



Cooler performance breadth in a viviparous skink relative to its oviparous congener



Félix Landry Yuan^a, Evan J. Pickett^b, Timothy C. Bonebrake^{a,*}

^a School of Biological Sciences, The University of Hong Kong, Hong Kong SAR, China

^b Faculty of Science, The University of Hong Kong, Hong Kong SAR, China

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ABSTRACT

Susceptibility of species to climate change varies depending on many biological and environmental traits, such as reproductive mode and climatic exposure. For example, wider thermal tolerance breadths are associated with more climatically variable habitats and viviparity could be associated with greater vulnerability relative to oviparity. However, few examples exist detailing how such physiological and environmental traits together might shape species thermal performance. In this study we compared the thermal tolerance and performance of two sympatric skink congeners in Hong Kong that differ in habitat use and reproductive mode. The viviparous *Sphenomorphus indicus* lives on the forest floor while the oviparous *Sphenomorphus incognitus* occupies stream edges. We quantified the thermal environments in each of these habitats to compare climatic exposure and then calculated thermal safety margins, potential daily activity times within each species' thermal optimal range, and possible climate change vulnerability. Although we did not detect any differences in thermal tolerance range or thermal environments across habitats, we found cooler performance in *S. indicus* relative to *S. incognitus*. Moreover, while optimal activity time increases for both skinks under a warming scenario, we project that the thermal safety margin of *S. indicus* would narrow to nearly zero, thus losing its buffering capacity to potential extreme climate events in the future. This research is thus consistent with recent studies emphasizing the vulnerability of viviparous reptiles to a warming climate. The results together furthermore highlight the complexity in how environmental and physiological traits at multiple spatial scales structure climate change vulnerability of ectothermic species.

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1. Introduction

In terrestrial ectotherms, extinctions due to climate change are predicted to increase in the tropics over the course of this century (Sinervo et al., 2010; Urban, 2015; Kubisch et al., 2016). The process by which this occurs is complex, since many aspects of life history can be affected by weather fluctuations, such as physiological development (Bestion et al., 2015) or reproduction (Zeh et al., 2012). However, it is generally thought that species are likely to be negatively impacted due to indirect effects on activity budgets rather than overheating or direct physiological impacts (Gunderson and Leal, 2015). For example, as the climate warms, more time is spent in cooler refuges, restricting behaviors that support survival and reproduction (Sinervo et al., 2010).

As behavior and physiology vary between species, it is expected that the risk of negative climate warming effects will vary

according to certain biological traits (Clusella-Trullas and Chown, 2014). In reptiles, reproductive mode is frequently associated with differences in thermal physiology, where viviparous (live-bearing) species are assumed to be more vulnerable to climate change than those showing oviparity (egg-laying) (Sinervo et al., 2010; Clusella-Trullas et al., 2011; Kearney, 2013; Pincheira-Donoso et al., 2013). Although both reproductive modes occur in the tropics (Webb et al., 2006) viviparous lizards and snakes (Squamata) tend to be found in greater proportion in cooler climates, relative to egg-layers, presumably because they have the capability to regulate the incubation temperatures of their offspring (Shine, 2005; Pincheira-Donoso et al., 2013). Therefore, it would be expected that viviparous species are less heat tolerant and thus more vulnerable to warming (Clusella-Trullas et al., 2011).

Similarly, the thermal environment of an ectotherm is expected to affect its vulnerability to climate change. Species that are exposed to a wide range of temperatures are expected to evolve the physiological or behavioral capacity to tolerate such variation. Therefore, ectotherms from more stable thermal habitats are

* Corresponding author.

E-mail address: tbone@hku.hk (T.C. Bonebrake).

predicted to be at a greater risk of extinction from climate change as their thermal tolerance breadths are expected to be narrower than species from highly variable environments (Deutsch et al., 2008; Huey et al., 2009; Clusella-Trullas et al., 2011; Bonebrake and Deutsch, 2012; Sunday et al., 2012). In addition to tolerance, thermal performance curves can vary as function of environmental contexts (Angilletta, 2009). For example a specialist-generalist trade off might be expected where greater temperature variability could be associated with lower relative maximal performance (P_{max}) in conjunction with a wider tolerance breadth, whereas, the opposite pattern would occur for stable thermal conditions (Gilchrist, 1995; Angilletta et al., 2010; McElroy, 2014; Phillips et al., 2014). Another possibility is that thermal physiology is driven by enzymatic processes, where there is greater relative performance for warm environment ectotherms, without any compensation in tolerance breadth; the hotter-is-better hypothesis (Huey and Kingsolver, 1989; Angilletta et al., 2010; Phillips et al., 2014).

Much of these concepts of temporal variability in temperature are further complicated by spatial heterogeneity in temperature. Habitats can provide the ideal temperature for species during variable weather conditions, for example cool microhabitats could permit foraging behaviors during hot weather. Therefore, the relationships between thermal performance curves or tolerance breadths can differ depending on the scale of habitat structure, which would thus lead to overestimates of extinction risk at larger scales (Huey et al., 2009; Logan et al., 2013). In such cases, spatial differences in microclimates within a given habitat type may confer greater tolerance to environmental variability than would be expected based on overall large scale trends in temperature.

In this study, we compared climate change vulnerability in two congeneric skink species, one oviparous and the other viviparous, that show sympatric distributions at regional scales, but differ in habitat use at finer spatial scales. Specifically, the viviparous species occupies forest habitats while the oviparous species strongly prefers stream edge habitats. We first determined (1) the extent to which the forest and stream habitats differed from one another by deploying copper lizard models quantifying each of their thermal environments as operative temperature (T_e), often employed to represent an ectotherm's instantaneous equilibrium body temperature in a given environment, with the assumption that there is no physiological or behavioral thermo-regulation (Dzialowski, 2005). We then determined (2) how thermal performance curves varied between both species. Finally we (3) modeled a simple warming scenario to determine which species shows greater climate change vulnerability with respect to projected changes in thermal safety margins and potential activity time.

2. Materials and methods

2.1. Study sites and organisms

Sphenomorphus incognitus (Thompson, 1912) is an oviparous skink that occupies rocks and boulders in stream or riparian areas, where it is often seen basking. Its distribution is generally restricted to tropical areas throughout Southern China, including Hainan Island, as well as Southern Taiwan and its nearby islands (Lau, 2005; S.P. Huang et al., 2006; W.S. Huang, 2010). *Sphenomorphus indicus* (Gray, 1853) differs in reproductive mode and habitat use, as it is viviparous and prefers forest floor, where it can be found under leaf litter, logs or stones, and occasionally basking in the open. Its distribution overlaps the entire range of *S. incognitus*, and further reaches higher latitudes in the Indian sub-continent and North-Central China, in addition to slightly higher elevations (Huang, 1996; Lau, 2005; Ji et al., 2006).

During the wet season of 2015, we collected T_e data and caught lizards throughout the New Territories of the Hong Kong Special Administrative Region (22.407°N 114.122°E). This region encompasses most of Hong Kong's land surface, with elevations ranging from 0 m at sea level to 957 m at the peak of Tai Mo Shan. However, we did not detect any *Sphenomorphus indicus* or *S. incognitus* at elevations greater than 600 m. Our study sites were Tai Po Kau Forest Reserve (121 m–221 m elevation), Mui Tsz Lam (85 m–163 m elevation), Shing Mun Country Park (196 m–471 m elevation) and Ng Tung Chai (226 m–427 m elevation), which all have both forest and stream habitats.

We caught lizards by hand and also conducted experiments throughout the period of April to October 2015. To avoid any differences due to stage of development (Telemeco, 2014), only mature lizards with full tails and no visible disease or impairment were used in experiments (14 and 11 individuals of *S. indicus* and *S. incognitus*, respectively).

Post-capture, we brought the skinks to the University of Hong Kong, where we housed them individually in terraria containing leaf litter, sticks, stones and moss, at an ambient temperature of 24 °C, which we measured with iButton® devices (DS1922L, Maxim Integrated, California, USA). We applied a one week period of acclimation at this temperature before experimentation to control for short-term plasticity in thermal physiology (Huang et al., 2006). We provided water and mealworms (*Tenebrio molitor*) ad libitum during the acclimation period and immediately after experimental trials. However, we fasted lizards for approximately 24 h before the start of each trial. If an individual lost its tail or became visibly ill during the course of the study, we excluded it from further experimentation and did not use its data. All lizards were returned to their site of capture once we completed the experiments.

2.2. Operative temperature models

We quantified the thermal environments using T_e s rather than measuring field body temperatures as the latter would involve catching and handling the skink, which could affect measurements (Hare et al., 2007; Luna and Font, 2013). Solely relying on data collected from skinks caught in the field would also fail to include body temperatures of lizards at times or places where catching them is not a possibility. We thus chose to employ copper models as an attempt to capture all thermal variation due to spatial and temporal effects.

In order to determine the T_e available in both habitats, we designed a single physical model to represent both species, and calibrated it accordingly (see Appendix and Fig. A1, available online). We fabricated these by cutting 3/4 in. diameter Type-M (0.032 in. wall thickness) copper pipes to a length expressed by adults of *Sphenomorphus indicus* and *S. incognitus* (60 mm). For temperature logging, we wrapped iButton® devices (DS1922L, Maxim Integrated, California, USA) in mesh and placed one inside each model, and plugged both ends with rubber stoppers (Logan et al., 2013).

In early September 2015, we deployed a total of 48 models across three sites (Mui Tsz Lam, Tai Po Kau Forest Reserve and Ng Tung Chai) with both habitat types, and set them to log temperature at 10 min intervals from the 3rd to the 27th of September. With the warmest and wettest time of the year being July and August, temperatures and precipitation in September are generally similar to those experienced during their peak reproductive period in May/June (personal observation; Dudgeon and Corlett, 2011).

Within each site, we interspersed models in two pairs of transects, with each pair consisting of two parallel transects placed approximately 20 m apart, with one following the stream and the other being in the forest. Each transect within a pair consisted of

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