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# Microhabitat use, diet, and performance data on the Hispaniolan twig anole, *Anolis sheplani*: Pushing the boundaries of morphospace

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## Abstract

Caribbean *Anolis* lizards are often cited as a textbook example of adaptive radiation. Similar morphologies (ecomorphs) have originated in similar ecological settings on different large islands in the West Indies. However, relatively little is known about one of the morphologically most specialized and divergent ecomorphs: the twig anoles. Here, we investigate aspects of morphology, dewlap size, locomotor and bite performance, structural habitat and diet of the poorly known twig anole, *Anolis sheplani* from Hispaniola. Few observations have previously been made of this species in its natural habitat, and few quantitative data on its natural history are available. *A. sheplani* is an extreme twig anole with respect to its morphology, performance capacities, and ecological niche. Males and females of this species do not differ from each other in body dimensions, performance or habitat use, but males do have a bigger dewlap than females. We present data for 25 individuals and compare them with data for other Greater Antillean anoles. It becomes apparent that twig anoles constitute a large component of the morphological, functional, and ecological diversity of *Anolis* lizards. Small twig anoles such as *A. sheplani* appear to be pushing the boundaries of morphospace and are thus crucial in our understanding of the evolution of phenotypic diversity.

***Keywords:*** Adaptive radiation; Ecomorph; Dewlap; Hispaniola; West Indies

## Introduction

*Anolis* lizards of the Caribbean are often cited as a textbook example of adaptive radiation (Schluter, 2000). On the different islands of the Greater Antilles, morphologically similar forms (termed ecomorphs) have originated independently in ecologically similar settings (Losos, 1992, 1994). Thus, an ecomorph is a group of species utilizing the same structural habitat, which are similar in morphology and behavior, but not necessarily closely related (Williams, 1972; Losos, 1994). These independent, convergent radiations make *Anolis* lizards a model group for evolutionary studies. Ecomorph classes differ in several aspects, including morphological (e.g., hind limb length, tail length, and lamellae number), behavioral (e.g., percentage of walks, jumps, and display), and ecological characteristics (e.g., perch diameter and perch height). For several of these features, the twig ecomorph is clearly an outlier (Losos, 1990a, b; Losos et al., 1994; Irschick and Losos, 1996, 1998; Beuttell and Losos, 1999), strikingly different

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from all other ecomorphs and often driving many of the evolutionary patterns observed (Vanhooydonck and Irschick, 2002). Surprisingly, relatively few studies have been dedicated to twig anoles, although they form an essential and crucial component of studies on anole communities and may give insights into the evolutionary limits of morphological differentiation. Strikingly, most of the available studies of twig anoles are based on small numbers of individuals, as most twig anoles are notoriously difficult to observe (Cast et al., 2000). For the twig anole species of Hispaniola, few or no quantitative data are available (Lenart et al., 1997; Cast et al., 2000; Schneider et al., 2000; Sifers et al., 2001).

Here, we present some basic data on the natural history of *Anolis sheplani*, the Baoruco twig anole. This species was, to our knowledge, never included in studies dedicated to anole communities in the Sierra de Baoruco, Dominican Republic (Lenart et al., 1997; Cast et al., 2000; Schneider et al., 2000; Sifers et al., 2001). *A. sheplani* is restricted to this mountainous area, occurring between roughly 820 and 1000 m (Schwartz and Henderson, 1991) and lives on bare vines and twigs like other twig anoles. We provide morphological, ecological, and performance data for *A. sheplani*, and report diet composition and habitat characteristics. We further test the hypothesis that twig anoles are not sexually dimorphic in size (Butler et al., 2000; Butler and Losos, 2002) and compare our data for *A. sheplani* to previously published data for other Greater Antillean anoles.

## Materials and methods

### Study area

Fieldwork was conducted during April 2005 at a site (elevation 922 m) near the town of Polo in the Sierra de Baoruco, Provincia de Barahona, República Dominicana. This mountainous area is characterized by mesic deciduous forest. The study site consists of a dirt road bordered by vegetation. The road is not accessible to vehicles and the area has remained relatively undisturbed. The vegetation consists of a mixture of coffee plants interspersed with native plants and trees growing up to 30 m, providing shade for the coffee plants.

### Study species

At the study site, we encountered seven different species of anoles which were assigned to six different ecomorphs: *Anolis cybotes* (trunk-ground), *Anolis distichus* (trunk), *Anolis coelestinus* and *Anolis singularis* (trunk-crown), *Anolis bahorucoensis* (bush), *Anolis barahonae* (crown giant), and *A. sheplani* (twig). *A. sheplani* is a small anole that sleeps on bare twigs and branches, 1–5 m above ground (Schwartz and Henderson, 1991). Individuals were caught by hand or noose, and kept individually in plastic bags. Flagging tape was used to indicate the perches, where the animals were caught so that they could be released at the exact site of capture within 48 h.

### Morphometrics

The following body, head, and limb dimensions were quantified to the nearest 0.01 mm for each individual using digital calipers (Mitutuyo): snout-vent length (SVL), tail length, head length, head height, head width, fore limb length, and hind limb length. Animals were weighed to the nearest 0.5 g using a Pesola spring balance. The number of subdigital lamellae under the fourth phalanx of the hind foot was counted in four individuals.

### Dewlap size

To quantify dewlap size, lizards were photographed in lateral view using a digital camera (Nikon D70), while pulling the base of the ceratobranchial forward with a pair of forceps, so that the dewlap became fully extended (as in Vanhooydonck et al., 2005). Photos were taken on a background grid for scaling (grid size: 0.63 cm × 0.63 cm). The outlines of the dewlaps were digitized on the digital photographs using tpsDig (Rohlf, 2003), allowing us to calculate the dewlap surface area ($cm^2$) for each individual.

### Diet

Immediately after capture, lizards' stomachs were flushed, and stomach contents were stored in a 70% aqueous ethanol solution. In the laboratory, all prey items were identified to order, subdivided into size classes (0–50 mm in classes of 5 mm), and weighed using a Mettler electronic microbalance. To allow comparison with dietary habits of other anoles in the Sierra de Baoruco (Lenart et al., 1997; Cast et al., 2000; Sifers et al., 2001), we calculated the importance value for each prey type (calculated as in Powell et al., 1990).

### Sprint speed

Sprint speeds were calculated by measuring the time needed to run 25 cm on a dowel (diameter 1.5 cm) placed at an angle of 45°. Different pairs of photocells, set at 25 cm intervals and connected to a portable computer, recorded the times at which the lizard passed the cells. Lizards were encouraged to run by tapping the base of the tail. Three trials were conducted for each individual at hourly intervals, and the highest speed recorded over a 25 cm interval was taken as that individual's maximum sprint speed ability. All performance measurements were conducted at a temperature between 28 and 30 °C, which matches the temperature of the field site (Sifers et al., 2001). This is also at or near the optimal performance temperature for several *Anolis* species (Huey and Webster, 1976; van Berkum, 1986).

## Bite force

Individual bite force capacity was measured using an isometric Kistler force transducer mounted on a purpose-built holder and connected to a charge amplifier (for details of setup see Herrel et al., 1999). Lizards were induced to bite five times, and the highest bite force generated was used as an estimator of maximal bite performance.

## Microhabitat use

For every lizard caught, habitat characteristics were measured to quantify the individual's use of the available habitat. Perch height, perch diameter, distance to nearest perch, and the diameter of the nearest perch were measured for 20 individuals.

## Comparison with other anoles

Data for 43 Greater Antillean anole species were gathered from the literature (Losos, 1990b; Irschick et al., 1997; Beuttell and Losos, 1999) and from our own unpublished data, representing six ecomorph types (crown-giant, trunk-crown, trunk, trunk-ground, grass-bush, and twig). A list of species is shown in the appendix. We examined morphological characteristics (mass, fore limb length, and hind limb length, all relative to SVL) that are traditionally used as a discriminator among ecomorph types (Williams, 1983; Losos, 1990a, b). Because ecomorph types typically differ in their use of arboreal microhabitats (Rand and Williams, 1969; Williams, 1972), we also compared perch height and perch diameter among species.

## Statistical analyses

All data were $\log_{10}$ transformed before analysis to fulfill the assumption of normality. Relations between variables were investigated using Pearson's correlation coefficients and regression analyses. For multiple regressions, the backward stepwise method was used to eliminate variables from the model, and unstandardized coefficients (*B*) are reported. General linear models (uni- or multivariate) were used to investigate

**Table 1.** Means and standard error (±1 SE) of the means for morphological, performance, and habitat characteristics of *A. sheplani*

| Characteristic | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *N* | Mean | SE | *N* | Mean | SE |
| Morphology | | | | | | |
| SVL (mm) | 9 | 38.61 | 0.76 | 16 | 37.40 | 1.13 |
| Mass (g) | 9 | 0.61 | 0.05 | 15 | 0.64 | 0.07 |
| Head length (mm) | 9 | 11.26 | 0.22 | 16 | 10.63 | 0.29 |
| Head height (mm) | 9 | 4.46 | 0.14 | 16 | 4.27 | 0.12 |
| Head width (mm) | 9 | 4.57 | 0.11 | 16 | 4.39 | 0.11 |
| Forelimb length (mm) | 9 | 10.38 | 0.35 | 16 | 10.09 | 0.29 |
| Hind limb length (mm) | 9 | 15.98 | 0.28 | 16 | 15.5 | 0.39 |
| Lamellae number | 4[a] | 15.50 | 0.58 | 4[a] | 15.50 | 0.58 |
| Tail length (mm) | 9 | 38.09 | 0.91 | 16 | 37.87 | 1.08 |
| Dewlap size ($cm^2$) | 9 | 0.54 | 0.02 | 14 | 0.24 | 0.02 |
| Performance | | | | | | |
| Sprint speed (cm/s) | 8 | 3.54 | 0.6 | 12 | 3.97 | 0.84 |
| Bite force (N) | 9 | 1.02 | 0.09 | 15 | 0.96 | 0.12 |
| Habitat | | | | | | |
| Perch height (m) | 7 | 2.24 | 0.28 | 13 | 2.08 | 0.17 |
| Perch diameter (cm) | 7 | 4.07 | 1.03 | 13 | 3.85 | 0.74 |
| Distance to nearest perch (cm) | 7 | 5.86 | 0.70 | 13 | 5.02 | 1.39 |
| Diameter nearest perch (cm) | 7 | 2.00 | 0.65 | 13 | 2.69 | 0.86 |

Results for males and females are reported separately. The number of individuals (*N*) used is indicated for all variables.

[a] Mean for males and females together, based on four individuals.

differences between sexes, including SVL as a covariate where necessary to control for differences in body size. For the comparison with other anoles, the number of variables was reduced using a Principal Component Analysis (PCA), with Varimax rotation.

## Results

### General

In 12 days of surveying the study area, 25 adult *A. sheplani* individuals were encountered and captured. All were collected between 10 and 15 h by patiently watching a tree and examining all twigs from trunk to edge. Table 1 provides absolute mean and standard error (SE) values of morphological, performance, and habitat characteristics for male and female *A. sheplani* separately. *A. sheplani* is a small anole with a mean SVL of 38.61 mm for males and 37.40 mm for females, and tails of comparable length (38.09 mm for males, 37.87 mm for females). Males have larger dewlaps than females (0.54 vs. 0.24 cm$^2$, respectively). Males were encountered on slightly wider (4.07 vs. 3.85 cm) and higher (2.24 vs. 2.08 m) perches than females, but these differences are not significant.

### Diet

One individual did not have any food in its stomach, so only 24 stomach contents were analyzed. Beetles (Coleoptera) were the most important food items found in these 24 stomachs. The importance value for Coleoptera was 146.55, very high compared with the values for other food items found (all importance values less than 47.99). Coleoptera were also found in the stomachs of other *Anolis* species occurring in this area (*A. bahorucoensis* and *A. coelestinus*) (Cast et al., 2000, own observations), but never as the dominant food item.

### Performance

Sprint speeds are very low for *A. sheplani* (males: mean = 3.54 ± 0.60 cm/s, for females: mean = 3.97 ± 0.84 cm/s). The animals appeared to be walking rather than running even at the highest speeds recorded. Notably, not all individuals managed to run over the entire 25 cm interval without stopping and some individuals could not be motivated to run at all, so mean sprint speeds are only based on 8 and 12 individuals for males and females, respectively. No relationship between sprint speed and body size was found in *A. sheplani* ($r = 0.22$, $F_{1,18} = 0.91$, $P = 0.35$).

In sharp contrast to their reluctance to run, all individuals were eager to bite when captured. Bite force capacity is strongly correlated to body size ($r = 0.74$, $F_{1,22} = 26.79$, $P < 0.001$), with bigger lizards biting harder. Bite forces are also tightly linked to head length ($R = 0.88$, $P < 0.001$), head height ($R = 0.64$, $P = 0.001$), and head width ($R = 0.72$, $P < 0.001$). A multiple regression analysis with head dimensions and SVL as independents retained a model with head length as the only variable. Thus, head length appears to be the most important morphological determinant of bite force in this species ($r = 0.80$, $B = 4.79$, $F_{1,22} = 38.28$, $P < 0.001$).

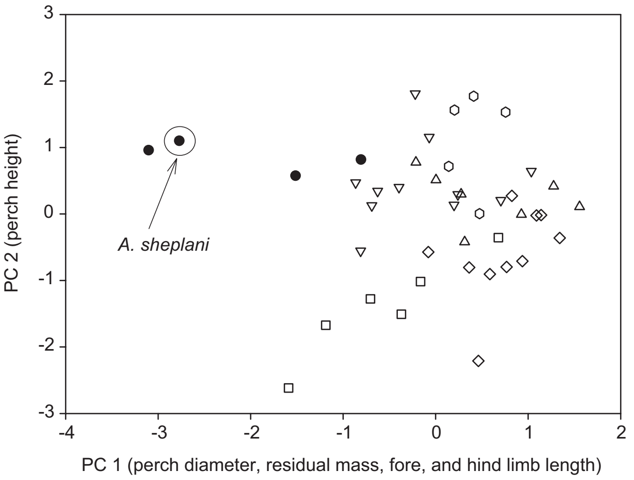

**Fig. 1.** Plot of the two principal components that resulted from a PCA on morphological (residual mass, fore and hind limb length) and ecological (perch height and diameter) data of 43 anole species of six ecomorph types. PC 1 (*x*-axis) is related to residual mass, limb lengths and perch diameter, and PC 2 (*y*-axis) is mainly determined by perch height. Each data point represents a different species, each symbol an ecomorph type: twig (circle), grass-bush (square), trunk-ground (diamond), trunk-crown (triangle down), trunk (triangle up), and crown-giant (hexagon).

### Sexual dimorphism

Male *A. sheplani* do not differ from females in SVL (ANOVA, $F_{1,24} = 0.72$, $P = 0.41$), nor in any of the other body dimensions (ANCOVA, covariate = SVL, all $F < 2.32$, all $P > 0.14$, no interaction effect SVL × sex). The only morphological characteristic that differs between sexes is dewlap size (ANCOVA, covariate = SVL, $F_{1,22} = 82.21$, $P < 0.001$, no interaction effect SVL × sex): males have a larger dewlap than females. Although the dimorphism in dewlap size is suggestive of a role in male–male or male–female signaling, relative dewlap size was not correlated with bite force ($r = 0.51$, $F_{1,7} = 2.46$, $P = 0.16$), nor with sprint speed ($r = 0.62$, $F_{1,6} = 3.80$, $P = 0.10$) in male lizards. Additionally, sexes also did not differ in relative bite force (ANCOVA, covariate = SVL, $F_{1,23} = 0.18$, $P = 0.67$, no interaction effect SVL × sex) or in maximal sprinting performance (ANOVA, $F_{1,19} \cong 0$, $P \cong 1$).

### Comparison with other anole species

Fig. 1 shows the relationship between the two principal components (PC) yielded by the PCA on morphological (residual mass, residual fore limb length, and residual hind limb length) and ecological (perch height and perch diameter) characteristics. PCs 1 and 2 explained 49.44 % and 25.67 % of the observed variation with eigenvalues of 2.47 and 1.28, respectively.

Different species of an ecomorph tend to cluster, especially in the grass-bush, crown-giant, trunk-ground and the twig ecomorphs. *A. sheplani* (indicated by an arrow in Fig. 1) resembles other twig anoles in having very low PC 1 values and relatively high PC 2 values. Like other twig anoles, *A. sheplani* perches high in the trees. Also, it is small with short limbs, like most typical twig anoles. Strikingly, nearly half of the variation on the first PC is generated by twig anoles with *A. sheplani* being one of the most extreme species, together with *A. occultus*.

## Discussion

We conclude that with respect to the morphological, ecological, and performance aspects considered here, *A. sheplani* is a real twig anole. Behaviorally, *A. sheplani* also accords well with the other twig anoles described previously (Losos, 1990b; Irschick and Losos, 1996). When disturbed, it responds by moving slowly to the other side of its perch and holding on tightly. Occasionally, individuals were observed moving slowly along their perches, but they were never observed jumping from one twig or branch to another. Twig anoles in general rarely jump from between branches, in contrast to most other anoles. Interestingly, *A. sheplani* appears to be an extreme twig anole in some of its morphological and ecological characteristics, diverging considerably from some of the better known twig anoles such as *A. angusticeps* and *A. valencienni*. With respect to locomotor performance, *A. sheplani* also appears to be somewhat of an outlier. While twig anoles are generally slower than other *Anolis* species, maximal sprint speeds in *A. sheplani* are very low even compared to other species in this ecomorph. For example, *A. angusticeps*, a Bahamian twig anole, has a mean maximal sprint capacity of 52 cm/s with a mean SVL of 43.18 mm, and *A. occultus* (Puerto Rico) runs at a mean of 25 cm/s (measured over 10 cm intervals) and has a mean SVL of 37.5 mm (own unpublished data, measured using the same experimental setup as described earlier). Moreover, *A. sheplani* has extremely short limbs for its body length, suggesting that its poor sprint capacity might have a clear morphological basis.

**Fig. 2.** Male *A. sheplani* displaying towards another male.

The sexes of *A. sheplani* do not differ in body size and shape, which is in accordance with the low degree of sexual size and shape dimorphism described for other twig anoles (Butler et al., 2000; Butler and Losos, 2002). As in the Jamaican twig anole *A. valencienni*, dewlap size is not correlated to aspects of male performance such as sprint speed or bite force suggesting this may be a general characteristic of twig anoles. Yet, dewlap size does differ between male and female *A. sheplani* suggesting it plays a role in intraspecific signaling. However, it has been suggested that males of twig anoles (*A. valencienni* and *A. angusticeps*) display infrequently relative to other ecomorphs (Losos, 1990b; Irschick and Losos, 1996). Moreover, twig anoles are generally considered to be non-territorial (Hicks and Trivers, 1983; Irschick and Losos, 1996). Unexpectedly, one of the male *A. sheplani* was observed displaying towards another male when returned to its original perch (Fig. 2) and thus, male–male signaling in *A. sheplani* might be more important than expected. Clearly more quantitative data on both the frequency and context of dewlap use in *A. sheplani* and twig anoles in general are needed to better understand the evolution of dewlap size and its role in these animals.

The high level of morphological and ecological divergence between *A. sheplani* and other anole species

**Table A1**

| Species | SVL (mm) | Mass (g) | Fore limb length (mm) | Hind limb length (mm) | Perch height (m) | Perch diameter (cm) | Ecomorph type |
|---|---|---|---|---|---|---|---|
| *Anolis sheplani* | 38.02 | 0.59 | 10.23 | 15.85 | 2.29 | 3.39 | Twig |
| *Anolis occultus* | 38.02 | 0.50 | 10.96 | 15.85 | 3.02 | 1.20 | Twig |
| *Anolis angusticeps* | 47.86 | 1.95 | 15.49 | 25.70 | 2.19 | 2.29 | Twig |
| *Anolis valencienni* | 72.44 | 6.46 | 25.70 | 38.02 | 1.41 | 42.66 | Twig |
| *Anolis frenatus* | 134.90 | 51.29 | 60.26 | 107.15 | 2.57 | 20.89 | Crown-giant |
| *Anolis equestris* | 134.90 | 46.77 | 63.10 | 91.20 | 3.98 | 50.12 | Crown-giant |
| *Anolis barahonae* | 154.88 | 77.62 | 67.61 | 112.20 | 4.07 | 79.43 | Crown-giant |
| *Anolis garmani* | 112.20 | 32.36 | 53.70 | 83.18 | 1.10 | 58.88 | Crown-giant |
| *Anolis cuvieri* | 123.03 | 44.67 | 60.26 | 91.20 | 3.98 | 60.26 | Crown-giant |
| *Anolis brunneus* | 63.10 | 5.13 | 22.91 | 40.74 | 2.34 | 3.31 | Trunk-crown |
| *Anolis fuscoauratus* | 42.66 | 1.20 | 16.60 | 31.62 | 1.00 | 9.55 | Trunk-crown |
| *Anolis carolinensis* | 67.61 | 5.50 | 27.54 | 38.90 | 1.26 | 15.85 | Trunk-crown |
| *Anolis biporcatus* | 91.20 | 19.05 | 30.20 | 57.54 | 1.41 | 7.94 | Trunk-crown |
| *Anolis singularis* | 38.90 | 1.29 | 15.14 | 23.99 | 2.14 | 5.01 | Trunk-crown |
| *Anolis punctatus* | 83.18 | 10.72 | 30.20 | 56.23 | 4.90 | 20.42 | Trunk-crown |
| *Anolis smaragdinus* | 58.88 | 4.57 | 21.88 | 38.90 | 3.02 | 15.14 | Trunk-crown |
| *Anolis coelestinus* | 61.66 | 5.89 | 26.30 | 43.65 | 1.32 | 22.91 | Trunk-crown |
| *Anolis stratulus* | 46.77 | 1.91 | 21.38 | 32.36 | 1.45 | 52.48 | Trunk-crown |
| *Anolis evermanni* | 63.10 | 5.62 | 30.90 | 45.71 | 1.17 | 109.65 | Trunk-crown |
| *Anolis grahami* | 93.33 | 22.91 | 44.67 | 70.79 | 1.74 | 81.28 | Trunk-crown |
| *Anolis sericeus* | 41.69 | 1.29 | 14.13 | 26.92 | 1.51 | 60.26 | Trunk |
| *Anolis lemurinus* | 48.98 | 2.29 | 19.50 | 38.02 | 2.29 | 13.80 | Trunk |
| *Anolis ortonii* | 43.65 | 2.19 | 16.60 | 28.84 | 1.20 | 31.62 | Trunk |
| *Anolis distichus* (Dom. Rep.) | 47.86 | 3.09 | 25.70 | 39.81 | 1.38 | 89.13 | Trunk |
| *Anolis distichus* (Florida) | 51.29 | 2.40 | 25.70 | 38.02 | 0.78 | 107.15 | Trunk |
| *Anolis brevirostris* | 44.67 | 2.29 | 22.91 | 35.48 | 1.35 | 42.66 | Trunk |
| *Anolis chloris* | 45.71 | 2.57 | 24.55 | 45.71 | 3.80 | 8.71 | Trunk |
| *Anolis trachydermis* | 45.71 | 1.82 | 18.62 | 39.81 | 1.10 | 12.02 | Trunk-ground |
| *Anolis capito* | 72.44 | 8.13 | 35.48 | 63.10 | 0.89 | 19.95 | Trunk-ground |
| *Anolis nitens* | 56.23 | 4.27 | 37.15 | 51.29 | 0.50 | 5.75 | Trunk-ground |
| *Anolis humilis* | 33.88 | 1.00 | 14.13 | 26.30 | 0.40 | 109.65 | Trunk-ground |
| *Anolis sagrei* | 58.88 | 5.62 | 26.92 | 42.66 | 0.36 | 223.87 | Trunk-ground |
| *Anolis cristatellus* (Puerto Rico) | 69.18 | 8.13 | 32.36 | 52.48 | 1.17 | 112.20 | Trunk-ground |
| *Anolis cristatellus* (Florida) | 64.57 | 7.24 | 30.90 | 50.12 | 0.91 | 144.54 | Trunk-ground |
| *Anolis lineatopus* | 58.88 | 5.50 | 30.20 | 50.12 | 0.71 | 61.66 | Trunk-ground |
| *Anolis gundlachi* | 64.57 | 7.08 | 33.11 | 52.48 | 1.29 | 56.23 | Trunk-ground |
| *Anolis cybotes* | 58.88 | 6.61 | 29.51 | 51.29 | 1.10 | 33.11 | Trunk-ground |
| *Anolis auratus* | 45.71 | 1.70 | 21.88 | 30.20 | 0.40 | 0.40 | Grass-bush |
| *Anolis olssoni* | 44.67 | 1.55 | 16.98 | 35.48 | 0.63 | 1.38 | Grass-bush |
| *Anolis pulchellus* | 45.71 | 1.51 | 17.78 | 31.62 | 0.28 | 87.10 | Grass-bush |
| *Anolis bahorucoensis* | 39.81 | 1.32 | 15.85 | 32.36 | 0.46 | 9.33 | Grass-bush |
| *Anolis limifrons* | 36.31 | 0.89 | 16.22 | 32.36 | 0.89 | 8.13 | Grass-bush |
| *Anolis krugi* | 46.77 | 2.40 | 20.89 | 35.48 | 0.63 | 158.49 | Grass-bush |

emphasizes the unique adaptive radiation of *Anolis* lizards. Our data for *A. sheplani* as well as for other elusive twig anoles such as *A. occultus* suggest an important role of twig ecomorphs in pushing the boundaries of morphological evolution within the group, driving a considerable part of the total morphological and ecological variation within anoles. Thus, twig anoles appear to be a unique model system for studies trying to understand the evolutionary pathways leading to high morphological diversity within clades.

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## References

Beuttell, K., Losos, J.B., 1999. Ecological morphology of Caribbean anoles. Herpetol. Monogr. 13, 1–28.

Butler, M.A., Losos, J.B., 2002. Multivariate sexual dimorphism, sexual selection, and adaptation in Greater Antillean *Anolis* lizards. Ecol. Monogr. 72, 541–559.

Butler, M.A., Schoener, T.W., Losos, J.B., 2000. The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. Evolution 54, 259–272.

Cast, E.E., Gifford, M.E., Schneider, K.R., Hardwick, A.J., Parmerlee Jr., J.S., Powell, R., 2000. Natural history of an Anoline community in the Sierra de Baoruco, Dominican Republic. Caribb. J. Sci. 36, 258–266.

Herrel, A., Spithoven, L., Van Damme, R., De Vree, F., 1999. Sexual dimorphism of head size in *Gallotia galloti*, testing the niche divergence hypothesis by functional analyses. Funct. Ecol. 13, 289–297.

Hicks, R.A., Trivers, R.L., 1983. The social behavior of *Anolis valencienni*. In: Rhodin, A.G.J., Miyata, K. (Eds.), Advances in Herpetology and Evolutionary Biology: Essays in Honor of E.E. Williams. Museum of Comparative Zoology, Cambridge, MA, USA, pp. 570–595.

Huey, R.B., Webster, T.P., 1976. Thermal biology of *Anolis* lizards in a complex fauna: the *cristatellus* group on Puerto Rico. Ecology 57, 985–994.

Irschick, D.J., Losos, J.B., 1996. Morphology, ecology, and behavior of the twig anole, Anolis angusticeps. In: Powell, R., Henderson, R.W. (Eds.), Contributions to West Indian Herpetology: a Tribute to Albert Schwartz. Contributions to Herpetology, vol. 12. Society for the Study of Amphibians and Reptiles, Ithaca, New York.

Irschick, D.J., Losos, J.B., 1998. A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. Evolution 52, 219–226.

Irschick, D.J., Vitt, L.J., Zani, P.A., Losos, J.B., 1997. A comparison of evolutionary patterns in mainland and Caribbean *Anolis* lizards. Ecology 78, 2191–2203.

Lenart, L., Powell, R., Parmerlee Jr., J.S., Lathrop, A., Smith, D.D., 1997. Anoline diversity in three differentially altered habitats in the Sierra de Baoruco, República Dominicana, Hispaniola. Biotropica 29, 117–123.

Losos, J.B., 1990a. Concordant evolution of locomotor behaviour, display rate and morphology in *Anolis* lizards. Anim. Behav. 39, 879–890.

Losos, J.B., 1990b. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. Ecol. Monogr. 60, 369–388.

Losos, J.B., 1992. The evolution of convergent structure in Caribbean *Anolis* communities. Syst. Biol. 41, 403–420.

Losos, J.B., 1994. Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. Ann. Rev. Ecol. Syst. 25, 467–493.

Losos, J.B., Irschick, D.J., Schoener, T.W., 1994. Adaptation and constraint in the evolution of specialization of Bahamian *Anolis* lizards. Evolution 48, 1786–1798.

Powell, R., Parmerlee Jr., J.S., Rice, M.A., Smith, D.D., 1990. Ecological observations on *Hemidactylus brookii haitianus* Meerwarth (Sauria: Gekkonidae) from Hispaniola. Caribb. J. Sci. 26, 67–70.

Rand, A.S., Williams, E.E., 1969. The anoles of La Palma: aspects of their ecological relationships. Breviora 327, 1–19.

Rohlf, F.J., 2003. tpsDig: digitize landmarks & outlines, version 1.37. Freeware at 〈http://life.bio.sunysb.edu/morph/index.html〉.

Schluter, D., 2000. The Ecology of Adaptive Radiation. Oxford series in Ecology and Evolution. Oxford University Press, New York.

Schneider, K.R., Parmerlee Jr., J.S., Powell, R., 2000. Escape behavior of *Anolis* lizards from the Sierra de Baoruco, Hispaniola. Caribb. J. Sci. 36, 321–323.

Schwartz, A., Henderson, R.W., 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History. University of Florida Press, Gainsville, FL.

Sifers, S.M., Yeska, M.L., Ramos, Y.M., Powell, R., Parmerlee Jr., J.S., 2001. *Anolis* lizards restricted to altered edge habitats in a Hispaniolan cloud forest. Caribb. J. Sci. 37, 55–62.

van Berkum, F.H., 1986. Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. Evolution 403, 594–604.

Vanhooydonck, B., Irschick, D.J., 2002. Is evolution predictable? Evolutionary relationships of divergence in ecology, performance and morphology in old and new world lizard radiations. In: Aerts, P., D'Août, K., Herrel, A., Van Damme, R. (Eds.), Topics in Functional and Ecological Vertebrate Morphology. Shaker Publishing, The Netherlands, pp. 191–204.

Vanhooydonck, B., Herrel, A., Van Damme, R., Irschick, D.J., 2005. Does dewlap size predict male bite performance in male Jamaican *Anolis* lizards? Funct. Ecol. 19, 38–42.

Williams, E.E., 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. Evol. Biol. 6, 47–89.

Williams, E.E., 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. In: Huey, R.B., Pianka, E.R., Schoener, T.W. (Eds.), Lizard Ecology: Studies on a Model Organism. Harvard University Press, Cambridge, Massachusetts, pp. 326–370.