies of thermal tolerance in multiple taxa across broad geographic scales. These devices are especially useful in advancing the field of thermal biology in developing countries where these devices are unavailable and where the costs associated with purchasing and importing conventional equipment (e.g., large environmental chambers) are prohibitive. The designs included in this study were developed through ongoing collaborations with researchers in the United States, Mexico, and Costa Rica (García-Robledo et al. 2016, García-Robledo et al. 2018a, b). We hope that these low-cost devices will continue to foster international collaborations, aiming to reduce the gap in data generation in developing countries due to the high cost of commercial laboratory equipment. By increasing the accessibility of low-cost thermal manipulation and measurement devices by researchers on a global scale, we can gain unprecedented insight into patterns of change.

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Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3083/full

Appendix S1: Assembly instructions for CT$_{\text{max}}$ device.
Appendix S2: Assembly instructions for CT$_{\text{min}}$ device.
Appendix S3: Instructions to modify a 3.2 ft$^3$ fridge into an environmental chamber.
Appendix S4: Assembly instructions for static temperatures thermostat (STC-1000).
Appendix S5: Assembly instructions for dynamic temperature controller.