



## Effects of oxygen on responses to heating in two lizard species sampled along an elevational gradient

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### ABSTRACT

Thermal tolerance is an important variable in predictive models about the effects of global climate change on species distributions, yet the physiological mechanisms responsible for reduced performance at high temperatures in air-breathing vertebrates are not clear. We conducted an experiment to examine how oxygen affects three variables exhibited by ectotherms as they heat—gaping threshold, panting threshold, and loss of righting response (the latter indicating the critical thermal maximum)—in two lizard species along an elevational (and therefore environmental oxygen partial pressure) gradient. Oxygen partial pressure did not impact these variables in either species. We also exposed lizards at each elevation to severely hypoxic gas to evaluate their responses to hypoxia. Severely low oxygen partial pressure treatments significantly reduced the gaping threshold, panting threshold, and critical thermal maximum. Further, under these extreme hypoxic conditions, these variables were strongly and positively related to partial pressure of oxygen. In an elevation where both species overlapped, the thermal tolerance of the high elevation species was less affected by hypoxia than that of the low elevation species, suggesting the high elevation species may be adapted to lower oxygen partial pressures. In the high elevation species, female lizards had higher thermal tolerance than males. Our data suggest that oxygen impacts the thermal tolerance of lizards, but only under severely hypoxic conditions, possibly as a result of hypoxia-induced anapnoea.

### 1. Introduction

Global climate change is expected to increase mean annual global temperatures by at least 0.8 °C, possibly more than 2 °C by 2050 (Collins et al., 2013). This change in the global climate will result in a massive restructuring of ecosystems worldwide and could lead to widespread species extinction (Thomas et al., 2004; Parmesan, 2006; Sinervo et al., 2010; Brusch et al., 2016). For this reason, concern is mounting for the longevity of many thermally sensitive species. Ectotherms are at particular risk because of the tight relationship between temperature and rates of physiological processes (Dawson, 1975; Huey and Stevenson, 1979). An increase in global temperatures can push many habitats outside of the physiological tolerance ranges of ectotherms (Brusch et al., 2016), leading to changes in growth, maintenance, reproduction, and survival (Bennett, 1980; Cloudsley-Thompson, 1999; Angilletta et al., 2002; Sinervo et al., 2010). Although thermoregulatory shuttling behavior may ameliorate some of these negative effects (Adolph, 1990; Buckley et al., 2015; Levy et al., 2015; Pincebourde et al., 2016), warming of the environment beyond

physiological tolerance ranges is expected to severely impact populations (Sinervo et al., 2010; Brusch et al., 2016). To better understand how climate change will affect terrestrial organisms and their habitats, we must investigate the thermal tolerances of ectothermic and thermally sensitive species from diverse and integrative perspectives.

A commonly used variable of thermal tolerance is the critical thermal maximum (CTMax). CTMax is defined as the maximum body temperature at which an organism is able to sustain basic vital physiological functions, with exposure to higher temperatures leading to death (Cowles and Bogert, 1944). Furthermore, studies have shown that the observable response to CTMax—loss of coordinated muscle function and righting response followed by the onset of spasms—occurs in all reptilian taxa studied (reviewed in Lutterschmidt and Hutchison, 1997b). Even with a long history of studies on CTMax, the mechanisms underlying the loss of righting response and onset of spasms remain poorly understood (Schulte, 2015). The oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis suggests that a decline in performance occurs due to the lack of oxygen delivery to body tissues at higher temperatures (Frederich and Pörtner, 2000). In recent years,

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**Table 1**  
Summary of Lizard Data and Experimental Design.

Site	Elevation (m)	Species	Treatment	P <sub>O<sub>2</sub></sub> (mmHg)	N	SVL (mm)	Mass (g)
Hospital Flats Campground	900	<i>S. occidentalis</i>	normoxia	144.0	12 (6M, 6F)	72.3 ± 1.6	15.0 ± 1.1
			hypoxia	41.2	10 (4M, 6F)	69.3 ± 6.6	15.7 ± 1.8
Kern River Trailhead	1475	<i>S. occidentalis</i>	normoxia	135.0	12 (4M, 8F)	66.1 ± 1.8	11.5 ± 0.9
			hypoxia	38.6	6 (2M, 4F)	67.8 ± 13.1	12.5 ± 2.2
Poison Creek	2100	<i>S. occidentalis</i>	normoxia	125.4	5 (3M, 2F)	69.8 ± 13.3	11.9 ± 2.3
			hypoxia	35.8	6 (3M, 3F)	73.8 ± 14.4	12.5 ± 2.5
		<i>S. graciosus</i>	normoxia	125.4	11 (4M, 7F)	55.1 ± 1.0	8.8 ± 2.1
			hypoxia	35.8	11 (6M, 5F)	57 ± 1.0	6.8 ± 0.4
Round Meadow	2680	<i>S. graciosus</i>	normoxia	117.2	11 (3M, 8F)	55.2 ± 0.8	6.4 ± 0.3
			hypoxia	33.5	11 (7M, 4F)	57.7 ± 0.9	7.0 ± 0.4

Note: Summary data on *Sceloporus occidentalis* and *S. graciosus* tested at four different sites along an elevational gradient in this study. The sample size (N) represents the number of lizards brought to the critical thermal maximum (CTMax). In some case, lizards did not gape or pant before attaining CTMax, so sample sizes for those tests may be smaller (see text).

this hypothesis has received a lot of attention (reviewed in Verberk et al., 2016). Several studies have shown that oxygen can be a limiting factor on thermal tolerances in water-breathing animals (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) and in air-breathing organisms (Verberk and Bilton, 2013, 2015; Verberk et al., 2013; Koopman et al., 2016; Shea et al., 2016), while most studies have not found support for OCLTT hypothesis in air-breathers, potentially because oxygen is so easily obtained (Klok et al., 2004; Stevens et al., 2010; McCue and De Los, 2013; Boardman and Terblanche, 2015). Fewer studies have tested this hypothesis in air-breathing vertebrates, and most have failed to support it (Seebacher and Franklin, 2011; Overgaard et al., 2012; Fobian et al., 2014; but see Smith et al., 2015; Shea et al., 2016).

Whereas the concept of oxygen limitation of air-breathing vertebrates has only recently received attention, there is a large literature showing that severe hypoxia can dramatically reduce the temperature set point of ectotherms, a phenomenon termed hypoxia-induced anapyrexia (Hicks and Wood, 1985; Dupré et al., 1986; Wood, 1991). Ectotherms exhibit a series of physiological and behavioral responses to hypoxia (Hicks and Wang, 2004), including initiation of panting at lower temperatures and choosing lower temperatures in a gradient, presumably to mitigate the metabolic costs of high body temperature under hypoxic conditions. In response to heating or while attempting to avoid heating beyond the preferred body temperature, many ectotherms exhibit gaping (opening of the mouth) and panting, potentially to enhance evaporative cooling (Heatwole et al., 1973); under hypoxic conditions, these behaviors may occur at lower temperatures to help the animal maintain a lower body temperature and therefore conserve oxygen (Wood and Gonzales, 1996). Although the temperatures at which animals exhibit gaping and panting behaviors do not necessarily reflect thermal tolerance in the way that the CTMax does, they represent robust and quantifiable behavioral responses to heating. While studies of hypoxia-induced anapyrexia do not directly test the OCLTT hypothesis because they do not demonstrate that physiological demand for oxygen outpaces the supply under normoxic circumstances, it is useful to compare the gaping threshold, panting threshold, and CTMax of animals under severe hypoxia to those observed during normoxia. Such comparisons may help explore what role, if any, oxygen plays in determining thermal tolerance. Further, they may reveal whether the OCLTT hypothesis is an appropriate model to apply to an ectothermic, air-breathing vertebrate. Furthermore, the vast majority of thermal tolerance studies in ectotherms, whether conducted under normoxic or hypoxic conditions, take place in captivity using acclimated laboratory animals. Given that thermal tolerance variables like the CTMax may be impacted by

acclimation (Spellerberg, 1972), it is desirable to conduct studies on animals in a natural setting shortly after capture.

We investigated the effect of inhaled oxygen partial pressures on the thermal tolerance of two species of lizards, *Sceloporus occidentalis* (western fence lizard) and *S. graciosus* (western sagebrush lizard), which are ideal species for thermal tolerance experiments due to the wealth of studies examining sensitivity to high temperatures in multiple lizard species (Cowles and Bogert, 1944; Brattstrom, 1965; Lutterschmidt and Hutchison, 1997b; Angilletta et al., 2002;). We conducted a field study examining the thermal tolerance of the two species across an elevational gradient, where ambient oxygen concentrations (e.g., environmental oxygen partial pressures, P<sub>O<sub>2</sub></sub>) vary. This experiment had several objectives. First, we examined how severe hypoxia impacts the gaping threshold, panting threshold, and CTMax of lizards along the elevational gradient to examine hypoxia-induced anapyrexia in a natural setting. Second, we took advantage of naturally occurring differences in P<sub>O<sub>2</sub></sub> to conduct an indirect test of the OCLTT hypothesis. If oxygen limits thermal tolerance, we predict that lizards will exhibit reduced thermal tolerance at higher elevations, where oxygen is lower. Third, we compared the thermal tolerance variables of the two species at the one elevation in which they overlapped, and of males and females of each species to examine potential species and sex differences in thermal tolerance and response to hypoxia.

## 2. Materials and methods

### 2.1. Study site and species

In the Sierra Nevada mountains of California, *S. occidentalis* is common at lower elevations and *S. graciosus* appears at higher elevations, with a narrow range of overlap. Lizards were sampled along an elevational gradient in the Sequoia National Forest in the Southern Sierra Nevada in the month of July. Four sampling locations were chosen (Table 1). Lizards were captured by hand or with a noose and stored in numbered tube socks for transport. Sample sizes are shown in Table 1. Mass (± 0.5 g), snout vent length (SVL, ± 1 cm), tail length (± 1 cm), time of capture, sex, and reproductive state (females only; carrying eggs=gravid, or not) were recorded for each lizard. Lizards were tested for gaping and panting thresholds and CTMax (see below) within 300 m of their capture location on the same day of their capture. Each lizard was tested only once. All procedures were approved by the Institutional Animal Care and Use Committee of the California Polytechnic State University (protocol #1506) and the California Department of Fish and Wildlife (scientific collecting permit #13265).

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