

# ASYNCHRONOUS EVOLUTION OF PHYSIOLOGY AND MORPHOLOGY IN *ANOLIS* LIZARDS

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Species-rich adaptive radiations typically diversify along several distinct ecological axes, each characterized by morphological, physiological, and behavioral adaptations. We test here whether different types of adaptive traits share similar patterns of evolution within a radiation by investigating patterns of evolution of morphological traits associated with microhabitat specialization and of physiological traits associated with thermal biology in *Anolis* lizards. Previous studies of anoles suggest that close relatives share the same “structural niche” (i.e., use the same types of perches) and are similar in body size and shape, but live in different “climatic niches” (i.e., use habitats with different insolation and temperature profiles). Because morphology is closely tied to structural niche and field active body temperatures are tied to climatic niches in *Anolis*, we expected phylogenetic analyses to show that morphology is more evolutionarily conservative than thermal physiology. In support of this hypothesis, we find (1) that thermal biology exhibits more divergence among recently diverged *Anolis* taxa than does morphology; and (2) diversification of thermal biology among all species often follows diversification in morphology. These conclusions are remarkably consistent with predictions made by anole biologists in the 1960s and 1970s.

**KEY WORDS:** Morphology, phylogenetic signal, thermal physiology.

Species-rich adaptive radiations typically diversify along several distinct ecological axes, each characterized by morphological, physiological, and behavioral adaptations (Simpson 1953; Pianka 1986; Schluter 2000; Strelman and Danley 2003; Ackerly et al. 2006). Whether these different traits diversify in similar ways is largely unstudied (Blomberg et al. 2003). Traits could diversify independently if each is subject to different selection pressures (Arnold 1987; Travis et al. 1999), if they have different genetic constraints (Falconer and Mackay 1996), or if the process of radiation tends to fill available ecological opportunities in a predictable

sequence (Williams 1972; Strelman and Danley 2003; Ackerly et al. 2006). We focus here on two general classes of traits—morphological and physiological—that exhibit extensive variation among species and that often evolve readily when subjected to strong selection (Bradley et al. 1999; Huey et al. 2000; Grant and Grant 2002; Bradshaw et al. 2004; Kingsolver and Nagle 2007; Angilletta 2009). *Anolis* lizards provide an excellent opportunity for a comparison of patterns of evolution of morphological versus physiological traits. Anoles form species-rich adaptive radiations that have diversified along numerous ecological niche axes that



reflect morphological and physiological adaptation (reviewed in Losos 2009). Early work on anoles from the four large islands of the Greater Antilles—where the anoles are the dominant component of lizard faunas and where anoles have been most-intensely studied for the past half century—suggested that thermal physiology (a key physiological variable for ectothermic vertebrates) varies more among closely related species than does morphology. For example, Ruibal (1961) noted that closely related species of Cuban anoles often differ dramatically in thermal physiology, but not in morphology. Rand (1964) drew similar conclusions from his field studies of anoles on Puerto Rico. Subsequently, Williams (1972) made a pioneering attempt to reconstruct the evolutionary history of the radiation of anoles in Puerto Rico; he hypothesized that anole adaptive radiations are characterized by a predictable sequence of ecological specializations. Williams specifically suggested that sympatric species first diverged in body size (via ecological character displacement) and subsequently into different “structural habitats” (i.e., perch height and diameter). This behavioral shift in structural habitat promoted coevolutionary changes in morphology (limb dimensions, head shape, and other traits), driven by the close functional relationship between morphology and locomotor ability on different perch types (Losos 2009). Williams hypothesized that, after filling the available structural habitats, anoles would secondarily diversify with respect to microclimate: ancestral structural habitat specialists (e.g., those adapted to using tree trunks near the ground) would diverge into multiple species occupying the same structural habitat, but living in thermally distinctive habitats (e.g., hot open habitats vs. cool shaded habitats); this divergence in turn would select for subsequent adaptive diversification of thermoregulatory behavior and of thermal physiology.

Regardless of the specific ecological and evolutionary mechanisms underlying this sequence, Williams’ hypothesis makes two implicit predictions that may be tested via phylogenetic comparative analyses. First, phylogenetic signal for body size and morphological traits associated with structural microhabitat specialization should be stronger than that for thermal physiology, the reason being that traits that evolve early in a phylogeny should be similar among members of the same clade, whereas those that evolve late in phylogeny will exhibit differences among more closely related species. Second, in a similar vein, the rate of evolutionary change in body size and in morphological traits associated with structural microhabitat specialization should have slowed through time, with greater change occurring early in phylogeny, whereas the rate for physiology should have increased through time and thus show the opposite pattern.

Here, we test these predictions using body length and measures of body shape that are strongly correlated with structural microhabitat specialization (reviewed in Losos 2009) as measures of morphology, and field active body temperature ( $T_b$ ) as an

indicator of physiology (see below for justification). Our analysis benefits from several advances that emerged in the decades following the pioneering studies by Collette (1961), Ruibal (1961), Rand (1964), and Williams (1972). Relevant data are now available for many species, beyond Cuba and Puerto Rico; phylogenetic information is now vastly more comprehensive and robust; and phylogenetically based comparative algorithms are now well developed.

## Materials and Methods

### MORPHOLOGY

We examined patterns of evolution in body size (snout–vent length) and shape (principal component axes generated from a suite of morphometric data) using a previously published dataset (Mahler et al. 2010). This dataset includes measurements of 20 morphological traits from adult males of 100 Greater Antillean species, with most traits characterizing head and limb dimensions that are demonstrably important to microhabitat specialization in anoles (Losos 2009).

### FIELD ACTIVE BODY TEMPERATURE

Thermal data were obtained from published and unpublished studies using species as the unit of comparative analysis. Our analyses include thermal data from many of the same Greater Antillean species for which morphological data are available as well as for a number of species from smaller Caribbean islands and the mainland. We compiled data on several traits (e.g., field active body temperatures [ $T_b$ ], critical temperatures, and temperatures selected in laboratory thermal gradients); however, we restrict our discussion here to field active  $T_b$ , because data for other traits were too sparse. Several factors suggest that  $T_b$  is a convenient and reliable indicator of a lizard’s underlying physiological sensitivity to temperature. Body temperature correlates strongly with habitat selection (high in open-habitat species, low in forest species; Ruibal 1961; Rand 1964; Clark and Kroll 1974; Huey 1974; Hertz 1981, 1992a,b; Huey et al. 2009). More importantly, field active  $T_b$  of anoles is also correlated with selected temperatures in laboratory thermal gradients ( $N = 9$ : nonphylogenetic  $r = 0.71$ ,  $P = 0.031$ ; phylogenetic  $r = 0.82$ ,  $P = 0.007$ ; P. E. Hertz et al., unpubl. data); with  $CT_{max}$  ( $N = 18$ : nonphylogenetic  $r = 0.51$ ,  $P = 0.030$ ; P. E. Hertz et al., unpubl. data); and with optimal sprint temperatures (van Berkum 1986). Finally, similar patterns hold in other lizard clades as well (Huey 1982; Huey and Kingsolver 1993; Huey et al. 2012).

Field active  $T_b$  data were collected by many investigators and are necessarily heterogeneous. To reduce noise, we used only data that met the following a priori criteria. The minimum acceptable sample size was 10 active individuals from a single population,

and data must have been collected across most hours that lizards were active. For many species, sufficient samples were available for different populations, collected in different seasons and by different investigators. Rather than treat each sample as independent, which would constitute pseudo-replication, we computed a single mean for each species via the following protocol. When possible, we included data only from the most comprehensive study. If multiple studies of the same species were equally comprehensive, we used an unweighted average of reported means (e.g., Ballinger et al. 1970; Campbell 1971 on *Anolis frenatus*). However, if populations were sampled at multiple altitudes (e.g., Hertz 1981 on *Anolis gundlachi*), we included only data from the lowest altitude. If multiple samples were collected from different habitats within a population (e.g., Huey 1974 on *Anolis cristatellus*), we used the unweighted average across samples and habitats. Time of year can also influence  $T_b$  values. Consequently, we determined whether data were collected in summer, winter, or year round. If data were available for only one season, we used that mean as the species value. If data were available for multiple seasons (e.g., Hertz 1992a on *Anolis cooki*), including “year-round” as a “season,” we computed the unweighted average across seasons. Data for 74 species met these criteria (Appendix A), but we analyzed data from only 62 because the phylogenetic positions of 12 species were unknown.

### PHYLOGENETIC ANALYSES

Our comparative analyses were conducted on trees that Mahler et al. (2010) reconstructed from an mtDNA sequence dataset comprising 187 anoles and two outgroup taxa. Mahler et al. (2010) generated ultrametric trees using the relaxed clock methods implemented in the program BEAST (Drummond and Rambaut 2007). Because we were concerned with relative, rather than absolute, node ages, we followed Mahler et al. (2010) in using trees with an arbitrary root age. We accounted for phylogenetic uncertainty by conducting all of our analyses on 901 trees drawn from this posterior distribution of Mahler et al.’s (2010) BEAST analyses.

### PHYLOGENETIC REGRESSION AND PRINCIPAL COMPONENTS ANALYSIS

Before conducting analyses of morphological trait evolution, we used phylogenetic regression and phylogenetic principal components analyses to obtain size-corrected multivariate shape parameters (Revell 2009). We generated 19 phylogenetically size-corrected measurements using the `phyl.resid` function in the R package PHYTOOLS (Revell 2009) and then included these measurements in a phylogenetic principal components analysis using PHYTOOLS’s `phyl.pca` function. We focus our attention below on the first three principal components produced by this analysis, which, based on loadings, we interpret primarily as measures of limb dimensions (PC1), toepad width (PC2), and an inverse con-

trast between number of toepad lamellae and head shape (PC3; Appendix B).

### PHYLOGENETIC SIGNAL AND THE TEMPO OF CHARACTER EVOLUTION

We used comparative phylogenetic analyses to examine Williams’ two predictions about patterns of trait evolution (body size,  $N = 100$ ; three shape dimensions,  $N = 100$ ; and field  $T_b$ ,  $N = 62$ ). We focused our attention on analyses of the most complete dataset available for each trait, but also conducted similar analyses on a reduced dataset (31 species) for which all three datasets are available (Appendix C). This reduced dataset comprises only Greater Antillean species because these are the only species included in our morphometric dataset.

#### Williams’ prediction 1: phylogenetic signal

Phylogenetic signal is a measure of how well interspecific variation in a trait is correlated with phylogenetic relationships (Revell et al. 2008). If body size and morphological traits diverged relatively early in the anole radiation but remained relatively unchanged during subsequent species diversification into distinct thermal habitats, then phylogenetic signal should be stronger for morphological traits than for traits associated with thermal physiology. This prediction results because multiple clades diverging over the same range of thermal physiologies (e.g., into both cool- and warm-adapted species in each clade) will produce convergent evolution across clades, leading to low phylogenetic signal. We used three approaches to test the hypothesis that phylogenetic signal differs between morphological and physiological traits.

First, we used Pagel’s (1999)  $\lambda$  statistic to evaluate phylogenetic signal. By multiplying the off-diagonal elements of the variance/covariance matrix describing a phylogenetic tree by values of  $\lambda$  ranging from 1 to 0, underlying phylogenetic structure is gradually eliminated. When  $\lambda$  is optimized via maximum likelihood, we expect to recover values at or near 1 when phylogenetic signal is strong, and values at or near 0 when phylogenetic signal is weak. We tested the extreme hypothesis that phylogenetic signal is lacking entirely by fixing  $\lambda$  at 0 and comparing the resulting likelihood score to the scores obtained from the original trees ( $\lambda = 1$ ).

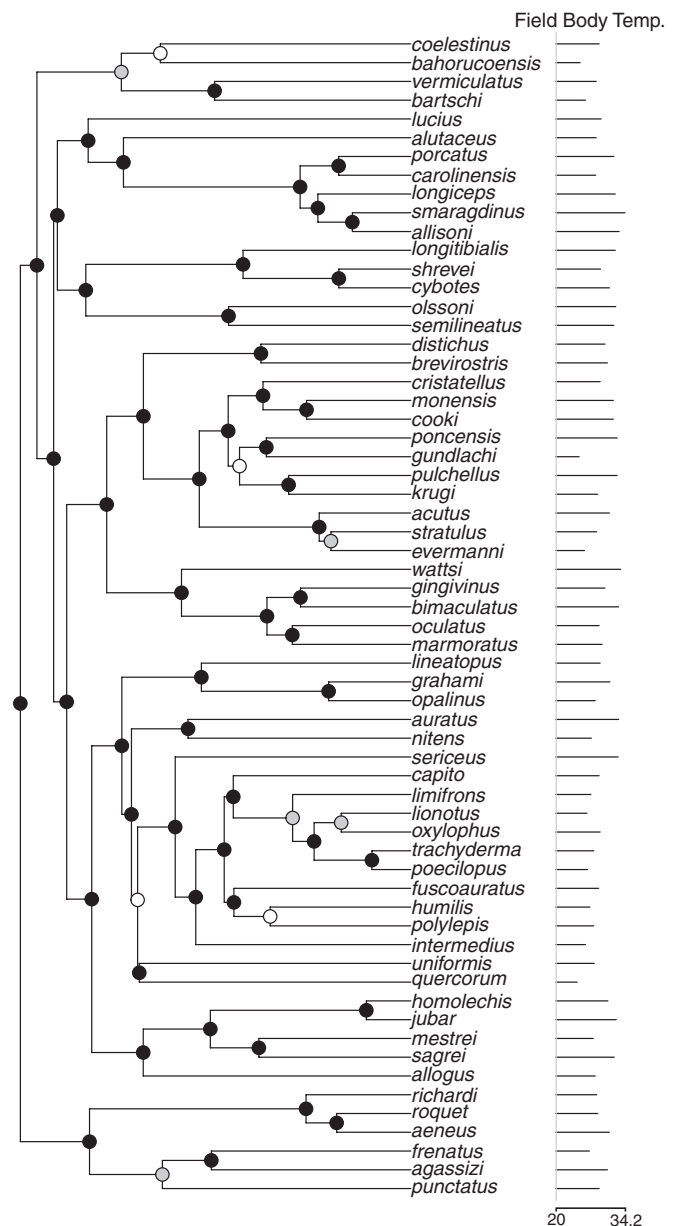
Second, we used Blomberg et al.’s (2003)  $K$  parameter, an alternative index of phylogenetic signal that may be more directly compared across characters and trees.  $K$  represents the ratio of observed mean squared error (MSE) over expected MSE, with values of  $K < 1$  indicating that related taxa resemble one another less than expected by a model of Brownian motion (BM; i.e., show a weak phylogenetic signal) and values  $> 1$  indicating that taxa are more similar than expected (i.e., show a strong phylogenetic signal). Blomberg et al. (2003) proposed two tests that evaluate the significance of  $K$ . We implemented one of these tests, which asks

whether the variance of independent contrasts calculated from the empirical data is lower than the variance of independent contrasts estimated after randomly reshuffling tip values. Estimation of  $K$  and tests for significant phylogenetic signal based on variance of independent contrasts are conducted in the R package PICANTE (Kembel et al. 2009).

Finally, we compared the fit of three alternative models of character evolution—BM, Ornstein–Uhlenbeck (OU), and white noise (WN)—using Akaike information criterion (AIC) values generated by the fitContinuous function in the GEIGER package for R (Harmon et al. 2008). The BM model uses a single rate parameter ( $k$ ) to characterize a phylogenetic random walk. The OU model, meanwhile, adds an additional parameter to characterize both the rate of the random walk ( $\beta$ ) and its central tendency ( $\alpha$ ; Hansen 1997; Butler and King 2004). Finally, the WN model eliminates phylogenetic signal by assuming that all trait values are drawn from a shared normal distribution. We expect traits with strong phylogenetic signal to exhibit considerably better (i.e., lower) AIC scores for the BM and OU models than for the WN model. Following Burnham and Anderson (2002), we compare AIC scores by computing the difference in scores between the optimal model and each alternative model ( $\Delta$ AIC values), with  $\Delta$ AIC values less than 2 suggesting substantial support for the alternative model, values of 3 to 7 indicating that the alternative is considerably less well supported and values exceeding 10 indicating that the alternative is very unlikely. We also calculate AIC weights ( $\omega$ ), which indicate the relative likelihoods of alternative models.

#### Williams' prediction 2: tempo of trait evolution over time

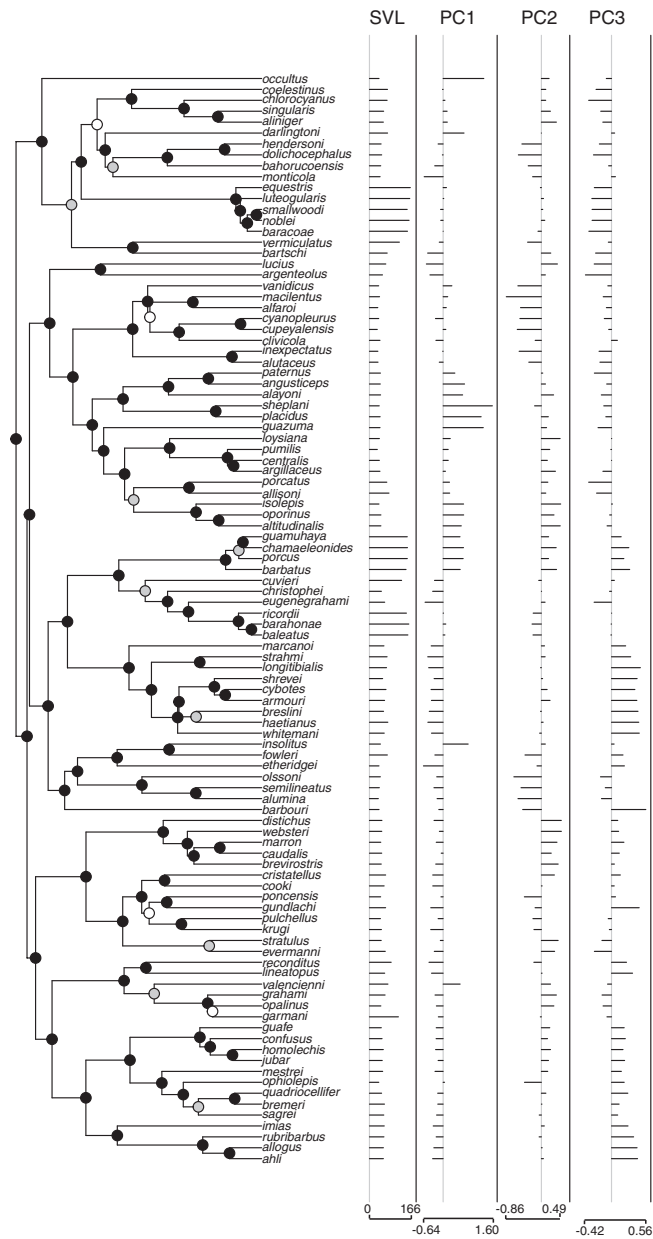
We used two methods to test Williams' prediction that morphological character evolution slowed over time while divergence of traits associated with thermal physiology sped up. First, we fit the evolutionary burst (EB) model implemented by fitContinuous, which includes a parameter characterizing exponential decline in a trait's rate of evolution over time; negative values for the decay parameter indicate a slow-down, whereas positive values indicate a speed-up (Blomberg et al. 2003; Freckleton and Harvey 2006; Harmon et al. 2010). Second, we used maximum likelihood to estimate Pagel's parameter  $\delta$  (Pagel 1999), again using the fitContinuous function of GEIGER.  $\delta$  transforms branch lengths exponentially to test whether the rate of character change shifted across the tree from root to tip.  $\delta < 1.0$  indicates that changes were concentrated early (more basally) in the tree, whereas  $\delta > 1.0$  indicates that change was concentrated late (nearer the tips). Because simultaneous estimation of multiple parameters via maximum likelihood is problematic, each of the Pagel parameters ( $\lambda$  and  $\delta$ ) was estimated independently after fixing the other at 1.



**Figure 1.** MtDNA phylogeny of taxa for which thermal data are available with branch lengths from molecular phylogenetic analyses conducted in MrBayes. Posterior probability (pp) values from Bayesian analyses conducted in MrBayes are indicated on each node with black circles indicating high support ( $pp > 0.95$ ), gray circles indicating moderate support ( $0.75 < pp < 0.95$ ), and white circles indicating low support ( $pp < 0.75$ ). Scale bars on the right indicate field body temperature (in  $^{\circ}\text{C}$ ).

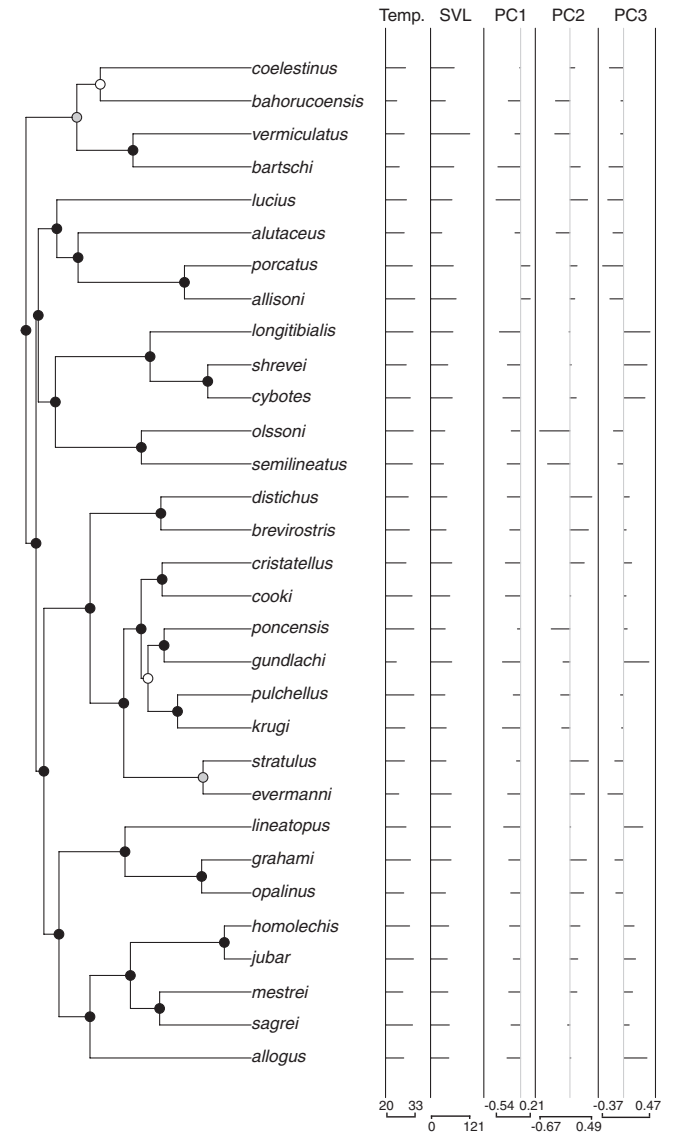
## Results and Discussion

All morphological and physiological traits we examined show conspicuous interspecific variation in *Anolis* (Appendices 1 and 2; Figs. 1–3). The body size (adult male SVL) of the largest species in our dataset (*Anolis equestris*, 166 mm) was more than five times greater than that of the smallest species (*Anolis cupeyalensis*,



**Figure 2.** MtDNA phylogeny of taxa for which morphometric data are available. Posterior probability (pp) values from Bayesian analyses conducted in MrBayes are indicated on each node with black circles indicating high support ( $pp > 0.95$ ), gray circles indicating moderate support ( $0.75 < pp < 0.95$ ), and white circles indicating low support ( $pp < 0.75$ ). Scale bars at the bottom of each trait are in millimeters for SVL and in PC units for each PC axis.

32 mm). Body shape varied substantially as well. For example, the femur of the longest-limbed species (*Anolis etheridgei*) is, when adjusted for size, more than twice as long as that of the shortest-limbed species (*Anolis sheplani*). Mean field active  $T_b$ , the trait we used to describe thermal physiology, differed nearly  $10^\circ\text{C}$  between the coolest ( $24.4^\circ\text{C}$  for *Anolis quercorum*) and



**Figure 3.** MtDNA phylogeny of taxa for which both thermal and morphometric data are available. Posterior probability (pp) values from Bayesian analyses conducted in MrBayes are indicated on each node with black circles indicating high support ( $pp > 0.95$ ), gray circles indicating moderate support ( $0.75 < pp < 0.95$ ), and white circles indicating low support ( $pp < 0.75$ ). Scale bars at the bottom of each trait are in  $^\circ\text{C}$  for temperature, millimeters for SVL, and PC units for each PC axis.

warmest ( $34.2^\circ\text{C}$  for *Anolis smaragdinus*) species, a range that is among the largest known within lizard genera (Table S6 in Sinervo et al. 2010).

Our comparative phylogenetic analyses support both predictions about the evolution of morphological and physiological traits derived from Williams' ecological scenario for anole diversification (Tables 1 and 2). Williams' first prediction is that body size and morphological traits associated with structural microhabitat specialization will be shared among groups of related species



**Table 1.** Average parameter values from analyses of character evolution calculated from 901 trees in the posterior distribution of a Bayesian relaxed clock analyses.

	Rate		Phylogenetic signal				Rate variation		
	BM k	OU		Pagel's $\lambda$ $\lambda$	Blomberg et al.'s $K$		Pagel's $\delta$ $\delta$	EB	
		$\beta$	A		$K$	$P$ value		Start	Change
Thermal	0.1029	0.2620	0.023	0.411	0.61	0.0158	4.069	0.0025	0.0474
SVL	0.0014	0.0014	2.01e-06	1	1.56	0.0010	0.761	0.0030	-0.0104
PC1	0.0020	0.0020	2.34e-09	1	1.12	0.0010	0.431	0.0096	-0.0227
PC2	0.0010	0.0010	5.77e-07	1	1.04	0.0010	0.923	0.0015	-0.0056
PC3	0.0004	0.0004	2.34e-09	1	1.53	0.0010	0.375	0.0017	-0.0205

and thus exhibit stronger phylogenetic signal than will thermal physiology, which will differ among closely related species that occupy distinct microclimates or macrohabitats. Analyses of phylogenetic signal support this prediction: morphological traits exhibit stronger phylogenetic signal than does thermal physiology, regardless of phylogenetic uncertainty and the method used to assess that signal (Tables 1 and 2). Maximum likelihood estimates of Pagel's  $\lambda$  for morphological traits are always 1 (Table 1), and AIC scores obtained when the underlying phylogenetic structure is left intact ( $\lambda = 1$ ) are considerably better than those obtained when phylogenetic structure is eliminated ( $\lambda = 0$ ;  $\Delta$ AIC values greater than 20 for each morphological trait). Blomberg et al.'s  $K$  values are above 1 for all morphological traits and also indicated significant phylogenetic signal (Table 1). By contrast, phylogenetic signal is extremely weak, or even absent, for field active  $T_b$  (Tables 1 and 2).

Our model fitting analysis reinforces these conclusions, lending further support to Williams' first prediction; the WN model of character evolution has an extremely poor fit to morphological traits relative to alternative models of character evolution that assume some degree of phylogenetic signal (Table 2). For thermal data, by contrast, the fit of the WN model is only slightly worse than that of the models that assume phylogenetic signal (Table 2). As is typical of traits that exhibit little phylogenetic signal (Blomberg et al. 2003; Ackerly et al. 2006), mean field active  $T_b$  also has a considerably higher rate of evolution (estimated via maximum-likelihood analysis under a simple Brownian model) than do either of the morphological traits that exhibit strong phylogenetic signal (Table 1). We obtain similar conclusions about phylogenetic signal when we conduct our analyses on only those 31 taxa for which data are available for both morphological and thermal traits, although evidence for signal in morphological traits is somewhat weaker in these analyses (Appendix C), possibly as a result of smaller sample size (Blomberg et al. 2003).

The apparent difference in the strength of phylogenetic signal for morphology and thermal physiology is probably not the re-

sult of measurements taken on different scales (see Blomberg and Garland 2002). However, it could be an artifact if field active  $T_b$  values have higher measurement error than do morphological values, as high measurement error tends to reduce phylogenetic signal (Ives et al. 2007). Correcting for measurement error requires estimates of trait variances (Ives et al. 2007), which unfortunately are not available for many of the values we compiled. The limited phylogenetic signal for  $T_b$  could also be a consequence of elevated environmental noise. Field active body temperature can be relatively plastic in some *Anolis* (Ruibal and Philibosian 1970), and can vary with behavior, time of day, season, and site (e.g., Huey 1974; Lister 1976; Hertz 1992a,b). However, both body size and relative limb length also differ among populations in different environments (e.g., Lazell 1972; Losos et al. 1994; Calsbeek et al. 2007); at least in some cases, these differences probably result from phenotypic plasticity rather than genetic differentiation (e.g., Roughgarden and Fuentes 1977). Therefore, it is not clear whether environmental influences affect some of the traits we examined more than others.

Our analyses also support Williams' second prediction concerning the tempo of trait evolution. Recall that Williams' scenario for anole diversification specifically predicts that the tempo of evolutionary change in body size and morphological traits will slow over time and that the rate of physiological diversification will speed up. For field active body temperature, the EB model recovers a positive rate change parameter and estimates of Pagel's  $\delta$  exceed 1; both methods suggest that diversification of this trait is indeed concentrated near the tips of the phylogeny (Table 1). However, both the lack of phylogenetic signal and the rapid rates of evolution for thermal physiology suggest that any inferences about a temporal shift in evolutionary rate over time should be interpreted cautiously (Ackerly et al. 2006); that is, the apparent high rates of thermal physiological evolution in the recent past make it difficult to draw inferences about rates of change in the distant past, when the anole radiation was in its early stages, or to extrapolate to anole faunas that may be at an earlier stage of diversification.

**Table 2.** Results of model-fitting analyses conducted on the largest possible dataset for each individual trait with 901 trees sampled from the posterior distribution of our Bayesian relaxed calibration analysis. The first column for each model indicates mean  $\ln L$  values and their standard deviations calculated from results for all 901 trees. The second column indicates mean AIC values and their standard deviations calculated from results for all 901 trees. The third column for each model indicates the difference in mean AIC values ( $\Delta$ AIC) among models with 0 indicating the optimal model and higher values indicating increasingly poorly support. The third column for each model indicates Akaike weights ( $\omega$ ). Bolded values indicate the preferred model and any models that are not substantially different from this model.

	Brownian motion					Ornstein-Uhlenbeck					Evolutionary burst					White noise						
	$-\ln L$ (SD)	AIC (SD)	$\Delta$ AIC	$\omega$	$\Omega$	$-\ln L$ (SD)	AIC (SD)	$\Delta$ AIC	$\omega$	$\Omega$	$-\ln L$ (SD)	AIC (SD)	$\Delta$ AIC	$\omega$	$-\ln L$ (SD)	AIC (SD)	$\Delta$ AIC	$\omega$	$-\ln L$ (SD)	AIC (SD)	$\Delta$ AIC	$\omega$
Thermal	<b>-143.38</b> (0.72)	290.77 (1.45)	7.01	0.013	0	-138.88 (0.28)	<b>283.76</b> (0.56)	0	<b>0.447</b>	0	-138.88 (0.28)	<b>283.76</b> (0.56)	0.001	<b>0.447</b>	-141.44 (0)	<b>286.89</b> (0)	3.13	<b>0.0934</b>	-141.44 (0)	<b>286.89</b> (0)	3.13	<b>0.0934</b>
SVL	<b>-3.05</b> (1.64)	<b>10.11</b> (3.27)	0	<b>0.458</b>	0	-3.06 (1.64)	<b>12.11</b> (3.27)	2.00	<b>0.168</b>	2.00	-2.26 (2.04)	<b>10.51</b> (4.08)	0.40	<b>0.374</b>	-60.02 (0)	124.03 (0)	113.93	<0.001	-60.02 (0)	124.03 (0)	113.93	<0.001
PC1	-19.61 (1.62)	43.21 (3.24)	4.65	0.086	0	-19.61 (0.90)	45.21 (3.24)	6.65	0.031	6.65	-16.28 (2.55)	<b>38.56</b> (5.10)	0	<b>0.882</b>	-60.01 (0)	124.03 (0)	85.46	<0.001	-60.01 (0)	124.03 (0)	85.46	<0.001
PC2	<b>16.09</b> (0.90)	<b>-28.18</b> (1.80)	0	<b>0.541</b>	0	16.09 (0.90)	<b>-26.18</b> (1.80)	2.00	<b>0.199</b>	2.00	16.35 (0.97)	<b>-26.71</b> (1.93)	1.47	<b>0.259</b>	-20.98 (0)	45.95 (0)	74.13	<0.001	-20.98 (0)	45.95 (0)	74.13	<0.001
PC3	58.66 (1.13)	-113.33 (2.26)	5.25	0.066	0	58.66 (1.13)	-111.33 (2.26)	7.25	0.024	7.25	62.29 (1.43)	<b>-118.58</b> (2.87)	0	<b>0.910</b>	3.13 (0)	-2.28 (0)	116.30	<0.001	3.13 (0)	-2.28 (0)	116.30	<0.001

By contrast, the EB and  $\delta$  models both support Williams' second prediction by suggesting that the rate of trait evolution for all four morphological traits slowed over time (Table 1), although the degree to which models involving a slow-down provided a better fit than those assuming simpler constant rate models varied among traits (Table 1). Given the replicated pattern of adaptive radiation seen in Greater Antillean anoles (sets of ecomorphs with similar morphology but very different thermal biology evolving on multiple islands; Ruibal 1961; Rand 1964; Williams 1972, 1983), differential measurement error and environmental noise are unlikely to be of major concern.

When we analyzed only those 31 species (all from the Greater Antilles) for which both morphological and thermal data are available, we continue to find support for Williams' first hypothesis concerning phylogenetic signal. Although values of Pagel's  $\lambda$  for some morphological traits are less than 1 and Blomberg's  $K$  values are similar among both morphological and thermal traits, the randomization tests for phylogenetic signal associated with Blomberg's  $K$  continue to recover significant signal only for the morphological traits. However, analyses of this dataset provide less support for Williams' second prediction about a decline in the tempo of morphological diversification. Consequently, this reduced dataset is less capable of distinguishing among the fit of alternative models, the evolutionary burst model is no longer favored over other models for PC1 and PC3, values of  $\delta$  are no longer less than one for SVL, PC1, and PC2, and the EB change parameter is positive for SVL and PC1 (Appendix C). We suspect these results are a consequence of the low power associated with analyses of a relatively small dataset rather than reflecting biases stemming from analyses of different sets of taxa.

We also note that Williams formulated his hypothesis on the basis of his studies of Greater Antillean anoles and our results support his predictions for this fauna. Additional thermal and morphological data are required to test whether these hypotheses also hold for species on the mainland and elsewhere. Although studies of ecological diversification among mainland anoles remain in their infancy, detailed studies of anoles on Lesser Antillean islands suggest that anoles on two species islands tend to differ most strikingly in body size, but may also differ importantly in thermal physiology (reviewed in Losos 2009). Moreover, Lesser Antillean anoles on one-species islands often appear to be undergoing local adaptation in response to landscape scale climatic variation (Thorpe et al. 2012).

## Conclusions

Our main conclusions are that (1) thermal biology exhibits more divergence among recently diverged *Anolis* taxa than does morphology; and (2) diversification of thermal biology often follows

diversification in morphology. These conclusions are remarkably consistent with those of Ruibal (1961) and Williams (1972). In their studies of Cuban and Puerto Rican species of *Anolis*, they noted that close relatives shared the same “structural niche” (i.e., used the same types of perches) and were similar in size and shape, but lived in different “climatic niches” (i.e., used habitats with different insolation and temperature profiles) and had different field active  $T_b$ s. Because morphology is closely tied to structural niche in *Anolis* (Losos 2009), their observations suggest that thermal physiology must be more labile evolutionarily than is morphology in these anoles, at least among relatively recently evolved species.

A half century has elapsed since Ruibal (1961) and Rand (1964) published their initial field observations, and four decades have elapsed since Williams (1972) presented his synthesis about the evolution of the anole radiation in Puerto Rico. Our results and conclusions, which are based on new analytical techniques and much larger datasets, closely match those of our predecessors. The concordance of our conclusions says something fundamental not only about *Anolis*, but also about the power of natural history and of careful observation to advance our understanding of ecology and evolutionary biology. Anyone who reads Ruibal (1961), Rand (1964), and Williams (1972) today will realize that those naturalists watched their lizards very carefully. Moreover, because they watched them through conceptually focused eyes, they saw the ecological and evolutionary implications of their observations long before the techniques and issues of contemporary evolutionary biology existed. To be sure, observations alone are sometimes misleading (Dayton 1973). But in the case of *Anolis*, Ruibal, Rand, and Williams really knew their lizards (*sensu* Hutchinson 1975)—and got it right.

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## Appendix A

## SUMMARY OF THERMAL DATA USED IN THE ANALYSES

<i>Anolis</i> species	$T_b$ (°C)
<i>acutus</i>	31.0 (McManus and Nellis 1973; Ruibal and Philibosian 1974)
<i>aeneus</i>	31.0 (Schoener and Gorman 1968; Roughgarden et al. 1981)
<i>agassizi</i>	30.6 (Rand et al. 1975)
<i>allisoni</i>	33.0 (Ruibal 1961)
<i>allogus</i>	28.1 (P. E. Hertz et al., unpubl. data; Ruibal 1961)
<i>alutaceus</i>	28.3 (J. B. Losos et al., unpubl. data)
<i>auratus</i>	32.9 (Ballinger et al. 1970; Vitt and Carvalho 1995)
<i>bahorucoensis</i>	25.0 (Cast et al. 2000; Sifers et al. 2001)
<i>barkeri</i>	24.0 (Birt et al. 2001)
<i>bartschi</i>	26.1 (Estrada and Novo 1987)
<i>bimaculatus</i>	32.9 (Roughgarden et al. 1981)
<i>biscutiger</i>	31.0 (Fitch et al. 1976)
<i>bonairensis</i>	33.4 (Bennett and Gorman 1979)
<i>brevirostris</i>	30.6 (Moster et al. 1992)
<i>capito</i>	28.9 (Vitt and Zani 2005)
<i>carolinensis</i>	28.2 (King 1966; Clark and Kroll 1974; Jenssen et al. 1996)
<i>coelestinus</i>	28.9 (Sifers et al. 2001)
<i>cooki</i>	31.8 (Huey and Webster 1976; Lister 1976; Hertz 1992a)
<i>crisatellus</i>	29.1 (Rand 1964; Huey and Webster 1976; Hertz 1992b; Lister 1976)
<i>cupreus</i>	29.9 (Tsuji et al., unpubl. ms.)
<i>cuprinus</i>	30.7 (Fitch et al. 1976)
<i>cybotes</i>	31.0 (Hertz and Huey 1981; Fobes et al. 1992; Cast et al. 2000)
<i>distichus</i>	30.1 (King 1966; Lister 1976; Lee 1980; Cast et al. 2000; Sifers et al. 2001)
<i>dolfusianus</i>	28.4 (Fitch et al. 1976)
<i>evermanni</i>	25.9 (Rand 1964; Hertz 1977)
<i>frenatus</i>	26.9 (Ballinger et al. 1970; Campbell 1971)
<i>fuscoauratus</i>	28.8 (Vitt et al. 2003)
<i>gemmosus</i>	21.0 (Fitch et al. 1976)
<i>gingivinus</i>	30.1 (Eaton et al. 2002)
<i>grahami</i>	31.1 (Rand 1967a; Lister 1976)
<i>gundlachi</i>	24.8 (Rand 1964; Huey and Webster 1976; Hertz 1981, 1992b)
<i>homolechis</i>	30.7 (P. E. Hertz et al., unpubl. data; Ruibal 1961)
<i>humilis</i>	27.0 (Fitch 1973, 1975; van Berkum 1988; L. J. Vitt, unpubl. data)
<i>intermedius</i>	26.1 (Tsuji et al., unpubl. ms.)
<i>jubar</i>	32.4 (J. B. Losos et al., unpubl. data)

<i>Anolis</i> species	$T_b$ (°C)
<i>krugi</i>	28.6 (Rand 1964)
<i>limifrons</i>	27.2 (Ballinger et al. 1970; Fitch 1973; R. B. Huey, unpubl. data; van Berkum 1988; L. J. Vitt, unpubl. data)
<i>lineatopus</i>	29.1 (Rand 1967b; Lister 1976)
<i>lionotus</i>	26.4 (Campbell 1971)
<i>longiceps</i>	32.2 (Powell 1999)
<i>longitibialis</i>	32.2 (Hertz and Huey 1981)
<i>lucius</i>	29.3 (Ruibal 1961)
<i>marmoratus</i>	29.5 (Huey and Webster 1975)
<i>mestrei</i>	27.7 (P. E. Hertz et al., unpubl. data)
<i>monensis</i>	31.8 (Lister 1976; R. Powell and T. A. Jenssen, unpubl. data)
<i>nebulosus</i>	29.8 (Jenssen 1970; Ramirez-Bautista and Benabib 2001)
<i>nitens</i>	27.3 (Vitt et al. 2001; L. J. Vitt, unpubl. data)
<i>oculatus</i>	28.9 (Brooks 1968; Malhotra and Thorpe 1993)
<i>olssoni</i>	32.3 (Smith et al. 1994)
<i>opalinus</i>	28.1 (Rand 1967a)
<i>oxylophus</i>	29.1 (Vitt et al. 1995)
<i>poecilopus</i>	26.5 (Campbell 1971)
<i>polylepis</i>	27.8 (Hertz 1974)
<i>poncensis</i>	32.6 (Rand 1964)
<i>porcatus</i>	31.9 (J. B. Losos et al., unpubl. data)
<i>pulchellus</i>	32.6 (Rand 1964)
<i>punctatus</i>	28.9 (Rand and Humphrey 1968; Vitt et al. 2003)
<i>quercorum</i>	24.4 (Fitch 1978)
<i>richardi</i>	28.4 (Roughgarden et al. 1981)
<i>roquet</i>	28.6 (Hertz 1981)
<i>sagrei</i>	32.0 (Corn 1971; Lister 1976; Lee 1980; J. B. Losos et al., unpubl. data)
<i>semilineatus</i>	31.9 (Hertz 1979)
<i>sericeus</i>	32.8 (Fitch 1973)
<i>shrevei</i>	29.2 (Hertz and Huey 1981)
<i>smaragdinus</i>	34.2 (Lister 1976)
<i>stratulus</i>	28.4 (Rand 1964)
<i>subocularis</i>	31.4 (Fitch et al. 1976)
<i>taylori</i>	29.1 (Fitch et al. 1976)
<i>townsendi</i>	30.9 (Carpenter 1965)
<i>trachyderma</i>	27.8 (Vitt et al. 2002)
<i>tropidolepis</i>	20.5 (van Berkum 1988)
<i>uniformis</i>	27.9 (Birt et al. 2001)
<i>vermiculatus</i>	28.3 (González Bermúdez and Rodríguez Schettino 1982; J. B. Losos et al., unpubl. data)
<i>wattsii</i>	33.3 (Roughgarden et al. 1981)

## Appendix B

## LOADINGS FROM PHYLOGENETIC PCA

	PC1	PC2	PC3
Head length	0.1645	0.1643	0.2240
Head width	-0.4680	0.5042	0.4511
Head height	-0.1336	0.4099	0.5550
Lower jaw length	0.0427	0.0797	0.1497
Jaw outlever	0.1184	0.0855	0.1558
Jugal to symphysis	0.1508	0.0005	0.0747
Femur length	-0.8847	-0.0476	0.1073
Tibia length	-0.9219	-0.1060	0.0380
Metatarsal IV length	-0.9429	-0.1702	0.0392
Toe IV length	-0.9111	-0.0765	-0.0103
Toe IV Lamellae width	-0.3819	0.7296	-0.2547
Humerus length	-0.6912	0.3808	0.1964
Radius length	-0.7325	0.4168	0.2275
Metacarpal IV length	-0.8359	0.2653	0.1238
Metacarpal IV Lamellae width	-0.3389	0.8364	-0.1514
Pelvis height	-0.5249	0.0324	0.4543
Pelvis width	-0.4187	0.5753	0.2384
Toe IV Lamellae number	-0.2856	0.2071	-0.7821
Foretoe IV Lamellae number	-0.1891	0.5543	-0.6504

## Appendix C

## RESULTS FROM ANALYSES OF A DATASET THAT INCLUDES ONLY THOSE TAXA FOR WHICH DATA ON ALL TRAITS ARE AVAILABLE

**Table C1.** Average parameter values from analyses of character evolution for a dataset that included only those taxa for which all types of trait data were available calculated from across 901 trees in the posterior distribution of a Bayesian relaxed clock analyses.

	Rate			Phylogenetic signal			Rate variation		
	BM <i>k</i>	OU		Pagel's $\lambda$ $\lambda$	Blomberg et al.'s <i>K</i>		Pagel's $\delta$ $\delta$	EB	
		$\beta$	$\alpha$		<i>K</i>	p value		Start	Change
Thermal	0.102	0.591	0.056	0.111	0.607	0.263	9.191	4.58e-05	0.117
SVL	0.001	0.0015	0.010	0.747	0.774	0.031	2.024	2.07e-04	0.021
PC1	0.0004	0.0006	0.008	0.855	0.820	0.017	1.826	1.43e-04	0.016
PC2	0.001	0.001	3.04e-06	1	0.984	0.002	1.031	0.002	-0.014
PC3	0.0005	0.0006	2.56e-09	1	1.176	0.001	0.739	0.001	-0.017



**Table C2.** Results of model fitting analyses conducted on a dataset consisting exclusively of taxa for which all types of data are available. The first column for each model indicates mean  $\ln L$  values and their standard deviations calculated from results for all 901 trees. The second column indicates mean AIC values and their standard deviations calculated from results for all 901 trees. The third column for each model indicates the difference in mean AIC values ( $\Delta$ AIC) among models with 0 indicating the optimal model and higher values indicating increasingly poorly support. The third column for each model indicates Akaike weights ( $\omega$ ). Bolded values indicate the preferred model and any models that are not substantially different from this model.

	Brownian motion				Ornstein–Uhlenbeck				Evolutionary burst				White noise			
	$-\ln L$ (SD)	AIC (SD)	$\Delta$ AIC	$\omega$	$-\ln L$ (SD)	AIC (SD)	$\Delta$ AIC	$\omega$	$-\ln L$ (SD)	AIC (SD)	$\Delta$ AIC	$\omega$	$-\ln L$ (SD)	AIC (SD)	$\Delta$ AIC	$\omega$
Thermal	-73.30 (0.62)	150.60 (1.24)	6.9	0.009	<b>-69.63</b> <b>(0.06)</b>	<b>145.30</b> <b>(0.13)</b>	1.60	<b>0.133</b>	<b>-69.63</b> <b>(0.06)</b>	<b>145.26</b> <b>(0.13)</b>	<b>1.60</b>	<b>0.132</b>	<b>-69.83</b> <b>(0)</b>	<b>143.66</b> <b>(0)</b>	<b>&lt;0.001</b>	<b>0.295</b>
SVL	<b>0.95</b> <b>(0.39)</b>	<b>2.10</b> <b>(0.78)</b>	0	<b>0.232</b>	<b>1.52</b> <b>(0.19)</b>	<b>2.95</b> <b>(0.38)</b>	0.86	<b>0.151</b>	<b>1.52</b> <b>0.19</b>	<b>2.95</b> <b>0.38</b>	<b>0.86</b>	<b>0.151</b>	<b>0.51</b> <b>(0)</b>	<b>2.97</b> <b>(0)</b>	<b>0.87</b>	<b>0.149</b>
PC1	<b>12.42</b> <b>(0.56)</b>	<b>-20.83</b> <b>(1.12)</b>	0	<b>0.316</b>	<b>12.80</b> <b>(0.38)</b>	<b>-19.59</b> <b>(0.75)</b>	1.24	<b>0.170</b>	<b>12.79</b> <b>(0.38)</b>	<b>-19.59</b> <b>(0.75)</b>	<b>1.24</b>	<b>0.170</b>	<b>10.96</b> <b>(0)</b>	<b>-17.91</b> <b>(0)</b>	<b>2.9</b>	<b>0.073</b>
PC2	<b>-1.63</b> <b>(0.45)</b>	<b>7.26</b> <b>(0.89)</b>	0	<b>0.440</b>	<b>-1.63</b> <b>(0.45)</b>	<b>9.26</b> <b>(0.89)</b>	2.00	<b>0.162</b>	<b>-1.33</b> <b>(0.60)</b>	<b>8.65</b> <b>(1.20)</b>	<b>1.39</b>	<b>0.219</b>	<b>-5.71</b> <b>(0)</b>	<b>15.42</b> <b>(0)</b>	<b>8.2</b>	<b>0.007</b>
PC3	<b>6.56</b> <b>(0.41)</b>	<b>-9.11</b> <b>(0.82)</b>	0	<b>0.405</b>	<b>6.56</b> <b>(0.41)</b>	<b>-7.11</b> <b>(0.82)</b>	2.00	<b>0.149</b>	<b>7.16</b> <b>(0.63)</b>	<b>-8.32</b> <b>(1.25)</b>	<b>0.79</b>	<b>0.273</b>	<b>0.04</b> <b>(0)</b>	<b>3.92</b> <b>(0)</b>	<b>13</b>	<b>&lt;0.001</b>