

Phylogenetic Comparative Analysis: A Modeling Approach for Adaptive Evolution

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ABSTRACT: Biologists employ phylogenetic comparative methods to study adaptive evolution. However, none of the popular methods model selection directly. We explain and develop a method based on the Ornstein-Uhlenbeck (OU) process, first proposed by Hansen. Ornstein-Uhlenbeck models incorporate both selection and drift and are thus qualitatively different from, and more general than, pure drift models based on Brownian motion. Most importantly, OU models possess selective optima that formalize the notion of adaptive zone. In this article, we develop the method for one quantitative character, discuss interpretations of its parameters, and provide code implementing the method. Our approach allows us to translate hypotheses regarding adaptation in different selective regimes into explicit models, to test the models against data using maximum-likelihood-based model selection techniques, and to infer details of the evolutionary process. We illustrate the method using two worked examples. Relative to existing approaches, the direct modeling approach we demonstrate allows one to explore more detailed hypotheses and to utilize more of the information content of comparative data sets than existing methods. Moreover, the use of a model selection framework to simultaneously compare a variety of hypotheses advances our ability to assess alternative evolutionary explanations.

Keywords: Ornstein-Uhlenbeck, Brownian motion, selective regime, adaptation, evolutionary model, *Anolis* lizards.

We have stressed throughout the important role that models of evolutionary change play in our statistical methods. Brownian motion models have been put to use for characterizing

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change in continuously varying characters, as has a Markov model in the case of dichotomous characters. New models, based on undoubtedly wicked mathematics, will gradually emerge. (Harvey and Pagel 1991)

The comparative method is a central tool for investigating the adaptive significance of organismal traits. A fundamental problem facing any interspecific comparative analysis is that the species compared are not independent: to a greater or lesser extent they share a common evolutionary history. Numerous methods have been devised to circumvent this problem (reviewed in Harvey and Pagel 1991; Miles and Dunham 1993; Martins 1996; Martins et al. 2002). However, as has long been recognized, the most popular methods for phylogenetic comparative analysis assume an inappropriate model of evolution (Westoby et al. 1995; Price 1997). In particular, a purely neutral model of evolution—Brownian motion—is used to model the evolutionary dynamics of a trait thought to be evolving in response to some selective factor (Harvey and Purvis 1991; Harvey and Rambaut 2000; Martins et al. 2002).

In his seminal article introducing the method of independent contrasts, Felsenstein (1985) recognized two cases in which Brownian motion (BM) may not be an appropriate model: when selection persists through time so that evolutionary changes on successive branches are correlated, and when different lineages are subject to the same selective regime (i.e., common environment, predators, food type, or habitat use). Both of these are to be expected in the presence of natural selection.

The use of BM is not limited to the method of independent contrasts. Although it is not always made explicit, BM is the underlying model of evolution in nearly all phylogenetic comparative methods for quantitative characters including phylogenetic autocorrelation (Cheverud et al. 1985), weighted least squares parsimony (Huey and Bennett 1987; Maddison 1991), phylogenetic regression (Grafen 1989), maximum likelihood (ML) methods for ancestral character state reconstruction (Schluter et al. 1997), and simulation methods (Martins and Garland 1991; Garland et al. 1993).

Perhaps because the BM model does not adequately de-

scribe change in adaptive characters, several investigators have attempted to improve the fit of the BM model in comparative analyses. These modifications fall into two basic categories. The first weakens the strength of the BM to the point that the model becomes nonphylogenetic and selects the best-fitting model from among this class (e.g., Mooers et al. 1999; Freckleton et al. 2002). The difficulty with this approach is that BM is a pure drift process, and one does not obtain a selection model from BM by merely weakening its strength. The second approach transforms the phylogeny in an attempt to improve the fit of the BM model. In particular, one transforms phylogenetic branch lengths or interspecific distance measures until the fit of the BM model is acceptable (Grafen 1989; Gittleman and Kot 1990; Garland et al. 1992; Pagel 1997). Although this approach results in statistically valid analyses, distortion of the phylogeny confuses interpretation of the model and makes it difficult to infer information about the evolutionary process.

The fundamental limitation of these BM-based methods is that they take no account of selection. Because the modifications referred to above remain based on a BM model of evolution, they share the essential features of BM, features that are at odds with the notion of natural selection. In particular, if two species are in different selective regimes, we expect their mean phenotypes to differ. In all BM-based models, however, all lineages share the same expected mean phenotype. Moreover, at least when stabilizing selection is present, we expect the variance in mean phenotypic traits to remain bounded. In BM-based models, by contrast, this variance grows with time in an unbounded fashion. These technical issues aside, biologists think about adaptive evolution as being driven by natural selection. Moreover, as we show in this article, tools are available to model selection directly. Why, then, would one only use a model that is purely neutral?

Hansen (1997) made an innovative contribution to the modeling of adaptive hypotheses. Following the suggestion of Felsenstein (1988), he proposed to model evolution by means of the Ornstein-Uhlenbeck (OU) process with multiple evolutionary optima. Although his approach is both powerful and flexible, it has received little attention (but see Hansen et al. 2000; Martins 2000; Blomberg et al. 2003; code for regression analysis of a limited, two-regime model is also available within the package COMPARE, Martins 2004). In this article, we show that the class of models introduced by Hansen (1997) is a powerful tool for comparative analysis in the presence of natural selection. Building on Hansen's foundation, we provide the mathematical background, interpretation, and computer code needed for comparative biologists to utilize these methods. We first show how the BM and OU models are related and briefly discuss the interpretation of the OU model. Next, we explain in some detail how one may model adaptive evo-

lution by hypothesizing the operation of different selective regimes along the various branches of the phylogeny. We discuss protocols for specifying a limited number of alternative models. Finally, we show how statistical model selection techniques for discriminating among evolutionary hypotheses may be applied. We illustrate the method using two worked examples.

The Ornstein-Uhlenbeck Model and Its Evolutionary Interpretation

The OU model is the simplest mathematical expression for an evolutionary process with selection. It differs from BM in that it possesses a selective optimum. It is important to note, however, that it includes BM as a special case. As one varies its parameters, one obtains a variety of distributions that are collectively consistent with phenotypic evolution under both drift and selection.

In order to better understand the OU process and the role it plays in our approach to comparative analysis, we will spend some time developing the model and discussing its evolutionary interpretation. Let us begin by considering the evolution of a quantitative character X along one branch of a phylogenetic tree. We can decompose the change in X into deterministic and stochastic parts. The former may be interpreted as the force of selection acting on the character, the latter as the effect of random drift and other, unmodeled, forces. Accordingly, the OU model has two terms:

$$dX(t) = \alpha[\theta - X(t)]dt + \sigma dB(t). \quad (1)$$

Equation (1) expresses the amount of change in character X over the course of a small increment of time: specifically, $dX(t)$ is the infinitesimal change in the character X over the infinitesimal interval from time t to time $t + dt$. The term $dB(t)$ is "white noise"; that is, the random variables $dB(t)$ are independent and identically distributed normal random variables, each with mean 0 and variance dt . The parameter α measures the strength of selection. When $\alpha = 0$, the deterministic part of the OU model drops out and equation (1) collapses to the familiar BM model of pure drift,

$$dX(t) = \sigma dB(t). \quad (2)$$

The parameter σ measures the intensity of the random fluctuations in the evolutionary process. Figure 1 shows the effect of varying σ in a simple BM process.

In the OU model equation (1), the force of selection is given by the deterministic term

$$\alpha[\theta - X(t)]dt. \quad (3)$$

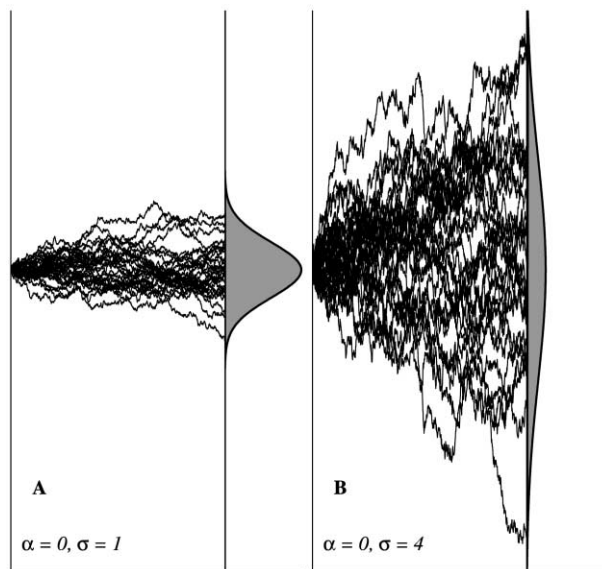


Figure 1: Effect of varying σ in a Brownian motion (BM) process. Plotted are random walks through time for a continuous character with phenotypic value along the Y-axis and time along the X-axis. At each small step in time, the phenotype has an equal and independent probability of increasing or decreasing in value. Increasing σ results in stronger random drift and a broader distribution of final states. Because Ornstein-Uhlenbeck (OU) processes contain a drift component, increasing σ also broadens the distribution of final states in OU processes. Each panel displays 30 realizations of the stochastic process and the distribution of final states (the Gaussian curves to the right of the random walks). The process is simulated from $t = 0$ to $t = 1$, with each realization having the same initial state. An animation of this process is provided in the online edition of the *American Naturalist*.

This term is linear in X , so it is as simple as it might possibly be. It contains two additional parameters: α measures the strength of selection, and θ gives the optimum trait value. The force of selection is proportional to the distance, $\theta - X(t)$, of the current trait value from the optimum. Thus, if the phenotype has drifted far from the optimum, the “pull” toward the optimum will be very strong, whereas if the phenotype is currently at the optimum, selection will have no effect until the stochasticity moves the phenotype away from the optimum again or there is a change in the optimum, θ , itself. Because of its dependence on the distance from the optimum, the OU process can be used to model stabilizing selection. The effect of varying α can be seen in figure 2.

Because the OU model reduces to BM when $\alpha = 0$, it can be viewed as an elaboration of the BM model. As a statistical model, its primary justification is to be sought in the fact that it represents a step beyond BM in the direction of realism while yet remaining mathematically tractable. As a model of evolution, the OU process is con-

sistent with a variety of evolutionary interpretations, two of which we mention here.

Lande (1976) showed that under certain assumptions, evolution of the species’ mean phenotype can take the form of an OU process. In Lande’s formulation, both natural selection and random genetic drift are assumed to act on the phenotypic character; the OU process’s optimum θ denotes the location of a local maximum in a fitness landscape. Felsenstein (1988) pointed out that in the event that this optimum itself moves randomly, the correct description of the phenotypic evolution is no longer exactly an OU process, but an OU process remains a good approximation.

Hansen (1997) raised questions concerning the timescale of the approach of a species’ mean phenotype to its optimal value relative to that of macroevolution. Specifically, he suggested that the macroevolutionary OU process he proposed could only operate on far too slow a timescale to be identical with the Landean OU process (cf. Lande 1980). He proposed a different interpretation based on the supposition that at any point in its history, a given phenotypic character is subject to a large number of conflicting selective demands (genetic and environmental) so that its present value is the outcome of a compromise among

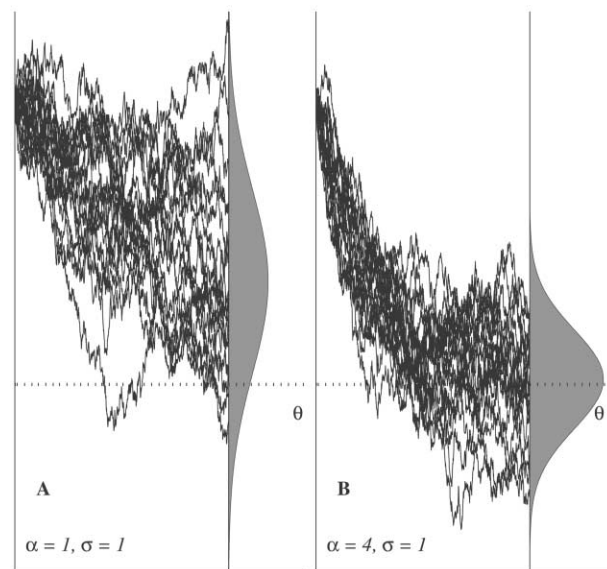


Figure 2: Influence of the selection-strength parameter α and optimum trait value θ on a trait evolving under an Ornstein-Uhlenbeck (OU) process. Larger values of α imply stronger selection and hence a more rapid approach to the optimum value θ (dotted line) as well as a tighter distribution of phenotypes around the optimum. Each panel displays 20 realizations of the OU process and the distribution of final trait values. The process is simulated from $t = 0$ to $t = 1$, with each realization having the same initial state and value of θ . See figure 1 for explanation of axes.

them. Under this interpretation, evolutionary changes on the macroevolutionary timescale occur as the balance among these selective forces shifts as the individual selective forces themselves undergo small, independent (or nearly independent) random changes. In other words, Hansen interprets the OU process as a qualitative model of the dynamics of peaks in an adaptive landscape.

Although questions of its interpretation remain open, it is clear that the OU process can be used to describe the evolution of a single lineage. One can blend in phylogenetic information by assuming that each lineage in the tree evolves according to its own OU process, that is, that there is one optimum per branch of the phylogeny. Complex evolutionary scenarios can be modeled by allowing different branches of the phylogeny to have different optima (fig. 3). We refer to this application of the OU process to evolution along a phylogenetic tree as the “Hansen model.” Each hypothesis that we wish to test is expressed as a particular arrangement of optima on the branches of the phylogeny. The arrangement of optima is naturally guided by any biological insight we may have into the selective regimes currently and historically operative in our study system. Each hypothesis yields a different distribution of phenotypes, which may then be used directly as the basis for an ML approach to statistical inference. We now describe, in some detail, the implementation of the Hansen model.

Nuts and Bolts

In this section, we demonstrate how the OU process can be integrated with phylogenetic information and biological hypotheses to give specific predictions on the distribution of trait values. Three components are needed: (1) a set of data on the distribution of a quantitative character across species, (2) a phylogeny with branch lengths showing the evolutionary history of the species in question, and (3) one or more hypotheses regarding the selective regimes operative on each of the branches in evolutionary time. In this framework, and in keeping with other comparative methods, components (1) and (2) comprise the data while the hypotheses (3) translate into models to be fit to the data. Each assignment of adaptive regimes to phylogenetic branches gives a distinct model that is then fit to the data. Model selection criteria, which take into account both number of parameters and goodness of fit, can then be applied as a basis for scientific inference.

We comment here on two issues involving the phylogeny: on polytomies and on the units in which branch lengths are reported. First, for the application of Hansen’s model, it is not necessary that the phylogeny be fully resolved: polytomies pose no difficulties in the computations. We stress, however, that in this approach, phylog-

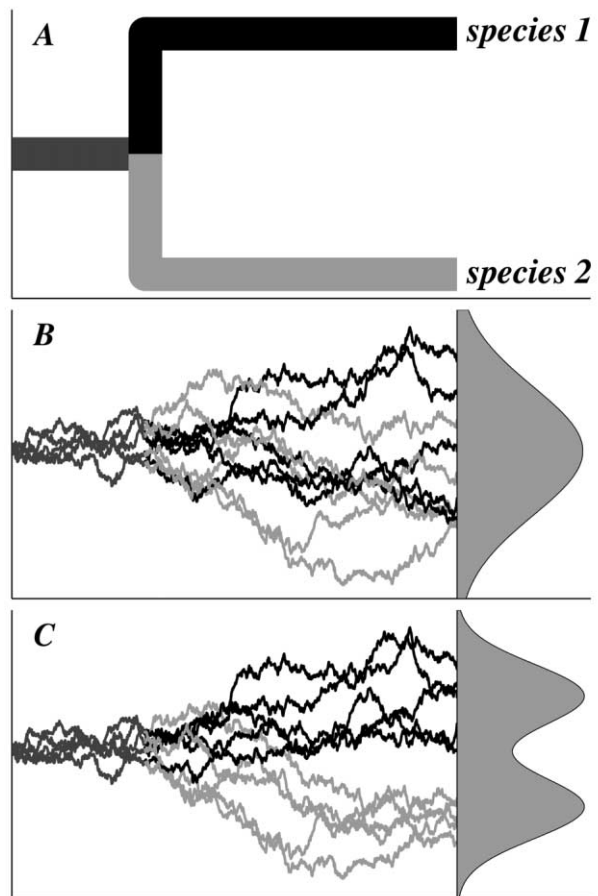


Figure 3: Simulations of Brownian motion (BM) and multiple-optimum Ornstein-Uhlenbeck (OU) processes with branching. Phenotypic value along Y-axis, time along X-axis. *A*, A single lineage evolves until a speciation event occurs from which two lineages (light gray, black) emerge. *B*, Lineages evolve according to BM, with light gray and black lineages evolving independently after the speciation event. *C*, Lineages evolve under an OU model. A single selective regime exists before the speciation event; two distinct selective regimes afterward. Distributions of the evolving quantitative character are shown at right. Brownian motion produces a unimodal trait distribution centered at the initial (ancestral) value, whereas the OU process results in a multimodal trait distribution with peaks near each optimum. An animation of this process is provided in the online edition of the *American Naturalist*.

enies are assumed to accurately reflect the evolutionary history of the system in question. Thus, polytomies are assumed to reflect true radiation and not phylogenetic uncertainty. The effect of phylogenetic uncertainty on comparative hypotheses is an important topic; in this article, we give only a brief indication of how phylogenetic uncertainty can be incorporated into the model-selection procedure. Second, the Hansen model requires phylogenetic branch lengths to be on a common timescale. Because the units of α and σ are directly related to time, inter-

pretation of these model parameters will be difficult if the phylogeny is not clocklike.

Figure 4 shows the simplest nontrivial phylogenetic tree. The phylogeny spans a total period of T years, and the speciation event at which species 1 and 2 diverged occurred at time $t = s$. The ancestral state, at time $t = 0$, is denoted by the unknown θ_0 , which will be estimated from the data.

We can write the quantitative character in vector format, with separate entries X_i for each lineage,

$$\mathbf{X}(t) = \begin{bmatrix} X_1(t) \\ X_2(t) \end{bmatrix}.$$

Under the BM model, the two lineages are supposed to have evolved together according to a purely random drift from $t = 0$ to $t = s$ (so that $X_1(t) = X_2(t)$ for $0 \leq t \leq s$). Thereafter, they continued to drift independently. The distribution of $X(T)$ under the BM model is bivariate normal with expectation and variance-covariance matrix

$$\begin{aligned} E[\mathbf{X}(T)] &= \begin{bmatrix} \theta_0 \\ \theta_0 \end{bmatrix}, \\ \mathbf{V} &= \sigma^2 \begin{bmatrix} T & s \\ s & T \end{bmatrix}. \end{aligned} \tag{4}$$

Because the mean and variance-covariance matrix completely determine the distribution of $\mathbf{X}(T)$, one can readily apply ML methods for the estimation of the parameters θ_0 and σ .

Similarly, the Hansen model gives a multivariate normal distribution for $\mathbf{X}(T)$. For illustrative purposes, let us make the hypothesis that species 2, after its divergence from species 1 at $t = s$, evolved under a new selective regime, characterized by the optimum trait value θ_2 (fig. 4). Species 1, by contrast, continued to evolve under the ancestral regime, which is characterized by the optimum θ_1 . In this model, again, the distribution of $\mathbf{X}(T)$ is bivariate normal. The expected mean trait values at the end of each evolutionary lineage can be computed from equation (A2) in the appendix in the online edition of the *American Naturalist*:

$$\begin{aligned} E[X_1(T)] &= \theta_0 e^{-\alpha T} + \theta_1 (1 - e^{-\alpha T}) \\ &= W_{10} \theta_0 + W_{11} \theta_1, \\ E[X_2(T)] &= \theta_0 e^{-\alpha T} + \theta_1 e^{-\alpha(T-s)} (1 - e^{-\alpha s}) \\ &\quad + \theta_2 [1 - e^{-\alpha(T-s)}] \\ &= W_{20} \theta_0 + W_{21} \theta_1 + W_{22} \theta_2. \end{aligned} \tag{5}$$

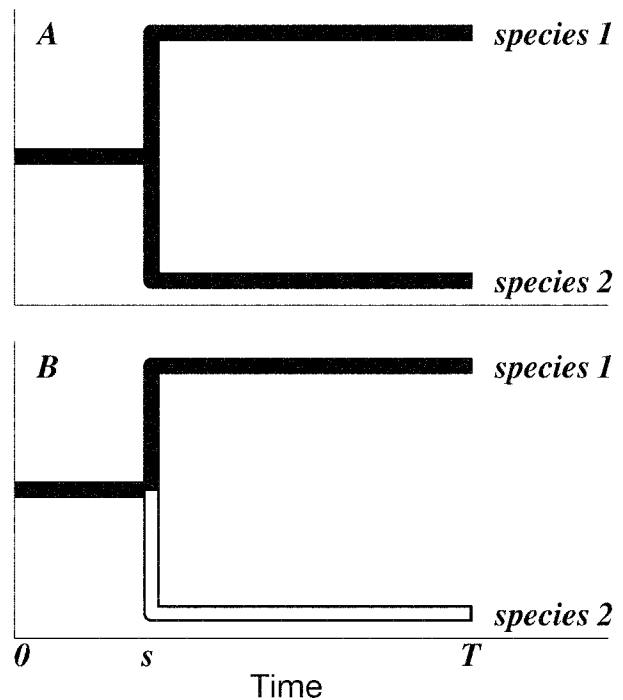


Figure 4: Specification of multiple optima in the Hansen model. *A*, Two species evolve according to a Brownian motion process with a speciation event at time s , after which they evolve independently. *B*, Two species evolving under an Ornstein-Uhlenbeck process. After the speciation event at time s , species 2 entered a new adaptive regime specified by θ_2 (white bar), whereas the lineage leading to species 1 has been evolving under the same adaptive regime with optima θ_1 (black bar) for its entire history.

We find that each expectation is a weighted sum of the parameters θ_0 , θ_1 , and θ_2 . Hence, we can write equation (5) in vector form as $E[\mathbf{X}(T)] = \mathbf{W}\boldsymbol{\theta}$, where \mathbf{W} is the matrix of weights and $\boldsymbol{\theta}$ the vector with entries θ_0 , θ_1 , and θ_2 . The variance-covariance matrix is

$$\mathbf{V} = \frac{\sigma^2}{2\alpha} \begin{bmatrix} 1 - e^{-2\alpha T} & e^{-2\alpha(T-s)}(1 - e^{-2\alpha s}) \\ e^{-2\alpha(T-s)}(1 - e^{-2\alpha s}) & 1 - e^{-2\alpha T} \end{bmatrix}.$$

It is important to note that both the expectation and the variance-covariance matrix tend to equation (4), as $\alpha \rightarrow 0$. Hence, the BM model is nested within the class of Hansen models. As before, because $\mathbf{X}(T)$ is distributed multivariate normally, it is easy to apply ML methods to estimate the parameters, which include α , θ_1 , and θ_2 in addition to σ and θ_0 . Because both the BM and Hansen models are multivariate normal (differing only in $E[\mathbf{X}(T)]$ and \mathbf{V}), their log-likelihood equation is

$$-2 \log \mathcal{L} = \{\mathbf{X}(T) - E[\mathbf{X}(T)]\}' \mathbf{V}^{-1} \\ \times \{\mathbf{X}(T) - E[\mathbf{X}(T)]\} + N \log(2\pi \det \mathbf{V}) \quad (6)$$

The only new wrinkle that arises with the Hansen model is due to the fact that α enters into equation (6) in a nonlinear fashion, and hence nonlinear optimization is needed to estimate this parameter. Full mathematical and computational details are given in the appendix; computer code is available at the authors' Web site (<http://www.tiem.utk.edu/~king>).

Examples

In this section, we provide a guide to the implementation of the Hansen model by means of examples; a technical description of the method can be found in the appendix. For each evolutionary hypothesis, we will obtain a model by assigning an optimum to each branch of the phylogeny. Therefore, we examine our hypotheses and determine how many optima each requires. One optimum will be required for each hypothesized selective regime. Next, we make our hypotheses phylogenetically explicit by "painting" the optima on the appropriate branches of the phylogeny. This association of hypothesized optima to branches is translated into a mathematical model in which, as we have seen above, the expected value of a species' trait is a weighted average where the weights depend on how long each lineage has evolved under each regime. Likelihood maximization then fits the parameter values for each model to the data. Finally, we compare the fit of the alternative models using standard model selection methods including the likelihood ratio test and information criteria (Akaike Information Criterion [AIC] and Schwarz Information Criterion [SIC]; Burnham and Anderson 2002).

Character Displacement in Lesser Antillean Anolis Lizards

Introduction. In our first example, we reexamine the case for character displacement in *Anolis* lizards of the northern Lesser Antilles. Each of these small islands supports either one or two species of anoles. A regular pattern of body sizes across islands exists: on the two-species islands, anoles differ substantially in size (one species large, the other small), while on the one-species islands, lizards are intermediate in body size (fig. 5). Previous workers (Schoener 1970; Lazell 1972; Williams 1972) have suggested that the differences in size among these species is the result of character displacement. That is, initially intermediate-sized species came into sympatry and evolved in opposite directions.

Because it contains more taxa for which we have body

size data, we use the phylogeny of Losos (1990), which is based on morphological (Lazell 1972) and protein-electrophoretic (Gorman and Kim 1976) data rather than the more recent molecular phylogenies based on mitochondrial sequences (Schneider et al. 2001; Stenson et al. 2004). We note, however, that the phylogenies differ significantly. Our primary purpose in this article is to illustrate means by which one may evaluate evolutionary hypotheses on the basis of a given phylogeny; we leave it to the interested reader to evaluate the effects of the differences in phylogeny on various forms of the character-displacement hypothesis. To assist the reader in this, we include with our computer code alternate phylogenies based on the data of Schneider et al. (2001) and Stenson et al. (2004).

In the late 1980s, with the advent of ancestral reconstruction methods, several workers reexamined phylogenetic versions of the character-displacement hypothesis (Losos 1990; Miles and Dunham 1996; Butler and Losos 1997). These studies can be criticized on at least two counts. First, to the extent that ancestral character-state reconstructions are model based, the evolutionary model used is neutral, that is, BM. A hypothesis of character displacement clearly implies selection, however, so that BM is an inappropriate model of this process. Second, it is very difficult to accurately estimate ancestral character values (Frumhoff and Reeve 1994; Butler and Losos 1997; Schluter et al. 1997; Oakley and Cunningham 2000; Polly 2001; Webster and Purvis 2002). We circumvent both difficulties here by testing alternative models that include selection and explicitly incorporate the character displacement hypothesis into the evolutionary model without requiring the estimation of ancestral states.

Alternative Evolutionary Models. We tested five different models of the evolution of body size (fig. 5). The two simplest models are naive and require no biological insight. These are BM and an OU process with one optimum, OU(1). The OU(1) models a single (global) optimum for all species. The next model adds two additional optima so that we have separate optima for large, intermediate, and small size; we call this model OU(3). This model incorporates the fewest assumptions while containing three optima. Internal branches are painted intermediate, whereas terminal branches are painted according to the ecological and body size conditions of the terminal taxa (i.e., isolated species are assumed to have evolved within the intermediate regime, whereas species that coexist with a congener are assumed to have evolved within the small regime if they are the smaller of the pair and within the large regime if they are the larger. The OU(4) model adds one additional parameter so that we can separately estimate the adaptive regime of the internal branches as an unknown ancestral

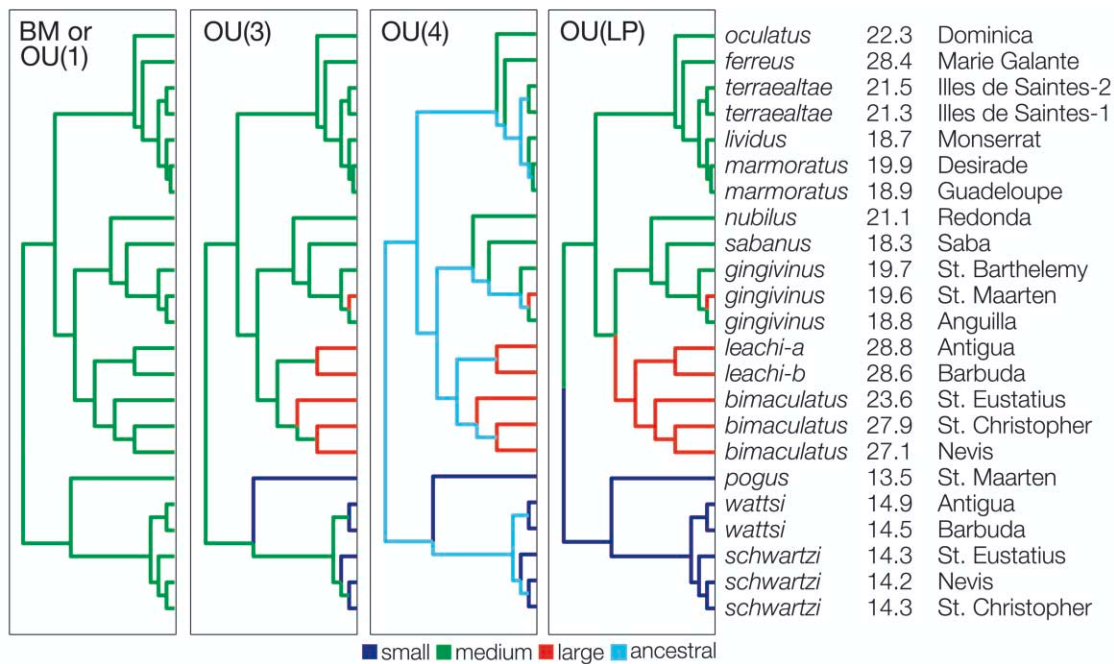
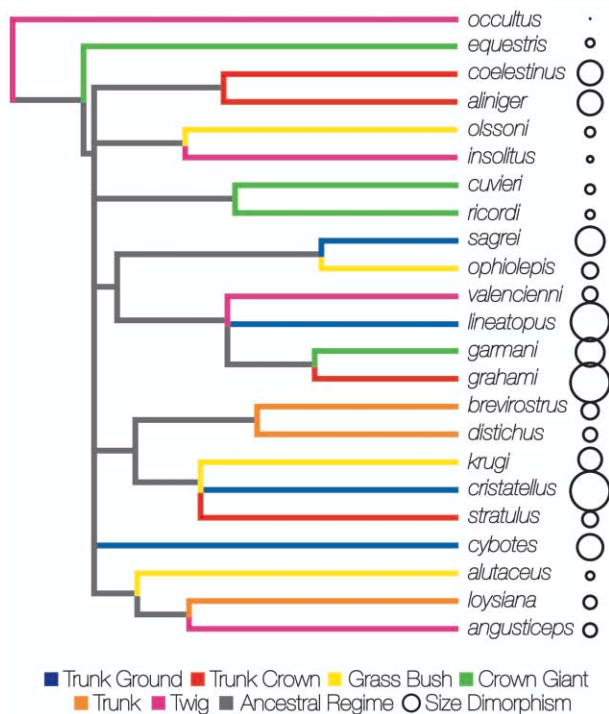


Figure 5: Alternative adaptive regime models for character displacement. *BM* = Brownian motion; *OU* = Ornstein-Uhlenbeck with one (1), three (3), or four (4) optima or based on linear parsimony (*LP*) reconstruction of colonization events (see text). Color codes indicate body size regimes. Timescale of the phylogeny is standardized to 1.0 from most basal node to terminal species. Data and phylogeny reproduced from Losos (1990) and Butler and Losos (1997). All species belong to the *Anolis bimaculatus* series. Species name, body size (mean values for jaw length of upper one-third of male specimens in millimeters), and island name are given.



regime. The final and most complex model is that implied by a linear parsimony reconstruction of the colonization events, that is, arrivals of second species on one-species islands. We call this model *OU(LP)*. Where species are inferred to have existed singly, the branches are painted with the intermediate optimum, and where species are inferred to exist with a congener, the branches are painted with the small optimum if the branch leads to the smaller species of the pair or with the large optimum if the branch leads to the larger species of the pair.

Results and Discussion. The overall fit of each of the five models is summarized in table 1. Each *OU* model was tested against *BM* using the likelihood ratio test, and all

Figure 6: Full adaptive regime model for size dimorphism associated with habitat type. Color codes indicate separate adaptive regimes for the different habitat types (ecomorphs). Diameter of circles are proportional to the degree of sexual size dimorphism ($\log[\text{male body length}/\text{female body length}]$). Data from Butler et al. (2000). Phylogeny (based on mtDNA) compiled from Jackman et al. (1997); Jackman et al. (1999; see Butler et al. 2000 for details). All species are within the genus *Anolis*. Timescale of the phylogeny is standardized to 1.0 from most basal node to terminal species.

Table 1: Performance of alternative models for body size evolution in the character displacement study

	BM	OU(1)	OU(3)	OU(4)	OU(LP)
$-2\log\mathcal{L}$	-34.66	-34.66	-40.21	-47.22	-49.69
AIC	-30.66	-26.66	-28.21	-33.22	-37.69
SIC	-28.39	-22.12	-21.40	-25.27	-30.88
LR		0	5.55	12.56	15.03
<i>P</i> value		1	.24	.028	.0046

Note: For each model, the likelihood values ($-2\log\mathcal{L}$), Akaike Information Criterion (AIC), likelihood ratio test value (LR), and associated *P* values are given. The LR tests were conducted for each model versus Brownian motion. Columns contain alternative evolutionary models. Model abbreviations are as follows: BM = Brownian motion, OU = Ornstein-Uhlenbeck with one (1), three (3), or four (4) optima or based on linear parsimony (LP) reconstruction of the colonization events (see text). For the OU(1) model, the best-fit $\alpha = 0$; therefore, the OU(1) and BM models are identical.

models were compared using the Akaike Information Criterion (AIC) and the more conservative Schwarz Information Criterion (SIC; also known as Bayes Information Criterion, or BIC). The likelihood ratio results were very similar to the AIC results. The best-fitting model, by any criterion, was the OU(LP), which was much better than BM. The worst-fitting model was not BM but OU(1). In fact, BM also performed better than OU(3) and was comparable in performance to OU(4). Similarly, the SIC picked out OU(LP) as the best but ranked it as only marginally better than BM.

The parameter estimates for these five models provide additional insight into model performance (table 2). The strength of selection (α) estimated for the OU(1) model is 0, and the algorithm failed to estimate a value for the optimum. The remaining parameters for the OU(1) model are identical to those estimated for the BM model. So the OU(1) model here describes BM but does so with two additional parameters (for which it is penalized). Parameter estimates for OU(3) and OU(4) are also problematic. The OU(3) model suggests weak selection with unrealistically small optima for the small and intermediate body size regimes (resulting in head lengths of 0.25 mm and 1.2 mm, respectively). The OU(4) model suggests very strong selection ($\alpha = 14.67$) and fails to estimate the initial state at the root of the phylogeny (see the section “Notes on the Implementation” in the appendix). The best performing model, OU(LP), suggests strong selection ($\alpha = 2.49$) with moderate drift ($\sigma = 0.22$; comparable to that estimated for the BM model $\sigma = 0.20$) and biologically reasonable optimal values.

We note that the value estimated for the root of the phylogeny is very small. However, because selection is strong, there is very little dependence of the traits of extant species on the value at the root. We can calculate the dependence as follows: the conditional expectation of the

phenotypic value at the end of the evolutionary process is a linear function of the root ancestral state and the optima along each tree segment of the lineage, weighted by the strength of selection. Using equation (A3) with $\alpha = 2.49$ and $T = 1$, the tip values on this phylogeny have an $e^{-(2.49)(1)}$ or 8% contribution from the ancestral root value and a 92% contribution from the optima along each lineage.

Our analysis of these data results in three main findings. First, the best model was an adaptive model describing character displacement under both strong selection and moderate drift. Second, the neutral BM model performed better than the “wrong” adaptive models, OU(1) and OU(3). Finally, the specification of the optima on the internal branches is critical to model performance and evolutionary conclusions. We note in passing that Freckleton et al. (2002), analyzing the same data, found support for the BM model over a “nonphylogenetic” model. They did not test an explicitly adaptive model. It is interesting to note that had we not considered the OU(LP) model, we would have selected a BM model over the more naive OU models. It is important to bring biological information to the formulation of hypotheses of adaptive evolution.

Sexual Dimorphism and Habitat Use in Greater Antillean Anolis Lizards

Anoles of the Greater Antilles are a well-studied example of ecological diversification (see Losos 1994 for a review).

Table 2: Parameters estimated for the five models comparing character displacement with alternative hypotheses

	BM	OU(1)	OU(3)	OU(4)	OU(LP)
α		0	.32	14.67	2.49
σ	.21	.21	.20	.47	.22
θ_0	2.95	2.95	3.99	... ^a	.86
θ_{small}		... ^a	-1.40	2.58	2.75
θ_{medium}			.18	3.11	3.24
θ_{large}			2.71	3.30	3.56
$\theta_{\text{ancestral}}$				2.83	

Note: The evolving character is log body size (mm). Model abbreviations are given in table 1. The model parameters (in rows) are as follows: α = strength of selection in OU models; σ = strength of random drift; θ_0 = estimated ancestral value for the most basal node of the tree; θ_k (k = small, medium, large, ancestral) = optima estimated for the different selective regimes. The Brownian motion model has only two parameters, σ and ancestor. The OU models have an additional parameter for the strength of selection and the one additional parameter for each optimum included in the model.

^a Ellipsis dots indicate cases where the algorithm failed to estimate a parameter (see “Notes on the Implementation” in the online edition of the *American Naturalist*).

Nearly the same set of six different ecomorphs has evolved on each of the Greater Antillean islands, and they have convergently evolved morphology to match their respective habitat types. These species are also characterized by a wide range of sexual size dimorphism (SSD). Previously, Butler et al. (2000), using phylogenetic simulation methods and a phylogenetic generalized least squares (phylo-GLS) regression of SSD on habitat type, established that SSD evolves in association with habitat use. The alternative models used in the phylo-GLS regression were BM and a single-optimum OU process. The OU model optimum, because it was left out of that model, was effectively fixed at a value of 0.

Alternative Evolutionary Models. We formulate three models to describe the evolution of SSD in this system. The first two are the neutral drift and single-optimum adaptive models used in the preceding example; BM and OU(1) respectively. The third is an adaptive model based on biological information. Specifically, we allowed a separate optimum for each of the six habitat types. We assigned optima on the terminal branches of each lineage according to the habitat type of the terminal taxon. We additionally estimated an “ancestral regime” optimum for all internal branches (fig. 6). We refer to this model as OU(7).

Results and Discussion. While again the BM model slightly outperformed OU(1), the OU(7) model performed much better than them both (table 3). The best model was again an adaptive one with strong selection ($\alpha = 1.44$). We estimated confidence intervals for the parameters using a parametric bootstrap (table 4). The optima for the low SSD ecomorphs (grass bush, crown giant, twig, and trunk) overlap broadly and differ substantially from the high SSD trunk ground and trunk crown types.

The conclusion that an association exists between habitat type and sexual size dimorphism and the finding of two broad SSD categories are consistent with the results of the earlier analysis (Butler et al. 2000), but the additional information gleaned here is that our data clearly support

Table 4: Model parameters estimated for the OU(7) model describing adaptive evolution of sexual dimorphism to habitat type

	OU(7)	95% CI
α	1.44	(.28, 5.83)
σ	.0885	(.045, .15)
θ_0	.228	(.0051, .28)
$\theta_{\text{trunk-ground}}$.327	(.23, .87)
$\theta_{\text{trunk-crown}}$.134	(-.014, .286)
$\theta_{\text{grass-bush}}$	-.0129	(-.40, .14)
$\theta_{\text{crown-giant}}$	-.0605	(-.54, .11)
θ_{twig}	-.0740	(-.56, .085)
θ_{trunk}	-.0513	(-.60, .14)
θ_{unknown}	.468	(.33, 1.47)

Note: Parameters α , σ , and θ_0 are as in table 2. The character evolving in this case is log sexual size dimorphism (SSD), thus the optima in the OU(7) model represent adaptive peaks for log SSD in each habitat type as well as a single ancestral optimal log SSD for the internal branches of “unknown” habitat type. Confidence intervals were obtained using a parametric bootstrap (see online appendix).

a multiple optimum model with strong selection over simpler models (single-optimum OU or BM). In addition to the greater detail afforded by the modeling approach, the analysis itself is simpler and easier to interpret. In the previous study, Butler et al. (2000) used the phylo-GLS method to adjust the association among species for the effects of phylogeny (removing putative phylogenetic covariance) and then conducted statistical tests on the “phylogenetically corrected” data. With such phylogenetically corrected data, the interpretation of the evolutionary process is harder because the analysis is conducted in a two-step process. Effectively, the first step “removes” the effect of drift, and the second step tests for association between the character and an ecological factor. However, no evolutionary biologist envisions the evolutionary process occurring this way; a model in which both the adaptive process and stochastic evolution are in intimate association is closer to our modern conception of the process of evolution.

Broader Conclusions

Hypothesis-Testing versus Model-Based Approaches to Comparative Studies

For our purposes, statistical approaches to scientific inquiry can be viewed as following two broad paths: the hypothesis-testing approach and the model-based approach. Models enter into both approaches but play different roles. Historically, the hypothesis-testing approach is the more commonly followed in comparative studies

Table 3: Performance of alternative models for the hypothesis of evolutionary association between habitat and sexual dimorphism

	BM	OU(1)	OU(7)
$-2 \log \mathcal{L}$	-38.35	-38.44	-72.71
AIC	-34.35	-30.44	-52.71
SIC	-32.08	-25.90	-41.36
LR		.086	34.4
<i>P</i> value		.96	.00004

Note: Abbreviations are as in table 1. The OU(7) model estimates an optimum for each habitat type plus one for an unknown ancestral type.

and is indeed the approach of comparative methods that employ a “phylogenetic correction.” In the hypothesis-testing approach, the scientific question is formulated as a null hypothesis. Sometimes alternative hypotheses are posed too; the most powerful examples of this approach test all possible alternative hypotheses simultaneously. In seeking to reject a hypotheses, the emphasis of this approach is on establishing what the phenomenon under study is not. The model-based approach, in contrast, attempts to establish what the phenomenon under study is, by developing approximations to it. Thus a variety of hypotheses are translated into explicit models and compared with data, and the best models are identified. By a process of model refinement, we can more closely examine which assumptions are supported and which are not. Information-based model selection statistics aim for a good balance between model complexity and explanatory power: each parameter added to the model must provide a significantly better explanation of the data.

In any comparative analysis, there are at least two levels at which a model of evolution can enter. At the most basic level, a model of evolution allows us to “correct” for the nonindependence of species. As Felsenstein (1985) first pointed out, because species are related to varying degrees, species-specific phenotypic characters are nonindependent. This fact complicates any statistical analysis of interspecific traits. A model of evolution combined with a phylogeny can be used to estimate the covariance structure of the interspecific data. This estimate can in turn be used to correct for the nonindependence. This goal falls in line with the hypothesis-testing approach. At this level, the signature of evolution’s history is merely noise that one desires to be rid of. Going beyond this level, one can compare models of evolution in an attempt to uncover details about the strength, direction, and history of evolution and differences in its action on different taxa. Using this method, one can potentially answer such questions as, do the data support evidence for both selection and drift? what is the strength of selection, relative to that of drift? what is the form of selection? and, can we identify selective optima?

Advantages of an Adaptive Model

In the Hansen model, evolutionary biologists have a tool with which to model natural selection directly. It therefore makes little sense to continue to use only purely neutral models of evolution when our interest is in characters that may be adaptive. Moreover, a direct modeling approach allows biologists to extract more information from their data. One can rigorously compare evolutionary models, glean specific details of the evolutionary process, and exploit the information inherent in long periods of evolu-

tionary stasis (Schwenk and Wagner 2001). We discuss these advantages in detail here.

Rigorous Model Comparison and the Details of the Evolutionary Process. Machinery for discrimination among alternative models is a major achievement of modern statistics. This machinery has been used extensively in phylogenetic systematics, but its application to comparative biology is still relatively new. Because many models will produce slightly different results, we need a rigorous basis for choosing which models are significantly better than others. In addition, we prefer the simplest model that accounts for most of the important variation. Thus, an important feature of model selection machinery is a penalty for additional parameters so that the improvement in fit must be substantial enough to outweigh the cost associated with an additional parameter.

However, applying sophisticated model selection techniques is not an improvement unless the models themselves are interesting. One gains little by using BM as an evolutionary model and rejecting it without any reasonable alternatives. In such a case, the most one can say is that pure drift is not a good model. We gain much more by comparing biologically interesting models. Models of the Hansen type, as a class, are biologically reasonable and capable of generating a wide range of evolutionary behaviors. One can obtain trait distributions characteristic of everything from pure drift to strong directional or stabilizing selection. Thus, using the Hansen model and model-selection techniques, one can ask questions such as, do the data give more support to scenarios involving two or three selective regimes? are the selective optima significantly different? which historical order of shifts in selective regime are supported? what is the strength of drift? and, what is the strength of selection?

The answers to these questions provide insight into the evolutionary process. However, in order to compare the strengths of selection and drift across studies, one must standardize timescales. This is because the influence of selection on the final trait values is a function of the combination αT . However, we can obtain a time-standardized measure of the strength of selection acting on the character of interest using equation (A3). This equation describes the conditional expectation for the trait value given the root character value. It computes the percentage of trait variation in our clade resulting from common ancestry (the influence of the root value) versus selection toward the optima along each lineage. It amounts to a weighted average of the selective optima where the weights are related to the times that each lineage has spent in each selective regime.

Information in Stasis. A further advantage of the modeling

approach is that long periods without phenotypic change are informative (Baum and Donoghue 2001). This fact is unexploited by existing parsimony-based approaches, which reduce even large data sets to the small number of changes that can be inferred. This not only frustrates the investigator who sees so little use made of her data but also “throws away” all data that document stasis. The conclusions of such an analysis will be the same whether or not stasis has occurred despite the fact that stasis is positive evidence for stabilizing selection.

If one has a phylogeny in which stasis has occurred, then one can fit a BM-based model. If the phenotypes of the extant species do not differ too widely, then one can even get a good fit. However, the intensity of random drift will be underestimated. If the phenotypes of the extant species differ widely, as would be the case, for example, if strong stabilizing selection with different optima were operative, then BM-based models will give a poor fit. As we have seen, however, OU-based models can accommodate multiple evolutionary optima. It is in this situation that the ability to distinguish between stabilizing selection (strong selection to different optima) versus low levels of drift (small σ) becomes an interesting advance over previous methods.

Our method is a simple way to utilize the information contained in the phylogeny. In our implementation, we chose to require that optima were constant in time except at discrete events where changes in selective regime occurred. We further insisted that these changes in regime coincide with phylogenetic branch points. These assumptions are arbitrary and are nothing more than an expedient to limit the number of hypotheses and simplify the equations. Other choices of more or less generality might easily be at least as useful. Any such choice, however, will lead to bias of one sort or another. In our case, our refusal to consider hypotheses in which changes in selective regime occur more frequently than speciation events results in an underestimation of the strength, α , of selection. Of course, because one typically has no independent information whatsoever about events deep in time or about historical environments, one is forced to live with such biases if one wishes to talk about the effects of past selection. We emphasize that nothing in our development depends on these arbitrary assumptions: regardless of how one specifies the OU-process optima, one obtains a tractable statistical model.

How Complex a Model Should One Use?

A related difficulty that has been noted previously (Price 1997) is that while BM has only one form, there are an infinite number of adaptive models possible. Thus, the question naturally arises, how detailed an adaptive scenario

should one use? Certainly the Hansen model is general enough to incorporate greater detail, such as fossil evidence that may suggest that selective regimes changed within branches (and not only at speciation events; see Hansen 1997). With more biological information, it would be possible to go to even further detail. The issue then becomes how much information in terms of data do we need in comparison with the complexity of the model? Clearly, we need to have more taxa (data points) than we have parameters to estimate (the number of optima plus three). Increasing the number of parameters will, in general, improve model fit but reduce the confidence we can place in parameter estimates. Information criteria, such as the AIC and SIC we employ in this article, are designed to balance these conflicting imperatives.

Uncertainty in the Phylogeny

Throughout the foregoing theoretical development, we have assumed that the given phylogeny is true. Let us say a few words here about the effects of uncertainty in the phylogeny itself. As we have shown, if we are given data X , a phylogenetic tree Φ , and a hypothesis \mathcal{H} regarding the disposition of selective optima along the branches of the phylogeny (how we have “painted” the tree), then the Hansen model gives us a likelihood

$$\mathcal{L}(\alpha, \sigma, \theta | \Phi, \mathcal{H}, \mathbf{X})$$

(see appendix). It is immediately evident that if we are able to express the uncertainty inherent in our estimation of the phylogeny itself in terms of a likelihood, $\mathcal{L}(\Phi)$, we thereby obtain a likelihood for the data that is unconditional on the phylogeny:

$$\mathcal{L}(\alpha, \sigma, \theta | \mathcal{H}, \mathbf{X}) = \mathcal{L}(\alpha, \sigma, \theta | \Phi, \mathcal{H}, \mathbf{X}) \mathcal{L}(\Phi).$$

Because of this fact, it is straightforward to gather the estimation of the phylogeny together with the estimation of the evolutionary process (modeled as an OU process) into a single model-selection procedure. We emphasize that the data on which the estimate of the phylogeny depend should be independent of the phenotypic data X .

Concluding Remarks

The current outlook for phylogenetic comparative methods is quite positive. The Hansen model for varying adaptive regimes is both realistic and flexible. It allows us to specify tractable models that differ only in particular portions of the phylogenetic tree so that we can focus our statistical power on the resolution of alternative hypotheses of interest. Unlike existing approaches, the adaptive mod-

els that we employ here are potentially very powerful for discriminating among evolutionary hypotheses. With these tools in hand, the prospects for our ability to make substantive statements about the evolutionary process based on character data from extant taxa and a phylogeny are improved.

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