



Oxygen concentration affects upper thermal tolerance in a terrestrial vertebrate



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ABSTRACT

We tested the oxygen limitation hypothesis, which states that animals decline in performance and reach the upper limits of their thermal tolerance when the metabolic demand for oxygen at high temperatures exceeds the circulatory system's ability to supply adequate oxygen, in air-breathing lizards exposed to air with different oxygen concentrations. Lizards exposed to hypoxic air (6% O₂) gaped, panted, and lost their righting response at significantly lower temperatures than lizards exposed to normoxic (21% O₂) or hyperoxic (35% O₂) air. A greater proportion of lizards in the hyperoxic treatment were able to withstand body temperatures above 44 °C than in the normoxic treatment. We also found that female lizards had a higher panting threshold than male lizards, while sex had no effect on gaping threshold and loss of righting response. Body size affected the temperature at which lizards lost the righting response, with larger lizards losing the response at lower temperatures than smaller lizards when exposed to hypoxic conditions. These data suggest that oxygen limitation plays a mechanistic role in the thermal tolerance of lizards.

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1. Introduction

Temperature is one of the most important environmental factors for ectotherms, influencing their biochemical and physiological processes (Cloudsley-Thompson, 1999) and affecting a range of functions from sensory input to immune response (reviewed in Angilletta et al., 2002). Global climate change imposed by anthropogenic greenhouse gas emissions poses a significant threat to terrestrial biodiversity in the twenty-first century (IPCC, 2014). The predicted global temperature increase over the next century could contribute to the extinction of 18% of all species by 2050 (Thomas et al., 2004), including up to 20% of lizard species (Sinervo et al., 2010). Ectotherms are expected to represent the bulk of this statistic because they are sensitive to micro- and macro-climatic changes due to the inherent temperature dependence of their physiological processes (Brusch et al., 2016; Sinervo et al., 2010; but see Kearney et al., 2009), especially given that their strong propensity for behavioral thermoregulation may weaken selective pressures for thermal adaptation (Buckley et al., 2015). For these reasons, the effects of temperature on the behavior and physiology of ectotherm species,

especially factors governing their thermal tolerance, is a growing area of interest.

Evaluations of thermal tolerance in terrestrial ectotherms have focused on the critical thermal maximum (CTmax¹) since Cowles and Bogert (1944) showed that reptiles demonstrate a stereotyped loss of coordinated motor function at a temperature just below the upper lethal temperature. These classic studies of CTmax also showcased the importance of reptiles as terrestrial model organisms for thermal tolerance because the highly stereotyped responses—loss of righting response followed by onset of muscular spasms at the CTmax—can be easily studied in a range of conditions and in species of varying body sizes (Lutterschmidt and Hutchison, 1997b). Despite scores of studies (reviewed in Lutterschmidt and Hutchison, 1997b) since Cowles and Bogert (1944), the physiological mechanisms responsible for the loss of coordinated motor function at high body temperatures remain unclear, largely due to the complex and differential ways in which temperature can affect proteins, cells, and organisms. These mechanisms range from effects of temperature on enzyme activity and enzyme-substrate interactions to the temperature dependence of the coordinated functioning of the nervous, endocrine, cardiovascular, and muscular systems (Schulte, 2015).

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¹ CTmax: critical thermal maximum.

An intriguing hypothesis for the physiological mechanism responsible for loss of motor function and coordination at high temperatures is the oxygen- and capacity-limited thermal tolerance hypothesis, or more simply the oxygen limitation hypothesis, which suggests that the upper thermal limits of complex animals are determined by oxygen delivery limitations that occur at high body temperatures (Frederich and Pörtner, 2000; Pörtner, 2001, 2002). That is, aerobic metabolism rises with increasing temperature, and at some point the ability of the circulatory system to deliver the necessary oxygen to the nervous system and muscles cannot keep up with oxygen demand, and the animal's ensuing anaerobic metabolism is insufficient to sustain prolonged energy demand. Support for the oxygen limitation hypothesis is mixed (reviewed in Verberk et al., 2016). Many studies on water-breathing animals have supported oxygen as a limiting factor (e.g., Pörtner, 2001; Pörtner and Knust, 2007; Verberk and Bilton, 2011; Verberk and Calosi, 2012; but see Clark et al., 2013; Ern et al., 2014; Norin et al., 2014). Fewer studies have been conducted on air-breathing organisms, where oxygen is more readily available than in water. These studies have focused mainly on invertebrates, and results have also been mixed, with some studies supporting the hypothesis (Koopman et al., 2016; Verberk and Bilton, 2013; Verberk and Bilton, 2015; Verberk et al., 2013) and others not (Boardman and Terblanche, 2015; Klok et al., 2004; McCue and De Los Santos, 2013; Stevens et al., 2010). Studies testing the oxygen limitation hypothesis in larger organisms, particularly terrestrial air-breathing vertebrates, are few, and for the most part oxygen limitation has not been supported as a mechanism behind thermal tolerance in these studies (Fobian et al., 2014; Overgaard et al., 2012; Seebacher and Franklin, 2011; Tattersall and Gerlach, 2005; but see Smith et al., 2015).

Given the paucity of experimental studies investigating the oxygen limitation hypothesis in terrestrial air-breathing organisms, we conducted an experiment in which we tested the effect of oxygen concentration of ambient air on thermal tolerance in lizards, one of the most thoroughly studied groups of terrestrial organisms in terms of thermal physiology (Angilletta et al., 2002; Brattstrom, 1965; Cowles and Bogert, 1944; Lutterschmidt and Hutchison, 1997b). We designed and built a multiplex device to deliver gases of various oxygen concentrations to lizards while heating them at a set rate. If oxygen availability limits thermal tolerance, we predicted that treatment with hypoxic air should result in lower thermal tolerance than exposure to normoxic air, and treatment with hyperoxic air should result in higher thermal tolerance than normoxic air.

2. Materials and methods

2.1. Ethical statement

All procedures were approved by the Institutional Animal Care and Use Committee of the California Polytechnic State University, which operates according to guidelines created by the National Institutes of Health.

2.2. Study site and study species

A total of 83 adult Western fence lizards (*Sceloporus occidentalis*, Baird and Girard, 1852) were collected from two sites (Logging Team facility and Poly Canyon) on the campus of California Polytechnic State University (Cal Poly), San Luis Obispo, California, USA. These sites are located on the central coast of California at an altitude of 72 m with an average annual high temperature of 21.8 °C, low of 8.5 °C, and precipitation of 48 cm (<http://www.usclimatedata.com>). This sample size was chosen to ensure sufficient power to detect potential effects of three oxygen treatments on thermal tolerance.

Sceloporus occidentalis is a heliothermic, Phrynosomatid lizard with a field active body temperature ranging from about 19 to 39 °C in its native range in the Western United States and south into Baja California

(McGinnis, 1966). It is a small to medium sized lizard, so the time needed to heat and cool the lizards to specific body temperatures in the lab is short. Because these lizards were caught from the wild and only kept in the lab for several hours before trials, they had little time to acclimate to laboratory conditions (which can happen as quickly as in the first 24 h), and results should be representative of their natural thermal tolerance (Hutchison and Dupré, 1992).

Lizards were collected by hand or by noose (fishing line on B'n'M Fishing crappie rods) and placed individually in tube socks for transport to the laboratory. Capture location and time of day were recorded for each lizard. In the lab, body mass (± 0.5 g), snout-vent length (SVL, ± 1 mm), and tail length were recorded. Sex and female reproductive state (gravid or not gravid) were recorded. After measuring thermal tolerance, blood samples were drawn from the post-orbital sinus to determine hematocrit. Blood was collected in heparinized microhematocrit tubes and centrifuged to separate the red blood cells from the plasma. These samples were taken after thermal testing was completed to avoid confounding experimental data with blood loss.

2.3. Measurements of thermal tolerance

We measured three variables: gaping threshold (lizard opens its mouth), panting threshold (lizard gapes and holds its mouth open for at least 4 s accompanied by heavy chest compressions), and loss of righting response. Gaping and panting behaviors reflect the lizards' attempt to utilize evaporative cooling to reduce body temperature (Tattersall et al., 2006), and the loss of righting response represents the failure of coordinated neural and/or muscular activity that occurs at high temperatures. The temperature at which the loss of righting response occurs, often used as a proxy for the CTmax in lizards, actually occurs just below the CTmax. The actual CTmax is better measured as the onset of muscular spasms (Lutterschmidt and Hutchison, 1997a). In a pilot study, all lizards we tested reached the upper lethal temperature without displaying any indication of spasms, so we chose to use the body temperature at which loss of righting response occurs (hereafter referred to simply as LORR²) as a measure of upper thermal tolerance. LORR is also appropriate because it represents the temperature at which performance declines, due to oxygen limitation according to our hypothesis (Verberk et al., 2016).

The three response variables were measured on the same day lizards were collected to avoid extensive acclimation to laboratory conditions (Art and Claussen, 1982; Hutchison and Dupré, 1992). To collect these data, we built a multiplex data acquisition apparatus, the Controlled Reptile Oxygen and Climate System (CROCS, Fig. 1), capable of heating animals in test chambers at a constant, designated rate with gases of varying oxygen concentration. This is accomplished via an Arduino UNO R3 microcontroller that controls flow of compressed gas from aluminum scuba tanks into an insulated metal box containing a heater (900w finned strip heater wrapped with 3/8" aluminum tubing) and digital temperature sensor (Adafruit MCP9808 High Accuracy I2C Temperature Sensor Breakout Board) and then into seven test chambers (8-inch respirometry chambers, Qubit Biology, Inc.) via silicone tubing. This arrangement, where air is heated via thermal conduction through an isolated coil of aluminum tubing contained within the heater box, was chosen to reduce the fire potential inherent when working with oxygen concentrations above 21%. Air exiting the heater passes through a diffuser manifold to disperse evenly from the heater into each of the seven chambers. When the heated air enters the chamber, additional diffusers route the heated air stream away from the lizard's snout to evenly heat the air in the chamber. Fiberglass insulation prevents excessive loss of heat to the environment from the two outer chambers. Prior to experimentation, we confirmed that the ambient temperature rises at equal rates in each of the seven chambers. Six of the test chambers

² LORR: body temperature at which loss of righting response occurs.

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