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Tempo and Mode of Performance Evolution across Multiple Independent Origins of Adhesive Toe Pads in Lizards

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Abstract

Understanding macroevolutionary dynamics of trait evolution is an important endeavor in evolutionary biology. Ecological opportunity can liberate a trait as it diversifies through trait space, while genetic and selective constraints can limit diversification. While many studies have examined the dynamics of morphological traits, diverse morphological traits may yield the same or similar performance and as performance is often more proximately the target of selection, examining only morphology may give an incomplete understanding of evolutionary dynamics. Here we ask whether convergent evolution of pad-bearing lizards have followed similar evolutionary dynamics, or whether independent origins are accompanied by unique constraints and selective pressures over macroevolutionary time. We hypothesized that geckos and anoles each have unique evolutionary tempos and modes. Using performance data from 59 species, we modified Brownian Motion (BM) and Ornstein-Uhlenbeck (OU) models to account for repeated origins estimated using Bayesian ancestral state reconstructions. We discovered that adhesive performance in geckos evolved in a fashion consistent with Brownian Motion with a trend, whereas anoles evolved in bounded performance space consistent with more constrained evolution (an Ornstein-Uhlenbeck model). Our results suggest that convergent phenotypes can have quite distinctive evolutionary patterns, likely as a result of idiosyncratic constraints or ecological opportunities.

Introduction

When investigating how the diversity (or lack thereof) of a trait arose, one of the first steps is to observe the variation present in the trait and investigate how the trait evolved through time, asking whether the trait has thoroughly explored a small part of trait space, or if the trait appears to have freely explored trait space. Thorough coverage of a limited region of trait space can suggest constrained evolution, possibly due to limited developmental or genetic variation, biomechanical constraints, or limited ecological opportunity to adapt and change. Alternatively, a trait may appear to have explored trait space in a less constrained fashion. This may be due to fewer developmental, genetic, or biomechanical constraints, the trait accessing more open niches, or the trait being under weak selection, drifting through trait space with little consequence.

Knowledge of how a clade has evolved through trait space can be integrated into a fuller understanding of that clade's evolutionary history. If a clade has exhibited constrained evolutionary patterns, future studies can investigate how the focal trait may be limited by developmental, genetic, or mechanical constraints, or how biotic interactions have influenced the diversification of the trait. For example, habitat use/morphology correlations have been reported to differ between Caribbean and South American anoles (Irschick et al. 1997; Macrini et al. 2003). These differences may suggest Caribbean and mainland anoles have filled trait space differently, possibly due to differences in development, genetics, biomechanical considerations, or differences in abiotic or biotic conditions in the Caribbean and mainland South America.

In addition, morphological traits can be constructed in alternative ways to accomplish the same adaptive function, and these alternative constructions may or may not require similar amounts of morphological change to enable the organism to adapt to changing adaptive requirements. For these reasons, studying performance directly as a trait, as is the case in our study, rather than morphology may give a clearer picture of ecological function and evolutionary dynamics (Arnold 1983; Wainwright and Reilly 1994). Evidence of a clade having evolved constrained in performance space could be explained by a variety of situations. Focal clades may not have had the genetic, developmental, or mechanical capabilities to diversify and explore performance space, or there may have been limited niche space available to diversify into, similar to as if a focal trait was a morphological trait. In addition, when considering performance niche space, limited successful performance options do not impose limited underlying morphological diversity. Few adaptive options can lead to convergent or parallel morphological evolution, including many-to-one mapping, when different morphologies perform similarly. Alternately, evidence of unconstrained-performance evolution could be explained by behavioral plasticity, phenotypic plasticity, adaptive change tracking adaptive peaks, as well as weak selection allowing performance to drift through performance space.

Modeling the evolutionary history of a trait also requires some knowledge or assumptions about the origin or origins of the trait in question. While many studies have focused on the relationship between convergent morphology and performance, few studies have compared the tempo and mode of performance evolution in a comparative framework (but see Harmon et al. 2003). By focusing on convergent traits, we can better understand how limiting factors such as constraints or limited ecological opportunities have shaped the evolution of our focal clades.

Evaluating the fit of Ornstein-Uhlenbeck (OU) and Brownian motion (BM) models of trait evolution to a focal clade can identify how constrained (OU) or unconstrained (BM) the evolution of the trait has been (Lande 1976; Hansen 1997). Brownian motion models the diffusion of a trait through trait space with two parameters, the root value and a stochastic rate parameter (σ^2). Alternatively, OU models extend BM models to represent constrained evolution towards a target value (θ). OU has the additional parameter α, which describes the rate of pull towards the target trait value θ. As α gets smaller and approaches zero, an OU model converges towards a BM model. BM models can also be extended to model a directional trend when a third parameter, μ, is non-zero, modeling the tendency of the trait value to consistently drift in a particular direction (positively or negatively) away from the root value.

In this study, we examine the evolutionary dynamics of performance in two groups of squamates: geckos and anoles. Adhesive toe-pads have evolved at least three times in Squamata: most famously in geckos, but also twice outside of Gekkota, in anoles and skinks. We define adhesive toe pads as having morphological traits such as setae or modified scales that generate both friction and adhesion (frictional adhesion; Autumn et al. 2006a). The results from previous studies have suggested one (Harrington and Reeder 2017) or multiple origins of toe pads within the 1700 described species of geckos (Underwood 1954; Haacke 1976; Russell 1976; Russell 1979; Irschick et al. 1996; Russell 2002; Gamble et al. 2012; Russell et al. 2015; Higham et al. 2016; Gamble et al. 2017). The adhesive system of lizards is an excellent system for investigating patterns of adaptation, constraint, and convergence. Gecko and anole toe pads are morphologically complex, being comprised of modified ventral scales with a free edge (lamellae) covered in small hair-like structures called setae. There is considerable morphological diversity among species at the macroscale *i.e.,* toe pad shape, skeletal features, and digital musculature (Russell 1979; Gamble et al. 2012) and at the microscale *i.e.,* setal morphology (Ruibal and Ernst 1965; Williams and Peterson 1982; Peattie 2007; Johnson and Russell 2009; Hagey et al. 2014). These structures are responsible for generating adhesion and friction on a variety of surface textures, self-cleaning, and not self-adhering (Hansen and Autumn 2005; Vanhooydonck et al. 2005; Autumn et al. 2006a; Huber et al. 2007; Persson 2007; Russell and Johnson 2007; Pugno and Lepore 2008b; Hu et al. 2012; Autumn et al. 2014; Russell and Johnson 2014) suggesting that while toe pads appear very diverse, there likely exists extensive constraints and limitations on their morphology and performance. It is likely that the evolution

and adaptation of adhesive performance in padded lizards has balanced selective pressures and opportunities with mechanical and developmental constraints, likely limiting the options open to evolution and adaptation.

We considered how gecko and anole toe pad adhesive performance evolved by fitting a variety of stochastic models of trait evolution. We fit models with shared or independent parameter values and/or models across geckos and anoles, incorporating ancestral state reconstruction results into our models, to test the hypothesis that independent origins differ in rate (tempo) or pattern (mode). If a single-rate model is a good fit to our entire adhesive performance dataset, this would suggest that the performance of padded lizards and their convergent morphologies evolved under similar processes, shared mechanical, developmental constraints, and/or similar selection dynamics. In contrast, if clade-specific models or parameters fit our data well, this would reveal a pattern of clade-specific evolutionary dynamics, likely associated with clade-specific constraints or ecological opportunities (Hansen 1997; Butler and King 2004; Yoder et al. 2010; Eastman et al. 2013). Considering patterns of performance evolution in conjunction with ancestral information improves our understanding of how historical processes of adaptation have shaped extant diversity, morphology, and performance.

Methods.

Estimation of the number of origins of toe pads across Squamata

To identify independent origins of adhesive toe pads in lizards, we used a large, species-level phylogeny of Squamata (Pyron and Burbrink 2013). While this phylogeny has topological differences as compared to other smaller, group-specific phylogenies (Sadlier et al. 2005; Brown et al. 2012; Gamble et al. 2012; Oliver et al. 2012), we do not feel these differences impacted our results. Also see Title and Rabosky (2016) for comments on the use of large macrophylogenies in diversification studies. We chose a time-scaled, ultrametric phylogeny because our models of trait evolution model trait change in relation to time rather than sequence divergence. We assigned presence or absence of toe pads to each species in the phylogeny (4162 species). Four species of skinks are known to have adhesive pads, *Prasinohaema virens*, *P. flavipes*, *P. prehensicauda*, *Lipinia leptosoma* (Williams and Peterson 1982; Irschick et al. 1996; Pianka and Sweet 2005). Of the three pad-bearing *Prasinohaema* species, only *P. virens* is in the Pyron and Burbrink (2013) phylogeny. In addition, only one species of *Lipinia* is in the phylogeny (*L.*

150 *pulchella*). We substituted *L. leptosoma* for *L. pulchella* without a loss of phylogenetic
151 information (Austin 1998) for a total of two pad-bearing skink species in our toe pad
152 presence/absence dataset. We assigned the presence of toe pads to all *Anolis* species in the
153 phylogeny (207 species) except *A. onca* (Peterson and Williams 1981; Nicholson et al. 2006). To
154 assign presence/absence to geckos, we modified generic-level assignments from Gamble et al.
155 (2012) adding information from Wilson and Swan (2010) and personal observations (TH), to
156 assign toe pad presence (472 species) or absence (188 species) to all 660 species of geckos in the
157 phylogeny (see Fig. 3 and Supplemental Material). The remaining lizard and snake species in the
158 tree were considered padless.
159 Using the complete phylogeny of Pyron and Burbrink (2013), we estimated the number
160 of origins of adhesive toe pads across squamates by combining Bayesian estimates of transition
161 rate matrices with stochastic character mapping. We estimated transition matrices for a binary-
162 state, Mk model with asymmetric transition rates allowing the rates of pad gain and loss to vary
163 (*i.e.,* q10 and q01 were not constrained to be equal) using the R package Diversitree (FitzJohn
164 2012). We then ran a Bayesian MCMC for 10,000 generations sampling every 100 generations,
165 with an initial burn-in of 3,000 generations, resulting in a posterior sample of 701 Q matrices. To
166 visualize our reconstructions, monomorphic clades were collapsed, resulting in a phylogeny with
167 118 tips. Using the posterior sample of Q-matrices, we generated 701 simmap phylogenies using
168 the R function *make.simmap* in the phytools package (Revell 2012). Of particular interest was
169 the number of independent origins of toe pads within geckos (Gamble et al. 2012). We therefore
170 counted the number of estimated origins in Gekkota across the simmap-generated
171 reconstructions to obtain a posterior sample of origins.
172
173 *Collection of performance data*
174 Previous studies of pad-bearing lizards have quantified adhesive performance in multiple ways
175 (Irschick et al. 1996; Autumn et al. 2006a; Autumn et al. 2006b; Pugno and Lepore 2008a;
176 Autumn et al. 2014; Hagey et al. 2014; Hagey et al. 2016). We chose to use the angle of toe
177 detachment, which was first used to quantify adhesive performance in frogs (Emerson 1991;
178 Moen et al. 2013) and subsequently in geckos (Autumn et al. 2006a; Hagey et al. 2014; Hagey et
179 al. 2016). The angle of toe detachment is directly related to the adhesive mechanics of setae
180 (Autumn et al. 2006a; Tian et al. 2006) and can be measured easily in the laboratory or field with

181 relatively simple equipment (see Supplemental Material). This approach quantifies the maximum
182 proportion of adhesion (negative normal force), relative to friction, generated by a species' toe
183 pad (see Fig. 1 and Methods). We quantified adhesive performance across three families of
184 geckos (Gekkonidae, Phyllodactylidae, and Diplodactylidae) and the genus *Anolis* (see
185 Supplemental Material). Our toe detachment observations were collected following previous
186 studies, using captive and wild caught specimens from the field (Costa Rica, Panama, Thailand,
187 and Australia) and the lab (Autumn et al. 2006a; Hagey et al. 2014; Hagey et al. 2016). We used
188 a variety of equipment setups that included powered rotational stages, stepper motors (including
189 Lego Mindstorm motors), and manual rotational stages. To measure angle of toe detachment,
190 live non-sedated lizards were suspended via the toe pad of a single rear toe from a vertical glass
191 microscope slide (Video links in Supplemental Material; Autumn et al. 2006a; Hagey et al. 2014;
192 Hagey et al. 2016). Variation in performance across toes has not been previously investigated
193 and so we strived to always test similar toes. Our trials alternated between the longest left and
194 right rear toes, or the center rear toes if all rear toes were similar in length. Using a single toe
195 eliminated confounding forces that would be generated by multiple toes acting in opposing
196 directions. During each toe detachment trial, the glass substrate was initially vertical with the
197 animal's toe pad generating friction relative to the substrate (and likely little adhesion *i.e.,* force
198 perpendicular and towards the glass). The glass substrate was then slowly inverted. When this
199 occurred, the setal shaft angle increased, generating adhesion and friction relative to the glass. At
200 the angle of toe detachment, the maximum ratio of adhesion to friction that the toe pad was
201 capable of generating was exceeded, and the animal fell onto a cushioned pad (see Fig. 1 and
202 video links in Supplemental Material). Toe-pad area has previously been shown to correlate with
203 the amount of friction generated by anole toe pads (Irschick et al. 1996), presumably due to the
204 fact that larger pads have more setae interacting with the substrate. This relationship has not been
205 investigated regarding toe detachment angle. While we would not predict toe-pad area to
206 correlate with toe detachment angle, due to the fact that detachment angle is weight independent
207 and likely related to setal morphology (Autumn et al. 2006a) and not the absolute number of
208 setae contacting the surface, this relationship still requires evaluation.
209 Our performance observations included measurements of over 250 individual lizards
210 from 59 species (13 species of anoles and 46 species of geckos; Fig. 3; see Supplemental
211 Material). Our dataset had a minimum of two observations per individual and maximum of 49,

212 with a mean of 9.1 observations per individual. We collected five or more observations from
213 91% of the individuals sampled. Observations from each individual lizard were fit to a Weibull
214 distribution, which is often used in "time-to-failure" analyses (McCool 2012). The Weibull scale
215 parameter, with standard error, was then estimated, representing each individual's detachment
216 angle (Hagey et al. 2016). To produce a mean value for each species, we calculated a weighted
217 average using each individual's estimated Weibull scale value, weighting by the inverse of its
218 estimated standard error. In six of our 59 focal species, we did not record individual identity for
219 each performance trial; therefore we estimated performance of these species as if all observations
220 were from a single individual (see Table S.1).
221
222 *Modeling trait evolution*
223 We performed all trait evolution analyses using untransformed performance data.
224 Natural-log transforming our data would artificially emphasize differences between small
225 detachment angles and reduce differences between large detachment angles. Our initial analyses
226 fit single and multi-regime BM and OU models of trait evolution via a maximum likelihood
227 approach with the use of *a priori* assigned clades using the R package OUwie (Beaulieu et al.
228 2012). We also conducted analyses not requiring *a priori* clade assignments using the R
229 packages AUTEUR (Eastman et al. 2011), fitting multi-regime BM models, and SURFACE
230 (Ingram and Mahler 2013), fitting multi-θ OU models (See Supplemental Material). In our
231 OUwie analyses we considered seven models in total, including species mean errors. Our two
232 simplest models were a Brownian motion model (BM1) and an Ornstein-Uhlenbeck model
233 (OU1) that each fit a single set of parameters. Our other five models fit unique parameter values
234 in various combinations to the gecko and anole clades. The decision to assign unique parameter
235 values to anoles and geckos followed the results obtained from our ancestral state reconstruction,
236 with anoles and geckos representing independent origins of toe pads, although we note that other
237 studies have suggested multiple independent origins within geckos (see Introduction and
238 Discussion). We fit the following models: a BM model with variable evolutionary rates (σ^2) and
239 single root value (BMσ^2), an OU model with single α and σ^2 parameter value and different
240 optima (θ) values (OUθ), an OU model with a single α but multiple rate (σ^2) and optima (θ)
241 parameter values (OUσ^2θ), an OU model with a single σ^2 but variable α and θ values (OUαθ),
242 and a OU model (OUσ^2αθ) in which all three parameters, σ^2, α, and θ, varied (Table 1; Beaulieu

et al. 2012). We then compared the fit of our seven models using AICc weights based on relative model likelihoods (Table 1; Burnham and Anderson 2002).

The models we have described so far can sometimes rely on unrealistic assumptions. These models estimate a trait value at the root, which is the phylogenetic weighted mean of tip states for our BM1 and OU1 models. In our case, toe pads have had multiple origins, with the backbone of the squamate phylogeny likely lacking toe pads. Our model assumptions regarding performance at the root of the tree, the most recent shared common ancestor of geckos and anoles, is inferred to have a performance that is near the average of geckos and anoles. This is almost surely in error. Incorrect root-node trait values can affect parameter estimate values and fit comparisons; for example, by allowing less change and/or a weaker α parameter value, mimicking Brownian Motion. To incorporate ancestral state information, we fit a set of BM and OU models that assumed independent origins for geckos and anoles using modified likelihood functions from the R packages *bayou* and *geiger* (Harmon et al. 2008; Pennell et al. 2014; Uyeda and Harmon 2014). We considered the lack of toe pads to have a performance value of 0°. Both the gecko and anole clades were assigned a root state of 0° and shifted to an OU or BM process model along their respective stem branch, with the timing of the initiation of the OU or BM model being allowed to vary along the branch, before diversification. When considering the likely evolution of setae from spinules, simple early structures likely initially generated friction but little adhesion, which would present itself as a low detachment angle. Higher detachment angles were likely achieved after the evolution of more complex setae (see Discussion). As a result, our assignment of detachment angles of 0° to padless species and the assumption that recently evolved toe pads have performance near zero is supported from a biomechanical and evolutionary point of view.

Stem branch dates were taken from the Pyron and Burbrink (2013) phylogeny. For geckos, the timing of the shift to an OU or BM process was constrained to occur between 168.8 mya (the timing of the divergence of geckos from other lizards) and 82.3 mya (the ancestral node of Gekkota). For anoles, the timing of the shift was constrained between 76.3 mya (the divergence of anoles from Corytophanidae) and 44.1 mya (the ancestral node of *Anolis*). We again considered single and multi-regime models of BM and OU, constraining our OU models to a maximum θ value of 90° (no species has been observed sticking to a surface with one toe beyond an angle of 45°). A total of 9 models incorporating ancestral information were

considered (models denoted by an asterisk, Table 1). We did not exhaustively fit all possible combinations of models, but instead let the results of earlier analyses guide our choices: BM with a shared σ^2 for both geckos and anoles (*BM1), Single-optimum OU with shared α and σ^2 parameters (*OU1), Brownian motion with a trend and shared mean, σ^2, and μ parameter, where μ describes the rate of the trend (*BMT), Brownian motion with a trend and shared σ^2, but different trend (μ) parameters for each clade (*BMTμ), an OU model with separate θ for each clade (*OUθ), OU with separate α and θ for each clade (*OU$\alpha\theta$), OU with separate σ^2 and θ for each clade (*OU $\sigma^2\theta$), OU with separate α, σ^2, and θ for each clade (*OU$\sigma^2\alpha\theta$), and lastly a BM model with a trend fit to geckos and an OU model fit to anoles (*BMT_G-OU_A). We computed AIC scores and AIC weights for each model using maximum likelihood optimization to evaluate which model was best supported by our data (Table 1). To supplement these analyses assuming one origin of toe pads within geckos, we also conducted a set of limited analyses assuming two origins of toe pads within Gekkota (see Supplemental Material).

In addition to this likelihood analysis, we fit the full *OU$\sigma^2\alpha\theta$ model using a Bayesian implementation in *bayou* (denoted *OU$\sigma^2\alpha\theta_{Bayesian}$ in Table 1). By considering our most complex model, we can compare posterior probabilities for inferring differences in parameters between clades. We set the following priors on the parameters: $\alpha \sim$ half-Cauchy(scale = 0.1), $\sigma^2 \sim$ half-Cauchy(scale = 0.1), $\theta \sim$ Uniform(min = 0, max = 90). Shift locations were given uniform priors over the length of the stem branches for geckos and anoles. We ran four chains for 1,000,000 generations and discarded the first 30% of the samples as burn-in. We then combined all the chains and estimated the median and 95% highest posterior density (HPD) interval for each parameter value.

For use in our comparative modeling, we modified the Pyron and Burbrink (2013) phylogeny by removing unsampled taxa. In a few cases we replaced closely related unsampled taxa with taxa for which we had performance measurements. We replaced *Afroedura karroica* and one of the closely related *Geckolepis* species with *A. hawequensis* and *A. loveridgei*, possibly overestimating the divergence between our two sampled *Afroedura* species. We also had performance observations from the recently described *Oedura bella,* substituting it for the closely related *O. gemmata* (Oliver et al. 2012; Oliver and Doughty 2016).

Results

Regarding our reconstruction of the number of independent origins of toe pads, our posterior sample of transition matrices had negligible autocorrelation for all parameters and high effective sample sizes, indicating convergence and adequate mixing. Transition rates were estimated to be highly asymmetric, with losses of toe pads occurring at rates an average of 16.8 times faster than gains (95% HPD 3.2 – 41.1). Our reconstruction favored three origins in squamates (geckos, anoles, and skinks, Fig. 2) but we were unable to rule out multiple origins within geckos. Within geckos, our reconstruction favored a single origin (53% of posterior reconstructions), followed by two origins (30%), with only 4% of reconstructions having three or more origins within geckos. 13% of our reconstructions contained no origins within geckos, modeling the root of squamates as having pads. It is worth noting that we observed some reconstructions in our posterior sample with transient assignments, in which toe pads transitioned from absent to present, back to absent along a single branch, generating no overall change but possibly inflating the number of origins we observed. In addition, we observed an origin of toe pads in the branch leading to *Hemidactylus* in 33% of our posterior reconstructions, complementing previous studies of toe pad origins in geckos (Fig. 2; Gamble et al. 2012).

We conducted a Shapiro-Wilk test of normality and found our performance data to not be significantly different from than expected for a normal distribution ($W = 0.98$, $p = 0.32$). We found toe detachment angle to vary widely across padded lizards (Fig. 3, Table S.1), ranging from 15° to over 40°. When we consider detachment angle among clades, we note detachment angle in anoles ranged from 15.7° to 23.3°; lower than in most gecko species. Gekkonid and phyllodactylid geckos showed the greatest variation, with detachment angles ranging from 23.4° to 40.5° (Fig. 3, Table S.1). Diplodactyline geckos exhibited intermediate performance between anoles and the gekkonids and phyllodactyls, exhibiting detachment angles between 15.0° and 30.1° (Fig. 3, Table S.1).

Considering our trait evolution analyses, our OUwie results did not find clear support for one particular model of trait evolution (Table 1). We found support for a single-rate BM model (BM1, AICc weight of 0.35) with weaker support for an OU model with clade specific σ^2, α, and θ values, (OU$\sigma^2\alpha\theta$ model, AICc weight of 0.19). When we examine our OU$\sigma^2\alpha\theta$ model parameter estimates, geckos were modeled under an OU model with a very small α value (2.1×10^{-9}), large σ^2 (3.6), and distant θ (> 1000), which converges towards BM with a trend

335 (Table 1). It is worth noting again that these models assume unrealistic ancestral states, with a
336 phylogenetic mean performance value for the ancestor of geckos and anoles, which almost
337 certainly did not have toe pads.

338 For our custom models of trait evolution, which improved upon our OUwie analyses by
339 incorporating constrained root state and timing of parameter shifts, our best fitting model was
340 one in which geckos evolved under a BM model with a trend, and anoles evolved under an OU
341 model (*BMT_G-OU_A, AIC weight = 0.37; Fig. 4), followed closely by a global Brownian Motion
342 with a trend model (*BMT, AIC weight = 0.35; Table 1). The third best-fitting model assigned
343 unique μ values to geckos and anoles (*BMTμ, AIC weight = 0.18). When independent OU
344 models are fit to geckos and anoles, the estimated gecko phylogenetic half-life was 208.2 million
345 years with an estimated θ of 90° (the maximum allowable performance value), compared to the
346 short half-life estimated for anoles of 0.33 million years and a θ of 19.4°. Support for a BM
347 model with a trend in geckos is indicative of very little statistical signal for bounded evolution, a
348 surprising result given the bounded nature of performance space (detachment angle being
349 constrained between 0° and 90°). This result is supported when assuming one or two origins in
350 Gekkota (see Supplemental Material). By contrast, there is support for an OU model in anoles, in
351 which anoles are very near their estimated θ value and have a very rapid phylogenetic half-life.
352 However, possibly due to the limited sampling of *Anolis* species in our dataset (14 species), the
353 *BMT and *BM_G-OU_A models are roughly equivalent when accounting for the fact that the
354 *BMT model has only four parameters, while the *BM_G-OU_A model has seven.

355 Considering our *$OU\sigma^2\alpha\theta_{Bayesian}$ model, although we observed overlap among parameters
356 estimated for geckos and anoles, the results again suggest that the phylogenetic half-life for
357 anoles is shorter than that of the geckos, with anoles much closer to their θ value, whereas gecko
358 evolution is relatively unconstrained (Fig. 5; Table 1). All parameter estimates reached
359 stationarity and had effective sizes of over 200 and were similar to maximum likelihood
360 estimates (Table 1).

361

362 Discussion

363 In this study, we modeled the evolution of adhesive performance considering gecko and anole
364 lizards. In order to incorporate historical information such as the repeated evolution of adhesive
365 toe pads in lizards, we conducted an ancestral state reconstruction. Our reconstruction favored a

single origin of toe pads within geckos, which is significantly fewer than previous work (Gamble et al. 2012), although we cannot rule out multiple origins (see Gamble et al. 2017). Our performance observations suggested toe detachment angle to be highly variable across species of padded lizards (14° to 40°, see Supplemental Material). Lastly our modeling results supported our hypothesis that independent toe pad origins would exhibit different tempos and modes of performance evolution. There was no evidence of substantial constraints on the evolution of gecko adhesive performance. In fact, we found consistent support for an unconstrained model of trait evolution in geckos, which indicates adhesive performance in geckos has evolved with ample evolutionary opportunity and few constrains. Conversely, anole performance appears to be limited to relatively low angles of toe detachment, suggesting strong constraints, consistent selection, or limited ecological opportunity.

Independent Origins of Toe Pads

Many previous studies have contributed to our understanding of independent toe pad origins within geckos (Underwood 1954; Haacke 1976; Russell 1976; Russell 1979; Irschick et al. 1996; Russell 2002; Higham et al. 2015; Russell et al. 2015; Higham et al. 2016), with recent studies suggesting between one (Harrington and Reeder 2017) and eleven origins (Gamble et al. 2012), including origins in the Phyllodactylidae family and on the stem of *Hemidactylus*. This is still a very active area of research (Gamble et al. 2017). Our reconstruction suggested a single origin at the base of geckos, although we did find some evidence suggesting *Hemidactylus* may represent an independent origin of toe pads within Gekkota (see Results, Fig. 2, and Supplemental Material), complementing results from Gamble et al. (2012), despite topological differences between the Gamble et al. (2012) and Pyron and Burbrink (2013) phylogenies regarding genera closely related to *Hemidactylus* (see Title and Rabosky 2016 regarding the use of macrophylogenies in comparative analsyes). While neither our study nor the Gamble et al. (2012) study allowed the rate of pad gain or loss to vary across clades, some clades may be predisposed to evolving or losing adhesive toe pads, resulting in clade-specific rates or gain or loss. There are multiple distantly related genera of geckos that exhibit adhesive structures on the tips of their tails strikingly similar to those on their toes such as *Lygodactylus* in the Gekkonidae family and New Caledonia and New Zealand genera in the Diplodactylidae family (Bauer 1998). These independent origins of adhesive tail pads may suggest that geckos are predisposed to

evolve adhesive pads, possessing easily co-optable developmental pathways as compared to other lizards.

In addition, if toe pad state is correlated with diversification rate, this may impact ancestral reconstruction results (Maddison 2006). Gamble et al. (2012) found toe pads to be associated with slightly higher rate of diversification, although this was not the case for Garcia-Porta and Ord (2013). Considering state-correlated diversification rate alongside an ancestral state reconstruction, Harrington and Reeder (2017) concluded a single origin of toe pads using a 'hidden states' binary-state speciation and extinction model (Maddison et al. 2007; Beaulieu et al. 2013; Beaulieu and O'Meara 2016), although Gamble et al. (2017) dispute these results due to potentially high Type 1 error rates (Davis et al. 2013; Maddison and FitzJohn 2015; Rabosky and Goldberg 2015). Future studies may want to consider incorporating character-state correlated diversification information into ancestral state reconstructions using the recently published nonparametric FiSSE (Fast, intuitive, State-dependent, Speciation-Extinction) approach (Rabosky and Goldberg 2017; Zenil-Ferguson and Pennell 2017).

When considering other lines of evidence such as the variation in toe hyperextension anatomy within geckos (Russell 1979), it is likely that the true number of origins within geckos lies somewhere between one and many (Gamble et al. 2017). Future studies investigating the origins of adhesive toe pads in lizards will benefit from considering multiple lines of evidence (Gamble et al. 2017). The adhesive toe pads of lizards vary in toe pad shape, spinule/seta morphology, skin-to-bone digital tendon system characteristics (Russell 2002), and the presence/absence of internal blood sinuses and paraphalanges (Russell 1976; Russell and Bauer 1988; Gamble et al. 2012). The presence of epidermal spinules may predispose lizards to express adhesive setae, with epidermal spinules having likely evolved into adhesive setae (Maderson 1970; Stewart and Daniel 1972; Russell 1976; Peterson 1983; Peattie 2008). Epidermal spinules appear to be common across geckos and other lizards, including Chamaeleonidae, Iguanidae, Leiocephalidae, and Polychrotidae (Maderson 1964; Ruibal 1968; Maderson 1970; Stewart and Daniel 1975; Peterson 1984; Bauer and Russell 1988; Irish et al. 1988; Peattie 2008; Vucko 2008). Russell et al. (2015) provide a stunning example in *Gonatodes*, highlighting variation in both setal and toe pad morphology suggesting that *Gonatodes* may represent an example of elongated spinules and enlarged ventral scales performing as a friction-generating pad.

Trait Evolution

We used angle of toe detachment as a measure of adhesive performance because it has a well-supported mechanistic basis (Autumn et al. 2006a; Tian et al. 2006), although other metrics exist (Irschick et al. 1996; Irschick et al. 2006; Stark et al. 2012; Crandell et al. 2014). Using this measure of performance, we saw striking differences between our focal clades. Species with the lowest detachment angles (mostly anoles, near 15°) only produce a maximum of 0.27 units of adhesion for one unit of friction, [using *tangent*(detachment angle) = adhesion/friction (Autumn et al. 2006a; Hagey et al. 2014)], whereas particular Gekkonidae geckos have detachment angles over 40° and produce up to 0.84 units of adhesion for every unit of friction, over three times as much as our lowest performing species.

Our trait evolution modeling analyses, which used modified models of trait evolution and our ancestral state reconstruction results, suggested that our observed pattern of gecko performance is well described by a BM with a trend model or a weak OU model with parameters converging towards a BM with a trend (large σ^2, distant θ, and small α values; Table 1; Fig. 4, 5). Both models suggest adhesive performance in geckos has evolved directionally, yet relatively unbounded. Conversely, our results suggest anoles, which are much younger than geckos, evolved rapidly in a bounded sub-section of performance space, similar to a conventional OU model (short phylogenetic half-life and a θ value near observed values; Table 1; Fig. 4, 5). However, likely due to limited sample size, we have only weak evidence against a Brownian Motion with a trend model.

These observed differences in performance and evolutionary tempo and mode mirror anole and gecko macro- and micro-adhesive morphology, ecology, and the fossil record. For example, geckos were found to be more variable in adhesive performance (Fig. 3) and also have a much wider range of toe pad shapes, setal morphology (Peattie 2007; Gamble et al. 2012), and ecology as compared to anoles. Geckos live in tropical, arid, and temperate environments on rocks, vegetation, and terrestrial substrates, whereas anoles are generally found in arboreal microhabitats in the Caribbean and South America. Mainland anoles have more detachment angle diversity as compared to Caribbean anoles. These differences may be related to mainland and Caribbean lizard community structure and ecological opportunity (Macrini et al. 2003; Losos 2009). As a result, geckos may be evolving within many different adaptive zones, while the limited variation in the ecology of anoles may be driving them towards one or a few adaptive

zones without selecting for novel adhesive morphology. Further work exploring the relationship between adhesive performance and habitat use of padded lizards is also crucial to place performance reported here in an ecological context. Conversely, the evolvability of the gecko and anole adhesive systems may be a driving factor, allowing geckos to diversify extensively, and limiting anole toe pad shape, setal morphology, or performance and hence limiting them to one or few adaptive zones. Our trait modeling results also complement studies of the fossil record. Studies of trait evolution can sometimes underestimate ancestral trait diversity (Mitchell 2015), but recent fossil evidence from anoles preserved in amber suggests a model in which anoles rapidly evolved their current phenotypes, with anole ecomorphs having changed little since the Miocene (Sherratt et al. 2015). The gecko fossil record is unfortunately less informative (Daza et al. 2014; Daza et al. 2016).

Our results provide an example of convergent traits evolving under different evolutionary histories, highlighting the importance of considering macroevolutionary dynamics when inferring historical contingency and ecological opportunity during adaptation. Our study also describes the evolution of a performance trait instead of morphological traits. Despite our results detailing strong evolutionary constraints on anole evolution that we did not find in geckos, there remain many open questions as to how lizard adhesive toe pads have evolved, how they work, and how they are used in the wild. Our results highlight the need to conduct more biomechanical, ecological, and developmental studies of padded lizards with an explicit consideration of their origins. Our results also illustrate the value in incorporating additional information into comparative phylogenetic methods. Without the use of our modified *bayou* model, we would not have identified differences between the evolution of performance in geckos and anoles and we strongly encourage researchers to investigate their model assumptions.

Acknowledgements

We would like to thank the National Science Foundation in collaboration with Aaron Bauer and Todd Jackman (Award #0844523), the National Geographic Society/Waitts Institute (Grant #W216-12), the BEACON Center for the Study of Evolution in Action (Request #302, #429), the NSF Collaborative Research grant: Arbor: Comparative Analysis Workflows for the Tree of Life (Harmon et al. 2013), and Sigma XI (#G200803150489) for funding, Matt Pennell for helpful discussions, Jon Eastman for help with analyses, Jon Boone for access to animals, Bobby

Espinoza, JR Wood, Jesse Grismer, Mat Vickers, Andrew Schnell, Scott Harte, Alyssa Stark, Peter Niewiarowski, Ali Dhinojwala, Jonathan Losos, Anthony Herrel, Shane Campbell-Staton, Kristi Fenstermacher, Hannah Frank, Martha Munoz, and Paul VanMiddlesworth for help collecting data in the lab and field, and multiple editors and anonymous reviewers for helpful comments. None of the authors declare any conflicts of interest.

Data Accessibility

See Supplemental Material

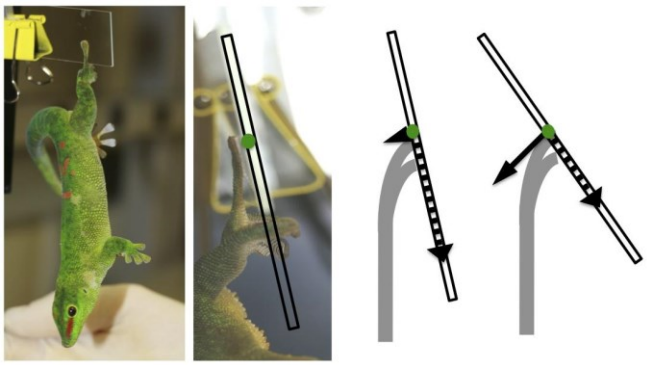


Figure 1. Angle of Toe Detachment Assay. To quantify toe detachment angle, a pad bearing lizard is suspended from a glass microscope slide by a single rear toe (left images). When the glass substrate is near vertical, the lizard's toe pad, and hence setae, are predominantly generating friction relative to the substrate (see right images, seta illustrated in gray, friction illustrated as dotted arrows). As the substrate is slowly inverted, the setae generate relatively less friction and more adhesion (see far right image, adhesion illustrated as solid arrow). At the angle of toe detachment, the setae can no longer maintain the proper orientation with the substrate to remain attached and the animal falls onto a cushioned base (see video links in Supplemental Material). As a result, the angle of toe detachment quantifies the maximum amount of adhesion, relative to friction, generated. Image modified from Hagey et al. (2014).

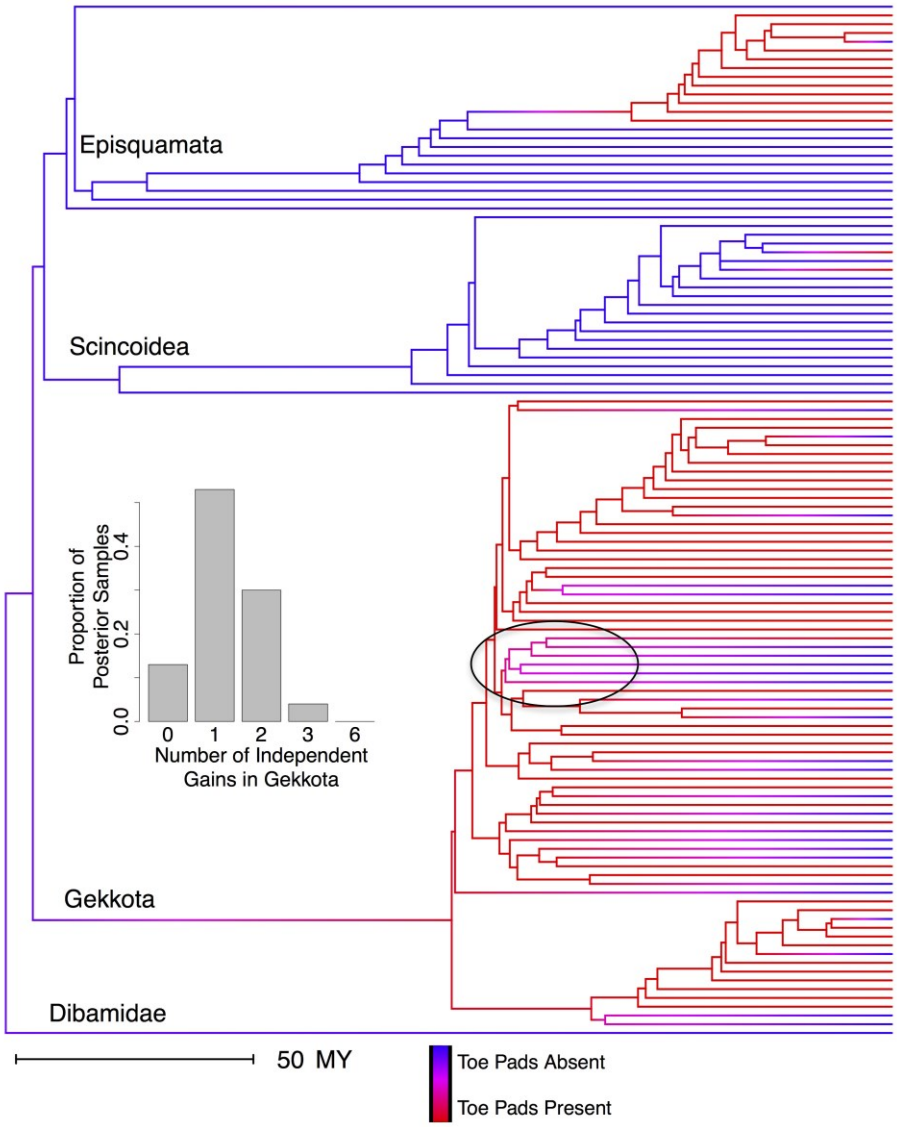


Figure 2. Toe Pad Ancestral State Reconstruction. We reconstructed the presence (red) and absence (blue) of adhesive toe pads across Squamata. We predicted toe pads likely evolved once within geckos, with many losses. The embedded histogram highlights the number of independent origins within Gekkota across our posterior sample of reconstructions (see Methods). Some of the reconstructions in our posterior sample yielded independent origins of toe pads in the stem leading to *Hemidactylus* (see Results). The root of the clade containing *Hemidactylus* is circled. For tip names see Supplemental Material.

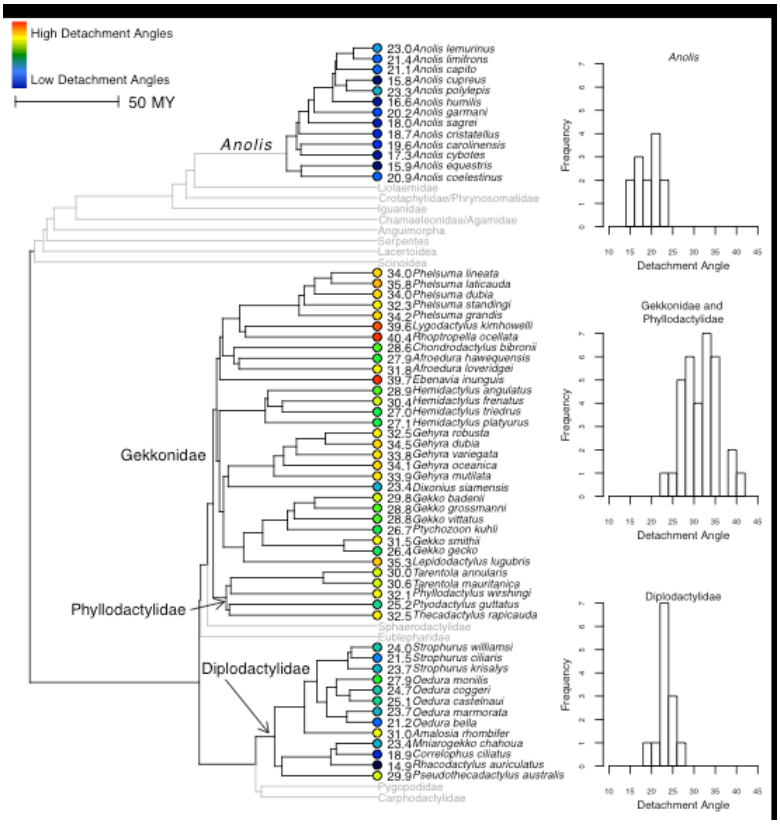


Figure 3. Phylogeny of Focal Padded Species with Performance Data. We quantified toe-detachment angle across 46 species of geckos and 13 species of anoles. Colored circles and numbers at the tips of the phylogeny represent each species' estimated detachment angle. Warmer colors represent higher detachment angles. We display prominent non-padded lizard groups to emphasize the evolutionary distance between anoles and geckos and to highlight the fact that not all families of geckos have toe pads (Carphodactylidae and Eublepharidae lack pads, Pygopodidae lacks limbs). Sphaerodactyls do possess adhesive toe pads, but we did not quantify their performance. Histograms to the right of the phylogeny illustrate the observed variation in performance within anoles, diplodactyls, and gekkonids and phyllodactylids. We found *Anolis* lizards to have the lowest detachment angles, followed by diplodactylids. Gekkonids and phyllodactylids had the highest and broadest range of detachment angles.

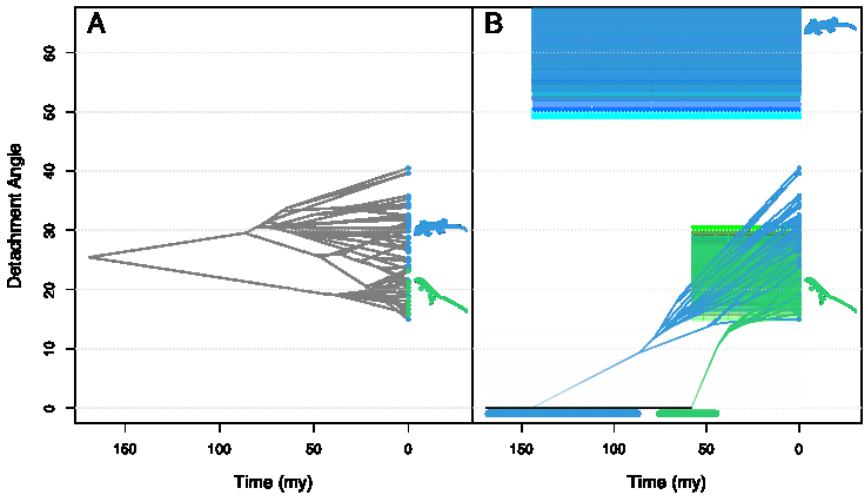


Figure 4. Ancestral state reconstructions using a single-regime BM model (A) and the median posterior parameter estimates for the *OU$\sigma^2\alpha\theta_{Bayesian}$ model (B) in *bayou*, which assumes independent origins of toe pads geckos and anoles. Anole data are displayed in green and gecko data in blue. B) median parameter estimates for the OU target value are indicated by colored dotted lines within the shaded bands indicating the expected densities of the stationary distributions. Horizontal bars below the X-axis indicate the constrained shift regions. Note the median predicted ancestral performance in plot A is estimating a toe detachment angle of approximately 25° for the shared ancestor of geckos and anoles, which likely lacked toe pads. See Supplemental Material for additional analyses assuming two origins of toe pads in Gekkota.

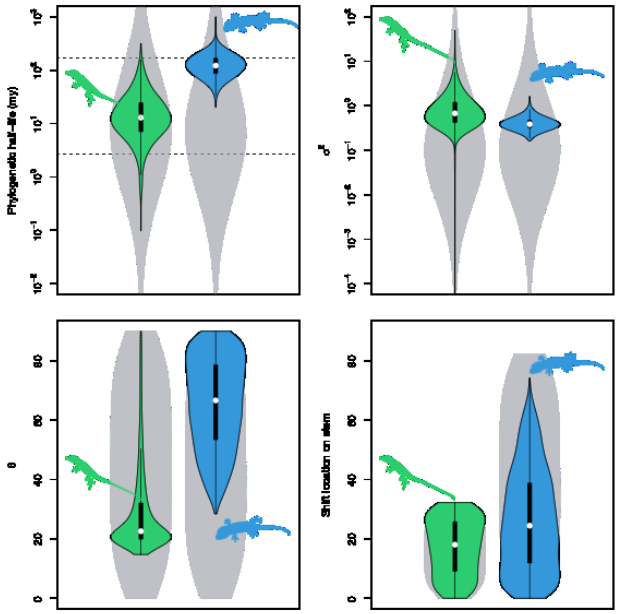


Figure 5. Posterior distributions from the *OU$\sigma^2\alpha\theta_{Bayesian}$ model. Anole data are displayed in green on the left of each plot. Gecko data are in blue on the right of each plot. White dots indicate median estimates for each parameter while black rectangles and whiskers indicate quartiles of the distribution. Gray violin plots indicate the prior distribution. The upper dotted line on the phylogenetic half-life plot indicates the root age of the Squamata phylogeny corresponding roughly to the value at which the OU model approaches a Brownian Motion model. The lower dotted line represents the value of phylogenetic half-life at which no two species in either phylogeny would have more than a 0.05% phylogenetic correlation, *i.e.,* the values at which our model simplifies into a white-noise model with independent, identically distributed trait values with no effect of phylogeny.

Offset Models	AIC_c Weights	Parameter Values			
		Rmax	g^2		
BMO	0.56	23.5	0.26		
		$\hat{R}$	g^2	AgGlds	
OU+Gb	0.19	19.0	0.46	33.2	Anoles
		>90.0	5.56	>1000	Geckos
		$\hat{R}$	g^2	AgGlds	
DCD	0.15	19.0	0.33	101.7	Anoles
		32.7			Geckos
		Rmax	g^2		
BM+J^2	0.12	23.5	0.26		Anoles
			0.26		Geckos
		$\hat{R}$	g^2	AgGlds	
DD1	0.12	25.5	0.26	>1000	
		$\hat{R}$	g^2	AgGlds	
OUm	0.05	18.9	0.42	100.8	Anoles
		45.6		200.4	Geckos
		$\hat{R}$	g^2	AgGlds	
OU+Y	0.05	19.0	0.39	194.0	Anoles
		32.4	0.39		Geckos

BAYES Models	AIC_c Weights	Parameter Values					
		Rmax$\hat{R}$	g^2	AgGlds	μ	Shift Time	
*BMT$_g$+OU$_s$	0.57	19.4	29.7	6.5	–	55.3	Anoles
		0.0	0.27	–	0.38	85.5	Geckos
		Rmax	g^2	AgGlds	μ	Shift Time	
*BMT	0.34	0.0	0.27	–	0.34	39.4	Anoles
						85.5	Geckos
		Rmax	g^2	AgGlds	μ	Shift Time	
*BMT$_\mu$	0.18	0.0	0.27	–	0.45	55.3	Anoles
					0.38	85.5	Geckos
		$\hat{R}$	g^2	AgGlds	μ	Shift Time	
*OU+Gd	0.04	19.4	33.1	6.3	–	55.5	Anoles
		90.0	0.31	208.1		39.6	Geckos
		$\hat{R}$	g^2	AgGlds	μ	Shift Time	
*OUJ	0.04	90.0	0.36	117.0	–	18.5	Anoles
						40.0	Geckos
		$\hat{R}$	g^2	AgGlds	μ	Shift Time	
*DDD	0.02	90.0	0.36	117.0	–	18.5	Anoles
		90.0				65.5	Geckos
		$\hat{R}$	g^2	AgGlds	μ	Shift Time	
*OUcd	0.01	90.0	0.41	2.3	–	31.4	Anoles
		90.0		90.9		55.5	Geckos
		$\hat{R}$	g^2	AgGlds	μ	Shift Time	
*OU$_s$b	0.01	90.0	0.30	90.9	–	31.4	Anoles
		90.0	0.41			55.5	Geckos
		Rmax	g^2	AgGlds	μ	Shift Time	
*BMI	0.00	0.0	0.30	–	0.00	0.0	Anoles
						0.0	Geckos
		$\hat{R}$	g^2	AgGlds	μ	Shift Time	
*OU+W_{Anoles}	–	22.6 (17.2, 41.1)	0.00 (0.00, 3.00)	13.9 (8.1, 65.4)	–	18.1 (1.8, 32.2)	Anoles
		65.7 (39.2, 90.8)	0.39 (0.22, 0.60)	131.3 (77.1, 247.7)		34.5 (0.6, 37.2)	Geckos

561

562 Table 1. Model of Trait Evolution Fits and Estimated Parameters. We evaluated multiple models
563 of trait evolution using the OUwie, and *bayou* packages. We ascribed model names based on
564 their use of a BM or OU procedure followed by parameters that were allowed to vary across
565 clades. We display AICc weights and parameter estimates for each model we considered, sorted
566 by their AICc weights. The models considered in our *bayou* analyses all incorporated constraints
567 (denoted by asterisks) limiting the trait value to 0° prior to the stem branches leading to geckos
568 and anoles. We report the predicted timing of the origins of toe pads in geckos and anoles (Shift
569 Time) in millions of years since the split of the stem segregating the clade from the rest of the
570 phylogeny. OU α values are displayed as phylogenetic half-life values ($ln[2]/\alpha$) in millions of
571 years. Our *bayou* Brownian Motion models also include root parameter values illustrating the
572 trait value at the root of the phylogeny. In BM models lacking a trend, in which the μ parameter
573 is zero, the root parameter value is also the clade mean. The μ parameter represents the expected
574 change in trait over time. Lastly, results from our $*OU\sigma^2\alpha\theta_{Bayesian}$ model included estimated
575 medians and 95% highest posterior density (HPD) intervals for each parameter, indicated in
576 parentheses under each value, displayed in the last row of the table.
577

Supplemental Material

Here we provide additional information including species level data, links to performance assay videos, additional results, and a description of how we measured performance in the field using purpose-built equipment.

File S.1. A .xlsx file listing our toe pad presence/absence assignments for all 4162 tips in the squamate phylogeny from Pyron and Burbrink (2013).

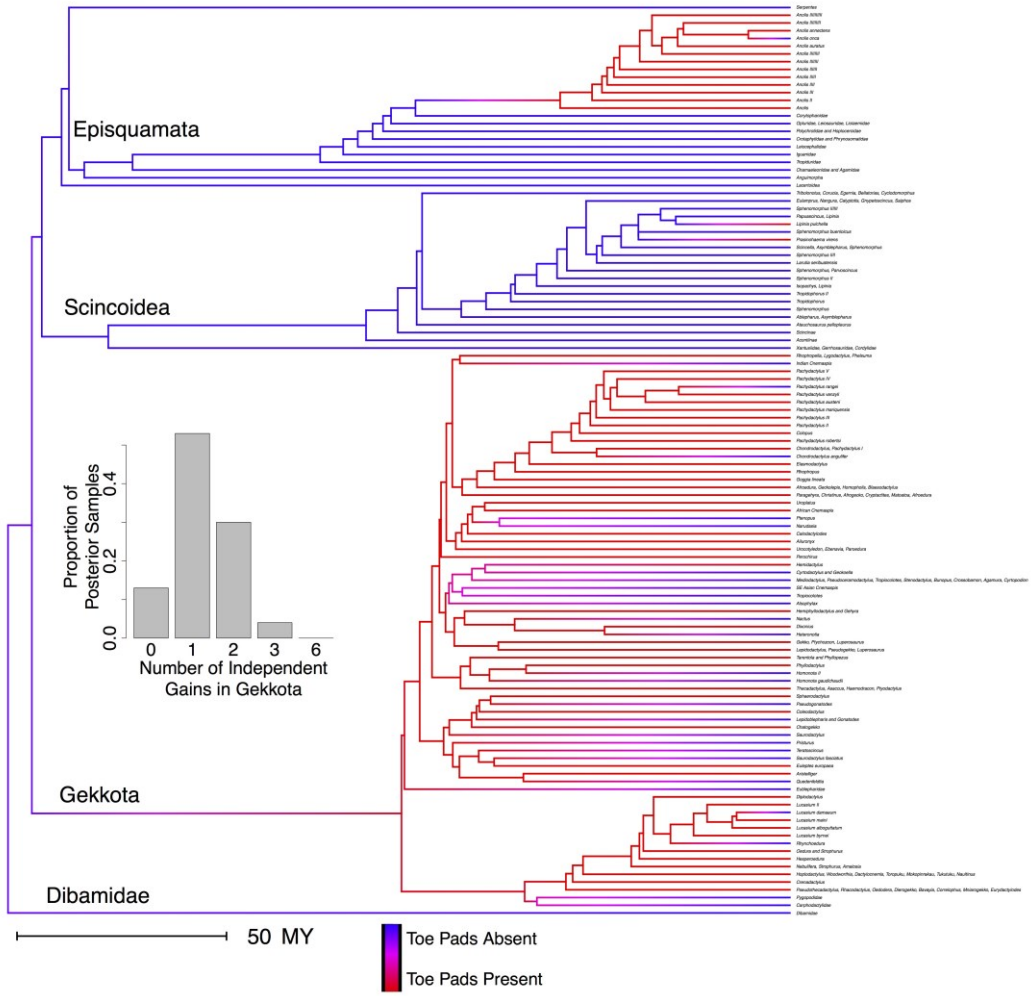
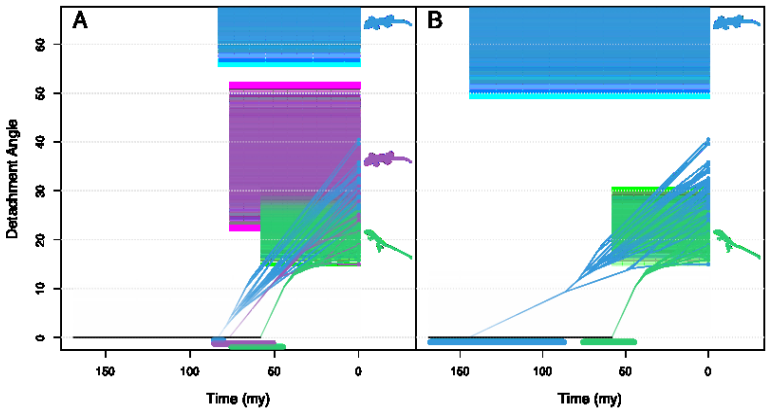


Figure S.1 Ancestral State Reconstruction with Tip Names (see Figure 2, Methods, and Results for additional information)

Modeling Trait Evolution Assuming Two Origins of Toe Pads within Gekkota

In addition to analyses assuming a single origin of toe pads within geckos, we considered an additional set of limited analyses assuming two independent origins of toe pads within Gekkota, one origin at the base of the Diplodactylidae family and a second at the base of the Phyllodactylidae and Gekkonidae clade. Our primary goal with these analyses was to determine whether two origins (which received some support in our reconstruction of toe pad evolution) changed our primary conclusions —namely, that Gekkota evolved under BM-like evolution with a trend with limited evidence of constraint.

Models fit using Maximum Likelihood to two-origin scenarios recover very similar dynamics, with Brownian motion with a trend being preferred over an OU model (AICs: BM with a trend = 264.3; OU = 296.3). Furthermore, even when an OU model is fit to our two gecko clades, they recover very BM-like dynamics with long phylogenetic half-lives (Gekkonidae/Phyllodactylidae = 136.7 my; Diplodactylidae = 193.0 my). Furthermore, we find little evidence for unique dynamics between the two putative origins (AICs: OU shared parameters = 297.4; OU independent parameters = 296.3), suggesting that the two gecko clades generally evolve under similar dynamics. We visualized our analysis by fitting the OU model described above in a Bayesian framework (left plot) with separate origins for Diplodactylidae (purple) and other Gekkonidae/Phyllodactylidae (blue). Both clades had long half-lives (Gekkonidae/Phyllodactylidae median = 91.5 my; Diplodactyline median = 64.8 my) and distant optima (Gekkonidae/Phyllodactylidae median [95%CI] = 67.6° [33.3°, 88.8°]; Diplodactyline geckos median [95%CI] = 46.1° ° [23.5°, 87.3°]). We compared this model to our Bayesian model from the main text (right plot). Note that although BM with a trend was preferred over OU models, OU models with distant optima and long phylogenetic half-lives approximate BM with a trend. Related to this point, estimates of half-lives are stronger in our Bayesian than the Maximum Likelihood analyses because we constrained the optima values using priors to not exceed 90° in our Bayesian analyses. However, for visualixation purposes, we view these differences as minimal. We conclude that even with multiple origins, the data suggest more gradual and unconstrained trait evolution across the geckos than in the *Anolis* lizards.



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[redacted]

Table S.1. Performance Observations. Species mean toe detachment angle and variance (displayed in parentheses). The number of individuals tested was not recorded for some species of anoles (number of individuals = NA) and were treated as observations from a single individual in our analyses.

File S.2 Performance Observations .xlsx file

Links illustrating our toe detachment assay on YouTube:
Far away view: https://www.youtube.com/watch?v=4EDUi9If-4c
Close up view: https://www.youtube.com/watch?v=HC-FdtGqv54

633 *AUTEUR and SURFACE Analyses*

634 In addition to our OUwie and modified *bayou* trait evolution analyses, we also considered BM
635 trait evolution using AUTEUR (Eastman et al. 2011), currently within the *geiger* package, and
636 shifts in the OU target parameter θ (assuming α, the strength of pull towards θ, and the rate of
637 diffusion, σ^2, are shared across clades) using the R package SURFACE (Ingram and Mahler
638 2013). These analyses each require different *a priori* information and use different model fitting
639 approaches. AUTEUR does not require *a priori* clade assignments and uses a reversible-jump
640 MCMC approach to fit multi-regime BM models, allowing either the rate of change (σ^2), mean
641 trait value (θ), or both parameters to vary between clades. We evaluated models with clade
642 specific σ^2 values (BMσ^2), clade specific θ values (BMθ), and models in which both θ and σ^2
643 could vary (BM$\sigma^2\theta$), all while including species-level trait value error. For each dataset, we
644 conducted two runs, evaluating chain convergence. All of our AUTEUR runs used one million
645 generations, sampling every five hundred generations.

646 The SURFACE package uses a step-wise AIC approach without *a priori* clade
647 assignments, varying the OU parameter θ for different clades until the AIC score can no longer
648 be improved. This package was designed to identify examples of convergence and so the second
649 phase of the analysis condenses previously identified regimes, allowing parameter values to be
650 shared between clades, and reducing the total number of unique parameter sets. We conducted
651 simulations to determine if the model identified by SURFACE contained a significant number of
652 regimes as compared to the number expected by chance under a single-rate BM model. We
653 simulated 500 datasets under BM using our cropped Pyron and Burbrink (2013) phylogeny. We
654 ran each simulated dataset through the forward and backward phases of SURFACE and tabulated
655 the number of regimes observed to generate a null distribution.

656 The results from our AUTEUR analyses, which considered multi-rate and multi-theta BM
657 models, found no significant changes in rate or mean across clades. All six of our runs, varying
658 σ^2 (BMσ^2), θ (BMθ), or σ^2 and θ concurrently (BM$\sigma^2\theta$) with two replicates each, estimated
659 similar parameter values ($\sigma^2 = 0.29 \pm 0.005$ SE, $\theta = 25.6 \pm 0.03$ SE, see Table below). We
660 display σ^2 and θ parameter estimates for each of our duplicate simulations (denoted as subscript
661 one or two). We concluded that our duplicate runs were converging by comparing σ^2 and θ
662 posterior probabilities of each branch between duplicated runs, finding them to be similar. We
663 also used the Heidelberger and Welch convergence diagnostic, which includes the Cramer-von-

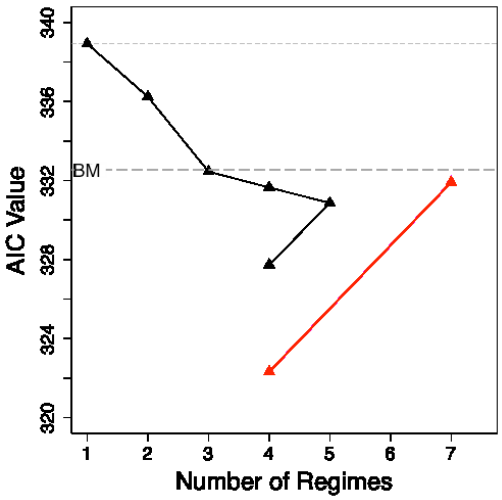
Mises statistic and the half-width test. In all of our analyses, the root and log-likelihood parameters passed both tests. We found effective sizes ranging from 598 to 2104 for our root and log-likelihood parameters across all our runs, which take into account autocorrelation between successive MCMC chain samples.

AUTHUR Models	σ^2	θ
$BM\theta_1$	0.31	25.5
$BM\theta_2$	0.31	25.5
$BM\sigma^2_1$	0.29	25.6
$BM\sigma^2_2$	0.29	25.7
$BM\sigma^2\theta_1$	0.28	25.6
$BM\sigma^2\theta_2$	0.29	25.6

Our SURFACE analyses originally found a multi-θ OU model with five regimes condensed into four made up of anoles and diplodactylid geckos, gekkonids and phyllodacylids, *Rhacodactylus auriculatus*, and three gekkonid species, *Lygodactylus kimhowelli*, *Rhoptropella ocellata*, and *Ebenavia inunguis*, Below we display parameter estimates and AIC scores for single-regime BM and OU (BM1 and OU1), and uncondensed and condensed models. During the stepwise SURFACE analysis our model AIC scores dropped as more regimes were added (black triangles; see Figure and Table below), starting at a single-theta OU model (upper dotted line, AIC = 338.9), until the analysis settled on a five-regime model (AIC = 330.9), scoring lightly better than a single-regime BM model (lower dashed line, AIC = 332.5). The analyses then looked for improvements to the AIC score by condensing regimes. By condensing the two small regimes within Gekkonidae into one, the AIC score and number of unique regimes were reduced to four and an AIC of 327.7. Although, when we consider the number of regimes expected under a single-rate BM model, we see that five regimes with one condensation event could easily occur by chance. In our 500 simulated datasets under single-rate BM, we found an average of 5.3 regimes, a mode of five, and a maximum of 11 regimes, with an average of 2.0 convergence events, a mode of two, and a maximum of six convergence events. These simulations suggest that a multi-theta OU model like the one we observed fitting our data best may have a low AIC score (327.7), but it is a pattern that can easily appear under a single-rate BM model (AIC = 332.5).

Considering the fact that our SURFACE analyses successfully fit divergent species to their own regimes (*Rhacodactylus auriculatus*, *Lygodactylus kimhowelli*, *Rhoptropella ocellata*,

and *Ebenavia inunguis*), we conducted a further analysis, manually condensing high performing diplodacylid geckos (*Amalosia rhombifer* and *Pseudothecadactylus australis*) into the gekkonid regime and recalculated the AIC score for this new, further condensed, model (red triangles; see Figure and Table below). We found our uncondensed seven-regime model had a higher AIC (331.9) as compared to the non-condensed five-regime model SURFACE found, yet when we condensed our modified model into four regimes, its AIC score (322.3) dropped well below the best condensed four-regime model identified by SURFACE. We believe this model was not chosen by the initial SURFACE analysis due the stepwise AIC approach SURFACE uses.



SURFACE Models	AIC	σ^2	α	θ
BM1	332.54	0.29	NA	25.4
OU1	338.93	0.33	0.003	25.7
$OU6_{Uncondensed}$	330.86	0.33	0.013	22.1 - *Anolis*, Diplodacylidae 33.2 - Gekkonidae, Phyllodactylidae 49.3 - *Lygodactylus*, *Rhoptropella* -8.2 - *Rhacodactylus* 49.1 - *Ebenavis*
$OU6_{Condensed}$	327.73	0.33	0.013	22.1 - *Anolis*, Diplodacylidae 33.2 - Gekkonidae, Phyllodactylidae 49.8 - *Lygodactylus*, *Rhoptropella*, *Ebenavis* -8.2 - *Rhacodactylus*
$OU6_{Modified\ Uncondensed}$	331.91	0.31	0.016	20.8 - *Anolis*, Diplodacylidae 33.0 - Gekkonidae, Phyllodactylidae 47.0 - *Lygodactylus*, *Rhoptropella* -0.3 - *Rhacodactylus* 46.0 - *Ebenavis* 39.7 - *Amalosia* 36.0 - *Pseudothecadactylus*
$OU6_{Modified\ Condensed}$	322.32	0.34	0.018	20.7 - *Anolis*, Diplodacylidae 32.8 - Gekkonidae, Phyllodactylidae, *Amalosia*, *Pseudothecadactylus* 45.5 - *Lygodactylus*, *Rhoptropella*, *Ebenavis* 1.2 - *Rhacodactylus*

Measuring Performance in the Field

Pad bearing lizards with higher detachment angles can likely use highly angled or inverted perches more easily, whereas species with lower detachment angles likely struggle to generate as much adhesion relative to friction and thus may be limited to vertical perches, although toe orientation and foot shape likely play a large role in inverted locomotion. In addition, there may exist a trade-off in high and low detachment angles regarding the production of friction versus adhesion. Species with a high detachment angle likely have setae and spatulae shaped to maintain proper contact with a substrate under high setal shaft angles, producing some amount of both adhesion and friction, but less absolute friction than if the setal shaft angle was near parallel with the substrate, translating the applied force into only friction (also see Pesika et al. 2007). Additional research considering the setal mechanics underlying detachment angle would be necessary to further describe this potential trade-off. In addition, rough surfaces offer a reduced surface area for a padded lizard to attach to, and as a result, higher detachment angles may allow setae to properly attach to the valleys and peaks of a rough surface (Sitti and Fearing 2003; Gillies and Fearing 2014; Gillies et al. 2014).

As part of this study, gecko performance was collected in Queensland, Australia using purpose-built equipment consisting of a Pacific Scientific Powermax 1.8° stepper motor (model #P21NRXB-LNN-NS-00), Vernier dual-range force sensor, Vernier three-axis accelerometer, Vernier sensorDAQ data-acquisition interface, and a Phidget bipolar stepper control board (#1063_1). Operation and data collection used a custom LabVIEW program (2011 version 11.0.1f2, National Instruments, Austin, TX, USA) running on a Gateway LT series netbook (LT2805u). The frame of our toe detachment equipment was custom-built and acted as a lever with a fulcrum in the center, force sensor at one end, and the lizard suspended from the other end (Fig. S.2).

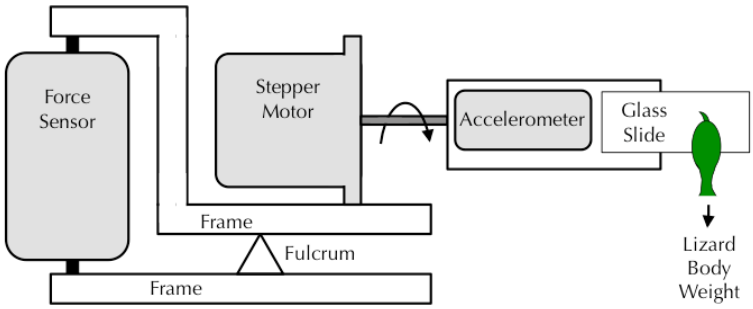


Figure S.2. Toe Detachment Field Equipment. We build a field-capable TAD device consisting of a force sensor, stepper motor, and multi-axis accelerometer. The upper frame of our apparatus acts as a lever with the fulcrum, allowing the force sensor (left side of image) to detect when a lizard detaches from the glass (right side of image). Our glass slide and accelerometer were attached to a large flat plate. The accelerometer was positioned to measure acceleration in the Y direction (vertical in our image) and Z direction (perpendicular to the mounting surface, out of the plane of the image, towards the reader).

An accelerometer, attached to the rotating glass surface, allowed us to determine the angle of the glass surface throughout the course of each trial. Raw toe detachment data consisted of three variables recorded over the course of each trial (acceleration in Y and Z directions and force). By calculating the arctangent of the ratio of the two acceleration measurements perpendicular to the axis of rotation, we could determine angle (Fig. S.2). When rotating, acceleration due to gravity was not linear; rather it changed slowly when near vertical. When near horizontal, acceleration due to gravity changed quickly.

Our force sensor recorded the corresponding change in force (Fig. S.3) and allowed us to pinpoint the instant the lizard detaches during a trial. We fit a three-parameter broken regression model to our force output data to pinpoint the moment the lizard detached (Fig. S.3). We estimated the y-intercept of a horizontal line fit to the force data before the lizard fell, the time point at which the lizard fell, and the y-intercept of a horizontal line fit to the force data after the lizard detached (Fig. S.3). Using our estimated time of detachment and our angle data (calculated from accelerometer data), we estimated the angle of the glass at the time of detachment (Fig. S.3).

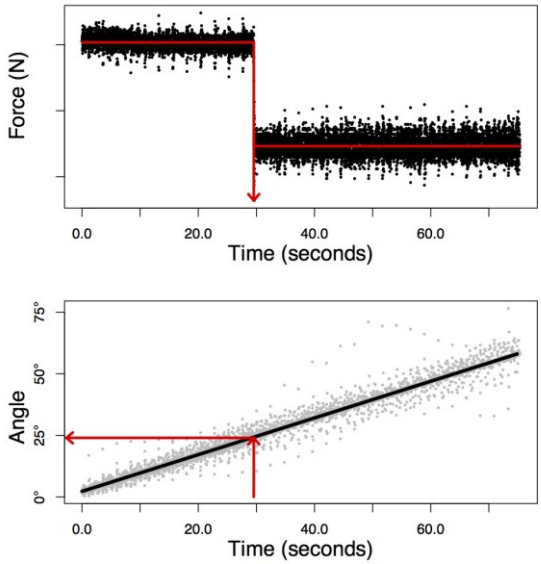


Figure S.3. Representative Toe Detachment Performance Trial. Representative data output from a single toe detachment trial is displayed. Time is on the X-axis. Raw force data (upper plot) displays our two estimated y-intercepts (red horizontal lines) and time of detachment (red vertical line, approximately 30 seconds in this example) estimated by a broken regression analysis. Raw acceleration data were used to estimate the angle of the glass slide through time (lower plot, gray points). The black line in our lower plot is the estimated substrate angle over the course of the trial. Our estimated angle of toe detachment is the point in which our estimated time of detachment intersects with our estimated angle, slightly under 25° in this example.

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