



Lack of supercooling evolution related to winter severity in a lizard



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ABSTRACT

As organisms move into higher latitudes, they may evolve physiological mechanisms to survive in harsher climates. One such mechanism is supercooling, the capacity to survive at subzero temperatures without freezing. While interspecific comparisons reveal greater thermal tolerances at higher latitudes in insects and vertebrates, evidence for intraspecific evolution in supercooling related to latitude is only evident in insects. We measured the supercooling points of lizards from 12 populations reared from hatch in common laboratory conditions to test for evolved differences in supercooling related to winter. Results indicate that winter harshness (depth or length) cannot explain supercooling points regardless of how data are analyzed, which suggests that populations have not evolved greater supercooling capacity. While our results are consistent with the idea that thermal physiology is evolutionarily conserved in vertebrates, we cannot reject several alternatives including the possibility that lizards are able to behaviorally avoid the extreme temperatures that would select for thermal evolution.

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1. Introduction

To survive direct exposure to subzero temperatures, ectotherms use one of two general strategies: freeze tolerance or freeze avoidance (for reviews see Bale (1987), Block (1990), Danks (2006) and Zachariassen (1985)). Tolerating the formation of ice in the body water (freeze tolerance) is common in invertebrates, but only present in a select few vertebrate ectotherms including some turtles, snakes, and frogs (Costanzo et al., 2001; Storey and Storey, 1988). On the other hand, freeze avoidance, which is also common in invertebrates, seems to be the norm in vertebrates (Costanzo et al., 1995). Supercooling is a common mechanism used by organisms that are freeze intolerant to avoid ice formation in tissues and involves lowering the temperature of body fluids below the crystallization temperature of water (i.e., $< 0\text{ }^{\circ}\text{C}$) without forming ice crystals. Although supercooling occurs as a natural consequence of solutes dissolved in the bodily fluids, it can be enhanced by the dual action of sugar or polyol production, such as glycerol, and the dehydration of cells (e.g., Sformo et al., 2010). Furthermore, supercooling capacity, which is usually also the

lower lethal limit of an individual, appears to be a trait that is greater in species that are freeze intolerant than in species that are freeze tolerant (Block, 1990). That is, freeze intolerant species can usually supercool to lower subzero temperatures than freeze tolerant species, which tend to foster ice nucleation at higher subzero temperatures.

Most of the previous research on the evolution of cold tolerance has focused on insects and, as predicted, shows that they have evolved an enhanced ability to deal with cold at higher latitudes using either tolerance or avoidance strategies (Addo-Bediako et al., 2000; David et al., 2003; Hoffmann et al., 2002; Zani et al., 2005). For example, enhanced cold tolerance is associated with higher latitudes in dipterans ranging from fruit flies, *Drosophila* (David et al., 2003) to pitcher-plant mosquitos, *Wyeomyia smithii* (Zani et al., 2005). Furthermore, lab experiments have shown that species occupying higher latitudes were not only more cold hardy than species from lower latitudes, but populations of the same species are more cold hardy at higher latitudes (Hoffmann et al., 2002). Insects from cold climates were also able to recover from cold exposure faster than those from more moderate climates (Ayrinhac et al., 2004; Hoffmann et al., 2002).

Despite the wealth of information on cold hardness related to latitude of ectotherms, very little research has been performed using vertebrates. A meta-analysis of the relationship between thermal tolerances and latitude including both invertebrates and vertebrates found support for the idea that tolerance to cold increases away from the equator (Sunday et al., 2011). However, the estimates of cold tolerance used by Sunday et al. (2011) were

Abbreviations: SCP, Supercooling point; EMNT, extreme annual minimum winter temperature; avg. EMMT, average annual minimum winter temperature; DMX0, number of days in a year with maximum daily temperature $< 0\text{ }^{\circ}\text{C}$; DMN-18, number of days in a year with minimum daily temperature $< 18\text{ }^{\circ}\text{C}$

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generalized for each species and not examined at the population level. The majority of previous vertebrate research involved critical thermal minima (CTMin) in reptiles. A few studies have reported differences in CTMin between populations (e.g., Brown, 1996; Tsuji, 1988; Weeks and Espinoza, 2013). For example, Weeks and Espinoza (2013) recently reported that although the CTMin (determined by loss of righting response) among populations of a South American gecko (*Homonota darwini*) did not correlate with latitude, CTMin did correlate with cooler climates. However, the effects of acclimation cannot be discounted in this and other studies due to the use of field-fresh animals in a number of these previous studies (but see Brown (1996), Tsuji (1988) and Yang et al. (2008)). A number of other studies failed to detect any difference in cold tolerance among populations (e.g., Gvoždík and Castilla, 2001; Manis and Claussen, 1986; Yang et al., 2008). Collectively these studies suggest that there are few differences in cold tolerance among populations in vertebrates that cannot be attributed to acclimation effects. Yet the capacity for vertebrates to evolve greater cold tolerance as they expand their range to higher latitudes is expected under the view that thermal-physiology traits are labile (e.g., Castilla et al., 1999; Hertz et al., 1983). To test the idea that cold tolerance has evolved in vertebrates, we studied the supercooling capacity of a small freeze-intolerant lizard that appears to have recently expanded its geographic range across a thermal gradient in western North America. We hypothesize that in response to selection by colder, longer winters, lizards at higher latitudes will have evolved lower supercooling points than those from lower latitudes.

2. Materials and methods

2.1. Study organism

To test for evolved supercooling ability in vertebrates, we used side-blotched lizards, *Uta stansburiana*. This species is widely distributed in western North America (from Baja California [23°N] to Washington State [47°N]) and appear to have little variation in mitochondrial DNA within the northern subspecies (*U. s. stansburiana*) (Corl et al., 2009). This latter result suggests a recent range expansion by this species, which we have mapped (Fig. 1). This map is based on our field observations, museum data available from VertNet (vertnet.org), and previous studies (e.g., McKinney, 1971; Parker and Pianka, 1975). We limited our study to animals from the northern subspecies, *U. s. stansburiana* (38.75°N–43.44°N; Fig. 1) because they occur over an environmental gradient related to winter cold; average minimum temperatures in the coldest month at our southern-most site (near Hawthorne, NV) = -4.3 °C; at our northern-most site (near Burns, OR) = -9.6 °C.

Side-blotched lizards are ideal study subjects in that adults are small (maturing in 9 mo. at 40 mm snout-vent length; Nussbaum and Diller, 1976; Zani and Rollyson, 2011), numerous (adult abundances range from 25 to 85 adults per ha in the northern portions of their range; summarized by Scouler et al., 2011), and overwinter in rock crevices in vertical cliffs that may subject them to thermal extremes (Cowles, 1941; Nussbaum et al., 1983). These thermal extremes are exacerbated by the fact that the vertical cliffs shed snow and therefore do not benefit from the insulative effects of snow. In the southern portion of their range, *Uta* can be active year round (Halpern and Lowe, 1968), whereas at high latitudes they are mostly inactive for 1–5 months during the winter (Nussbaum et al., 1983). Thus, our source populations spanned only 4.7°N latitude (Fig. 1), but occurred across an environmental gradient thought to be related to cold tolerance. Therefore, we predict that populations from sites with harsher winters will have

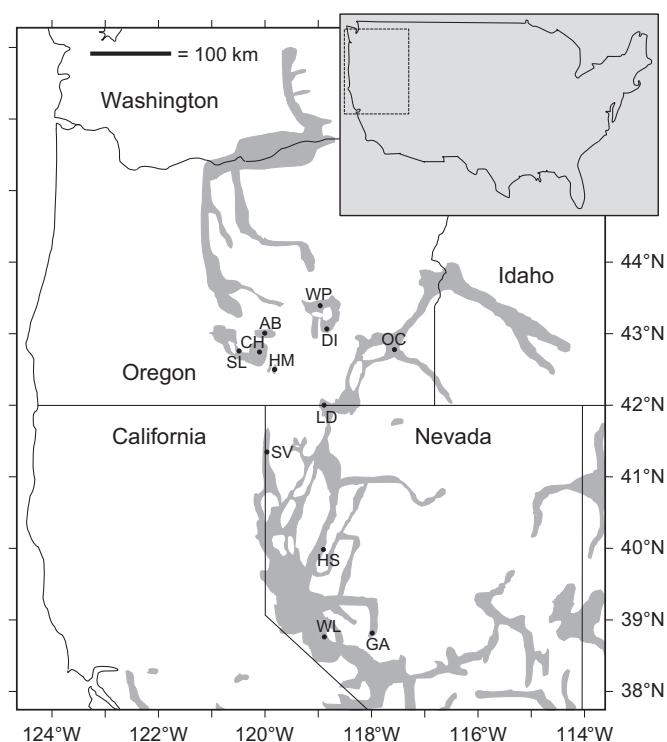


Fig. 1. Map of western United States showing collection localities of the 12 populations of *Uta stansburiana* used in this study. See Table 1 for site names and latitude of origin. Shading indicates habitats and elevations suitable for side-blotched lizards and is based on personal observations and historical collections (see methods). While *Uta* occur at higher latitudes, these locations all occur at lower elevations (and therefore less harsh winters) than our study sites. Inset shows map of United States with study area indicated by dashed box.

greater evolved supercooling abilities than those from southern latitudes.

Although we did not collect data from all sites, we were able to characterize the hibernation environment at one long-term study site, Wrights Point, in eastern Oregon. For this site we recorded temperatures approximately 0.75 m deep in a crevice from 2011 to 2014 using WatchDog Temp8K (Spectrum Technologies, Aurora, IL) dataloggers. This crevice was chosen because we observed lizards using it in the fall just prior to winter (P.A. Zani, pers. obs.). This crevice depth was likely more shallow than what lizards actually use in nature based on additional observations during winter. We compared these data to the corresponding hourly air temperatures (T_a) from a weather station located 11 km away at the Eastern Oregon Agricultural Research Center (<http://oregonstate.edu/dept/EOARC>). We only included data from November–February since our field observations indicate this is when lizards reliably use the deep crevices as retreat sites. We compared temperature observations using reduced major axis regression to estimate the temperature in the crevices used by lizards. This model was considered appropriate since there is error associated with both x and y variables.

2.2. Growth and acclimation conditions

To minimize non-genetic sources of variation (e.g., acclimation) among populations, we reared animals in identical conditions from hatching before assaying supercooling ability. To do this, we collected adult female (12–16 females per site) and male (4–5 males per site) lizards from 12 distinct populations in Nevada and Oregon (Fig. 1) in the spring of 2013 (March–May). We shipped lizards overnight to the University of Wisconsin–Stevens Point and maintained animals in an animal care facility. Cages were

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