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# Variation in the thermal ecology of an endemic iguana from Mexico reduces its vulnerability to global warming

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ABSTRACT

The persistence of reptile populations in a specific location is influenced by individuals' capacity to regulate their body temperatures, among other factors. Anthropogenic climate change may pose a risk to the survival of ectothermic animals due to their dependence on external heat sources to thermoregulate. In this study, we calculated indices of thermal habitat quality, thermoregulatory precision, and thermoregulatory effectiveness for the endemic spiny-tailed iguana *Ctenosaura oaxacana*. We evaluated these indices and the thermoregulatory behavior of the iguanas in the four types of vegetation that provide the most favorable conditions for thermoregulation. We also performed our experiments during both the wet and dry seasons to capture the full range of thermal conditions available to *C. oaxacana* over the course of a year. Finally, we evaluated the potential niche for the iguana in the years 2020, 2050, and 2080. Thermoregulation depends on both seasonal and environmental factors in this species. We found that thermoregulation effectiveness in both wet and dry seasons depends not only on the thermal conditions of the immediate environment, but also on the cover vegetation and habitat structure available across the range of habitats the species uses. Thus, heterogeneous habitats with dispersed vegetation may be most suitable for this species' thermoregulatory strategy. Likewise, niche modeling results suggested that suitable habitat for our study species may continue to be available for the next few decades, despite global warming tendencies, as long as cover vegetation remains unaltered. Our results suggest that thermoregulation is a complex process that cannot be generalized for all ectothermic species inhabiting a given region. We also found that temperature changes are not the only factor one must consider when estimating the risk of species loss. To understand the necessary thermal conditions and extinction risk for any ectothermic species, it is necessary to focus studies on the species' general ecology.


## 1. Introduction

The inability of reptiles to regulate their body temperatures as birds and mammals do is one of the principal reasons why reptiles' behavior and physiology depend on the temperature of the environment. This dependence can make reptiles and other ectotherms particularly vulnerable when environmental temperatures change (Mosauer and Lazier, 1933; Bogert 1939; Cowles 1942; Cowles and Bogert, 1944). The persistence of reptile populations in a given site depends, among other factors, on individuals' capacity to regulate their body temperatures through behavioral strategies (Christian et al., 1983; Adolph, 1990; Bauwens et al., 1996; Webb and Shine, 1998), that may include changes in activity periods (Carrascal and Díaz, 1989; Van Damme et al., 1989; Bauwens et al., 1996), and movement between cool and warm microhabitats (Kearney 2002).

Efficient thermoregulation is a complex strategy influenced by numerous factors, both directly and indirectly (Huey and Stevenson, 1979). For example, the sex and reproductive condition of individuals are intrinsic characteristics of the biology of a species (Gardener-Santana and Beaupre, 2009), while competition for resources, pressure from predators, and habitat composition or heterogeneity, seasonality, and even time of day are extrinsic factors that condition and modify the thermoregulatory capacity of individuals within their natural distributional range (Hertz

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et al., 1993; Angert et al., 2002; Sartorius et al., 2002; Kerr and Bull, 2004; Díaz et al. 2005; McConnachie et al., 2009). Further, it has become evident that anthropogenic climate change will compromise the thermoregulatory efficiency of some ectotherms, making their thermal environment more hostile (Root et al., 2003) by pushing the species into higher regions of their range of tolerated temperatures (Ruibal, 1961; Parsons, 1989). In fact, it is estimated that some species are already experiencing environmental temperatures that surpass the optimal temperatures for individuals to such a degree that it compromises their thermoregulation (Huey et al., 2009).

Since the previous century, researchers have tried to answer the question of how reptiles thermoregulate, and several methodologies have been developed as part of this work. The protocol of Hertz et al. (1993) has driven substantial advances in the estimation of fundamental indices of thermoregulation in lizards. It introduced two primary indices: thermoregulatory precision (*db*), which is the average degree to which ectotherms experience body temperatures outside the set-point range, and thermal quality of the habitat where the species is distributed (*de*), which indicates how closely the available thermal environment in a habitat matches the selected temperature range. Blouin-Demers and Weatherhead (2001) introduced an alternative thermoregulatory effectiveness index (*de*–*db*) to address difficulties with the index of Hertz et al. (1993) (for more details, see Blouin-Demers and Weatherhead 2001). The index *de*–*db* is a measure of how much an animal departs from thermoconformity. In addition to these indices, other parameters have been developed to estimate the vulnerability of a species to changes resulting from global warming (Sinervo et al., 2010) or from direct degradation of habitat due to human activity (Ballesteros et al., 2007). These measures include the thermal exploitation index (Ex), which quantifies the extent to which a species exploits its thermal opportunities (Christian and Weavers 1996), and hours of restriction, which estimates how many hours per day a reptile can be active, while staying within its thermal limits (Sinervo et al., 2010). Through niche modeling based on bioclimatic layers estimated for future years, Kearney et al. (2009) and Sinervo et al. (2010) have described possible modifications in the activity of lizards in response to changing environmental temperatures. They predict that if warming continues at its current rate, 56% of the viviparous lizards and 46% of the oviparous lizards in Mexico may disappear by 2050.

It is likely that lizards with limited distributions will be at greater risk, due to their reduced capacity for adaptation to drastic changes in their environment (Malcolm et al., 2006). In addition, recent studies also indicate that some tropical species may have a greater risk of extinction due to increased temperature than temperate species (Huey et al., 2009; Huey et al., 2012; Tewksbury et al., 2008).

It has been suggested that tropical environments exhibit relatively constant and homogeneous temperatures over time (Huey et al., 2009), so that tropical species thermoregulate efficiently within narrow ranges. In contrast, those species that inhabit temporally heterogeneous environments tend to interact more often with warm and cool habitats and exhibit wider thermal tolerances (Soulé, 1963). These ideas predict that species from temporally thermally homogeneous environments are more specialized in their thermoregulation than those which are distributed in variable environments, which has led some researchers to propose that tropical species with restricted distributions may be seriously threatened by anthropogenic climate change (Deutsch et al., 2008; Tewksbury et al., 2008; Huey et al., 2009; Huey and Tewksbury, 2009; Kearney et al., 2009; Bonebrake and Mastrandrea, 2010; Dillon et al., 2010; Huey et al., 2012; Urban et al., 2012). Despite recognizing the vulnerability of tropical species to anthropogenic warming, new results have suggested that these species may have a greater ability to respond to and tolerate these conditions than previously thought (Logan et al., 2013). Many of these results incorporate spatial thermal variability and collect data across different seasons to ensure a complete description of the species' thermal ecology.

In the context of these previous findings, we analyzed the thermal ecology of the endemic spiny-tailed iguana *Ctenosaura oaxacana* in a spatially thermally heterogeneous zone in southern Oaxaca, México. This species is considered critically threatened and exhibits a distribution restricted to a few vegetation associations in the Isthmus of Tehuantepec. It is threatened by poaching and habitat destruction due to extensive ranching (Köhler and Hasbun, 2001; Köhler, 2004; SEMARNAT, 2010; Rioja et al., 2012). In this study, we evaluated whether the thermoregulatory behavior of the iguana will allow it to tolerate anthropogenic climate change, including the effects of seasonality and the type of vegetation association in which the thermoregulation is taking place.

## 2. Materials and methods

### 2.1. Description of the species and study area

*C. oaxacana* is an arboreal iguana endemic to the state of Oaxaca in Mexico, separated from *C. quinquecarinata* by Köhler and Hasbun (2001). It is considered "critically endangered" by the International Union for the Conservation of Nature (Köhler, 2004) and is listed on the Norma Oficial Mexicana NOM-059-SEMARNAT-2010 in the "threatened" category (SEMARNAT, 2010). The population is severely fragmented, and it is estimated that habitat loss has increased considerably in the last 50 years due to human activity. In addition, extensive ranching and agriculture have recently become the most economically important activities for the people of Montecillo Santa Cruz, the nearest population center to the distribution of *C. oaxacana*; other activities of lesser importance include commerce and hunting of wildlife (Rioja et al., 2012).

The study site has an area of approximately 35 $km^2$ and is located to the north of the Lower Laguna, in the southern part of the Isthmus of Tehuantepec, Oaxaca (16°;22'00"-N, 94°;35'12"-W and 16°;24'10"-N, 94°;34'47"-W). The nearest community is Montecillo Santa Cruz, Municipality of San Francisco del Mar. This region is located in the northeastern part of the isthmus-Chiapan coastal plain, between the Sierra Madre de Chiapas and the Pacific Ocean (Zizumbo and Colunga 1982).

The climate is tropical, with an average annual temperature of 27.6 °C, average annual precipitation of 800 mm (INEGI, 1995), and clearly defined seasonality. The wet season occurs from May to October, with a midsummer drought in August, whereas the dry season occurs from November to April (Zizumbo and Colunga 1982).

The spiny-tailed iguana (*C. oaxacana*) in this area has access to five different vegetation associations. We chose to evaluate three of these due to their degree of abundance according to Rioja et al. (2012), and one more due to the level of disturbance we observed as a result of human and cattle activity. The vegetation associations we evaluated were: 1-Pasture: flat and open areas that flood during the wet season and that are characterized by an herbaceous stratum composed of cereals, herbs, isolated and dispersed "morro" trees (*Crescentia alata* Kunth 1819), and bushes. The most common plants are cereal species such as *Aristida* sp. and *Trisetum* sp. 2-Nanchal: semi-open areas with primarily herbaceous and bushy strata; the density of bushes is greater than in pastures, and the dominant species is the "nanche" (*Brysonima crassifolia* Kunth, 1822). 3-Tropical deciduous forest: closed areas with spiny, deciduous bushes and trees up to four meters tall. The most common