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Primary Article

Living the High Life: *Sceloporus malachiticus* from High Elevations Perform Better at Extreme Temperatures

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Summary

It is well known that activity, including sprint speed, is highly temperature dependent in ectothermic organisms. Because temperature changes across elevations, the wide elevational range of the lizard *Sceloporus malachiticus* in Costa Rica is an enigma. We tested thermal sensitivity of sprint speed in *S. malachiticus* from high (3500m) and low (2200m) elevation populations near Savegre Lodge in San Gerardo de Dota, Costa Rica. To test the hypothesis that lizards from low elevations have narrower thermal envelopes than lizards at high elevations, we conducted temperature controlled sprint trials on noosed lizards from both elevations. Lizards from both populations performed comparably at ambient temperature; however, high elevation lizards were faster at both extremes suggesting phenotypic differences between populations which may be explained by genetic variation or phenotypic plasticity. Such studies are essential to understanding the fundamental processes underlying speciation and adaptation.

Introduction

The lizard *Sceloporus malachiticus* is found in Costa Rica and western Panama at elevations ranging from 600-3800 m (Savage, 2002). The wide range of this lizard is perplexing as species turnover rate is generally high across elevation gradients in the tropics. In fact, Fischer and Lindenmayer (2005) estimate that 90% of variability in lizard species richness can be explained by elevation. The daily activities of ectotherms are highly dependent on temperature which is known to decrease significantly with increasing elevation; temperature drops by approximately 0.56 degrees Celsius for every one hundred meter increase in elevation (Terborgh, 1977). In addition, variability across a year at any given location in the tropics is small when compared to the temperate zone (Figure 1). Species across elevations experience different, yet constant temperatures so that they become more highly specialized and are adapted to narrower thermal envelopes than their temperate zone counterparts (Janzen, 1967).

It may be expected that the thermal sensitivity of a lizard's sprint speed is dependent on that individual's habitat, with those species living in warmer areas performing better at higher temperatures, and those in colder habitats performing better at lower temperatures. Additionally, those living in habitats with greater temperature variability would be expected to demonstrate wider tolerance ranges and performance breadths. A study by Van Berkum (1986) of Anolis lizards supports this hypothesis; maximal sprint speeds and performance breadth were correlated with median body temperature of individuals in their natural environments. However, this may not be universal; Hertz et al. (1983) found no difference in optimal temperature range between Agamid lizard populations from varying temperature habitats.

Differences in thermal sensitivity across elevational populations may exist, either through phenotypic plasticity and/or genetic differentiation. Genetic variation might allow each population to perform best within a different thermal range (Hertz and Huey, 1981; Hertz et al., 1983). For example, higher elevation lizards may have developed adaptations decreasing optimal temperature in response to specific selective pressures, enabling them to perform better at lower temperatures. Phenotypic plasticity, on the other hand, may allow genetically identical populations to alter phenotype in response to varying environmental conditions. If either of these cases were true for *Sceloporus malachiticus*, we would expect high elevation populations to be more active at lower temperatures. Alternatively, lizards may not experience different thermal envelopes across elevational ranges if they are able to compensate for environmental change with behavioral adaptations, for example by altering time spent basking in the sun (Adolph, 1990; Grant and Dunham, 1990).

Sprint speed is a common measure of lizard performance (Van Berkum, 1988), and is an important determinant of survival, and hunting and breeding success (Savage, 2002; Husak et al., 2006). Reptile behavior and physiology are limited by temperature more than any other environmental factor (Pinch and Claussen, 2003), and it is well established that temperature affects sprint speed in lizards (Hertz et al., 1983; Pinch and Claussen, 2003). Our study tests the hypothesis that lizards *Sceloporus malachiticus* from high and low elevations have different temperature

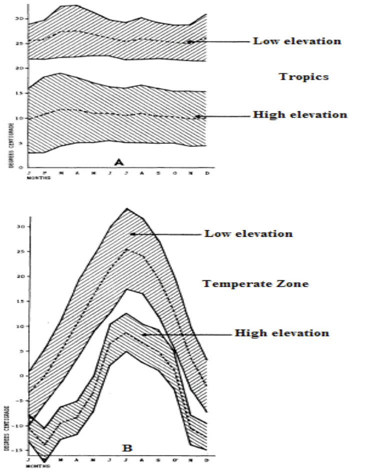

Figure 1. Temperature Ranges across Elevational Habitats (Janzen, 1967) In the tropics, temperature varies more in a day than in a year, which is in stark contrast to the temperate zone. Although tropical lizard species experience only a narrow thermal envelope, as elevation increases temperature range increases. Thus, lizards from high elevations experience both colder and warmer temperatures on a daily basis than do the lizards from low elevations.

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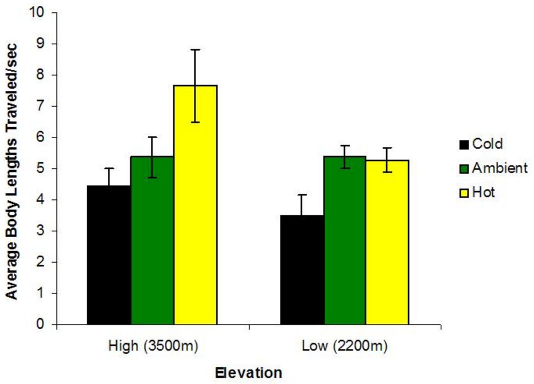

Figure 2. Comparison of Average body lengths traveled/second between elevations. High elevation lizards perform better at temperature extremes; they were almost significantly faster than low elevation individuals under hot (*P*= 0.1160) and cold (*P*= 0.2012) conditions, but not at ambient (*P*= 0.9867).

sensitivities, with lower elevation populations showing narrower thermal envelopes, by measuring sprint speed in response to temperature manipulations.

Results

High elevation lizards performed better at extreme temperatures (Figure 2). Lizards from high elevations had an average speed of 4.44 body lengths traveled per second (±0.55) in cold temperatures, 5.36 (±0.66) in ambient temperatures, and 7.65 (±1.16) in hot temperatures. Lizards traveled faster with increased temperature. Low elevation lizards had an average speed of 3.49 body lengths traveled per second (±0.66) at cold temperatures, 5.37 (±0.37) at ambient, and 5.27 (±0.39) at hot temperatures. Low elevation lizards did not increase their speed as temperature rose from ambient to hot. In fact, the average speed decreased slightly, although this was not significant.

Discussion

High elevation lizards performed better at both extreme temperatures. Although this trend was not statistically significant at the .05 level, this was likely due to small sample sizes, and may still indicate phenotypic differences between high and low elevation populations. These phenotypic differences could be explained by either genetic variability or phenotypic plasticity (Hertz et al. 1983). High elevation lizards may have been selected for adaptations that decrease their optimal temperature and are therefore enabling them to operate at lower temperatures with minimal negative effects. Phenotypic plasticity, on the other hand, may have allowed lizards to physiologically adjust to activity at a wider range of temperatures without genetic diversion (Spencer and Grimmond, 1994).

Crowley et al. 1985 found similar thermal sensitivities in two populations of *Sceloporus undulatus* which differed by temperature, but not elevation. This could suggest that factors other than temperature, for example oxygen level, may have influenced the variable performance of our lizards across elevational gradients. However, the fact that both populations performed comparably at ambient temperatures in our study suggests that temperature, rather than oxygen level, accounted for differences in sprint speed performance between populations.

Future studies should attempt to distinguish between genetic variation and phenotypic plasticity as possible explanations for the observed phenotypic differences in thermal sensitivity across elevational populations. Measuring sprint speed of lizards from different elevations raised in identical laboratory conditions could provide some insight. This method was used by Wilson (2001) to compare jumping performance of striped marsh frogs across geographic areas with varying climates. Future studies may also test directly for genetic variation between populations by looking at the population genetics of hemoglobin. Some organisms, such as Deer Mice, have shown genetic variation in hemoglobin across elevations (Snyder, 1981).

Our results may provide insight into the fundamental processes underlying speciation and adaptation. If the observed phenotypic differences across populations can be explained by genetic variation, this may suggest that the current range of this *Sceloporus malachiticus* population is a relatively recent occurrence. These populations may, in fact, be in the process of speciation. Phenotypic plasticity, on the other hand, would indicate that *Sceloporus malachiticus* is unique among tropical ectotherms. Generally, in the tropics, species turnover rate is high across elevational gradients. Janzen's classic 1967 article entitled "Why mountain passes are higher in the tropics" showcases how elevation can affect speciation in the tropics. According to Janzen, tropical organisms exposed to narrower temperature ranges should be more highly adapted to their specific niche than temperate organisms exposed to a wider range of temperatures. The lizard *Sceloporus malachiticus* appears to be enough of a generalist to thrive across a wide range, despite temperature changes across the elevational gradient.

Methods

Capture

Lizards were captured by a combination of noosing and hand capture. The noose consisted of a loop of fishing wire on the end of a stick. Most lizards were cornered and then grabbed by hand. After capture, lizards were placed in small, breathable cloth bags and transported to Savegre Lodge. Ten lizards were captured at 3500 meters and eight lizards were captured at 2200 meters. Mass and body length were measured before placing them in a box where they were left for twenty minutes before exposing them manipulated temperatures.

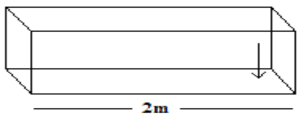

Figure 3. Track Diagram. Lizards were run on a two meter lone track after they were placed at one end of it (arrow).

Speed Trials

Boxes obtained from the Lodge were used to create hot, ambient, and cold environments. In the cold box we placed a bag of ice and in the hot box we attached two lamps. Temperature of the ambient box was left unmanipulated. Over the hot and cold boxes, we placed a shirt or sweater to better maintain temperatures over time. Once the box had reached the appropriate temperature (32 degrees Celsius for the hot box, 20 to 23 degrees Celsius for the ambient box, and 14 degrees Celsius for the cold box), we placed a single lizard inside for fifteen minutes.

Each lizard was tested after exposure to cold, ambient and hot temperatures in a random order. After fifteen minutes, lizards were removed from the box and placed him inside our makeshift, two-meter long cardboard track (Figure 3). To encourage the lizard to move, we tapped it on the hindquarters and also tapped the ground behind it, chasing it to the other end. Each lizard went through three timed trials per temperature manipulation.

Acknowledgements

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