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Rapid Change in the Thermal Tolerance of a Tropical Lizard

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ABSTRACT: The predominant view is that the thermal physiology of tropical ectotherms, including lizards, is not labile over ecological timescales. We used the recent introduction (~35 years ago) of the Puerto Rican lizard *Anolis cristatellus* to Miami, Florida, to test this thermal rigidity hypothesis. We measured lower (critical thermal minimum [CT_{min}]) and upper (critical thermal maximum [CT_{max}]) thermal tolerances and found that the introduced population tolerates significantly colder temperatures (by ~3°C) than does the Puerto Rican source population; however, CT_{max} did not differ. These results mirror the thermal regimes experienced by each population: Miami reaches colder ambient temperatures than Puerto Rico, but maximum ambient temperatures are similar. The differences in CT_{min} were observed even though lizards from both sites experienced nearly identical conditions for 49 days before CT_{min} measurement. Our results demonstrate that changes in thermal tolerance occurred relatively rapidly (~35 generations), which strongly suggests that the thermal physiology of tropical lizards is more labile than previously proposed.

Keywords: thermal tolerance, ecological timescale, phenotypic change, climate change, tropical ectotherms, *Anolis*.

Introduction

The general view is that climate change will have a major impact on biodiversity by increasing the extinction risk of many species or changing their distributions (Pounds et al. 1999; Moritz et al. 2008). This view is based on the implicit assumption that species are relatively fixed entities, unable to respond to rapid changes in ecological conditions, including climatic variables, over an ecological timescale. Nevertheless, evidence that some organisms are able to respond to climatic changes over short timescales has begun to emerge (e.g., Grant and Grant 2002; Walther et al. 2002; Bradshaw and Holzapfel 2006). However, the rate at which species respond to climate change may be clade specific (e.g., Willis et al. 2008; Huey et al. 2009).

Ectotherms, including lizards, are widely used as a

model system to address questions regarding the impact of thermal environment on the evolution of physiological traits (e.g., Huey and Kingsolver 1993; Bauwens et al. 1995; Angilletta 2009). Multiple lines of evidence suggest that thermal physiology of diverse lizard clades is highly conserved (i.e., the conservatism hypothesis; Bogert 1949; Hertz et al. 1983; van Damme et al. 1990), leading to the prediction that lizard thermal physiology lacks evolutionary lability (reviewed in Hertz et al. 1983). Two mechanisms have been proposed to account for the apparent conservatism of lizard thermal physiology. First, behavior buffers thermal physiology from directional selection (Huey et al. 2003). Second, genetic constraints limit the ability of physiological traits to respond to environmental changes (van Damme et al. 1990; Huey et al. 2009; Sinervo et al. 2010). The conservatism of lizard thermal physiology has led to the prediction that lizards are particularly susceptible to rapid changes in climatic conditions (Huey et al. 2009; Sinervo et al. 2010). A recent survey of lizard populations across a vast geographic area partially supports this prediction by documenting local extinctions of species or populations over the last few decades (Sinervo et al. 2010). This problem is predicted to be most acute for tropical lizards, in which thermal conservatism is generally accompanied by a lack of phenotypic plasticity in response to thermal conditions (Tsuji 1988; Ghalambor 2006; Huey et al. 2009; and references therein).

Over the past two decades, ecologists and evolutionary biologists have taken advantage of human-mediated species introductions to evaluate the responses of populations to novel environments over evolutionarily brief time intervals (e.g., Lee 1999; Huey et al. 2000; Herrel et al. 2008). The results of these studies are particularly robust when the age and putative source of the introduction is known, because this allows for direct comparisons between the introduced population and its source (e.g., Reznick et al. 1990; Losos et al. 1997; Kolbe et al. 2012). Here, we take advantage of the recent introduction (~35 years ago) of the tropical Caribbean lizard *Anolis cristatellus* to a sub-

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tropical region of North America, where winter temperatures are markedly colder than in the ancestral region.

Anolis cristatellus is native to the Greater Puerto Rican Bank, but established populations were first recorded in Miami, Florida, in 1975 (Schwartz and Thomas 1975). A phylogeographic study of *A. cristatellus* using mitochondrial DNA data demonstrates that the source of the Miami introduction used in this study was located within Las Cabezas de San Juan region, a continuous area of xeric forest located in northeastern Puerto Rico (Kolbe et al. 2007). Given the history of this introduction over the past 35 years, the source and introduced populations have experienced two distinct temperature regimes (fig. 1A). In particular, minimum air temperatures during the winter months can average 10°C cooler in Miami than in Puerto Rico. However, this pronounced difference in temperature is not present with regard to the maximum temperature experienced by the introduced and source populations. Therefore, this introduction provides a unique opportunity to evaluate the lability of thermal physiology over an ecological timescale.

The natural history of *A. cristatellus* is well known, making this species an excellent system with which to test predictions of the conservatism hypothesis. First, *A. cristatellus* has served as a model organism for studies of thermal ecology and physiology of anoles and tropical lizards in general (e.g., Hertz 1992a, 1992b; Hertz et al. 1993). Second, previous research has documented that, within the island of Puerto Rico, *A. cristatellus* populations occupying distinct thermal habitats do not differ in thermal physiology, particularly in preferred temperature (Hertz et al. 1993), critical thermal maximum (CT_{max} ; Huey and Webster 1976), and optimal sprint temperature (Gunder-son and Leal 2012). Finally, *A. cristatellus* have served as an empirical example of how behavioral thermoregulation may buffer populations from experiencing divergent selection pressures when they inhabit different thermal regimes (Huey et al. 2003).

In this study, we ask whether thermal physiology, specifically cold tolerance (critical thermal minimum [CT_{min}]) and heat tolerance (CT_{max}) have diverged between the introduced and source populations of *A. cristatellus*. The conservatism hypothesis predicts that both populations should exhibit similar values of CT_{min} and CT_{max} . However, if traits are labile, we predict that CT_{min} should have diverged between populations; specifically, we predict that individuals from Miami should tolerate colder temperatures than individuals from Puerto Rico. For the Miami population, we also evaluate whether CT_{min} varies across seasons (early spring vs. fall), periods during which lizards experienced distinct thermal regimes. Because of the tropical evolutionary history of *A. cristatellus*, we predict that

CT_{min} should not vary across seasons (Janzen 1967; Ghalambor et al. 2006).

Material and Methods

Anolis cristatellus is a medium-sized (males can reach 76 mm in snout-vent length), gray-brown, sexually dimorphic, arboreal lizard that is commonly found perching on the lower portion of tree trunks. We collected *A. cristatellus* at two sites. On the island of Puerto Rico, lizards were collected at Las Cabezas de San Juan region (18°16.204'N, 65°37.845'W), located in northeastern Puerto Rico, at an elevation of 10 m. In Miami, Florida, lizards were collected in the vicinity of the village of Pinecrest (25°40.167'N, 80°17.138'W).

Lizards were brought to our laboratory and housed individually in plastic cages (29 cm × 21 cm × 21 cm) with a wooden dowel perch. Cages were located inside an environmental control chamber kept under a 12L : 12D photoperiod cycle at a constant temperature of 28°C and 60% relative humidity. Lizards were watered daily and were fed crickets every other day.

Experimental Design

The CT_{min} and CT_{max} are the lower and upper body temperature thresholds, respectively, at which a lizard loses the ability to right itself (Huey and Stevenson 1979). These metrics are often used as indicators of ecological death (i.e., physiological impairment, which would be lethal if maintained). We first explored whether the CT_{min} of *A. cristatellus* from the Miami population varies across seasons. Lizards were collected in the vicinity of the village of Pinecrest during April 10–11, 2010 (early spring), and on October 1, 2010 (early fall). The CT_{min} of lizards collected during the spring was measured during April 17–19, 2010, and the CT_{min} of lizards collected during the fall was measured during October 22–23, 2010. With the exception of one female that was measured as part of the collection of spring data, all other lizards used in this study were male. Lizards from Puerto Rico were not included in this experiment, because ambient temperatures at Las Cabezas de San Juan are relatively constant throughout the year (fig. 1A).

We next tested whether CT_{min} has diverged between lizards from Puerto Rico and Miami. We collected lizards at Las Cabezas de San Juan on August 9, 2010, and measured their CT_{min} during September 9–13, 2010, for comparison with the CT_{min} of the Miami lizards that were collected in the fall. Individuals from both populations had experi-

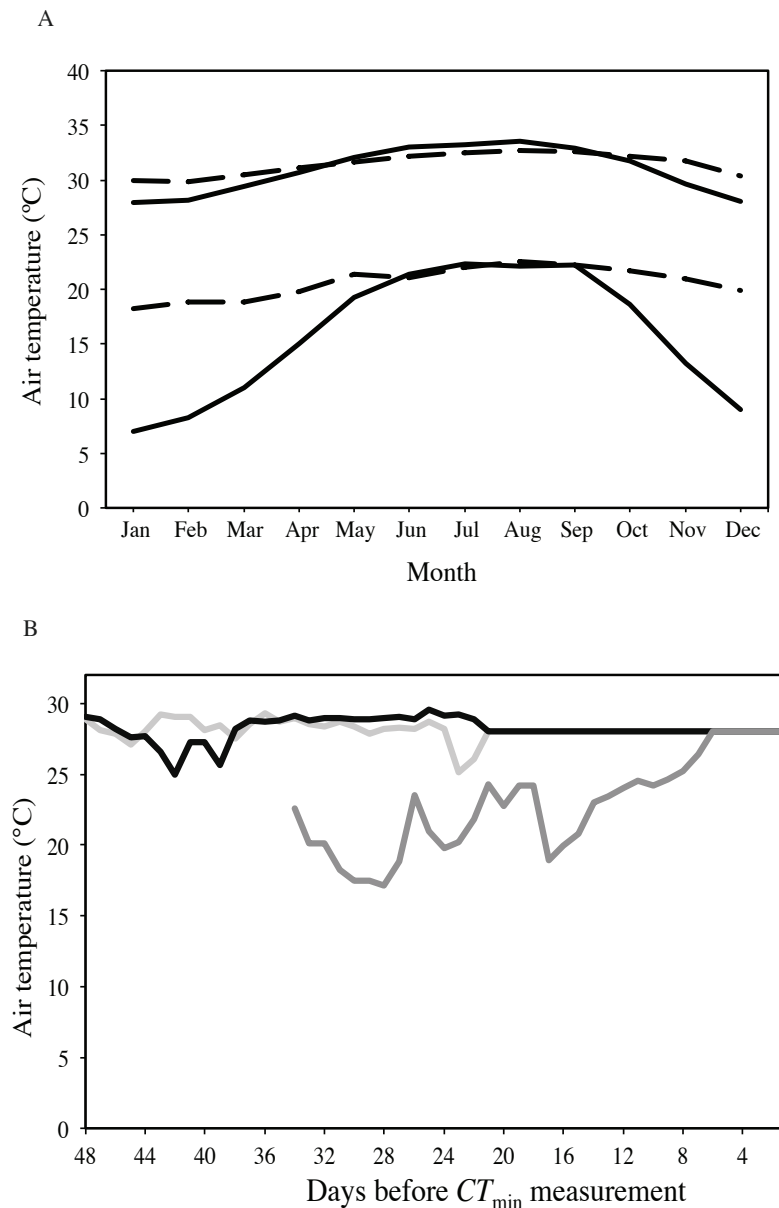


Figure 1: Ambient air temperatures experienced by individuals of *Anolis cristatellus* from the introduced and source populations. *A*, Average extreme air temperatures for each month over the past 40 years in Miami, Florida (solid lines) and “Las Cabezas de San Juan” region of Puerto Rico (dashed lines). The upper lines represent extreme maximum temperatures, whereas the lower lines represent the extreme minimum temperatures. *B*, Daily mean air temperatures experienced by individuals from Miami in the spring (dark gray line) and fall (light gray line) and Puerto Rico in the fall (black line) before critical thermal minimum (CT_{min}) measurements. The lines include the temperature experienced in the field 28 days before lizard collection as well as temperatures experienced in the laboratory.

enced similar temperature regimes in their respective habitats for 4 weeks before collection (fig. 1*B*) and were maintained under identical laboratory conditions for 21 days before testing.

Finally, we tested for differences in the CT_{max} of lizards from Miami and Puerto Rico. As was the case for the fall

measurements of CT_{min} , individuals were maintained under identical laboratory conditions for 21 days before data collection. Lizards from Miami were collected on December 23, 2011, and their CT_{max} was measured on January 15, 2012. Lizards from Puerto Rico were captured February 4, 2012, and their CT_{max} was measured February 26, 2012.

Measurement of CT_{min}

To measure CT_{min} , we placed the tip of a long thermocouple probe (~ 1.5 m, 40 gauge) inside the cloaca of a lizard and secured it to the base of the lizard tail with a small piece of surgical tape. The probe was connected to an Omega digital thermocouple thermometer (model HH603A, type T, sensitivity $\pm 0.1^\circ\text{C}$), which allowed lizard body temperature to be monitored continuously throughout the experiment. Next, the lizard was loosely tethered to a piece of cardboard (29 cm \times 21 cm) with a piece of dental floss looped around the waist, taking the precaution that limb movement was not affected. The cardboard was placed inside an incubator (Percival model I30NLC8) maintained at a temperature of 2°C . Lizards were removed from the incubator to assay righting ability at the following target body temperatures: 14.0, 13.0, 11.5, 10.0, 9.0, 8.0, and 7.0°C . Righting ability was evaluated by placing the lizard onto its back with tweezers and gently pinching the hind limbs with the tweezers to induce a righting response over a 20-s period. If the lizard righted itself, it was placed back inside the incubator to be tested at the next-lower target body temperature. If the lizard was unable to right itself, it was placed back inside the incubator until its body temperature decreased by 0.5°C and was then removed and assayed again. A lizard that failed to right itself this second time was left out of the incubator and allowed to slowly warm up at room temperature. As the lizard warmed up, we tested its righting ability at 0.5°C intervals. The CT_{min} of a lizard was recorded as the lowest body temperature at which it righted itself during the cooling or warming phase of the experiment. The experiments followed approved ethical and institutional guidelines for animal care.

Measurement of CT_{max}

To measure CT_{max} , we affixed a thermocouple probe inside the cloaca of lizards and tethered them to a piece of cardboard as described above for CT_{min} . To increase their body temperature, the lizards were placed under a 150-W double-mirror incandescent light bulb. We tested each lizard for righting ability at 1°C intervals starting at 36°C .

Climatic Data

We obtained air temperature data for Miami and Puerto Rico at two timescales: long-term temperature data (i.e., collected over the past 40 years) and short-term data (i.e., the thermal regime experienced by the lizards in the field for 28 days before collection). Long-term temperature data

were compiled to explore the typical temperature extremes experienced by Miamian and Puerto Rican lizards since the approximate time of the introduction. These data were obtained from the Southwest Regional Climate Center at the University of North Carolina, Chapel Hill. Miami data were gathered from National Climatic Data Center (NCDC) weather station 085658 and include records for the period 1970–2010. Puerto Rico data were collected from NCDC station 668412, located at the Roosevelt Roads Naval Base, which is within Las Cabezas de San Juan region, and include records for the period 1970–2003 (records were unavailable for the years 1999–2000 and 2004–2010). From these data, we calculated the monthly mean extreme maximum air temperature and the monthly mean extreme minimum air temperature (fig. 1A).

We also obtained average daily temperatures for the 4 weeks (i.e., short-term timescale) preceding the day of lizard capture in Miami and Puerto Rico. These measurements provided an opportunity to evaluate the similarity of the thermal conditions at both sites immediately before individuals were captured. In the case of the Miami population, data were obtained for both the spring and fall collecting periods. These short-term data were compiled from the NCDC Global Summary of the Day online database (Miami, NCDC station 722020; Puerto Rico, NCDC station 998247).

Statistical Analyses

Data on CT_{min} and CT_{max} were not normally distributed. After confirming homogeneity of variances with *F*-tests (all $P > .05$), we used nonparametric Wilcoxon rank-sum tests to test for differences in thermal tolerance. Short-term climatic data did not meet the assumption of homogeneity of variances, and data on minimum temperatures for Miami during the fall were not normally distributed. We tested for differences in short-term climatic data using the Welch's *t*-test for unequal variances on rank-transformed climatic data (see Ruxton 2006 for a detailed description of this approach). All tests were two-tailed at $\alpha = 0.05$. Analyses were conducted using the R statistical programming language (R Development Core Team 2009).

Results

Long-term climatic data demonstrate that, throughout the year, maximum air temperatures in Puerto Rico (i.e., Las Cabezas de San Juan region) and Miami have been very similar; however, minimum air temperatures have been considerably different (fig. 1A). The difference is most pronounced during the winter months (November–March), when average minimum air temperatures are of

ten over 10°C cooler in Miami than in Puerto Rico (fig. 1A).

Heat tolerance, CT_{max} , did not differ between lizards from Miami and Puerto Rico (median CT_{max} for Miami lizards, 39.0°C, $n = 11$; median CT_{max} for Puerto Rico lizards, 39.0°C, $n = 10$; $P = .970$). However, lizards from Miami had significantly lower CT_{min} than lizards from Puerto Rico, which indicates that lizards from Miami have greater cold tolerance (fig. 2). The median CT_{min} of fall Miami lizards (10.0°C, $n = 8$) was 3.1°C lower than that of Puerto Rican lizards (13.1°C, $n = 12$; $P < .001$). The population difference in CT_{min} was observed despite the fact that, over a period of 28 days before lizard collection, mean daily air temperatures (\pm SD) did not differ significantly between sites (Miami, $28.2^\circ \pm 0.9^\circ\text{C}$; Puerto Rico, $28.4^\circ \pm 1.1^\circ\text{C}$; $P = .120$; fig. 1A), and mean daily minimum temperatures differed only by a magnitude of 1.8°C (Miami, $25.0^\circ \pm 0.9^\circ\text{C}$; Puerto Rico, $26.8^\circ \pm 1.9^\circ\text{C}$; $P < .001$).

Short-term field temperature data indicate that Miami lizards collected during the early spring experienced significantly colder temperatures than those collected during the early fall (fig. 1B). Spring lizards experienced a mean air temperature 6.5°C colder than that experienced by fall lizards (spring, $21.7^\circ \pm 3.0^\circ\text{C}$; fall, $28.2^\circ \pm 0.9^\circ\text{C}$; $P < .001$) and a mean minimum air temperature 8.4°C colder than that experienced by fall lizards (spring, $16.6^\circ \pm 2.7^\circ\text{C}$; fall, $25.0^\circ \pm 0.9^\circ\text{C}$; $P < .001$). Despite the difference in thermal regime, the CT_{min} of Miami lizards collected in early spring (9.3°C; $n = 10$) and early fall (10.0°C; $n = 8$) did not differ significantly ($P = .098$; fig. 2).

Discussion

Our results reject the hypothesis of thermal conservatism by demonstrating changes in the thermal physiology of a tropical lizard species over an ecological timescale (~ 35 years). The approximately 3°C differences in CT_{min} between the introduced population and its source is in the direction predicted by the temperature regimes of each habitat, particularly with respect to the minimum air temperatures experienced during the winter (fig. 1A). This strongly suggests that the physiological differences can be adaptive, because increased cold tolerance could benefit lizards from Miami in a number of ways. Most obviously, greater cold tolerance should increase the probability of survival during cold winter temperatures. Other positive effects could be less conspicuous. For example, increased cold tolerance could increase the time available for activity during the winter, allowing more time for foraging and decreasing vulnerability to predation by limiting the amount of time that lizards are unable to move as a result of cold incapacitation.

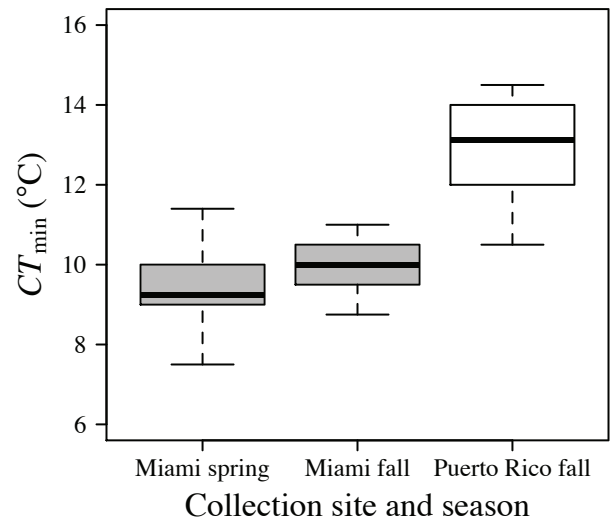


Figure 2: Box plots of the critical thermal minimum (CT_{min}) values of lizards from Miami and Puerto Rico measured in the spring and fall. Boxes encompass the second to third interquartile range, whiskers span the range of the data, and the thick bars indicate the median values.

As predicted, we found no difference between the CT_{max} of lizards from Miami and that of lizards from Puerto Rico. Figure 1A shows that, over the period that *Anolis cristatellus* has been in Miami, the maximum ambient temperature experienced by the source and introduced populations is nearly identical. The observed values of CT_{max} are nearly identical to those previously reported for multiple populations of *A. cristatellus* within Puerto Rico (Huey and Webster 1976).

Our results suggest that divergence in thermal tolerance (CT_{min}) occurred rapidly (within ~ 35 generations) in a population of *A. cristatellus*. Faster rates of divergence in thermal physiology have been shown in other taxa, such as *Drosophila* and sticklebacks (e.g., Hoffman et al. 2003; Barrett et al. 2010); however, given our knowledge of the thermal physiology of tropical lizards, which includes extensive work in *A. cristatellus* (Huey et al. 2003; Gunderson and Leal 2012; and references therein), our findings are unexpected (Huey et al. 2009; Sinervo et al. 2010). The predominant view across tropical lizards is that conservatism is the rule in thermal physiology, particularly over an ecological timescale.

Why the introduced *A. cristatellus* do not support the predictions of the conservatism hypothesis is an open question. The expectation of conservatism is based on the prediction that behavior can buffer thermal physiology from selection (reviewed in Huey et al. 2003) and that the temperature sensitivity of physiological traits lacks evolutionary lability, particularly over ecological timescales

(e.g., Sinervo et al. 2010). Behavioral thermoregulation allows individuals to modify the selective environment (i.e., thermal regime) that they experience, thereby leading to a reduction or possible elimination of divergent selection pressure on thermal physiology (Bogert 1949), known as the “Bogert effect” (reviewed in Huey et al. 2003). However, the strength of the Bogert effect should be limited by the heterogeneity of the thermal environment. In Puerto Rico and Miami, *A. cristatellus* sleep on top of broad leaves exposed to the night air when temperatures are lowest and when spatial thermal heterogeneity is at a minimum (Porter and Gates 1969; Huey et al. 1989). The long-term data for Miami (fig. 1A) show that ambient temperature can drop at least 3°C below the lizards’ median CT_{min} , which suggests that nighttime air temperatures can be a strong selective force. Our results suggest that, in situations in which behavioral thermoregulation cannot buffer selection on thermal physiology, tropical lizards may have the evolutionary lability to respond to new climatic conditions.

Adaptive phenotypic plasticity is an alternative mechanism that could account for the difference between the introduced and native populations of *A. cristatellus*, including seasonal acclimation in adults or irreversible developmental plasticity induced during embryonic or juvenile development (reviewed in Gienapp et al. 2008; Somero 2010). Seasonal acclimation has been demonstrated in other taxa, including temperate lizards (e.g., Wilson and Echternacht 1987, 1990; Tsuji 1988; Du et al. 2010). However, studies testing seasonal thermal acclimation in tropical anoles, including *A. cristatellus*, have found lack of support for this mechanism (Rogowitz 1996a, 1996b; but see Corn 1971). Two additional lines of evidence suggest that acclimation does not account for the observed differences in CT_{min} between the source and introduced populations. First, before collection, Miami lizards in the spring experienced a mean air temperature 6.5°C cooler and a mean minimum air temperature 8°C cooler than those experienced by fall lizards (see “Results”). Under acclimation, we would expect the CT_{min} of Miamian lizards to be lower in the spring than in fall (Tsuji 1988), but this pattern was not observed (fig. 2). Second, lizards from Miami and Puerto Rico experienced very similar environmental temperatures in the field for at least 28 days before collection (see the short-term temperature results) followed by identical laboratory conditions (i.e., 28°C air temperature) for approximately 21 days before measurement (fig. 1B). Under acclimation, we would expect the CT_{min} of Miami and Puerto Rico lizards to converge after experiencing similar thermal regimes for 49 days; however, populations still exhibited significant differences in thermal tolerance (fig. 2).

Another possibility is that temperatures experienced

during incubation or juvenile development have an effect on thermal physiology (Jensen et al. 2008; Angilletta 2009; Hoffman and Todgham 2010), although a recent synthesis of data for ectotherms suggests that adaptive developmental plasticity in response to thermal variation is rare (Angilletta 2009; Du et al. 2010). Extensive data on anole natural history suggest that it is unlikely that Miamian and Puerto Rican embryos will experience divergent thermal regimes. In Puerto Rico, *A. cristatellus* and other species in the *cristatellus* species group exhibit strong seasonality in breeding, which is primarily driven by changes in ambient temperature (Gorman and Licht 1974; Losos 2009). A strong seasonality in the breeding cycle has also been documented for *Anolis sagrei* in southern Florida, in which individuals are not reproductive from November through February (Lee et al. 1989). Thus, *A. cristatellus* in Miami is unlikely to be reproductively active during the months when environmental temperatures differ substantially between Miami and Puerto Rico. Additional studies are needed to explore the possibility that incubation temperature can influence the CT_{min} of *A. cristatellus*.

In summary, regardless of the mechanism, the adaptive lability of thermal tolerance in *A. cristatellus* over an ecological timescale is unexpected and provides a glimpse of hope for tropical lizards under the current conditions of rapid climate change. The relatively rapid divergence in CT_{min} suggests the possibility that the physiological traits of tropical ectotherms are evolutionarily labile. However, their flexibility might be masked by the Bogert effect, which can compromise the accuracy of models predicting the evolutionary potential of thermal physiology. It should not be overlooked that it remains to be tested whether the lability of thermal tolerance is also present for the CT_{max} (i.e., whether species or populations challenged with warmer temperatures would be able to respond to those challenges by increasing their upper thermal tolerance). At present, this remains an open question for most species of tropical ectotherms, particularly vertebrates. Human-mediated introductions or habitat disturbances in which populations experience warmer environments than those experienced by their source populations provide a unique opportunity to evaluate the lability of CT_{max} over time scales relevant to predictions of global climate change (e.g., Angilletta et al. 2007). These systems are ripe for additional research, including gathering much-needed empirical data to address the evolutionary potential of physiological parameters over short periods of time.

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A male *Anolis cristatellus* in its native habitat in the Caribbean island of Puerto Rico. Photograph by Manuel Leal.