

Thermoregulatory Behavior Simultaneously Promotes and Forestalls Evolution in a Tropical Lizard

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Submitted January 11, 2017; Accepted July 21, 2017; Electronically published October 25, 2017

Online enhancements: appendix.

ABSTRACT: The role of behavior in evolution has long been discussed, with some arguing that behavior promotes evolution by exposing organisms to selection (behavioral drive) and others proposing that it inhibits evolution by shielding organisms from environmental variation (behavioral inertia). However, this discussion has generally focused on the effects of behavior along a single axis without considering that behavior simultaneously influences selection in various niche dimensions. By examining evolutionary change along two distinct niche axes—structural and thermal—we propose that behavior simultaneously drives and impedes evolution in a group of *Anolis* lizards from the Caribbean island of Hispaniola. Specifically, a behavioral shift in microhabitat to boulders at high altitude enables thermoregulation, thus forestalling physiological evolution in spite of colder environments. This same behavioral shift drives skull and limb evolution to boulder use. Our results emphasize the multidimensional effects of behavior in evolution. These findings reveal how, rather than being diametrically opposed, niche conservatism and niche lability can occur simultaneously. Furthermore, patterns of niche evolution may vary at different geographic scales: because of thermoregulatory behavior, lizards at high and low elevation share similar microclimatic niches (consistent with niche conservatism) while inhabiting distinct macroclimatic environments (consistent with niche divergence). Together, our results suggest that behavior can connect patterns of niche divergence and conservatism at different geographic scales and among traits.

Keywords: niche evolution, behavior, thermoregulation, Caribbean, lizard, Bogert effect.

Introduction

For nearly a century, behavior has been recognized as a key pacemaker for evolution (discussed in Huey et al. 2003; Duckworth 2009). On the one hand, behavior can facilitate evolutionary change; as organisms explore novel environments, they experience new selective pressures that can lead

to phenotypic adaptations and speciation (Miller 1956; Lande 1981; Wyles et al. 1983; Bateson 1988; West-Eberhard 1989; Sol et al. 2005). Mayr (1963) proposed, for example, that shifts in behavior were key initial changes precipitating the prolific morphological diversification of tropical birds. An alternative school of thought contends that behavior often plays a constraining role in evolution (Bogert 1949; Bartholomew 1964; Wake et al. 1983; Brandon 1988). Organisms can choose microhabitats to which they are already well adapted, preventing exposure to directional selection, even in the face of changing environmental conditions. The Bogert effect (sensu Huey et al. 2003) is a prime example of this process: rather than shifting their physiology, ectotherms such as reptiles and insects use regulatory behaviors to buffer their physiology from selection, even as environments change across space or through time (Huey 1982; Angilletta 2009). In this context, behavior constrains rather than facilitates evolutionary divergence.

Both perspectives have empirical support, but considering them a dichotomy overlooks the connectivity among a species' multiple niche dimensions (Hutchinson 1957; Holt 2009). By simultaneously affecting diverse aspects of the niche, a single behavior can mold the natural selection pressures on multiple phenotypic traits (Lewontin 1983; Levins and Lewontin 1985; Huey et al. 2003). For example, a population may be adapted to eat a particular type of food found in certain microhabitats with specific microclimates. By behaviorally shifting to eat a different food that occurs in a separate microhabitat, the population may have to adapt not just to the new diet item but also to new structural habitat and microclimatic niche conditions. In other words, behavioral shifts in the use of any resource may have multiple potentially contrasting effects on trait evolution (Levins and Lewontin 1985; Huey et al. 2003), but these kinds of effects remain empirically unexplored.

Anolis lizards provide a unique opportunity to test the multidimensional effects of behavior on evolution because both their physiology and morphology are tightly linked to

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habitat choice (Losos 2009). The form-function relationship between structural habitat (i.e., the matrix of structural supports these arboreal lizards utilize) and morphology is well established (Losos 1990; Garland and Losos 1994; Irschick and Losos 1999), supplying concrete hypotheses for how behavioral changes in microhabitat use will affect morphological evolution. Similarly, the effects of thermal habitat use (i.e., the matrix of thermal patches in a habitat) on thermal physiology in anoles are also well understood (Ruibal 1961; Rand 1964; Hertz 1974, 1981, 1992*a*, 1992*b*; Huey et al. 2009), and anoles are known to shift their habitat use at different elevations (Rand 1964; Schoener and Schoener 1971; Hertz and Huey 1981; Schwartz 1989). In other words, habitat choice by anoles may impact both their physiology and their morphology.

We focus our study on the *Anolis cybotes* species complex (the cybotoids) from the Caribbean island of Hispaniola. The thermal biology of these lizards makes them an excellent subject for the study of the role of behavior in evolution. Despite being distributed across a broad altitudinal range (from sea level to more than 2,500 m), lizards in this complex have quite similar body temperatures (Hertz and Huey 1981; Muñoz et al. 2014). Similarly, heat tolerance (CT_{max}) remains nearly constant ($\sim 40^{\circ}C$) across this elevational range (Muñoz et al. 2014). In many lizards, including many species of anoles, both body temperature and thermal tolerance are labile, often shifting substantially over shallower thermal clines (Hertz 1979; van Berkum 1988; Labra et al. 2009; Rodríguez-Serrano et al. 2009; Bonino et al. 2011; Muñoz et al. 2016). In contrast, the minimal change in body temperature in the cybotoids over such large elevational transects suggests that behavioral thermoregulation, potentially involving shifts in microhabitat use, may be occurring.

We address four specific hypotheses in this study. We first predicted that thermoregulatory behavior changes with altitude, such that montane lizards behaviorally compensate for their colder environments. Second, we predicted that thermoregulation at high elevation is accomplished by a shift in structural microhabitat away from these lizards' ancestral arboreal niche to capitalize on more exposed and thus warmer substrates, namely boulders (Rand 1964; Schoener and Schoener 1971; Hertz and Huey 1981; Schwartz 1989). Third, we tested the hypothesis that behavioral shifts in microhabitat use involve adaptive shifts in skull, limb, and toe pad morphology. Specifically, we predicted that boulder-dwelling lizards evolved a flattened body form and fewer toe pad scales as well as differences in hind limb length. Lizards utilizing boulders and cliff faces are typically characterized by dorsoventral flattening, which eases their movements into narrow crevices and tight spaces under boulders (Vitt et al. 1997; Arnold 1998*a*; Revell et al. 2007; Goodman and Isaac 2008). Anoles perching close to the ground tend to have fewer adhesive toe scales (lamellae) than arboreal anoles because lamellae assist with clinging to vertical surfaces (Collette 1961; Glossip and Losos 1997;

Stuart et al. 2014). Shifts in relative limb length are also often associated with boulder use in lizards, although the direction of change varies, with longer hind limbs evolving in some lineages and shorter hind limbs evolving in others (Leal et al. 2002; Goodman 2007; Revell et al. 2007; Goodman et al. 2008; Collar et al. 2011; Muñoz et al. 2015; Blom et al. 2016). Why limb length evolves in different directions is not fully understood (Cartmill 1985; Pounds 1988; Losos and Sinervo 1989; Losos et al. 1993; Losos and Irschick 1996; Arnold 1998*b*). As a result, we predict that the shift to using boulders will lead to a change in limb length, but we do not specify the predicted direction of this change. Finally, using a common garden experimental design, we tested whether such morphological shifts are evolved or due to phenotypic plasticity.

Material and Methods

Species and Study Sites

The *Anolis cybotes* species complex is found throughout the island of Hispaniola (Schwartz 1989; Glor et al. 2003), across habitats ranging from tropical lowland forests and lowland xeric scrub forest to cold montane pine forests. Importantly for this study, *A. cybotes* and its close relatives are distributed across wide elevational ranges in the island's two principal mountain chains, the Cordillera Central and the Sierra de Baoruco, or the eastern and western mountains, respectively (fig. A1; figs. A1, A2 are available online). Lizards in this group found at elevations higher than 1500 m have been designated as separate species—*Anolis shrevei* in the eastern mountains and *Anolis armouri* in the western mountains (Schwartz 1989)—but these populations are phylogenetically nested within populations described as *A. cybotes* (Glor et al. 2003; Wollenberg et al. 2013). *Anolis armouri* and *A. shrevei* are each more closely related to lowland populations of *A. cybotes* in the same mountain range than they are to each other (Glor et al. 2003; Wollenberg et al. 2013), suggesting that the invasion of high-elevation environments occurred independently. We studied *A. cybotes* at four sites in this study, one low- and one high-elevation site in each mountain chain. Study sites in the Sierra de Baoruco were located in Los Patos, Barahona Province (45 m), and in Loma del Toro, Sierra de Baoruco National Park, Independencia Province (2,258 m), and sampling days were June 11–16, 2012. Study sites in the Cordillera Central were located in the Francisco Alberto Caamaño Deñó National Park, Azua Province (13 m), and in Valle Nuevo National Park, La Vega Province (2,450 m), and sampling days were June 3–8, 2012 (table 1).

In contrast to the mesic, broadleaf forests found near sea level, the montane habitats of Hispaniola are covered in pine forest stands interspersed with savannas and rocky outcrops (Martin et al. 2011). Previous research has found that both *A. armouri* and *A. shrevei* are notably absent from

Table 1: Summary environmental information for localities visited and for lizards' preferred temperature ranges

Locality	Coordinates	Altitude (m)	Mean $T_e \pm 1$ SD ($^{\circ}\text{C}$)	Preferred thermal range T_{sel} ($^{\circ}\text{C}$; N)	Thermal habitat quality $\bar{d}_e \pm 1$ SD ($^{\circ}\text{C}$)
Cordillera Central (east):					
Low: Caamaño	18°26.119'N, 70°35.546'W	13	30.4 \pm 3.9	29.1–31.3 (17)	3.27 \pm 2.17
High: Valle Nuevo	18°43.800'N, 70°36.000'W	2,450	23.6 \pm 10.1	26.8–31.4 (19)	7.68 \pm 5.76
Sierra de Baoruco (west):					
Low: Los Patos	17°57.300'N, 71°11.288'W	45	31.3 \pm 4.7	28.3–30.4 (21)	3.65 \pm 3.54
High: Loma de Toro	18°17.244'N, 71°42.749'W	2,320	18.2 \pm 6.3	28.8–32.7 (23)	12.99 \pm 5.21

Note: This study was conducted at low- and high-elevation sites in the two main mountain ranges—the Cordillera Central (east) and the Sierra de Baoruco (west)—on the Caribbean island of Hispaniola. The mean operative temperature, T_e (i.e., the expected temperature of nonthermoregulating lizards), is substantially lower at high elevation than near sea level. Despite this environmental difference, lizards at high elevation have preferred thermal ranges (T_{sel}) nearly identical to their low-elevation counterparts, indicating a greater mismatch between their preferred temperature and the available thermal habitat (higher \bar{d}_e). To compensate for their colder habitats, high-elevation lizards are predicted to thermoregulate more effectively than their low-elevation counterparts (table 2). Measurement of T_e and T_{sel} are described in “Material and Methods.” Thermal habitat quality, \bar{d}_e , describes the deviation between the operative temperature (T_e) and the preferred temperature range (T_{sel}), such that a value of 0 indicates that T_e falls within T_{sel} (high thermal quality), and progressively greater numbers indicate increasing mismatch between T_e and T_{sel} (low thermal quality).

the deep forest and instead primarily occur in savannas and other clearings (Hertz and Huey 1981; Williams 1983). To gather body and operative temperature data, we centered our study sites on the open clearings adjacent to the deep forest. Nonetheless, during our experiments (described below) we periodically searched for lizards in deep forest. None of these searches yielded any lizards, confirming that they were primarily restricted to clearings and forest edges.

Measurement of Thermoregulation Efficiency

Behavioral thermoregulation occurs when an organism uses behavior to actively maintain a particular mean and variance of body temperature (Cowles and Bogert 1944; Huey 1982). To determine whether lizards were actively regulating their body temperature, we measured the efficiency (E) of thermoregulation, which estimates how well organisms are able to stay within their preferred temperature range, given their local thermal conditions (Hertz et al. 1993). To estimate E (described in detail below), we needed to know field-measured body temperatures (T_b), the preferred thermal conditions for the lizards (T_{sel}), and the environmental (operative) temperature (T_e) at each of the sites, which we measured as follows.

Operative Temperature. The operative environmental temperature (T_e) is the steady-state temperature of an organism in the absence of physiological thermoregulation (Bakken 1992). To estimate T_e at each site, we deployed 44 lizard models containing an iButton temperature sensor (DS1921G,

Maxim). Models were built from electroformed copper matching the shape and color of an adult male *A. cybotes* (Bakken and Angilletta 2014; Muñoz et al. 2014). We examined lizard color by measuring reflectivity of the head, body, and tail using an Ocean Optics USB 2000 spectrometer. Reflectivity values were recorded as percent reflectance relative to a barium sulphate white standard using an Ocean Optics R400 ultraviolet-visible (UV-VIS) reflectance probe, which was attached to a DT-1000 tungsten halogen/deuterium UV-VIS light source (Ocean Optics, Dunedin, FL). Note that we are assuming that the reflectivity in the visible range is also representative of the near infrared. The matte brown paint color for lizard models was selected by comparing sampled lizard reflectance to various paint samples. More details for building model are provided by Muñoz et al. (2014).

To establish transects for placing copper lizard models on perches, we walked a certain number of meters into the study site (with number of meters determined using a random number table). From that point we then picked a direction in which to walk (0° – 360° in 45° increments), with direction also chosen using a random number table. On the basis of previous work (Schwartz 1989; Glor et al. 2003; Wollenberg et al. 2013), these lizards are most commonly observed on boulders and arboreal vegetation within 1.5 m of the ground. Following Hertz (1992a), we placed copper models on tree trunks and boulders in roughly equal numbers at each site. Substrate choice (trunk vs. boulder), device height (0–150 cm in 15-cm increments), and orientation for perches (0° – 360° in 45° increments) in each transect were all chosen using a random number table. Models recorded T_e

every 10 min from 0600 to 1900 hours for 6 continuous days, providing an average of 1,714 copper model hours of sampling per site.

As discussed above, the high-elevation lizards (*A. armouri* and *A. shrevei*) are found in open clearings adjacent to deep forest (in which they are notably absent; Hertz and Huey 1981; Williams 1983). We centered our study sites in the savannas and rocky clearings where these lizards occur. We did not explicitly quantify habitat availability (i.e., the relative abundance of boulders and trees) in our study sites, because it would have been arbitrary to decide which trees were available to lizards. Hence, we measured the operative temperatures of boulders and trees found in the savannas and in the surrounding forest edges. Thus, our study design does not allow us to explicitly quantify lizard preference for forest or clearings or for the perches within them. However, our approach does allow us to compare the distribution of operative temperatures on the two most commonly utilized substrates in the habitats where lizards occur and to test whether lizard perch use in those habitats confers a thermoregulatory advantage.

Body Temperature. On the same days that we recorded T_e , we also measured T_b from wild adult male lizards. Following established methods (Hertz 1992a; Muñoz et al. 2014), two researchers walked slowly through each habitat and captured adult lizards using a noose tied to the end of a 3–3.7-m telescopic panfish pole (Cabela's, Sidney, NE). We measured T_b (to the nearest 0.1°C) through the cloaca using a thermocouple (type T, 5SC series, 36 gauge [0.13-mm diameter], OMEGA Engineering) connected to a temperature logger (HH603A; Omega). We marked lizards using nontoxic paint to prevent resampling during our experimental period.

Preferred Temperature Range. The preferred temperature range or the set point range (T_{sel}) refers to the central 50% of body temperatures measured in lizards that have been put in a thermal gradient and allowed to choose where to sit (i.e., in the absence of environmental constraints; Huey 1982; Hertz et al. 1993). We measured T_{sel} from wild-caught adult male lizards from all localities ($N = 17$ – 23 per population; table 1). Before experiments, lizards were maintained in environmentally controlled reptile facilities at Harvard University. Lizards were kept at 29.4°C and under a 12L:12D cycle for less than a week after capture. Lizards were not fed in the 24 h before experiments. The thermal arena consisted of a pine box with eight identical lanes (91 cm × 15 cm × 14 cm) covered with chicken wire. We laid a bed of gravel over heat cables (150 W; Zoo Med) in an air-conditioned room, creating a stable temperature range of 18°–40°C in each lane. Before experiments, we inserted a thermocouple (type T, 5SC series, 40 gauge [0.076-mm diameter], OMEGA Engineering) ~1 cm into the cloaca of each lizard and secured it to

the base of the tail using medical tape. The probe was connected to a digital temperature logger (HH147U, Omega). Lizards acclimated to the experimental chamber for 30 min before the beginning of the experiment. Temperature loggers recorded T_b every 10 min during each 4-h experimental trial. Trials started at 0830 and 1330 hours, and we put equal numbers of lizards from each population into each time trial.

Thermoregulatory Efficiency. We calculated thermoregulatory efficiency (E) for adult males observed in the wild as follows: $E = 1 - \overline{d_b}/\overline{d_e}$, where $\overline{d_b}$ and $\overline{d_e}$ refer to the mean deviation of T_b and T_e from T_{sel} , respectively (Hertz et al. 1993). A highly efficient thermoregulator would have a low $\overline{d_b}$ (meaning they are effective at maintaining temperatures within their preferred range), even in habitats in which operative temperatures diverge from the preferred range (i.e., high $\overline{d_e}$), leading to values of E close to 1. As organisms become more behaviorally passive with respect to temperature, the ratio between $\overline{d_b}$ and $\overline{d_e}$ increases, and E approaches 0. Following Hertz et al. (1993), we set confidence intervals on E through bootstrap resampling of our empirical distributions of T_e and T_b . Specifically, we computed $\overline{d_e}$ and $\overline{d_b}$ by randomly drawing samples (with replacement) of n observations of T_e and T_b , where n is the total number of observations. We estimated the confidence interval from 1,000 replicates of random resampling.

Structural Microhabitat Use

For each lizard captured for T_b measurement (described above), we also recorded two key aspects of microhabitat use at first observation: substrate type and perch height. Perch types included rocky substrates (boulders, ledges), woody substrates (branches, logs, roots, trunks, and twigs), leafy substrates (vines and leaves), man-made substrates (fence posts and walls), and the bare ground (soil). We compared boulder use with arboreal perch use (woody and leafy substrates) using the G -test of goodness-of-fit. We excluded a few observations of lizards on unusual perches, such as a coconut ($n = 1$) and a conch shell ($n = 1$). We also excluded man-made substrates (posts and gates) that were only available at low elevation. All other perches (boulders, branches, leaves, logs/stumps, tree roots, tree trunks, and twigs) were found in abundance at all sites. Following previous studies (Hertz 1981; Muñoz et al. 2014), we also recorded how exposed to sunlight the lizards were; lizards were considered to be exposed if 50% or more of their bodies was in direct sunlight. We compared observations of exposed (full sun), partially exposed (filtered), and shaded lizards among populations using a G -test for goodness-of-fit. To avoid resampling, all captured lizards were marked using nontoxic ink.

Morphological Analysis

To obtain morphological measurements, we captured adult male lizards ($n = 20\text{--}31$) from each locality. We took digital images (1200 dpi) of toe pads using a flatbed scanner, from which we measured lamella number (number of adhesive scales under the fourth toe). We then generated full skeletal images using a portable X-ray machine (Kodex). From each image, we measured body size (represented by snout-vent length [SVL]; the distance from the tip of the snout to the cloaca), femur length, tibia length, fourth metatarsal length, and fourth hind toe length. All skeletal measurements were gathered using the Object-J plugin in Image-J (ver. 1.47; Abramoff et al. 2004). We measured head height (the distance from under the base of the jaw to the top of the head) using digital calipers (Mitutoyo) to the nearest 0.01 mm. All morphological traits were log transformed before analysis. We tested for differences in morphological traits between high- and low-elevation lizards within transects using ANCOVA, with morphological traits as separate dependent variables, SVL as the covariate, and elevation (high vs. low) as the fixed effect.

Common Garden Experiment

In July 2012, we collected 20 gravid females each from the high- (Loma de Toro) and low- (Los Patos) elevation sites in the Sierra de Baorucu. We kept these females in environmentally controlled facilities (room temperature = 29.4°C) at Harvard University. Females were housed with one male from their native locality. Each enclosure consisted of a 30-cm³ polyester/nylon mesh cage (BioQuip Products) and included a felt cage carpet, two bamboo dowels for perching, and a small pot with moist soil for laying eggs. Cages were illuminated with full spectrum lighting, which was maintained at a 12L:12D cycle. Lizards were misted twice daily and fed 1.25-cm vitamin-dusted crickets three times per week.

Cages were checked three to four times per week for eggs from August to December 2012. Despite several months of effort (through May 2013), only two eggs were laid by females from the high-elevation population (Loma de Toro) under our laboratory conditions, and no changes in husbandry induced the females to become gravid again. Thus, we chose to rear young from eggs excised directly from females. In June 2013, we collected 10 heavily gravid females from Loma de Toro and surgically removed the shelled eggs from the oviduct. Eggs were immediately transferred to cell culture dishes containing moistened vermiculite, where they remained until hatching. Hatchlings were immediately placed in individual cages with temperature, lighting, feeding, and misting conditions as described above. We fed juvenile lizards vitamin-dusted *Drosophila* twice weekly until they reached approximately 20 mm in body size (SVL), at which point they were switched to a diet of 1.25-cm vitamin-dusted crickets.

We reared male lizards to adulthood (8–10 months) and then measured skull and limb dimensions, as described above. As with adults, we tested for differences in morphological traits between high- and low-elevation laboratory-reared lizards using ANCOVAs, with SVL as the covariate and elevation (high vs. low) as the fixed effect.

Results

Thermoregulatory Efficiency Increased with Altitude

The set-point range (T_{set}) varied little between high- and low-elevation populations of lizards (table 1). On average, operative temperatures (T_e) in montane environments are about 7°C below lizards' preferred temperature range (table 1; fig. 1), indicating lower thermal quality (higher \bar{d}_e) at high elevation. Lizards in these cool montane habitats are effective thermoregulators ($E = 0.93$; table 2), meaning that they maintain their body temperatures within their preferred thermal range, despite the available environment tending away from the preferred range (table 2). This near-perfect behavioral efficiency appears to stem from montane lizards effectively utilizing the relatively narrow sliver of their habitat matching their ancestral preferred thermal conditions (fig. 1C, 1D). At low elevation, in contrast, lizards are more behaviorally passive (lower E ; table 2), with the distribution of body temperatures closely mirroring the distribution of operative temperatures (fig. 1A, 1B). This correspondence likely results because their warmer habitats more closely match their thermal preferences: at low elevation, operative temperatures were, on average, 1°C warmer than the preferred range (i.e., lower \bar{d}_e) than at high elevation (fig. 1; table 1). In other words, lowland lizards do not need to thermoregulate as precisely to remain within their preferred range, whereas montane lizards must thermoregulate to accomplish the same feat and appear to do so effectively.

Microhabitat Use Differed between High- and Low-Elevation Sites

At high elevation, most operative temperatures (T_e) were below lizards' preferred range, but there were clear differences in thermal habitat quality between boulders and trees. Nearly all (93%) of the T_e 's measured on trees were below lizards' preferred range, in contrast to 70% of the T_e 's measured on boulders (fig. 1). Whereas lowland lizards predominantly (68% of observations) perched on arboreal vegetation (tree trunks, roots, leaves, branches), most lizards at high elevation were observed on rocky substrates (83% of observations; tables 2, A1; tables A1, A2 are available online; G-test for differences in boulder use between high- and low-elevation lizards; $P < .001$ for both mountain chains). Concomitant with the substrate switch, nearly all lizards at high elevation occupied habitats exposed to the sun (table A2;

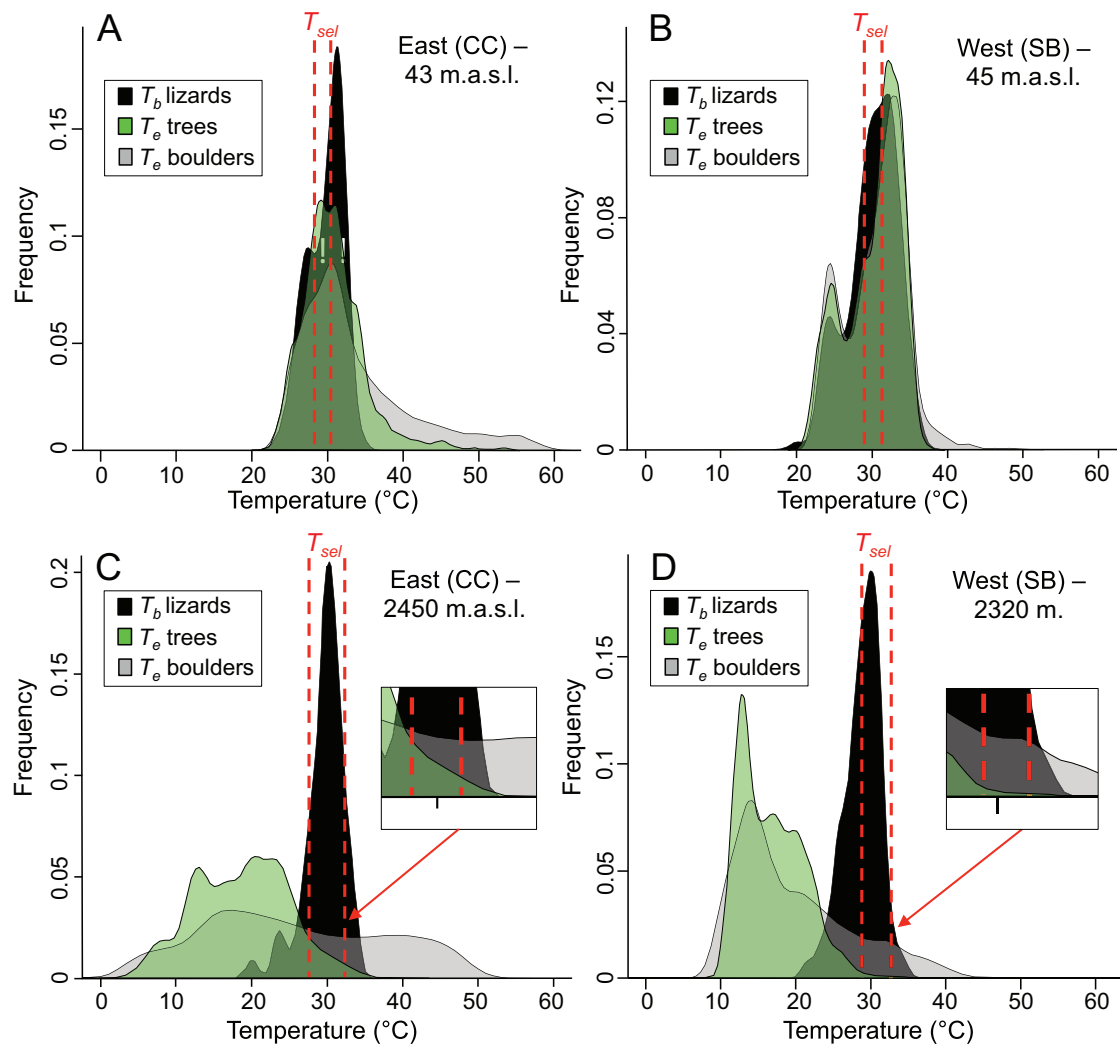


Figure 1: Montane lizards thermoregulate efficiently, despite living in thermally challenging habitats. *A, B*, Low-elevation sites. *C, D*, High-elevation sites. In each panel, the distribution of field-measured lizard body temperatures is shown in black, with the preferred temperature range measured in the laboratory indicated with red dashed lines. The distribution of T_e measured on boulders (gray) and trees (green) are overlaid. At low elevation (*A, B*), the temperature range of boulders, trees, and body temperatures overlap with T_{sel} , indicating that lizards do not need to thermoregulate precisely to maintain temperatures within their preferred range. In contrast, at high elevation lizards maintain body temperatures warmer than their local ambient conditions. The distribution of substrate temperatures shows that boulders fall within the preferred range more often than trees (insets). CC, Cordillera Central; SB, Sierra de Baoruco.

fig. A2; *G*-test for differences in perch exposure between high- and low-elevation lizards: $P < .001$ for both mountain chains). In short, perching on boulders provides montane lizards with a thermoregulatory advantage, enabling them to be highly efficient thermoregulators in relatively cold habitats.

*Montane Lizards Evolved Flatter Skulls
and Shorter Hind Limbs*

Morphological analyses of wild-caught adults revealed that montane cybotoid anoles have more dorsoventrally flat-

tened skulls relative to lowland lizards (table 3; fig. 2). Montane lizards also had relatively shorter hind limbs than lowland lizards, a result that stems from reduction in the length of the femur, tibia, and metatarsus but not the fourth toe (table 3; fig. 2). High- and low-elevation lizards did not differ in lamella number.

The common garden experiment revealed that the morphological differences observed among wild-caught lizards were evident in the laboratory-reared generation as well (table 3; fig. 2). As with wild-caught adults, laboratory-reared lizards from high-elevation habitats had dorsoventrally flattened heads, shorter femora, and shorter tibiae than low-

Table 2: Summary data for behavioral variables used to determine thermoregulatory efficiency

Locality	<i>N</i>	Boulder and arboreal use (%)	Mean perch height \pm 1 SD (cm)	Mean T_b \pm 1 SD ($^{\circ}$ C)	Thermoregulatory efficiency <i>E</i> (95% CI)
Cordillera Central (east):					
Low	104	11.3, 66.2	42.5 \pm 41.8	30.3 \pm 3.6	.368 (.364–.371)
High	58	77.6, 5.2	30.2 \pm 29.7	29.7 \pm 2.6	.930 (.929–.931)
Sierra de Baoruco (west):					
Low	83	2.3, 69.8	102.3 \pm 41.9	29.8 \pm 2.3	.670 (.693–.697)
High	68	88.2, 2.9	26.1 \pm 29.7	28.9 \pm 2.4	.929 (.928–.930)

Note: Lizards at high elevation are effective at maintaining body temperatures (T_b) as high as their lowland counterparts, despite living in considerably colder habitats (see also table 1; fig. 1). Consequently, their thermoregulatory efficiency *E* (the ability of lizards to maintain body temperatures within the preferred range, given its thermal habitat) is nearly perfect (i.e., *E* is close to 1). Lizards at high elevation utilize boulders more often than arboreal perches, although perch height remains roughly the same across elevation. Full substrate use given in table A1, available online. Measurement of body temperature, perch use, and thermoregulatory efficiency are described in “Material and Methods.” CI, confidence interval.

elevation lizards, although metatarsus length was not found to differ (table 3).

Discussion

The Bogert Effect Occurs through Shifts in Habitat Use

The extent to which ectotherms, such as lizards, can use behavior to buffer the effects of thermal variation has received renewed attention in light of global climate warming (Huey et al. 2009; Kearney et al. 2009; Sunday et al. 2014; Buckley et al. 2015). This topic, first discussed in the middle of the last century (Bogert 1949; Huey et al. 2003), has become particularly relevant in studies of tropical forest lizards because these organisms are currently functioning near their

upper limits (Huey et al. 2009). Our results suggest that behavior can be remarkably effective at buffering lizards from thermal variation. Specifically, the Bogert effect—physiological buffering through thermoregulation—is occurring in the high-elevation cybotoids from Hispaniola because these lizards appear to have adjusted their behavior, rather than their physiology, to their colder habitats.

The proximate mechanism underlying the Bogert effect in *Anolis armouri* and *Anolis shrevei* involves behavioral shifts in habitat use. Specifically, we found that lizards at high elevation are found in relatively more open habitats, where they perched primarily on boulders. Whereas nearly all temperatures measured on trees were below the set point range, rocky perches were nearly 5 $^{\circ}$ C warmer, providing a distinct thermoregulatory advantage to montane lizards.

Table 3: Regression results for comparisons of morphological variables across elevation

Trait	West: wild caught			East: wild caught			West: common garden		
	Coefficient	$F_{2,54}$	<i>P</i>	Coefficient	$F_{2,41}$	<i>P</i>	Coefficient	$F_{2,18}$	<i>P</i>
Head height	.054 \pm .005	215.6	8.13 \times 10 $^{-16}$.062 \pm .017	207.7	5.80 \times 10 $^{-4}$.085 \pm .015	41.06	1.68 \times 10 $^{-5}$
Femur	.027 \pm .004	179.3	5.86 \times 10 $^{-10}$.047 \pm .009	433.4	1.45 \times 10 $^{-5}$.048 \pm .011	33.46	5.18 \times 10 $^{-4}$
Tibia	.045 \pm .004	209.7	2.00 \times 10 $^{-16}$.054 \pm .008	667.7	7.35 \times 10 $^{-8}$.049 \pm .011	41.94	3.53 \times 10 $^{-4}$
Metatarsus	.025 \pm .004	91.81	6.04 \times 10 $^{-7}$.044 \pm .012	191.2	7.57 \times 10 $^{-4}$.018 \pm .012	19.09	.146
Fourth toe	.049 \pm .041	1.58 ^a	.239	.015 \pm .012	1.579	.216	.012 \pm .013	13.05	.336
Lamella no.	-.001 \pm .007	2.84 ^b	.894	.021 \pm .019	.579 ^c	.279

Note: ANCOVA for individual morphological traits showing differences in skull and limb dimensions between lowland and highland lizards. Montane lizards have more dorsoventrally flattened skulls and shorter femora, tibiae, and metatarsi relative to lowland lizards. All differences persisted in the common garden experiment, except for metatarsus length. For each regression, the model coefficient (\pm 1 SEM), *F* value with degrees of freedom, and significance value (*P*) are given. Separate analyses were performed for wild-caught lizards from each mountain chain (east and west) and for laboratory-reared lizards. For wild-caught lizards, the dependent variables examined were head height, head width, femur, tibia, metatarsus, fourth toe, and lamella number. For laboratory-reared lizards, the same variables except for lamella number were included (because no differences were detected in the wild-caught lizards).

^a $F_{2,53}$.

^b $F_{2,40}$.

^c $F_{2,39}$.

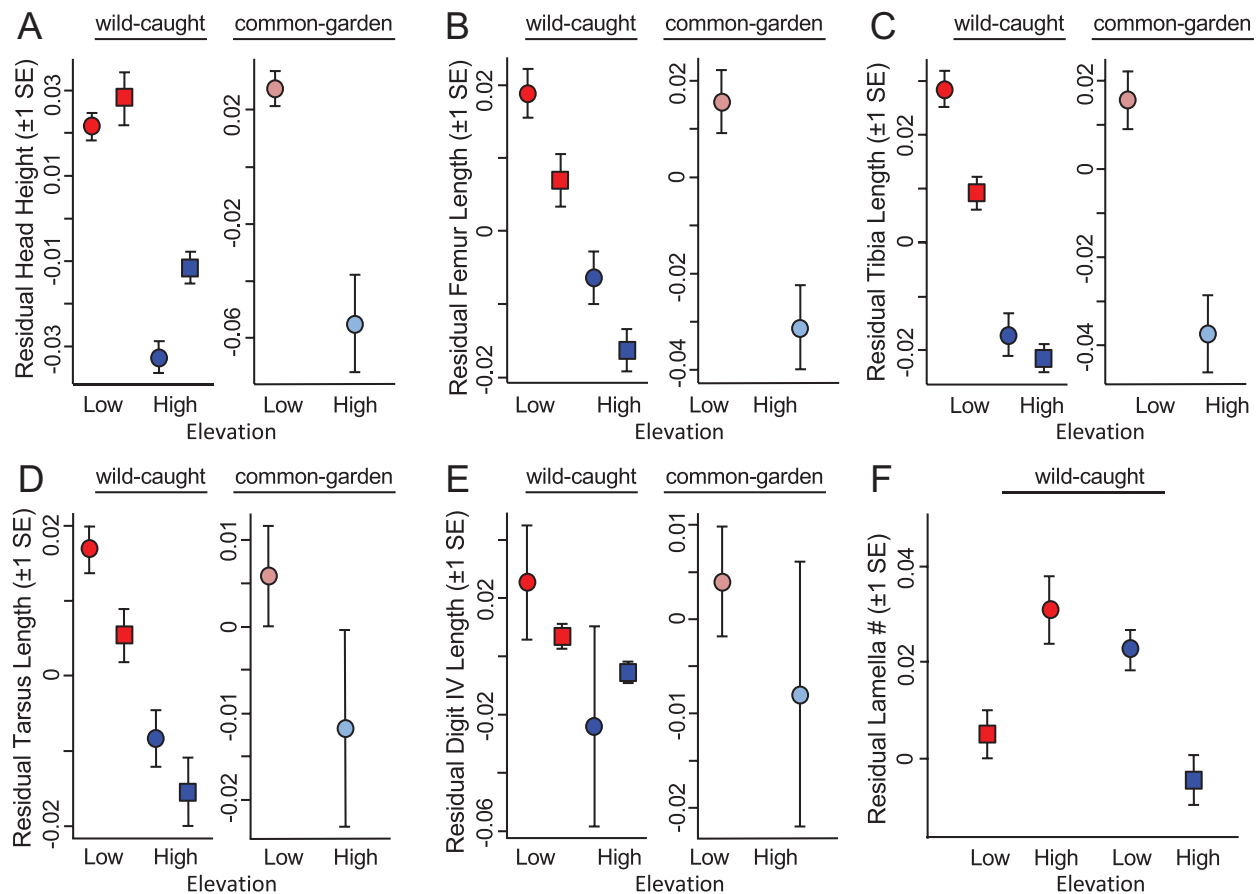


Figure 2: Skull and limb dimensions diverged between high- and low-elevation populations of lizards, with population means for size-corrected residuals (± 1 SEM) shown. Dark blue indicates wild-caught lizards from high elevation, and light blue indicates laboratory-reared lizards. Dark red indicates wild-caught lizards from low elevation, and pink indicates laboratory-reared lizards. Circles correspond to lizards from the western mountains (Sierra de Baoruco) and squares to lizards from the eastern mountains (Cordillera Central). The utilization of boulders at higher elevation corresponds to a significant decrease in head height (A), femur length (B), tibia length (C), and metatarsus length (D), but no shifts were detected in the fourth toe (E) or in lamella number (F). All shifts except metatarsus length were also found in the common garden experiment. Expanded ANCOVA results are given in table 3.

Behavioral Inertia Meets Behavioral Drive

While rendering evolutionary shifts in physiology unnecessary (Muñoz et al. 2014), behavioral thermoregulation occurred through a shift in structural supports, setting the stage for morphological adaptation (Huey et al. 2003). In other words, the same behavioral shift that precludes divergence in thermal physiology (behavioral inertia) may have concurrently driven divergence in morphology (behavioral drive).

Although *Anolis cybotes* is commonly known as the large-headed anole, we found that montane populations in this group have compressed skulls compared with their low-elevation counterparts. The adaptive value of this morphology is clear: rock-dwelling lizards—including these montane anoles (Hertz and Huey 1981)—often quickly scramble

into crevices and under boulders when threatened (Cooper et al. 2000; Stapley and Keogh 2004), a behavior facilitated by a flattened body shape. In contrast, arboreal lizards tend to flee up and around vegetation (Williams 1983; Cooper 1997; Cooper and Whiting 2007), a strategy unaffected by head size. Both *A. armouri* and *A. shrevei* are also known to retreat under rocks and logs under inclement weather conditions (Schwartz 1989).

In addition to skull compression, we also found that montane lizards evolved relatively shorter hind limbs, a result that echoes findings in *Petrosaurus*, another rock-dwelling lizard group (Revell et al. 2007). Relatively short hind limbs are thought to assist with climbing by maintaining the lizard's center of balance close to the surface (Sinervo and Losos 1991; Losos et al. 1993; Van Damme et al. 1997; Zaaf and Van Damme 2001). However, further

study on how montane lizards move on boulders (running, jumping, climbing, and clinging) is needed to illuminate the mechanistic relationship between boulder use, locomotor patterns, and limb length evolution.

Whereas changes in skull and limb morphology accompany the shift to boulders at high elevation, we detected no differences in toe scalation among populations. This may be due, in part, to the fact that high- and low-elevation lizards perched equally high off the ground and within the expected range for trunk-ground lizards (i.e., <1.5 m above the ground; table 2). Our findings of morphological divergence in limb and skull dimensions further suggest that physiological similarity is not due to gene flow precluding differentiation (e.g., Peterson 1995).

The adaptive radiation of *Anolis* lizards in the Caribbean is characterized by two distinct phases: morphological adaptation to structural habitat early in the radiation (i.e., the evolution of ecomorphs), followed by physiological adaptation within ecomorph clades to different thermal and hydric environments (reviewed in Williams 1972; Losos 2009). As a result, closely related anoles often exhibit morphological similarity and physiological differentiation (Hertz et al. 2013). Our results show, however, that this pattern does not hold in all cases. Rather than diverging physiologically to occupy different habitats, the cybotoids took an alternative tack, diverging in thermoregulatory behavior rather than physiology. The different path of the cybotoids compared with other anoles, however, is a result of geographic context. Whereas the cybotoid taxa are allopatric and adapt to broad-scale environmental differences across elevation (Schwartz 1989; Glor et al. 2003; Wollenberg et al. 2013), the divergence in thermal microhabitat among closely related species usually occurs among sympatric species that are thought to partition thermal habitat to minimize interspecific interactions (Ruibal 1961; Rand 1964).

Niche Conservatism, Behavior, and the Multidimensional Niche

Our central finding is that regulatory behavior—in this case, thermoregulation—and the evolutionary stasis it promotes can concomitantly lead to trait divergence, emphasizing the dual role of behavior in evolution. In light of these conclusions, we argue that investigating how behavior shapes the evolutionary process should involve an “exploration of the vectors and tensions that link these multidimensional roles” (Huey et al. 2003, p. 363). Behavioral shifts to preferred thermal microclimates are a widespread phenomenon in vertebrates (Rand 1964; Hertz 1981; Adolph 1990; Hertz et al. 1993; Harvey and Weatherhead 2010) and invertebrates (Watt 1968; Kingsolver 1983; Sømme 1989; Merrill et al. 2008; Ashton et al. 2009), setting the stage for both behavioral inertia and behavioral drive to be at play. For example, mir-

roring our finding in Hispaniolan anoles, spiny lizards (*Sceloporus*) in the western United States are arboreal at low elevation and ground-dwelling at high elevation; this shift in habitat use is thought to relate to behavioral thermoregulation (Adolph 1990). Although the Bogert effect has most often been examined in the context of thermal physiology, behavioral buffering can also affect other aspects of physiology. For example, Appalachian salamanders distributed across altitudinal gradients behaviorally shift habitat use to seek their preferred hydric microclimates, which sets up the possibility that buffering behaviors for hydric physiology may also influence evolution in nonphysiological parameters (Farallo and Miles 2016).

Especially since Hutchinson’s seminal work (1957), the multidimensionality of the niche has been recognized (Holt 2009). Less appreciated, however, is that niche dimensions, although distinct, are not independent of each other. As a result, shifts in resource use can affect multiple niche axes, simultaneously impinging on multiple selective pressures (Levins and Lewontin 1985; Huey et al. 2003). Our findings thus provide an important perspective on the ongoing debate about niche conservatism. The extent to which species’ niches are labile or conserved is a topic of keen interest in evolutionary biology (reviewed in Wiens et al. 2010). On the one hand, the tendency for ecological niches to remain stable across evolutionary timescales is a common pattern in nature and has been implicated in a variety of evolutionary phenomena, including allopatric speciation and latitudinal diversity patterns (Wiens and Graham 2005; Kozak and Wiens 2006; Buckley et al. 2010). On the other hand, rapid shifts in species’ niches have also been detected, leading to communities of closely related species with little ecological overlap (discussed in Losos 2008; Pearman et al. 2008).

Patterns of niche divergence or conservatism are often inferred from macroclimatic data. We argue that behavioral inertia can make such inferences misleading. For example, on the basis of macroclimatic data (e.g., climate layers resolved to 1 km²; Hijmans et al. 2005), thermal niche overlap between *A. cybotes* and the two highland taxa, *A. armouri* and *A. shrevei*, is low (Schoener’s $D = 0.396$ and 0.135 , respectively; see appendix), indicating that the thermal conditions between high and low elevation differ substantially. However, the thermal niches for these species are considerably less differentiated at the microclimatic scale because of behavioral thermoregulation (fig. 1). In other words, examination of macroclimatic data alone would lead to interpretation of niche divergence among taxa, whereas consideration of microclimatic and behavioral data suggests niche conservatism.

Even when species’ behavior and physiology are taken into consideration, we emphasize the need for caution about extrapolating evolutionary patterns from a single aspect of a species’ niche to overall patterns of niche evolution. Given

that different aspects of a species' niche can evolve in different ways, we suggest that the tendency to study niche evolution along a single axis may often be too narrowly focused. Indeed, several studies have found that different niche axes can evolve in different ways, suggesting that niche conservatism and divergence can occur simultaneously (Böhning-Gaese and Oberrath 1999; Vitt et al. 1999; Lindeman 2000; Freckleton et al. 2002). This finding may stem, in part, from the multiple interacting roles of behavior in evolution.

More broadly, the connection between behavioral drive and behavioral inertia offers an opportunity to unify studies of climate, behavioral ecology, and phenotypic evolution into a common framework. For example, behavioral shifts are one of the key ways in which organisms can respond to climate warming (Williams et al. 2008; Kearney et al. 2009; Huey et al. 2012). While serving to buffer organisms, a less explored corollary is that such behavioral shifts may simultaneously expose organisms to distinct selective pressures along different niche axes, in turn impelling evolution. Multiple potentially contrasting selective pressures can be operating simultaneously, leading to patterns of both stasis and divergence, and behavior may be the bridge that links these outcomes.

Acknowledgments

We thank K. Boronow, E. Cook, M. Landestoy, and I. Shields for field assistance and the Ministerio de Medio Ambiente y Recursos Naturales (Dominican Republic) for permits. We thank J. L. Bronstein, M. Kearney, and two reviewers for their thoughtful feedback, which greatly improved the manuscript. A. Algar and Y. Stuart provided feedback and support with methods on the manuscript. Funding was provided by the National Science Foundation (DEB award 0918975 and a Doctoral Dissertation Improvement Grant) and a Sigma Xi Grant-In-Aid.

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