Testing models of biological diversification: morphological evolution and cladogenesis in the neotropical furnariiidae (Aves: Passeriformes)

Santiago Javier Claramunt Tammaro
Louisiana State University and Agricultural and Mechanical College, sclara1@tigers.lsu.edu

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TESTING MODELS OF BIOLOGICAL DIVERSIFICATION:
MORPHOLOGICAL EVOLUTION AND CLADOGENESIS IN THE
NEOTROPICAL FURNARIIDAE (AVES: PASSERIFORMES)

A Dissertation

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Santiago Javier Claramunt Tammaro
Licenciado en Ciencias Biológicas
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A la memoria de mi padre.
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ABSTRACT

In this dissertation I explored the processes that generated high species diversity in a continental adaptive radiation of passerine birds: the family Furnariidae. Although there is a vast amount of information on the microevolutionary mechanisms that generate speciation and adaptation, much less is known about the processes underlying large-scale patterns of diversity. I used new techniques that exploit information contained in phylogenetic trees to investigate the diversification process in Furnariidae at a macroevolutionary scale.

First, I conducted the first quantitative study that demonstrated that the Furnariidae constitute a case of rapid diversification in both species numbers and morphology as compared to six closely related families. To evaluate phenotypic diversity, I developed a new multivariate extension of the variance, which I called 'proper variance', and a new simulation procedure to test for differences in phenotypic diversity when complete phylogenies are not available. I found that the Furnariidae, although not particularly diverse in body size, is unusually diverse in shape. These results support the idea that the Furnariidae constitute a continental adaptive radiation.

To explore processes responsible for high species diversity in the Furnariidae, I first investigated the effect of dispersal ability on species proliferation. Assuming that dispersal in birds is highly influenced by flying ability, I used an index of wing shape as a surrogate for flying ability. Using a nearly complete species-level phylogeny of the Furnariidae and a recently developed method, I found a negative correlation between flying ability and speciation rates, suggesting that low dispersal has stimulated species proliferation in Furnariidae.

Finally, I investigated the effect of three key innovations on furnariid diversification: adaptations for trunk climbing, spiny-tail morphologies, and skull kinesis. I found that increases in diversification rates are not associated with major morphological changes. In addition, I found that climbing specialization had a negative effect on speciation rates, but that the spiny-tail
morphology was positively correlated with speciation rates. These results provide mixed support for a role of key innovations promoting speciation.

My results suggest a stronger role of geographic isolation (low dispersal) than ecological opportunities in species diversification in the continental radiation of the Furnariidae.
CHAPTER 1

INTRODUCTION

Understanding the processes that generated biological diversity is one of the main challenges of evolutionary biology. The basic components of the diversification process are speciation (cladogenesis) and phenotypic evolution (anagenesis). The phenotype of a lineage can influence its chances of speciation and extinction, and speciation and extinction can influence the observed patterns of distributions of phenotypes. The study of this interplay between speciation and phenotypic evolution is essential for understanding the origin and evolution of biological diversity.

An important aspect of the study of diversification is to disentangle how ecological factors and interactions influence the diversification process. Ecological factors can determine the geographic distribution of lineages and are responsible for selective pressures that stimulate phenotypic evolution and result in adaptations. In addition, theoretical, experimental, and field evidence suggest that ecological factors are responsible for divergent natural selection among populations, which can then accelerate phenotypic divergence between populations and generate reproductive isolation (Dodd 1989, Schluter 2001, McKinnon et al. 2004, Coyne & Orr 2004). In theory, geographic isolation alone can result in speciation, and a vast amount of information has been generated on the influence of geographic barriers, dispersal events, and geological history on patterns of cladogenesis. On the other hand, many believe that speciation without selection is highly unlikely (Turelli et al. 2001, Sobel et al. 2009, Butlin et al. 2009). In particular, an effect of divergent selection produced by ecological factors is at the core of proposed mechanisms for rapid diversification in adaptive radiations (Simpson 1953, Schluter 2000, Price 2008, Gavrilets & Losos 2009).
The various interpretations of the process of diversification can be organized in two general models of diversification. The first can be called a 'neutral' model of diversification, in which geographic isolation alone plays a preponderant role on speciation. In this model, speciation is triggered by barriers to dispersal and results in ecologically equivalent species. Phenotypic evolution and adaptation in this model occurs gradually along lineages and is not particularly associated with speciation events. Ecology may play a role in the neutral model by determining the distribution of organisms and barriers. However, the model is neutral in the sense that does not consider competition for niche space.

The second model can be called an 'ecological' or niche model, and is represented by the ecological theory of adaptive radiation (Schluter 2000). The basic mode of speciation in this model is ecological speciation, in which ecologically driven, divergent selection plays a fundamental role in both phenotypic evolution and cladogenesis. Divergent selection arises by ecological differences in the environment or by competitive interactions with coexisting species. In particular, this model predicts that ecological opportunities, in the form of open niche space, stimulate diversification at large scales (Simpson 1953, Schluter 2000).

Theoretical and empirical evidence revealed how both neutral and niche-based mechanisms can produce speciation and phenotypic differentiation (Coyne & Orr 2004, Price 2008). However, the preponderance of the different mechanisms in generating biological diversity at large scales is not well known. Much empirical research has been done on adaptive radiations (Givnish & Sytsma 1997, Grant 1999, Schluter 2000, Gavrilets & Losos 2009). Because adaptive radiations represent profuse manifestations of both speciation and phenotypic change, they offer rich material for the study of evolutionary mechanisms. Moreover, understanding the mechanisms responsible for high diversity in adaptive radiations may provide a bridge between microevolution and macroevolution, and may help to explain large-scale patterns of diversity.
However, most evidence for the effect of ecological factors on diversification has come from adaptive radiations in geographically isolated places (Losos & Ricklefs 2009), such as Darwin’s finches (Grant 1999), Caribbean anoles (Losos & Thorpe 2004, Losos 2008), cichlids in African lakes (Stiassny & Meyer 1999), and various Hawaiian radiations (Robichaux et al. 1990, Lovette et al. 2002, Gillespie 2004). The study of continental adaptive radiations has lagged behind. The study of continental radiations is important because continents are where most terrestrial diversity has evolved. Moreover, continental radiations may differ from island radiations in patterns of cladogenesis and phenotypic evolution (Richman & Price 1992, Benkman 2003, Kozak & Wiens 2006). The scale and complexity of the geographical and ecological settings, as well as the difficulties in extrapolating current process to old divergences complicate microevolutionary studies of continental radiations. However, developments on the use of phylogenetic information for inferring evolutionary processes are making feasible large-scale studies of diversification with extant taxa (Nee et al. 1994, Hansen & Martins 1996, Pagel 1999, Paradis 2005).

In this dissertation, I explore the use of new phylogenetic techniques for the study of the processes that influenced the continental adaptive radiation of the passerine family Furnariidae. The Furnariidae has been regarded as one of the most spectacular examples of a continental adaptive radiation (Fitzpatrick 1982, James 1982, Remsen 2003). With nearly 290 species, the Furnariidae is one of the richest bird families in the Western Hemisphere. In addition, furnariids show an astonishing ecological diversity. They occupy every terrestrial and water edge habitat in South America (Skutch 1996, Remsen 2003), from the driest deserts to the wettest tropical forests, including all the bird microhabitats defined for the Neotropical region (Stotz et al. 1996). Concomitantly, furnariids show a tremendous diversity in ecomorphological adaptations including some extreme cases of morphological specialization among passerine birds (Skutch
1996, Remsen 2003, Fjeldså et al. 2005). Fjeldså et al. (2005) considered Furnariidae to be the most morphologically diverse avian family. However, attempts to assess the ecomorphological diversity of Furnariidae were limited to a few traits and qualitative comparisons (James 1982, Fjeldså et al. 2005). In the past, the taxonomic delimitation of Furnariidae was ambiguous regarding the inclusion of the woodcreepers (Dendrocolaptinae). Woodcreepers show advanced climbing adaptations rivaling those of the woodpeckers (Richardson 1942, Feduccia 1973, Marantz et al. 2003); therefore, their inclusion in Furnariidae increases the range of adaptive forms in the family. Recent studies of the phylogenetic relationships in the group, however, have revealed that woodcreepers are indeed nested within traditional recognized furnariids (Irestedt et al. 2002, Chesser 2004, Moyle et al. 2009). In agreement with phylogenetic relationships, I will refer to Furnariidae as composed of three subfamilies: Sclerurinae, Dendrocolaptinae, and Furnariinae. Within Furnariidae, three traditional groups will be treated as tribes: Furnariini, Synallaxini, and Philydorini.

In addition to their tremendous ecomorphological variation and specialization, other characteristics make Furnariidae an ideal group to study the process of diversification at a continental scale. First, because they are of South American origin and have not expanded much into other regions (they are strictly Neotropical, and only 6 of 290 species are found strictly outside South America itself), the study of diversification will be less influenced by intercontinental processes. Second, basic distributional and ecological information for each species is currently available (Stotz et al. 1996, Remsen 2003). Finally, basic understanding of the ecomorphology of birds allows relating the phenotypic variation of the Furnariidae to its ecological adaptive function (Richardson 1942, James 1982, Leisler & Winkler 1985).

The dissertation is divided in three research chapters (2 to 4). In Chapter 2, I test the notion that the Furnariidae is exceptionally diverse in both species numbers and morphology. I
compared levels of species richness and morphometric diversity between the Furnariidae and all other six closely related families in the infraorder Furnariides. In chapters 3 and 4, I explore two main predictions of the neutral and ecological models of diversification in the Furnariidae. In the neutral model, geographic isolation is the major driver of speciation. Therefore, a reduction in dispersal ability of lineages is likely to increase the chances of speciation because make them more sensitive to geographic barriers. The ecological model, on the other hand, predicts that exposure to different ecological settings trigger speciation. Lineages with increased dispersal are more likely to colonize newly formed habitats or regions. Because dispersal into new areas exposes lineages to new selective regimes, dispersal may have a positive effect on speciation (Simpson 1959, Rosenzweig 1995, Schluter 2000, Price 2008). Therefore, the two models make contrasting predictions on the role of dispersal on diversification. In Chapter 3, I investigate the effect of dispersal on diversification in Furnariidae, using a species-level phylogeny of the entire family and a morphological index of wing shape as a surrogate for flying ability.

A crucial component of the ecological model is the role of ecological opportunities in stimulating diversification (Simpson 1953, Schluter 2000). Abundance of ecological opportunities due to low accessibility by continental clades is one of the main explanations for rapid radiations in oceanic island (Rosenzweig 1995, Givnish & Sytsma 1997, Grant 1999, Schluter 2000, Gillespie et al. 2004). In continents, however, ecological opportunities may be scarcer because of competition within rich biotas. As stated above, high dispersal may increase the ability of lineages to find ecological opportunities if structured geographically. In addition, lineages can 'create' ecological opportunities by changing the way they interact with the environment, i.e. changing their phenotype. The ecological theory predicts that evolutionary novelties that allow lineages to explore new niches can stimulate diversification (Simpson 1953, Schluter 2000). These evolutionary novelties are called key innovations (Hunter 1998). In
Chapter 4, I explore the existence of key innovations in Furnariidae. As a first approach, I explore morphologies related to locomotion and bill kinesis that are present in furnariids but are absent or are rare among closely related families, and are in Passeriformes in general. In Chapter 5, I discuss the major finding of my research and propose lines of future inquiry for understanding the processes that influenced the diversification of the Furnariidae in particular, and continental radiations in general.
CHAPTER 2

DISCOVERING EXCEPTIONAL DIVERSIFICATIONS AT CONTINENTAL SCALES: THE CASE OF THE ENDEMIC FAMILIES OF NEOTROPICAL SUBOSCINE PASSERINES*

INTRODUCTION

Adaptive radiations represent exceptional examples of biological diversification that involve two central processes in evolutionary theory: speciation and adaptation (Simpson 1953, Givnish 1997, Schluter 2000). The study of adaptive radiations has shed light on the role of ecological factors in phenotypic evolution and adaptation, the process of character displacement, the effect of key innovations, the evolution of ecological specialization, and the rise of reproductive isolation (Givnish & Sytsma 1997, Grant 1999, Schluter 2000). These studies have had a pervasive influence on our current understanding of the origin and evolution of biological diversity. However, most detailed studies of adaptive radiations have focused on clades occurring on islands (e.g., Darwin’s finches, Grant 1999, Caribbean Anolis, Losos & Thorpe 2004, Hawaiian silverswords, Robichaux et al. 1990) or isolated lakes (cichlids of East African lakes, Stiassny & Meyer 1999). The study of continental radiations has been more challenging due to larger geographic and taxonomic scales. Moreover, the mere identification of adaptive radiations is more difficult. Some continental clades that are both species-rich and ecologically diverse are often old; therefore, a slow process of cladogenesis and gradual change, instead of evoking fast adaptive radiation, can explain their diversity. Other continental clades that represent cases of rapid speciation and adaptation show subtle ecomorphological differentiation (Richman & Price 1992, Benkman 2003). Finally, some species-rich continental clades show signs of niche conservatism (Kozak & Wiens 2006). Those cases in which species proliferation

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is not accompanied by ecological differentiation are better regarded as "non-adaptive radiations" (Gittenberger 1991, Givnish 1997, Rundell & Price 2009).

For these reasons, developing practical methods to discover exceptional diversifications at large scales is important. Adaptive radiations are characterized by higher species proliferation and higher ecomorphological differentiation as compared to other groups of otherwise similar characteristics. Therefore, as a large-scale approximation, exceptional diversifications can be discovered in a comparative study of species diversity and phenotypic diversity (Magallón & Sanderson 2001, Losos & Miles 2002, Chakrabarty 2005). If a clade shows exceptionally high levels of species richness and phenotypic diversity, then it becomes a candidate for an adaptive radiation. Further investigations on the adaptive nature of the phenotypic variation, the relationship between traits and ecology, and the role of ecology in speciation are necessary to confirm that the clade is an adaptive radiation in a more strict sense (Givnish 1997, Grant 1999, Schluter 2000, Clabaut et al. 2007).

Magallón & Sanderson (2001) proposed a method for discovering clades with exceptionally high or exceptionally low species richness given their ages. Using simple models of cladogenesis (Raup 1985, Nee 2006), they derived formulas for the expectations and confidence intervals under the null hypothesis that all clades in the group are diversifying at the same rate. A similar method for phenotypic diversity is lacking. Losos & Miles (2002) proposed a non-parametric bootstrap test to determine whether a clade has higher phenotypic diversity than clades of otherwise similar characteristics. However, Losos & Miles' (2002) method does not take into account the effect of clade age on phenotypic diversity. Most neutral models of quantitative trait evolution predict an increase in phenotypic diversity with clade age (Slatkin 1981, Felsenstein 1988, Hansen & Martins 1996, O’Meara et al. 2006, Wainwright 2007); therefore, it is critical to take time of divergence into account in comparative analyses of phenotypic diversity. In
addition, phylogenetic relationships within clades influence the resultant phenotypic diversity (O’Meara *et al.* 2006). Therefore, even when the phylogenies are unknown, it is important to not ignore phylogeny but to incorporate its effects as much as possible (e.g. Losos 1994, Martins 1996). Ackerly & Nyffeler (2004) described a modified F-test for comparing the variances of a single trait of two sister clades that incorporates the uncertainties of an unknown phylogeny, and Sidlauskas (2007) proposed a simulation-based approach to test alternative explanations for differences in phenotypic diversity. Both methods were envisioned for the comparison of two sister clades; therefore, they are not immediately useful for comparing the morphometric diversity of multiple, possibly non-sister, clades.

Here I demonstrate new methods to discover exceptional phenotypic diversifications. The methodology is simple enough to apply at any taxonomic level, yet it considers the three main factors in the diversification process: time, speciation, and phenotypic differentiation. Furthermore, even though the method is not phylogenetic in the sense that it does not require a species-level phylogeny of the clades, it takes into account some aspects of the unknown phylogenetic structure. Before describing the method, I discuss the advantages and disadvantages of some multivariate indices of phenotypic diversity, and I propose a new index that takes covariation into account. I then apply the new methodologies to a diverse clade of Neotropical passerines in the infraorder Furnariides (Moyle *et al.* 2009). Within this clade, the family Furnariidae has been considered an adaptive radiation, but no quantitative evidence has been presented so far in support of this assertion.

**The Furnariides**

The infraorder Furnariides (Moyle *et al.* 2009) is endemic to the Neotropical region and comprises 51% of the species of suboscine passerines, and 11% of the species in the entire order
Passeriformes. It contains a diverse array of passerine birds currently classified in seven (Irestedt et al. 2002, Remsen et al. 2009) or nine families (Moyle et al. 2009).

Within this clade, the family Furnariidae has been regarded as one of the most spectacular examples of a continental adaptive radiation (Fitzpatrick 1982, James 1982, Remsen 2003). With nearly 225 species, the Furnariidae is one of the richest bird families in the Western Hemisphere. In addition, furnariids show an astonishing ecological diversity. They occupy every terrestrial and water edge habitat in South America (Skutch 1996, Remsen 2003), from the driest deserts to the wettest tropical forests, including all the bird microhabitats defined for the Neotropical region (Stotz et al. 1996). Concomitantly, furnariids show a tremendous diversity in ecomorphological adaptations including some extreme cases of morphological specialization among passerine birds (Skutch 1996, Remsen 2003, Fjeldså et al. 2005). Fjeldså et al. (2005) considered Furnariidae to be the most morphologically diverse avian family. However, attempts to assess the ecomorphological diversity of Furnariidae were limited to a few traits and qualitative comparisons (James 1982, Fjeldså et al. 2005). In addition, recent studies of the phylogenetic relationships in the group have revealed that two specialized clades are successive sister clades to core furnariids (Irestedt et al. 2002, Chesser 2004) and may be better regarded as separate families: Scleruridae and Dendrocolaptidae (Moyle et al. 2009). The former is composed of two specialist genera: leaf-litter specialist *Sclerurus* leaffossers, and *Geositta* miners of dry, open landscapes. The Dendrocolaptidae (woodcreepers) show advanced climbing adaptations rivaling those of the woodpeckers (Richardson 1942, Feduccia 1973, Marantz et al. 2003). Here, I present the first comprehensive quantitative study of the morphometric diversity of furnariids and relatives, and I use the methods described below to investigate whether any of the families in the suborder Furnariides has the characteristics of an adaptive radiation.
METHODS

Divergence Times

Because both speciation and phenotypic evolution are time dependent, considering the age of each clade for the comparative analysis is critical. Furthermore, for the analysis of diversification, it is important to distinguish between the age of origin of the clade (stem-group age) and the age of the most recent common ancestor (MRCA) of the clade (crown-group age) (Hennig 1965, Magallón & Sanderson 2001). In particular, because significant variation cannot accumulate in a clade until more than one lineage is present, the analysis of phenotypic diversity requires estimates of crown ages (Collar et al. 2005).

I estimated the age of the MRCA of each family using a molecular phylogeny. DNA sequences of 23 species of Furnariidae representing all families were taken from Chesser (2004). The aligned data matrix consists of a total of about 1900 bases from two mitochondrial genes (ND3 and COII) and intron 7 of the nuclear gene β-fibrinogen (BF7). I included additional taxa to ensure that the node corresponding to the MRCA of each family is represented in the dataset. For Furnariidae sensu stricto, recent molecular evidence indicates that the genus Xenops is sister to the rest of the family (Moyle et al. 2009). For Dendrocolaptidae both 'strong-billed' and 'intermediate' woodcreepers were included (Irestedt et al. 2006, Moyle et al. 2009). For Thamnophilidae, Terenura, by itself or together with a small group of genera, represents the sister clade of the remaining genera (Irestedt et al. 2004, Brumfield et al. 2007, Moyle et al. 2009). Within Rhinocryptidae, Scytalopus and Pteroptochos belong to the two most distantly related clades within the family (Chesser 2004, Rice 2005, Maurício et al. 2008, Moyle et al. 2009). Grallariidae seem to be divided into a clade of large birds in the genus Grallaria, and a clade of small birds (Grallaricula, Hylopezus, Myrmothera) (Chesser 2004, Rice 2005, Moyle et
al 2009). For the families composed of two genera (Scleruridae, Formicariidae, Conopophagidae), I included one species of each genus. For Melanopareiidae, which contains a single genus of unknown relationships, I included *Melanopareia torquata* and *M. elegans*, the most geographically distant species in the genus. Finally, I included two species of the sister suborder Tyrannides (Chesser 2004, Moyle et al. 2009) to root and calibrate the tree as explained below. ND3 sequences of *Chamaeza campanisona* and *Terenura sharpei* were taken from Brumfield et al. (2007).

New sequences were generated as follows. DNA was extracted from ca. 25 mg of tissue using DNeasy kits (Qiagen Inc.). The ND3 gene was amplified and sequenced with primers L-10755 and H-11151 (Chesser 1999), and COII with primers NF3COII (Sanín et al. 2009), and SCTRCOII (Claramunt et al. in press). The BF7 intron was amplified using primers FIB-BI7U and FIB-BI7L (Prychitko and Moore 1997). For sequencing, additional internal primers FIBI7-397U and FIBI7-439L (Chesser 2004) were used. Each 25 µl PCR reaction contained approximately 60 ng template DNA, 1.5 mM MgCl₂, 0.2 mM dNTPs each, and 0.1 U Taq DNA polymerase (New England Biolabs). Thermocycling conditions started with an initial denaturation of 94°C for 2 minutes, followed by 34 cycles of 30 sec. at 94°C denaturation, 30 sec. at 55°C annealing (45°C for ND3), and 30 sec. at 72°C extension, and ending with a final extension of 10 minutes (5 minutes for ND3) at 72°C. PCR products were purified using PEG precipitation. A BigDye® Terminator kit (Applied Biosystems) was used for the cycle sequence reaction, and products were cleaned in Sephadex columns before electrophoresis in an ABI 3100 Genetic Analyzer. New sequences were deposited in GenBank (accession numbers GU371838–GU371848). BF7 sequences were aligned using Clustal W 2.0.9 (Thompson et al. 1994).

Phylogenetic reconstruction under the Maximum Likelihood (ML) criterion was performed in RAxML 7.0.4 on the Cipres Portal V (Stamatakis et al. 2008), which uses fast algorithms to
find ML trees under the GTR+Γ finite-sites model of nucleotide substitution. I explored four data partitioning schemes corresponding to mitochondrial sequences being treated as: 1) a single concatenated sequence; 2) partitioned by gene; 3) partitioned by codon position; and 4) partitioned by both gene and codon position. BF7 sequences were always treated as a separate partition. In addition, I explored models with an invariant sites parameter (I). I obtained trees and ML values for all combinations of partitioning schemes and models, and used the small sample size version of the Akaike Information Criterion (AICc) to choose the most appropriate model (Posada & Buckley 2004, Sullivan & Joyce 2005). The number of free parameters in each partitioning scheme was six for the GTR+Γ model (or seven for the GTR+Γ+I models) multiplied by the number of partitions, plus 53 corresponding to the number of branch length estimates (Posada & Buckley 2004). Finally, using the optimal model, I conducted 1000 bootstrap replicates to assess clade support.

To obtain a calibrated tree, I used the Penalized Likelihood (PL) method implemented in the program r8s version 1.71 (Sanderson 2002). I used the cross-validation (CV) procedure to determine the best smoothing parameter value for the PL function (Sanderson 2002). The program also provides a chi-squared statistic to test the fit of a model with a single rate across the tree (a strict molecular clock). Although relative divergence times are sufficient for the present analyses, I calibrated the tree to allow comparisons of ages and rates with other studies. Furnariides fossils are scarce, relatively young, and their phylogenetic affinities too poorly known to be used for calibration (Claramunt and Rinderknecht 2005); therefore, I used molecular calibrations (Arbogast et al. 2002). The first calibration point corresponds to the basal node of the tree and is based on an estimate of 61 million years (Ma) for the age of the most recent common ancestor of Furnariides and Tyrannides (Barker et al. 2004). The second calibration point is based on an estimate of the rate of mtDNA evolution for a pair of closely related
dendrocolaptids (Weir and Schluter 2008). Using ND3 and COII sequences, and the same model used by Weir & Schluter (2008, GTR+Γ), I estimated a maximum likelihood genetic distance between the two least divergent dendrocolaptids in my dataset (Xiphorhynchus fuscus and Drymornis bridgesii) using PAUP* (Swofford 2003). The resultant distance and the 2.6% rate of mtDNA evolution correspond to an age of 7.1 Ma for the MRCA of these two species. Before combining the two calibration points in a single analysis I investigated the agreement between the branching times produced by the two calibration points when used separately.

**Morphological Variables**

I measured a total of 890 study skins representing 86% of the species and 100% of the genera in the Furnariides (Table 2.1). Most specimens are housed in the Louisiana State University Museum of Natural Science (LSUMZ), but specimens from other museums were included to complete the taxonomic coverage (see Acknowledgments).

<table>
<thead>
<tr>
<th>Family</th>
<th>Specimens</th>
<th>Species</th>
<th>Measured</th>
<th>Total</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Furnariidae</td>
<td>356</td>
<td>211</td>
<td>225</td>
<td>94</td>
<td></td>
</tr>
<tr>
<td>Dendrocolaptidae</td>
<td>115</td>
<td>50</td>
<td>51</td>
<td>98</td>
<td></td>
</tr>
<tr>
<td>Scleruridae</td>
<td>86</td>
<td>17</td>
<td>17</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>Formicariidae</td>
<td>20</td>
<td>11</td>
<td>11</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>Grallariidae</td>
<td>40</td>
<td>33</td>
<td>49</td>
<td>67</td>
<td></td>
</tr>
<tr>
<td>Rhinocryptidae</td>
<td>48</td>
<td>34</td>
<td>52</td>
<td>65</td>
<td></td>
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<tr>
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<td>4</td>
<td>4</td>
<td>100</td>
<td></td>
</tr>
<tr>
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<td>11</td>
<td>9</td>
<td>10</td>
<td>90</td>
<td></td>
</tr>
<tr>
<td>Thamnophilidae</td>
<td>206</td>
<td>194</td>
<td>220</td>
<td>88</td>
<td></td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td><strong>890</strong></td>
<td><strong>553</strong></td>
<td><strong>625</strong></td>
<td><strong>86</strong></td>
<td></td>
</tr>
</tbody>
</table>
I measured 11 linear variables that represent the size and shape of major functional modules of the bird external anatomy: bill, wing, tail, and feet. I measured bill length from the anterior border of the nostril to tip of the bill, and bill width and depth (vertically) at the level of the anterior border of nostrils. I measured three wing variables, all from the carpal joint and without flattening the natural curvature of the closed wing: (1) wing length to the longest primary (the traditional “wing length” measure) as a general measure of wing extent; (2) wing length to the tenth primary, the most distal one in furnarioids, which is related to the shape of the wing tip; and (3) length to the first secondary feather, which represents the width of an open wing (“wing width”). Tail maximum and minimum length were taken from the base of the central rectrices to the longest and to the shortest rectrices respectively. The third measure, an index of tail width, was measured as the width of the central rectrix at its midlength. I measured tarsus length and hallux length (including the claw) as measures of leg length and foot size respectively. All measurements were taken with a Mitutoyo Digimatic Point Caliper and loaded directly into an electronic spreadsheet using an input interface.

All variables were log-transformed so the differences between observations in the logarithmic space are proportional differences in the original space (Ricklefs & Travis 1980, Ricklefs & Miles 1994, Gingerich 2000). Therefore, two clades will show the same level of morphological diversity if they have the same variation in size and shape proportions. Otherwise, the variance of a clade with larger species will be higher just because of the larger absolute values of the raw measures (Cheverud et al. 1989).

Finally, I analyzed body size and shape variation separately under a strict geometrical concept of size and shape in which two individuals have the same shape only if they have the same proportions (Mosimann 1970, Bookstein 1989, Jungers et al. 1995). I computed the size of each species as the mean of the eleven log-transformed variables of the species. Then, I
calculated a shape vector for each species, with a shape value for each variable, by subtracting the size of the species from each variable (Mosimann 1970, Mosimann and James 1979). One fundamental advantage of Mosimann's method is that it is immune to the phylogenetic structure of interspecific data because the resultant size and shape of a species does not depend on the values of other species. Regression and Principal Component techniques are affected by phylogenetic non-independence (Revell 2009).

**Estimation of Phenotypic Diversity**

Phenotypic diversity can be measured in several ways (Wills et al. 1994, Foote 1997). Some measures are based on ranges and consider only the limits of the morphospace occupied, whereas others, based on variances or quantiles, take into account the density distribution of all the species in the morphospace (Wills et al. 1994). In this study I use measures of the second type because they better represent the dispersion of a clade in all portions of the morphospace. Moreover, common models of continuous character evolution are parameterized using variances, and specific theoretical results and modeling techniques are available when variances are used to quantify morphospace occupation (Slatkin 1981, Martins 1994, Pie & Weitz 2005, Ricklefs 2006, O’Meara et al. 2006).

Multivariate measures of variation can differ in two additional properties: 1) whether they are linear measures of morphospace size, or are hypervolumes; and 2) whether they take covariation into account. One of the most widely used multivariate extensions of the variance is the generalized variance $GV = |\Sigma| = \prod \lambda_j$, in which $|\Sigma|$ is the determinant, and $\lambda_j$ are the eigenvalues of the covariance matrix (Sokal 1965). Although the generalized variance has been proposed as index of multivariate dispersion in morphometrics (Sokal 1965, Goodman 1968, Cheverud et al. 1989), its use has been criticized because it collapses to zero when the number of real dimensions in the sample is fewer than the number of variables (Van Valen 1974, 1978,
Ashton and Rowe (1975, Mustonen 1997). This arises when the number of observations is fewer than the number of variables, when two or more variables are nearly perfectly correlated, or when one or more variables have little variation. In all these cases, the hypervolume collapses to zero even when most other traits vary significantly and are uncorrelated.

As an alternative to the generalized variance, Van Valen (1974) proposed the total variance, defined as the sum of the squared Euclidean distances of each observation from the centroid but also equals the sum of the variances of the original variables. The total variance and related measures, such as the mean pairwise squared Euclidean distance (Pie & Weitz 2005), are widely used as morphological diversity indices because they are computed easily and are unbiased. Because the total variance is a sum of distances, it does not have the disadvantages of the measures of hypervolume described above. Another advantage of the total variance is that it can be partitioned into size and shape components; the total variance of the log-shape matrix as defined above is the shape component, and the difference between the total variance of the original log matrix and total variance of the log-shape matrix is the residual log size, or the contribution of size to the total variation (Darroch & Mosimann 1985).

The main disadvantage of the total variance is that it does not take into account covariation among traits. This is true whether this measure is calculated using the original variables or using Principal Component scores because the Euclidean distance structure is the same. In other words, the sum of the variances also equals the sum of the eigenvalues, which represent the variances along the PC axes. To take covariation into account, I developed a new measure of multivariate variance. Following ideas in previous works (Derrickson & Ricklefs 1988, Wills et al. 1994, Ricklefs & Nealen 1998), the new measure is conceptually based on the constant-density contour ellipsoid related to the distribution of the observations in the multivariate space. The size and shape of the ellipsoid is determined by the degree of scatter and
the amount of correlation in the data, and is expressed in the length of its major and minor axes. Therefore, a simple sum of the major and minor axes would give a linear measure of total spread. This sum can be calculated using the eigenvalues of the covariance matrix:

\[ \text{Total Axis Length} = 2c \sum_{j=1}^{p} \sqrt{\lambda_j} \]  

in which the square root of an eigenvalue is proportional to the length of a semi-axis of the ellipsoid, and \( c \) is a constant that controls the size of the ellipsoid. For data that follow a multinormal distribution, when \( c^2 = \chi^2_p(\alpha) \) the ellipsoid encompasses a proportion \( \alpha \) of the observations, in which \( \chi^2_p(\alpha) \) is the chi-square distribution with degrees of freedom \( p \) equal to the number of variables (Johnson & Wichern 2002). However, for descriptive or comparative purposes, it is unnecessary to refer to a specific equiprobability contour of a multinormal distribution. Therefore, I propose the

\[ \text{Proper Variance} = \left( \sum_{j=1}^{p} \sqrt{\lambda_j} \right)^2 \]  

as a new multivariate generalization of the variance, the only one that requires the use of the eigenvalues for its computation (also called "proper values"). In contrast to the total variance, the proper variance decreases with an increase in correlations, which reduces the length of the minor axes of the ellipsoid (Figure 2.1). In addition, in contrast to the generalized variance, the proper variance does not collapse to zero with a decrease in dimensionality. Even in the extreme case of complete correlation among all the variables, the proper variance will express the variance along the single remaining axis of variation (i.e., the one corresponding to the first eigenvalue).

Mustonen (1997) developed a measure of total dispersion with similar characteristics, but the proper variance has the advantage of being computationally simpler.
Figure 2.1 Hypothetical clades A and B have the same variance for traits X and Y ($\sigma^2_X = \sigma^2_Y = 4$) but different covariance ($\sigma_{XY}^2 = 1, \sigma_{XY}^2 = 3.5$). The total variance fails to detect the difference in morphospace occupation between the two clades ($TV_A = TV_B = 8$), whereas the proper variance correctly identifies clade A ($PV_A = 15.7$) as more diverse than clade B ($PV_B = 11.9$). The ellipses correspond to the 95% equiprobability contour, and major and minor axes were drawn at the corresponding $c^2 = \chi^2_{df=2}(0.95) = 5.99$. Points are a sample of 100 observations from a bivariate normal distribution with the parameter specified above.

Although the computation of the total variance is straightforward, the proper variance requires the estimation of a covariance matrix and its eigenvalues. When sample size is small in relation to the number of variables, traditional formulae for estimation of the covariance matrix can result in poor estimation of eigenvalues (Schäfer & Strimmer 2005). For this reason, in addition to traditional estimators, I used shrinkage estimators of the covariance matrix. Finally, I evaluated the effect of sample size on both types of estimators using resampling rarefaction with 500 replicates (Foote 1992).

**Analysis of Diversification**

I used simple models of diversification to generate null expectations for species numbers and phenotypic diversity and their corresponding confidence intervals. Clades that fall outside these confidence intervals are candidates for adaptive radiations. To generate a null model of cladogenesis, I used a uniform birth-death branching process (Raup 1985, Nee 2006). I
estimated a net diversification rate \( r = \lambda - \mu \) (i.e. the speciation rate minus the extinction rate) for the entire suborder Furnariides using its total number of species and crown age, and computed confidence intervals for expected number of species trough time using Magallón and Sanderson's (2001) formulae implemented in the GEIGER library (Harmon et al. 2008) in R language for statistical computing (R Development Core Team 2008). I repeated the analysis using three levels of relative extinction \( \varepsilon = \mu / \lambda = 0, \varepsilon = 0.5, \) and \( \varepsilon = 0.95, \) and computed probabilities of obtaining a clade size \( \geq N \) for a given age, where \( N \) is the number of species (species-richness) of the clade. The number of species of each family was taken from Dickinson (2003), with modifications following Remsen et al. (2009).

For testing for exceptional phenotypic diversity I assumed a Brownian motion process to model gradual evolution of traits on random branching trees (Raup & Gould 1974, Slatkin 1981, Pie & Weitz 2005). In contrast to the case of species richness, there are no formulae to estimate rates, expectations, or confidence intervals for variances in the absence of phylogenetic information. Therefore, I used Monte Carlo methods to generate a null distributions of phenotypic diversity values. The first step is estimating rates of phenotypic evolution based on the empirical data. For the multidimensional Brownian motion process, the intrinsic rate of evolution is modeled by the evolutionary rate matrix \( R \) (Revell & Harmon 2008) composed of a diagonal of variances \( \sigma^2 \) and off diagonal covariances among traits. When the phylogeny is known, matrix \( R \) can be estimated directly (Revell & Harmon 2008, Revell & Collar 2009). Because a phylogeny of all species of Furnariiides has not been developed yet, I used an alternative approach based on the relationship between the observed covariance matrix \( V \) of a clade, age, and the evolutionary matrix \( R \). When \( N \) species originated \( t \) units of times ago, the expected covariance matrix among traits is simply \( V = Rt \) (Lande 1979). However, lineages do not originate simultaneously but speciate gradually producing phylogenetic trees. The phylogeny
implies that most pairs of species diverged later than the MRCA of the entire clade. For the univariate case, O’Meara et al. (2006) derived a formula that relate variance and time under a Brownian motion process that incorporates the phylogeny:

\[ E(v) = \sigma^2 (t - \text{mean}(C)), \]

(2.3)
in which \( \sigma^2 \) is the characteristic rate of the Brownian process, \( t \) is the crown age of the entire clade, and \( \text{mean}(C) \) is the average of the entries of the \( N \) by \( N \) phylogenetic or tree matrix \( C \) (the \( T \) matrix of Felsenstein 1973, 2004). Each element \( c_{ij} \) of the phylogenetic matrix is the time elapsed from the basal node of the tree to the most recent common ancestor of species \( i \) and \( j \) (Felsenstein 1973, 2004, Hansen & Martins 1996) and represents the shared history between species \( i \) and \( j \) in the tree; therefore, \( \text{mean}(C) \) can be interpreted as the average relatedness of all species in the clade. Assuming that the same relationships between variance, time, and phylogeny hold in the multivariate case, the rate matrix \( R \) of multivariate evolution can be estimated as

\[ R = \frac{V}{t - \text{mean}(C)}. \]

(2.4)

A phylogeny is still required for using equation (2.4) but only for calculating \( \text{mean}(C) \); thus, trees of a specific age and species richness can generate samples of possible average relatedness values. Simulations suggest that equation (2.4) results in reliable estimates of \( R \) for modeling multivariate evolution in Furnariides (Appendix A).

I conducted two types of analyses. The first explores visualizing the relationship between clade age and phenotypic diversity, and detecting clades that seem to depart from the background model. The second is a statistical test for whether a specific clade has significantly higher (or lower) phenotypic diversity than expected given a background rate of phenotypic evolution. Both analyses required two rounds of simulations, one for generating a collection of Brownian rate
matrices that represent a background rate of evolution, and the other for generating a distribution of expected phenotypic diversity values. For the exploratory analysis, I first estimated an observed covariance matrix $V$ for all Furnariides as a whole. Then, I generated 1000 trees of the same species richness as and age as the suborder Furnariiides using the function `birthdeath.tree()` in the GEIGER library (Harmon et al. 2008), which generates trees according to a uniform birth-death branching process (Nee 2006), and a new function for rescaling trees (Appendix B). For each tree, I used equation (2.4) to calculate a rate matrix $R$. In the second round of simulations I generated 1000 simulated clades, each one evolving at a rate determined by one of the rate matrices $R$. Simulated clades were generated using function `birthdeath.tree()` using the speciation and extinction rates estimated for Furnariides from the cladogenesis analysis. To generate a distribution of ages similar to the one shown by the nine families, the time to stop tree-growth was controlled by a random number following a normal distribution with a mean and standard deviation equal to the mean and standard deviation of the ages of the nine families. In each resultant tree, I simulated the evolution of 11 continuous traits following a Brownian motion model using function `sim.char()` in the GEIGER library. In each case, a different rate matrix $R$ from the collection of matrices generated above was used, accounting in this way for uncertainties in the estimate of $R$ due to the lack of a species level phylogeny. For each resultant table of $N$ species by 11 traits, I estimated the size variance and the shape proper variance using the methods explained in the previous section.

Testing whether a specific clade has significantly higher phenotypic diversity than expected, however, requires a different null distribution for each clade that depends not only on age but also on number of species. Even though evolution under a Brownian motion model depends only on time and is independent of speciation events, the number of species can influence the expected variance through its influence on the average relatedness within the clade (Ackerly &
Nyffeler 2004, Ricklefs 2006, O'Meara et al. 2006). Under a random branching process, species-rich clades are generated when, by chance, they experience multiple speciation events early in time (Phillimore & Price 2008). This makes the average relatedness within rich clades lower, on average, than within species-poor clades, producing a positive relation between the number of species and the observed variance (Ricklefs 2006). Therefore, the null distribution of phenotypic diversity values needs to be generated for a specified age and number of species. An additional advantage of generating null distributions for specific clades is that another source of bias is eliminated. If a clade has evolved at a higher rate, then it may bias the null distribution of phenotypic diversity values towards higher values thus increasing type II error rates.

Accordingly, in the second type of analysis I generated null distributions of phenotypic diversity for specific Furnariides families (focal clades). I generated a collection of Brownian rate matrices as above but using an observed covariance matrix $V_i$, species numbers, and age for Furnariides after excluding the focal family $i$, thus avoiding the bias produced by the focal family evolving at a faster (or lower) rate. In the second round of simulations, I generated 1000 trees of the same age and species richness as the focal family. On these trees, I simulated the evolution of 11 continuous traits following a Brownian motion model using the $R_i$ matrices generated in the first round of simulations to generate 1000 simulated character matrices under the null model. Finally, I computed the size and shape variances of each matrix, and estimated the quantiles of their distribution. If the observed variance of the focal family fell outside the 95% percentile, then it was considered significantly more diverse than expected. To examine possible effects of extinction on the estimates of rates and expected variances, I repeated the simulations using trees generated by a birth-death process using a relative extinction rate $\epsilon = 0.5$, and 0.95. All computations and analyses were performed in R language using functions in libraries CORPCOR (Schäfer & Strimmer 2005) for shrinkage estimates of covariance matrices, APE (Paradis et al.
2004), and GEIGER (Harmon et al. 2008). New functions and example codes used for the simulations are provided in Appendix B.

RESULTS

Divergence Times

The best model for the phylogenetic analysis was the fully partitioned GTR+Γ+I (-log Likelihood = 17068, AICc = 34237); models with reduced number of partitions or without invariants were significantly worse (more than 40 AIC units greater than the best model); however, the tree topology recovered was identical for all except the worst models. Branching times estimated separately using the basal node calibration and the dendrocolaptid node calibration were highly congruent (simple linear regression: slope = 1.14, $R^2 = 0.999$); therefore, I combined the two calibration points in a final Penalized Likelihood analysis. The molecular clock model with a single substitution rate across the tree was rejected (Chi-square = 1621, df = 29, $P < 0.001$), and the cross-validation procedure indicated an optimal smoothing parameter of 0.63 for the Penalized Likelihood function. The resultant chronogram with branches proportional to time is depicted in Figure 2.2.

Patterns of Morphometric Diversity

Different methods for estimating the covariance matrix produced different estimates of the proper variance (Figure 2.3). The standard method underestimated the proper variance, whereas shrinkage methods overestimated it. In both cases the bias decreased quickly as sample size increased. The average of both estimates is quite stable above a sample size of only five to ten species. For the rest of the analyses, I used this average as the best estimate of the proper variance.
Figure 2.2 Calibrated phylogeny of the Furnariides. The chronogram was obtained using the Penalized Likelihood method on a Maximum Likelihood tree from the analysis of two mitochondrial genes (ND3 and COI) and one nuclear intron (BF7). Numbers above branches are bootstrap values. Time before the present in millions of years (Ma).

The total variance and the proper variance resulted in moderately similar rankings of the families according to their overall (size and shape) morphometric diversity (Figure 2.4a and b). However, using the total variance the most diverse family is Thamnophilidae, whereas using the proper variance the most diverse family is Furnariidae. For shape variation, both variances
Figure 2.3 Rarefaction curves showing the dependence of the proper variance on sample size up to 30 species. For Furnariidae (Fu) the estimates using the shrinkage covariance matrix (upper dashed line) and the regular covariance matrix (lower dashed line) as well as the average between the two estimates (continuous line) are shown. For the four species poor families Conopophagidae (Co), Scleruridae (Sc), Formicariidae (Fo), and Melanopareiidae (Me), only the average of the two estimates is depicted.

indicate that Furnariidae is the most diverse, but there are important differences in the assessment of shape variation for other families. For example, the total variance suggests that Conopophagidae is second only to Furnariidae in shape diversity (Figure 2.4c), whereas the proper variance indicates that Conopophagidae is among the three families with lowest shape diversity (Figure 2.4d). The Conopophagidae consists of only two genera, *Conopophaga* and *Pittasoma*; although clearly different in body size, they are similar in body shape and limb proportions. Inspection of the first three eigenvalues of the shape matrices reveals that, whereas in Furnariidae the shape variance is distributed in several dimensions (0.100, 0.046, 0.030), most of the shape diversity in Conopophagidae is concentrated in a single axis of variation (0.199, 0.008, 0.006). Seven of the eleven variables measured contribute to this single axis of variation in Conopophagidae (Principal Component Analysis loadings not shown). By not taking this
covariation into account, the total variance overestimates the shape diversity in the Conopophagidae.

![Figure 2.4 Morphometric diversity in nine families of the passerine infraorder Furnariides (see Figure 2.2 for family codes). (a) Total variance partitioned into its size and shape components using Darroch and Mosimann’s (1985) method. (b) Unpartitioned (size and shape) proper variance. (c) Shape total variance. (d) Shape proper variance.](image)

**Patterns of Diversification**

The net rate of clade diversification for the Furnariides was 0.114 species per million years assuming no extinctions, and 0.109 and 0.069 species per million years with intermediate ($\epsilon = 0.5$) and high ($\epsilon = 0.95$) extinction rates respectively. The families Furnariidae, Dendrocolaptidae, and Thamnophilidae have significantly more species than expected under a null model without extinction (Figure 2.5) (probability of obtaining the standing diversity or however, assuming a relative extinction rate $\epsilon = 0.5$, the species richness of Dendrocolaptidae is higher: $P < 0.001$ for Furnariidae and Thamnophilidae; $P = 0.01$ for Dendrocolaptidae); marginally non-significant ($P = 0.05$), and with a high extinction rate ($\epsilon = 0.95$) only
Thamnophilidae remains as an exceptionally diverse family \((P = 0.04)\), while Furnariidae does not \((P = 0.09)\). On the opposite side of the spectrum, Melanopareiidae is significantly less diverse than expected given its age assuming no extinction (Probability of obtaining the extant diversity or lower, \(P = 0.035\)), although they are not exceptionally species-poor in the models with medium to high levels of extinction \((\varepsilon = 0.5: P = 0.12, \varepsilon = 0.95: P = 0.051)\).

![Figure 2.5 Observed and expected number of species for Furnariides families as a function of age (see Figure 2.2 for family codes). Shaded areas correspond to 95% confidence regions assuming no extinction (dark gray), a relative extinction rate \(\varepsilon = 0.5\) (medium gray), and a relative extinction rate \(\varepsilon = 0.95\) (light gray). The line corresponds to the expected number of species assuming no extinction. Fu* = Furnariidae sensu lato (including Dendrocolaptinae and Sclerurinae as subfamilies). Clade age (crown age) in millions of years (Ma).](image)

Patterns of body size and shape diversity through time in Furnariides families coincide in general terms with the simulated clades generated using single background rates of cladogenesis and phenotypic evolution (Figure 2.6). However, some families lie at the periphery of the distribution of simulated clades suggesting that it is unlikely that they experienced the same
background rate of diversification. Specifically, the families Dendrocolaptidae and Thamnophilidae have high body size and shape diversity for their ages, and the family Formicariidae has low body size and shape diversity for its age (Figure 2.6). The family Furnariidae, either sensu stricto or sensu lato, seems to be highly diverse in body shape, but not particularly diverse in body size (Figure 2.6). These four families were subjected to focal tests. The families Thamnophilidae and Dendrocolaptidae were significantly more diverse than expected in size \( (P < 0.025 \text{ for both}) \), but only the Dendrocolaptidae was also significantly more diverse in shape \( (P < 0.02, \text{ Figure 2.7}) \). The family Formicariidae, on the other hand, was significantly less diverse than expected for both size and shape \( (\text{both } P < 0.02, \text{ Figure 2.7}) \). Finally, Furnariidae was not significantly more diverse in body size \( (P > 0.1) \), but it was significantly more diverse in shape than expected under the null model \( (P < 0.01, \text{ Figure 2.7}) \).

**Figure 2.6** Relationships between phenotypic diversity in size (a) and shape (b) as a function of clade crown age for nine families of the passerine infraorder Furnariides (see Figure 2.2 for family codes). Gray dots are 1000 simulated clades generated with a pure birth random branching process and a Brownian motion model of trait evolution using an evolutionary rate matrix estimated for all Furnariidae species. Fu* = Furnariidae sensu lato (including Dendrocolaptinae and Sclerurinae as subfamilies). Clade age (crown age) in millions of years (Ma).
The same conclusions regarding size and shape diversity held when Furnariidae was treated as including Dendrocolaptinae and Sclerurinae as subfamilies. The analysis with moderate and high relative extinction rates resulted in similar distributions of simulated diversities and confidence intervals, leading to the same statistical conclusions as the models without extinction.

**Figure 2.7** Test for whether a specific clade has significantly higher (or lower) phenotypic diversity than expected given a background rate of phenotypic evolution. Null distributions are kernel density curves of 1000 variances obtained by simulating clades of the same number of species and age as the focal clade but with a background rate of phenotypic evolution estimated from the most inclusive clade after excluding the focal clade. White areas under the curves correspond to the lower or upper 5% of the simulated variances. Arrows indicate the observed percentile of focal clade.

**DISCUSSION**

**Testing for Differences in Phenotypic Diversity**

In this study I introduced two new techniques for the comparative study of phenotypic diversity at large scales. The first is a new way of quantifying variation in multivariate space that improves measures currently used by taking covariation into account. Covariation between to
traits in the morphospace is due to two processes: 1) genetic, developmental, and functional constraints (Lande 1979, Pigliucci & Preston 2004, Klingenberg 2008), and 2) phylogenetic relationships among species (Felsenstein 1988, Hansen and Martins 1996). A key aspect of modern comparative methods is to separate these two sources of covariation (Felsenstein 1985, Harvey & Pagel 1991). However, in comparative studies of phenotypic diversity the first step is to estimate the extent of morphospace occupation regardless of the different sources and ultimate causes of variation and covariation. For this reason, the measurements of morphospace occupation or disparity do not need to be corrected for phylogenetic covariation.

The second technique introduced here is a Monte Carlo method for testing for differences in phenotypic diversity. Because it takes into account time of divergence and number of species of the clades, this method can be used in broad-scale comparisons including groups of different age and taxonomic rank. Most previous methods for comparing phenotypic diversity in contemporaneous clades assume that clades are either similar in age (Losos & Miles 2002) or are sisters (same age of origin, Ackerly & Nyffeler 2004, Sidlauskas 2007). However, Sidlauskas' (2007) method could be modified to compare non-sister clades; therefore, it can be an alternative to the test described in this study.

Sidlauskas (2007) proposed a simulation-based approach to test alternative explanations for differences in phenotypic diversity. Specifically, he investigated the role of crown age, relative extinction rate, and rate of phenotypic evolution in generating the observed difference in morphometric diversity between the two clades. As in the present study, he generated trees using simple birth-death models, and simulated traits following a Brownian motion model. Simulations are repeated for different combinations of parameter values. Finally, the probability that a given parameter combination generated the observed diversity is computed, and these probabilities are used in hypothesis testing. He applied the method to two sister clades of South American fishes,
and found that the method is capable of detecting a significant difference in rates of evolution between the two clades. However, differences in crown age between clades could also explain the differences in phenotypic diversity; only after considering the low likelihood of high differences in crown age assuming a random branching model, a difference in rates became a more plausible explanation. As compared to the method proposed in this study, Sidlauskas' (2007) method is more labor-intensive in both parameter choice and computing. The range and number of parameter values has to be chosen by the investigator, and for each parameter combination at least one tree and trait simulation is required. In his example of South American characiform fishes, the test for differences in rates required 120 sets of simulations (Sidlauskas 2007), whereas the method proposed here would require only two sets (one for generating background rates using the second clade and one for generating the simulated trait matrices for the focal clade).

The Monte Carlo method proposed here can be applied to a variety of organisms, including fossil taxa, provided that estimates of crown ages are available. That the method does not require a phylogeny for all species included makes it useful for large-scale studies, or studies involving poorly known groups. Because continents often contain large clades spanning a wide range of ages, this method is especially useful for discovering exceptional continental diversifications. However, the lack of phylogenetic information comes with a cost. A significant result may arise even if the rates of trait evolution are the same. If a clade has experienced a burst of diversification early in its history, then it will show lower average relatedness among its constituting species, and high phenotypic diversity (Ackerly & Nyffeler 2004, Ricklefs 2006, O'Meara et al. 2006). This problem is shared by all the methods that do not use phylogenetic information. Although the method proposed here accounts for variation in average relatedness, the real tree might be highly unlikely under the random branching models used here. Therefore,
the method cannot distinguish whether the higher phenotypic diversity of a clade was produced by a higher rate of phenotypic evolution or by an unusual pattern of cladogenesis. Differences among clades in models of trait evolution may also result in significant results. As in many statistical tests, a significant result may be produced because of violations of the assumed models. To distinguish between these alternative explanations, a phylogeny is required. If phylogenetic information for all the included species is available, then the most appropriate model of trait evolution can be selected based on data, rates can be estimated, and tests for differences in rates can be performed with more rigorous and powerful methods (Pagel 1999, Mooers et al. 1999, Butler & King 2004, O'Meara et al. 2006, Revell & Harmon 2008, Collar et al. 2009, Revell & Collar 2009).

**Diversification in Furnariiides**

This study is the first detailed analysis of large-scale diversification patterns in the infraorder Furnariides. A uniform diversification rate across families cannot explain the variation in species richness among Furnariides. Two families, Furnariidae *sensu stricto* and Thamnophilidae, stand out as exceptionally species-rich clades (Figure 2.4), suggesting that their net rate of diversification was higher than that of other members of the infraorder. Interestingly, the family Dendrocolaptidae, the sister clade of Furnariidae is also exceptionally species-rich (Figure 2.7), but Scleruridae is not, suggesting that the rate of diversification changed at some point at the base of the Furnariidae-Dendrocolaptidae clade. These conclusions, however, depend on the levels of extinction assumed. With high levels of extinction ($\epsilon = 0.95$) only the Thamnophilidae remains as an exceptionally rich family. Although relative extinction rates $\epsilon = 0.95$ may be considered exceptionally high (Magallón & Sanderson 2001), Ricklefs (2007) estimated a relative extinction rate $\epsilon = 0.954$ for South American passerine clades; however, confidence intervals around the estimates were broad. That the four fossils furnariids described from the
Pleistocene are all extinct species (Tonni 1977, Noriega 1991, Tonni & Noriega 2001, Claramunt & Rinderknecht 2005) also suggests high levels of extinction in the recent past. With such high levels of extinction the birth-death process becomes highly stochastic, and clades with high numbers of species are increasingly more likely. More phylogenetic and paleontological information is needed to estimate speciation and extinction rates in Furnariides with more precision.

Another critical assumption of the analysis is the validity of a uniform birth-death process for modeling cladogenesis in Furnariides. This model predicts a positive relationship between clade age and species richness. A lack of such a relationship in several datasets has called into question the usefulness of uniform birth-death models (Ricklefs 2007, 2009, Rabosky 2009a). For all Furnariides families there is no correlation between crown age and species richness ($\rho = -0.1, P = 0.8$). However, when the two clades that seem to be evolving at a faster rate are excluded (Thamnophilidae, and the Furnariidae/Dendrocolaptidae clade), the remaining families show a strong and significant correlation between age and richness ($\rho = 0.90, P = 0.015$, Figure 2.6). Therefore, the lack of a correlation among all Furnariides families seems not to be a significant departure from a birth-death model but the result of a shift in diversification rates in two clades.

The present analysis is the first to demonstrate quantitatively that the Family Furnariidae is exceptionally diverse in external shape, and this holds whether it is analyzed as a large clade that includes Dendrocolaptidae and Scleruridae, or sensu stricto, or assuming different levels of relative extinction. Thamnophilidae, on the other hand, is exceptionally diverse in body size, but not in shape. The family Dendrocolaptidae was also exceptionally diverse in shape (Figure 2.7), but not Scleruridae, suggesting that the rate of phenotypic evolution changed at the base of the Furnariidae-Dendrocolaptidae clade. This result parallels the finding for rates of cladogenesis.
Actually, the logarithm of species richness was highly correlated with phenotypic diversity in Furnariides in both body size ($\rho = 0.86$) and shape ($\rho = 0.91$), whereas the correlations with crown age were lower for body size ($\rho = 0.30$) and zero for shape ($\rho = 0.00$). Qualitatively similar results were found using phylogenetic independent contrasts. For Brownian models of phenotypic evolution a correlation between number of species and phenotypic diversity is expected because average relatedness decreases in large phylogenies (see Methods). For example, the simulated clades also showed correlations between log(species) and phenotypic diversity; however, these correlations were lower in magnitude (body size: $\rho = 0.32$; shape: $\rho = 0.70$) and similar to correlations between crown age and phenotypic diversity (body size: $\rho = 0.39$; shape: $\rho = 0.67$). Therefore, the strength of the correlations between log(species) and phenotypic diversity in Furnariides seems to exceed the effect of relatedness and may indicate a contribution of speciational or punctuated phenotypic evolution (Slatkin 1981, Gould & Eldredge 1977). Phenotypic change may be associated with speciation either through developmental instabilities due to founder effects (Gould & Eldredge 1977) or through ecological speciation (Schluter 2000, 2001). In addition, gradual phyletic evolution can produce a similar pattern if the coexistence of more lineages generates divergent selection (Ricklefs 2004). Further studies are warranted to explore these possibilities.

The clade Furnariidae-Dendrocolaptidae shows the characteristics of an adaptive radiation: high rates of cladogenesis and high phenotypic diversity. Moreover, the estimated phenotypic diversity for Furnariidae and Dendrocolaptidae may be conservative because they are highly variable in other traits not represented in the morphometric matrix. For example, bill curvature varies from the extremely decurved bill of the dendrocolaptid genus *Campylorhamphus* to the upturned bills of *Xenops* and *Megaxenops*. Foot morphology is also more heterogeneous in the Furnariidae-Dendrocolaptidae clade, which show variation in the relative length of toe IV and
claw curvature (Richardson 1942, Feduccia 1973). Finally, in addition to the variation in feather length, the tail in Furnariidae and Dendrocolaptidae shows notable variation in structural details such as rachis thickness, which are adaptations to trunk climbing (Tubaro et al. 2002), barb integration, including extreme cases of weak barb development like *Sylviorthorhynchus* (Remsen 2003), and feather tip morphology, which varies from rounded to extremely pointed (Fjeldså et al. 2005). Other families in the suborder Furnariidae are more homogeneous in these external morphological details, which perhaps was one of the reasons several of them were considered a single family in the past (Formicariidae). Therefore, by not including these traits, the phenotypic diversity of Furnariidae and Dendrocolaptidae may have been underestimated.

Adaptive radiations are characterized by adaptive or ecomorphological diversity (Schluter 2000, Clabaut et al. 2007). Although the adaptive nature of a specific trait in a particular species may not be known for Furnariidae and Dendrocolaptidae, the magnitude of the variation across taxa is almost certainly not neutral and represents variation associated principally with feeding behavior and locomotion. The avian bill is the main tool for food capture and handling, and its variation in size and shape is strongly correlated with bill function and performance (Lederer 1975, Greenberg 1981). Wings generate thrust for flight, and variation in their size and shape is related to such important factors as food searching behavior (Leisler & Winkler 1985, Rayner 1993), and predator-escape behavior (Swaddle & Lockwood 1998). The tail is used in locomotion in different ways: as a rudder and brake in flight (Thomas 1996), as support for part of the body weight in climbing birds (Richardson 1942, Norberg 1986, Tubaro et al. 2002), and as a brace during locomotion through closed vegetation by several small furnariids (Remsen 2003). Finally, hind limbs are used in different types of locomotion (Zeffer et al. 2003), including perching and climbing (Richardson 1942, Feduccia 1973). The ecological theory of adaptive radiation proposes that ecological pressures played a central role not only in generating
adaptations but also in the speciation process and the build up of a clade’s species diversity in adaptive radiations (Schluter 2000, Price 2008). Further studies are warranted to test whether this was the case for the Furnariidae-Dendrocolaptidae continental radiation.
CHAPTER 3

THE EFFECT OF DISPERAL ABILITY ON DIVERSIFICATION:
FLIGHT AND SPECIATION IN A CONTINENTAL ADAPTIVE
RADIATION

INTRODUCTION

Dispersal plays two fundamental roles in evolution. First, dispersal is related to the process of range expansion and is a crucial first step in the process of colonization of new areas. Second, dispersal is the major force behind gene flow and the maintenance of genetic cohesion within lineages. These two major effects of dispersal means that dispersal may play a dual or opposing role in the diversification process. On the one hand, because of its role in range expansion and colonization, dispersal can stimulate diversification. Species distributed over large geographic areas are more likely to be divided by barriers and to develop population structure, a requirement for geographic speciation (Mayr 1970, Rosenzweig 1995, Coyne & Orr 2004). In addition, populations in recently colonized areas may be exposed to new ecological conditions, which may stimulate ecological speciation (Rosenzweig 1995, Schluter 2000, Price 2004). On the other hand, high dispersal ability may inhibit speciation by maintaining gene flow among populations (Mayr 1970, Bohonak 1999, Coyne & Orr 2004). Although both the stimulating effect and the inhibitory effect of dispersal have played a role during the diversification of organisms, it is not well understood when one of these effects predominates during the generation of biological diversity. An examination of the relationship between dispersal ability and diversification in real clades may disclose the preponderant influence of one or the other process on diversification.

The main problem in the comparative study of dispersal is that it is exceptionally difficult to quantify. At the organismal level dispersal is a highly stochastic process that depends on specific environmental conditions and behavioral decisions of particular individuals, producing typically
skewed distributions and high variance in dispersal distance even within a single species (Paradis et al. 1998). In addition, the evolutionary effects of dispersal may depend more on rare long-distance dispersal events than on the more frequent small-scale movements (Ibrahim et al. 1996, Levin 2006, Clayton et al. 2009). More importantly, to relate dispersal to the diversification process, measurement of dispersal tendencies at large temporal scales is important (Barton 1999). Therefore, even detailed data on current dispersal may not be sufficient for the study of diversification.

A potentially more fruitful approach is to quantify dispersal ability based on phenotypic features (Bohonak 1999, Van Bocxlaer et al. 2010). This approach has stimulated research on dispersal in plants (Levin et al. 2003) and marine invertebrates. In plants, dispersal syndromes can be inferred from size, color, quality (fleshiness) and morphology (ornamentations or appendages) of fruits and seeds (van der Pijl 1982, Hughes et al. 1994), and several studies have used these characteristics to investigate the relationship between dispersal and diversification (Tiffney & Mazer 1995, Dodd et al. 1999, Price & Wagner 2004, Moore & Donoghue 2007). In marine invertebrates, dispersal distance is related to the duration of a pelagic larvae stage, which can be inferred from morphological characteristics (Shanks et al. 2003). Developmental modes in marine invertebrates have been shown to influence geographic range size, genetic differentiation, and diversification (Burton 1983, Jablonski 1986, Hellberg 1996, Lester & Ruttenberg 2005, Paulay & Meyer 2006).

In this study, I use a simple index of wing shape that has roots in aerodynamic theory to investigate the relationship between dispersal ability and diversification in the Furnariidae. This Neotropical avian family is ideal to investigate the relationship between dispersal and diversification for several reasons. First, furnariids are widespread in the Neotropical region, and especially in South America; therefore, they may be informative about the continental-scale
processes that produced the most diverse avifauna in the world (Ricklefs 2002). Second, they show a wide range of dispersal abilities as inferred from behavior (Remsen 2003) and wing morphology (see below). Finally, Furnariidae represents a continental-scale adaptive radiation, with lineages adapted to all major biomes in South America (Stotz et al. 1996), extreme cases of habitat specialization (Remsen 2003), and exceptionally high diversification rates and phenotypic diversity (Chapter 2, Claramunt in review). Therefore, models of ecological diversification, in which dispersal stimulates diversification (Rosenzweig 1995, Schluter 2000, Price 2008) should be particularly applicable to the Furnariidae radiation.

METHODS

Wing Morphology and Dispersal Ability

As an index of dispersal ability, I used a simple descriptor of wing shape, Kipp’s index (Kipp 1959), which relates the length of the primary feathers to the length of the secondary feathers as follows:

\[ K = 100 \times \frac{W_L - S_1}{W_L} \]

in which \( W_L \) is the standard length of the closed wing taken from the carpal joint to the tip of the longest primary feather without flattening the natural curvature of the wing (Baldwin et al. 1931), and \( S_1 \) is the distance from the carpal joint to the tip of the first secondary feather, the most distal secondary feather and nearest to the carpal joint (Figure 3.1). The key feature of Kipp's Index is that it is related to the aspect ratio of the wing (Lockwood et al. 1998), and according to models of bird flight aerodynamics, economic long-distance flight is achieved with high aspect ratio (Rayner 1988, Norberg 1995, Videler 2005, Pennycuick 2008). Moreover, empirical evidence demonstrates that Kipp's index is related to migratory behavior (Lockwood et
al. 1998), natal dispersal distance (Dawideit et al. 2009), and genetic differentiation (Burney & Brumfield 2009).

![Figure 3.1](image.png)

**Figure 3.1** Measurement of the standard wing length (WL) and the distance to the first secondary (S1) for the calculation of Kipp's index. The measurements are made on the closed wing (left). The open wing shows how these measurements relate to wing extent and wing width.

I measured WL and S1 in 289 species of Furnariidae, using at least three male specimens when available, using a Mitutoyo Digimatic Point Caliper. I also measured nine additional variables for computing an index of body size: 1) "primary 10" from the carpal joint to the tip of the last primary feather; 2) bill length from nares; 3) bill width at nares; 4) bill depth at nares; 5) tail length to the longest central rectrix; 6) tail length to the shortest external rectrix; 7) width of central rectrices; 8) tarsus length; and 9) hallux length (see Chapter 2 for further details). Log-body size was calculated as the mean of the 11 log-transformed variables (Mosimann 1970, Mosimann & James 1979). Most specimens were measured at Louisiana State University Museum of Natural Science (LSUMZ), with the majority of additional specimens measured at the American Museum of Natural History and the Field Museum of Natural History (see
Acknowledgments for a complete list of institutions). Using a total of 1156 specimens, I calculated Kipp's Index for the 279 species also included in the phylogenetic analysis, which represents 98.6% of the species in the family.

In addition, I evaluated the relationship between Kipp's Index and aspect ratio in Furnariidae. I estimated the aspect ratio of furnariid species using specimens deposited at LSUMZ in which wingspan was measured at the time of preparation, and a spread wing or an outline of it was preserved. Only fully spread wings with a straight leading edge were used. Digital photographs of spread wing preparations or scanned wing tracings were used to calculate the area of a single wing using the software ImageJ 1.42q (Wayne Rasband, National Institute of Health, http://rsb.info.nih.gov/ij). Then, I estimated aspect ratio ($AR$) as,

$$AR = \frac{WS^2}{TA} \quad (3.2)$$

in which $WS$ is the wingspan and $TA$ is the total area, which includes not only twice the area of the single wing but also the root box area (i.e., the area of the body between the wings, Figure 3.2). See Pennycuick (2008) for details of the method for calculating total wing area.

![Figure 3.2](image_url)  
**Figure 3.2** Wingspan and total area used for calculation of aspect ratio.
Phylogeny

The analyses used in this study require a species-level phylogeny. I used a species-level phylogeny of the Furnariidae inferred from DNA sequences of three mitochondrial (COII, ND3, ND2) and three nuclear genes (BF7, RAG1, RAG2) (Derryberry et al. in prep.). Mitochondrial and BF7 sequences were generated for ca 600 specimens at the LSU Museum of Natural Science. RAG1 and RAG2 sequences for at least one species per genus were taken from Moyle et al. (2009), or sequenced at LSUMNS. Phylogenetic analysis started with the selection of the most appropriate partition scheme followed by selection of the most appropriate model of evolution for each partition using model selection techniques (Posada and Buckley 2004, Sullivan & Joyce 2005, McGuire et al. 2007, Li et al. 2008). The resultant partitioned model was used to infer a calibrated phylogeny using Bayesian methods in BEAST (Drummond & Rambaut 2007). The tree was calibrated using: A) the age of the split between tyrannoids and furnarioids (Barker et al. 2004); and B) multiple biogeographic calibration nodes based on the last rapid uplift of the northern Andes, which separates multiple lineages, and the formation of the Isthmus of Panama, which allowed multiple furnariids lineages to colonize Central America. For further details on phylogenetic reconstruction and calibration see Derryberry et al. (in prep.).

Statistical Analysis

Correlation between variables was evaluated using a generalized least-squares (GLS) approach in which the effect of phylogenetic relationships on covariation is included as the covariation structure of the model (Martins & Hansen 1997, Garland & Ives 2000). A lambda transformation of the phylogentic tree (Pagel 1999) was used to determine the strength of the phylogenetic effect on the correlation between variables, and the optimal value of lambda was estimated simultaneously with the linear model (Freckleton et al. 2002).
To test the effect of dispersal ability as measured by Kipp's Index on diversification, I used a Yule model with covariates, which is a pure-birth model of cladogenesis in which the per-lineage speciation rate depends on one or more variables as determined by a generalized linear model (Paradis 2005). In the present analysis it takes the form:

$$\ln \frac{\lambda_i}{1 - \lambda_i} = \beta x_i + \alpha$$

(3.2)

in which $\lambda_i$ is the speciation rate of lineage $i$, $x_i$ is the value of Kipp's Index, and $\beta$ and $\alpha$ are the parameters (slope and intercept respectively) of the linear model. To model the diversification process through history, the method requires not only trait values for each species but also values for every node in the tree, which are estimated assuming a Brownian motion model of trait evolution. Kipp's Index values were log-transformed and centered to meet distributional assumptions of the method. Then, I estimated ancestral character states using maximum likelihood following Schluter et al. (1997). Finally, species values and ancestral values together with the phylogeny were used to fit a Yule model with covariates using non-linear numerical optimization of a likelihood function (see Paradis 2005 for further details). The likelihood of a null model that includes only the intercept term was also computed and used in a likelihood ratio test for comparing the null and the alternative model. I also investigated two other factors that may influence diversification: log-body size and clade-specific effects. The latter were tested by fitting a Yule model with covariates using a categorical variable indicating membership to any of the three subfamilies of Furnariidae (Furnariinae, Dendrocolaptinae, and Sclerurinae).

I evaluated two critical assumptions of the Yule model with covariates. First, I evaluated whether the assumption of no extinction is appropriate. Even low levels of extinction can dramatically reduce the statistical power of the test (Paradis 2005). Fossil remains of several extinct species of furnariids indicate unequivocally that extinction has occurred in the family.
(Tonni 1977, Noriega 1991, Tonni & Noriega 2001, Claramunt & Rinderknecht 2005). However, a more relevant question is whether extinction has been pervasive enough to leave a signal in the phylogenetic tree of extant species. To evaluate this possibility, I estimated speciation and extinction rates using the phylogeny by fitting a uniform birth-death model (Nee et al. 1994, Nee 2006). Second, I evaluated the appropriateness of a Brownian motion model of trait evolution used in ancestral character reconstruction. I used model selection techniques to evaluate a number of simple models of trait evolution: Brownian motion, Ornstein-Uhlenbeck, which is a Brownian model with a central tendency (Butler & King 2004), lambda transformation of branch lengths (Pagel 1999), speciational (Pagel 1999), and 'early burst' (Harmon et al. in review).

Analyses were conducted in the R language for statistical computing (R Development Core Team 2009). Code for adjusting phylogenetic GLS models was kindly provided by R. P. Freckleton. Ancestral state reconstruction using likelihood was performed using function ace() and the Yule model with covariates was fitted using function yule.cov(), both part of the APE library (Paradis et al. 2004). Parameter estimation of the birth-death model of diversification was conducted using function birthdeath() in the same library. Parameter estimation, log-likelihoods and AIC values for the five models of Kipp's Index evolution were obtained using function fitContinuous() of the GEIGER library (Harmon et al. 2008).

RESULTS

Kipp's Index in the Furnariidae ranges from 5.9% in *Phacellodomus ferrugineigula* to 37% in *Geositta antarctica*, but most species had intermediate values (1st quartile =12.3; median: = 15.7; 3rd quartile = 18.8). Among the smallest furnariids there are genera, such as *Acrobatornis*, *Metopothrix*, *Siptornis*, *Microxenops*, and *Xenops*, with high Kipp's Indices, but also genera with low Kipp's indices, such as *Synallaxis*, *Certhiaxis*, and *Hellmayrea*. The highest values are found in intermediate-sized birds like *Geositta*, *Cinclodes*, and *Berlepschia*, but in the same size range
there are birds with very low Kipp's indices, such as species of *Thripadectes*, *Geocerthia*, and *Automolus*. Finally, the largest species, all woodcreepers, have only intermediate values of Kipp's Index. Overall, there was a negative relationship between Kipp's Index and body size (Figure 3.3).

A phylogenetic GLS model relating Kipp's Index and aspect ratio showed no significant phylogenetic signal (Lambda < 0.01; Likelihood ratio test for Lambda ≠ 0: Chi-square = -0.001, d.f. = 1, P = 1), and ordinary and phylogenetic linear models gave similar results: Kipp's Index was strongly related to aspect ratio (phylogenetically adjusted $R^2 = 0.66$, Figure 3.4).

Kipp's Index was negatively correlated with diversification. Clades with high indices tend to be small, and clades with low indices tend to be species-rich (Figure 3.5). The effect of Kipp's

**Figure 3.3** Relationship between body size and Kipp's Index for 278 species of Furnariidae. Body size was calculated as the mean of 11 log-transformed linear measurements. Regression line from a phylogenetic generalized least-squares model ($R^2 = 0.02$, $\hat{\beta} = -4.5$, $F = 6.5$, d.f. = 1, $P = 0.01$).
Figure 3.4 Relationship between Kipp's Index and aspect ratio for 36 species of Furnariidae. Numbers correspond to species in Table 3.1. Regression line from a phylogenetic generalized least-squares model ($R^2 = 0.66, F = 68.4$, d.f. = 1, $P < 0.001$). Wing outlines representing low (left, *Synallaxis erythrothorax* LSUMZ 180728, female, 15.8g) and high (right, *Glyphorynchus spirurus* LSUMZ 180713, female, 15.3g) Kipp's Index and aspect ratio.

Index on the diversification rate was significant (model deviance: -957; null deviance: -949; Chi-square = 7.8, d.f. = 1, $P = 0.005$) with a negative effect ($\hat{\beta} = -0.80$, SE = 0.20; $\hat{\alpha} = -1.8$, SE = 0.050, Figure 3.6). The signal of extinction is not present in the phylogeny. The birth-death model fit returned an essentially pure-birth Yule model (log-likelihood = 474.5; net diversification rate = 0.14, confidence interval: 0.13, 0.16; relative extinction rate $\varepsilon = 0$, confidence interval: 0, 0.11); therefore, a pure-birth model seems a valid approximation for the analysis of diversification of extant furnariid species. On the other hand, a pure Brownian model was not the most appropriate model for Kipp's Index evolution; a lambda model, in which internal branches are shorter than terminal branches, fit the data better (Table 3.2). Accordingly,
Table 3.1 Morphometric variables and estimates of flight performance parameters for 35 species of Furnariidiae. Linear measurements in cm, areas in cm². Sample size (n), wingspan (WS), total area (TA), aspect ratio (AR), wing length (WL), secondary 1 length (S1), and Kipp's Index.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>WS</th>
<th>WA</th>
<th>TA</th>
<th>AR</th>
<th>WL</th>
<th>S1</th>
<th>Kipp</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Anabacerthia variegaticeps</td>
<td>1</td>
<td>27.9</td>
<td>77</td>
<td>184</td>
<td>4.2</td>
<td>87.9</td>
<td>70.8</td>
<td>19.4</td>
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<tr>
<td>2. Asthenes dorbignyi</td>
<td>1</td>
<td>21.0</td>
<td>40</td>
<td>104</td>
<td>4.2</td>
<td>60.3</td>
<td>56.2</td>
<td>6.9</td>
</tr>
<tr>
<td>3. Asthenes ottonis</td>
<td>2</td>
<td>18.6</td>
<td>36</td>
<td>86</td>
<td>4.0</td>
<td>58.1</td>
<td>52.1</td>
<td>10.3</td>
</tr>
<tr>
<td>4. Asthenes virgata</td>
<td>2</td>
<td>22.3</td>
<td>52</td>
<td>125</td>
<td>4.0</td>
<td>66.8</td>
<td>61.9</td>
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<td>5. Campylocinetus pusillus</td>
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<td>29.7</td>
<td>87</td>
<td>205</td>
<td>4.3</td>
<td>92.4</td>
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<td>6. Cinclodes taczanowskii</td>
<td>1</td>
<td>34.0</td>
<td>115</td>
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<td>116.1</td>
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<td>41</td>
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<td>56.3</td>
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<td>86</td>
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<td>97.3</td>
<td>78.8</td>
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<td>234</td>
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<td>107.0</td>
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<td>104.2</td>
<td>85.6</td>
<td>17.8</td>
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<td>126.9</td>
<td>100.7</td>
<td>20.6</td>
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<td>85.8</td>
<td>66.8</td>
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<td>107</td>
<td>4.8</td>
<td>70.8</td>
<td>54.4</td>
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<td>82</td>
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<td>56.6</td>
<td>51.0</td>
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<td>9.9</td>
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<td>24.5</td>
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<td>64.0</td>
<td>7.7</td>
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<td>19.6</td>
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<td>88</td>
<td>4.3</td>
<td>59.5</td>
<td>51.8</td>
<td>13.0</td>
</tr>
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<td>19. Premnornis guttuligera</td>
<td>2</td>
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<td>41</td>
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<td>66.2</td>
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<td>13.6</td>
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<td>109</td>
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<td>113.5</td>
<td>92.6</td>
<td>18.4</td>
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<td>21. Schizoeacca griseomurina</td>
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<td>58.4</td>
<td>51.8</td>
<td>11.3</td>
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<td>22. Sclerurus guatemalensis</td>
<td>2</td>
<td>28.4</td>
<td>75</td>
<td>183</td>
<td>4.4</td>
<td>87.6</td>
<td>74.8</td>
<td>14.7</td>
</tr>
<tr>
<td>23. Synallaxis brachyura</td>
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<td>19.4</td>
<td>34</td>
<td>90</td>
<td>4.2</td>
<td>54.6</td>
<td>49.1</td>
<td>10.0</td>
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<td>18.2</td>
<td>32</td>
<td>81</td>
<td>4.1</td>
<td>55.2</td>
<td>49.3</td>
<td>10.7</td>
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<td>18.7</td>
<td>34</td>
<td>87</td>
<td>4.0</td>
<td>56.2</td>
<td>51.1</td>
<td>9.2</td>
</tr>
<tr>
<td>26. Syndactyla rufosuperciliata</td>
<td>1</td>
<td>25.1</td>
<td>62</td>
<td>146</td>
<td>4.3</td>
<td>77.6</td>
<td>66.8</td>
<td>13.9</td>
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<td>27. Upucerthia jelskii</td>
<td>1</td>
<td>27.6</td>
<td>78</td>
<td>181</td>
<td>4.2</td>
<td>83.9</td>
<td>75.7</td>
<td>9.8</td>
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<td>28. Xenerpestes minlosi</td>
<td>1</td>
<td>16.6</td>
<td>29</td>
<td>65</td>
<td>4.2</td>
<td>54.3</td>
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<td>18.7</td>
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<td>29. Xenerpestes singularis</td>
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<td>17.9</td>
<td>31</td>
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<td>55.3</td>
<td>44.8</td>
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<td>30. Xenops minutus</td>
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<td>19.5</td>
<td>33</td>
<td>78</td>
<td>4.8</td>
<td>60.2</td>
<td>47.1</td>
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<td>31. Xiphocolaptes proceropirhynchus</td>
<td>1</td>
<td>41.0</td>
<td>174</td>
<td>404</td>
<td>4.2</td>
<td>131.0</td>
<td>111.1</td>
<td>15.1</td>
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<td>32. Xiphorhynchus erythroptygius</td>
<td>1</td>
<td>35.8</td>
<td>115</td>
<td>270</td>
<td>4.8</td>
<td>113.4</td>
<td>88.1</td>
<td>22.3</td>
</tr>
<tr>
<td>33. Xiphorhynchus flavigaster</td>
<td>1</td>
<td>33.1</td>
<td>104</td>
<td>240</td>
<td>4.5</td>
<td>101.5</td>
<td>84.4</td>
<td>16.8</td>
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<td>34. Xiphorhynchus susurrans</td>
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<td>89</td>
<td>206</td>
<td>4.5</td>
<td>95.1</td>
<td>77.2</td>
<td>18.9</td>
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<td>35. Xiphorhynchus triangularis</td>
<td>3</td>
<td>38.0</td>
<td>123</td>
<td>294</td>
<td>4.9</td>
<td>120.0</td>
<td>94.0</td>
<td>21.6</td>
</tr>
</tbody>
</table>
Figure 3.5 Distribution of Kipp's Index values across the phylogeny. Values at nodes are maximum likelihood ancestral reconstructions.
I repeated the ancestral trait reconstruction using a lambda transformation of the tree (Pagel 1999). The result of fitting the Yule model with covariates using the new ancestral reconstructions was similar to the previous result (model deviance = -958; Chi-square = 8.4, d.f. = 1, \( P = 0.004 \); \( \hat{\beta} = -0.84 \), SE: 0.21; \( \hat{\alpha} = -1.8 \), SE: 0.050).

**Figure 3.6** Predicted speciation rates as a function of Kipp’s Index in Furnariidae as estimated by the Yule model with covariates.

**Table 3.2** Diagnostics of models of Kipp's Index evolution.

<table>
<thead>
<tr>
<th>Model</th>
<th>Sigma</th>
<th>Parameter</th>
<th>Log-likelihood</th>
<th>AIC</th>
<th>( \Delta )AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lambda</td>
<td>0.0035</td>
<td>0.92</td>
<td>59.0</td>
<td>-112</td>
<td>-</td>
</tr>
<tr>
<td>Speciational</td>
<td>0.011</td>
<td>0.41</td>
<td>52.8</td>
<td>-100</td>
<td>12</td>
</tr>
<tr>
<td>Ornstein-Uhlenbeck</td>
<td>0.010</td>
<td>0.06</td>
<td>38.4</td>
<td>-71</td>
<td>41</td>
</tr>
<tr>
<td>Delta</td>
<td>0.0029</td>
<td>3.00</td>
<td>35.5</td>
<td>-65</td>
<td>47</td>
</tr>
<tr>
<td>Brownian</td>
<td>0.0072</td>
<td>-</td>
<td>24.3</td>
<td>-45</td>
<td>67</td>
</tr>
<tr>
<td>Early burst</td>
<td>0.0072</td>
<td>0</td>
<td>24.3</td>
<td>-43</td>
<td>60</td>
</tr>
</tbody>
</table>
The effect of body size on diversification was not significant (model deviance: -949; Chi-square < 0.01, d. f. = 1, \( P = 0.98 \)) in contrast to the clade effect (model deviance: -958; Chi-square = 9.1, d. f. = 2, \( P = 0.011 \)). Therefore, I fit a final Yule model including both Kipp's Index and a clade effect. This model resulted in a decrease in deviance (-961); however, this model was not a significant improvement over the model with Kipp's Index only (Likelihood ratio test: Chi-square = 3.8, d.f. = 2, \( P = 0.15 \)).

**DISCUSSION**

**Kipp's Index, Flying Ability, and Dispersal**

The aspect ratio of the wing has a strong influence on flight performance. According to aerodynamic models of avian flight, high aspect ratios reduce the cost of transport of level flight (Norberg 1995, Pennycuick 2008). Birds that spend most of their time airborne have high aspect ratio wings, and birds with poor flight capabilities have low aspect ratio wings (Rayner 1988, Videler 2005). Other components of the flight apparatus, such as the volume and type of the pectoral muscles, may also have an influence in flight performance, but they are usually correlated with wing shape (Videler 2005). However, wingspan and wing area data are not currently available for most bird species; therefore, related indices such as Kipp's provide a convenient surrogate, especially for large-scale studies involving tropical birds.

Kipp's Index varies considerably among birds and is qualitatively related to flying ability. According to Kipp (1959), among European birds, swifts have the highest indices (71-75%) followed by terns (66-71%); gulls, boobies, shorebirds, and swallows have medium-high values (50-65%). In most other birds, the distance between the longest primary and the first secondary is less than half the wing length (Kipp's Index < 50%). Water birds, raptors, bee-eaters and open-country passerines have intermediate values (35-50%), whereas woodpeckers and most passerines are in the 20-35% range. Only two European species have Kipp indices well under
20%: *Troglydus troglodytes* (15-16%) and *Cettia cetti* (16-17%). Among passerines, Lockwood et al. (1998) found that migratory species had higher Kipp's indices than their sedentary relatives.

The Furnariidae shows a wide range of Kipp's Index values indicating a wide variety of flight abilities. Among the birds with the highest indices are *Geositta* and *Cinclodes* (25-37%), two unrelated genera that inhabit temperate to cold regions and that are strong fliers, even in strong wind conditions (Remsen 2003). Also with relatively high Kipp's indices (22-27%) are genera that inhabit the canopy of tropical forests, such as *Acrobatornis*, *Metopothrix*, *Microxenops*, and *Siptornis*. Among the tropical genera, *Berlepschia* has the highest value (32%). The sole species of this genus inhabits the canopy of palm swamps across the Amazon basin. Presumably, a high aspect ratio may allow *Berlepschia* to fly economically from palm to palm, or between swamp patches. However, most furnariids have low Kipp's indices as compared to European birds (Kip 1959). Three quarters of the furnariid species have Kipp's indices under 19%. Birds that inhabit dense vegetation in open areas or the understory, such as *Synallaxis*, *Phacellodomus*, *Automolus*, and *Thripadectes*, show the lowest Kipp’s indices. These species are probably in the lower limit of Kipp's Index among flying birds. On the other hand, Kipp's indices under 15% and even under 10% are common among Neotropical passerine families such as *Formicariidae*, *Rhinocryptidae*, *Grallariidae*, *Melanopareiidae*, and *Thamnophilidae* (Claramunt, unpublished data).

Dispersal in birds was traditionally presumed to be determined by behavioral choices about when, where, and how far to disperse. For example, limited dispersal in tropical birds was attributed to behavioral flightlessness or fear of flying over inhospitable habitat (Diamond 1981, Laurance et al. 2004). However, recent evidence suggests that flying ability may have an important role on dispersal. Dawideit et al. (2009) found that a multi-predictor model including Kipp's distance (*WL – SI*) and bill depth explained 33% of the variation in natal dispersal.
distance among British birds. This percentage of the total variation should be considered high given that natal dispersal distances in birds typically have large variances (Paradis et al. 1998, Sutherland et al. 2000), and a high percentage of the variation in natal dispersal distance is probably unpredictable because it reflects the fortuitous history of dispersing individuals. Moore et al. (2008) investigated flight performance in nine tropical passerines plus a hummingbird, and found that six of them could not fly 300 meters over water, implying an important flight performance limitation in the dispersal capabilities of these species. Dispersal ability was estimated from 'dispersal challenge' experiments conducted in Gatun Lake, in the Panama Canal, in which captured birds were released from a boat at incremental distances from shore (Moore et al. 2008). I calculated Kipp's indices for the species used in Moore et al. (2008) and found that it is strongly related to the mean distance flown by each species (Figure 3.7), corroborating the expected causal link between wing morphology and flight performance. This suggests a mechanistic explanation for reduced dispersal in tropical birds, in which reduced flight performance determined by the characteristics of the flight apparatus limits the dispersal ability of species.

Ultimately, behavioral and morphological causes of dispersal are expected to be correlated. Birds with a strong flight apparatus are more likely to engage in long distance flights or flights over inhospitable habitats, whereas birds with a weak flight apparatus are less likely to do so (Rayner 1988, Vedeler 2005, Pennycuick 2008). The advantage of using wing morphology for the study of dispersal is that it is easy to quantify. Furthermore, the fact that wing morphology is evolutionarily conservative (Table 3.2) permits inferences of ancestral states and, more generally, the use of phylogeny-based methods for the study the evolutionary process. If
Figure 3.7 Relationship between Kipp's Index and mean distance flown over water for 10 species of tropical birds. Wing measurements were taken at LSUMZ for four males of each species. Mean distance flown was taken from table 3 in Moore et al. (2008). Species: (1) *Epinecrophylla fulviventris*, (2) *Myrmeciza exsul*, (3) *Hylophylax naevioides*, (4) *Thamnophilus atrinucha* (Thamnophilidae), (5) *Habia fuscicauda* (Cardinalidae), (6) *Xiphorhynchus susurrans* (Furnariidae), (7) *Manacus vitellinus* (Pipridae), (8) *Mionectes oleagineus* (Tyrannidae), (9) *Pipra mentalis* (Pipridae), and (10) *Phaethornis longirostris* (Trochilidae). Kipp's Index is plotted in a logarithmic scale.

Additional studies corroborate a strong link between Kipp's Index, flight performance, and dispersal, then this simple morphological index has the potential to stimulate the study of dispersal in birds and its effects not only on diversification but also on population structure, metapopulation dynamics, biogeography, and conservation.

**Dispersal and Diversification**

Studies of dispersal and diversification in birds are scarce. Owens et al. (1999) and Phillimore et al. (2006) explored the relationship between the number of species in family-level taxa and multiple biological predictors. They found that a categorical index of dispersal propensity was the strongest predictor of diversification, having a positive effect on diversity. On the other hand,
Belliure et al. (2000) found a negative relationship between estimates of dispersal distance (Paradis et al. 1998) and subspecies richness (as a surrogate for population differentiation) for a group of European birds. Mayr & Diamond (2001) studied the relationship between overwater dispersal and degree of subspecific differentiation in Melanesian birds; they found the highest degree of geographic variation in species with intermediate dispersal propensity. Finally, Burney and Brumfield (2009) found that genetic differentiation across the Andes and two major Amazonian rivers was correlated with foraging strata: birds that inhabit the forest canopy had lower level of genetic differentiation, a phenomenon that they interpreted as the effect of a higher dispersal propensity in canopy birds.

As for other volant organisms, studies are also few. Genetic differentiation in bat species across the Strait of Gibraltar was not significantly related to aspect ratio or wing loading (García-Mudarra et al. 2009). Studies of wing shape and genetic structure in insects produced mixed results (Zera 1981, Liebherr 1988).

Earlier broad-scale comparisons suffered from considering species or higher-level taxa as independent data points in statistical analyses. Methods that compare number of taxa with the presence or absence of traits fail to distinguish whether the a pattern of correlation is produced by changes in rates of diversification related to the trait, or a scenario in which more taxa possess a specific trait because of an asymmetry in trait evolution (Duda & Palumbi 1999, Maddison 2006). Only those methods that make intense use of phylogenetic information, such as the Yule model with covariates, are able to disentangle these alternative processes (Paradis 2007). Although differences in the methods used may explain part of the discrepancy in the results, it is likely that a universal simple relationship between dispersal and diversification does not exist.
The Intermediate Dispersal Hypothesis

An alternative explanation that can reconcile the existence of positive and negative relationship between dispersal and diversification is what can be called the "intermediate dispersal hypothesis". In this model, diversification rates are maximized at intermediate levels of dispersal (Mayr 1963, Diamond et al. 1976, Mayr & Diamond 2001, Price & Wagner 2004, Phillimore et al. 2006, Paulay & Meyer 2006). Lineages with very low dispersal ability are expected to be geographically restricted and hence have few opportunities for geographic speciation. On the other hand, species with extremely high dispersal ability are expected to be distributed over wide areas but have reduced chances of speciation due to maintenance of genetic cohesion through gene flow. Only lineages with intermediate dispersal abilities can experience a dynamic of range expansion and geographic subdivision that promote speciation.

In a continuous scale of dispersal ability, this model can be represented as a curvilinear or bell-shaped relationship between dispersal and diversification (Figure 3.8). The key feature of this model is that depending on the exact shape of the curve and the range of dispersal abilities shown by the organisms under study, both negative and positive correlations between dispersal and versification can be observed. Among organisms with low dispersal ability a positive correlation is expected, whereas among organisms with high dispersal ability a negative relationship is expected. Finally, organisms with intermediate dispersal abilities may not show any significant linear trend, although a curvilinear relationship is expected if variation in dispersal ability covers a broad range.

The shape of the curve may also depend on the scale and configuration of the geographic scenario. In a continuous geographical scenario, such as small continent with no major barriers, even low levels of dispersal may inhibit diversification. This would produce a shift in the
maximum diversification rates towards lower values of dispersal ability and result in mainly a negative relationship between dispersal and diversification (Figure 3.9b). On the other hand, in an oceanic archipelago, low dispersal may confine lineages to single islands, in which case opportunities for geographic speciation are limited. Only lineages that can disperse over water and colonize multiple islands can diversify (Cowie & Holland 2006). In this case, diversification may be maximized at higher levels of dispersal ability, and result in the dominance of a positive relationship between dispersal and diversification (Figure 3.9a).

Finally, although the intermediate dispersal pattern is driven by geographic speciation, extinction may have an effect on the shape of the curve. Because of its effects on local persistence, recolonization, and geographic range size, high dispersal is expected to decrease extinction risk (McKinney 1997, Purvis et al. 2000a, 2000b, Gaston & Blackburn 2002, Jones et al. 2003). If the incidence of extinction is high in relation to speciation, then diversification will...
Figure 3.9 Alternative scenarios of the relationship between dispersal and diversification. a – Continents, small regions, weak geographic barriers; b – Archipelagos, strong barriers, high local extinction risk.

be maximized at higher levels of dispersal. Therefore, extinction can increase the region of the curve that shows a positive relationship between dispersal and diversification (Figure 3.9a).

The intermediate dispersal hypothesis in the context of the configuration of the geographic setting can reconcile the result from studies of dispersal and diversification in birds. The three studies concerning continental birds found a negative relationship between dispersal and diversification (Belliure et al. 2000, Burney & Brumfield 2009, this study). Given that many Neotropical birds, like most furnariids, are among the birds with the lowest dispersal ability, the relationship between dispersal and diversification within continental avifaunas is likely to be predominantly negative. In archipelagos, on the other hand, diversification is inhibited at lower dispersal levels, producing the intermediate pattern found by Mayr & Diamond (2001). Finally, at the global scale the effect of high dispersal ability is reminiscent of an archipelago, first because intercontinental dispersal can stimulate diversification (Voelker et al. 2009, Moyle et al. 2009, Van Bocxlaer et al. 2010), and second because the inhibitory effect of dispersal is diminished because even high dispersal potential may not be sufficient to maintain genetic cohesion across continents. This may explain the positive pattern found by Phillimore et al. (2006) for avian families of the world.
Alternatively, dispersal ability may evolve fast and lineages may experience phases of colonization, when they have high dispersal ability, and phases of speciation, when they have low dispersal ability: a taxon cycle process (Wilson 1961, Ricklefs & Bermingham 2002). In theory, taxon cycles can yield the highest rates of speciation because at some phases lineages combine large geographic distributions with low dispersal ability, increasing the probability of multiple speciation events. Moyle et al. (2009) proposed that rapid shifts in dispersal ability may explain extremely high speciation rates during the transcontinental diversification of white-eyes (Zosteropidae). Distinguishing between a taxon cycle model and a more stable intermediate dispersal model may be possible. Taxon cycle models predict a faster rate of flying ability evolution than a stable intermediate dispersal model. Using phylogenies and measures of dispersal ability such as Kipp's Index it may possible to distinguish between these to models with empirical data. Further development of both appropriate quantitative measurements of dispersal and appropriate phylogenetic analytical methods will be essential to advance our knowledge of the role of dispersal on diversification.
CHAPTER 4

EVOLUTIONARY NOVELTIES IN FURNARIIDAE AND THEIR EFFECT ON RATES OF CLADOGENESIS: A SEARCH FOR KEY INNOVATIONS

INTRODUCTION

Key innovations are evolutionary novelties in any aspect of an organism's phenotype that confer them a functional advantage in relation to ancestral phenotypes or coexisting organisms (Simpson 1953, Schluter 2000). A key innovation may allow a lineage to use ecological resources previously not in use or underutilized by other lineages. Therefore, key innovations may create new niches and put lineages in new 'adaptive zones' (Simpson 1953). Alternatively, a key innovation may confer competitive advantage over other lineages using a common resource. In general, key innovations may benefit a lineage in regard not only to competition but also to any non-neutral ecological interaction such as parasitism, predation, or mutualism (Schluter 2000). Examples of key innovations are the specialized toepads of Anolis lizards (Jackman et al. 1997, Losos 2009) and the decoupling of pharyngeal and oral jaws in cichlids (Liem 1973, Hulsey et al. 2006). Among birds, wood-drilling adaptations in woodpeckers (Bock 1999) and gaping adaptations in the Icteridae (Beecher 1951) are two classical examples, although their effects on diversification have not been quantified.

According to the ecological theory of adaptive radiation, key innovations may enhance diversification (Simpson 1953, Schluter 2000). The effect of key innovations on speciation may have multiple causes. First, key innovations expand the adaptive landscape of lineages (or increase its dimensionality, Nosil & Harmon 2009), creating new adaptive peaks and valleys that produce more opportunities for divergent natural selection, the engine of ecological speciation. The effect of divergent selection on speciation is enhanced if traits under ecological natural selection are also involved in mate recognition, and thus may also produce behavioral prezygotic
isolation (Schluter 2001, McKinnon et al. 2004, Price 2008). Second, key innovations may allow lineages to expand their geographic range to new regions, resulting in increased opportunities for geographic isolation and speciation (Rosenzweig 1995, Price 2008).

Finally, key innovations may be particularly relevant to continental radiations. The rapid evolution of many clades on oceanic islands has been attributed to the abundance of ecological opportunities in depauperate habitats (Rosenzweig 1995, Schluter 2000). In contrast, continental radiations evolved in old and diverse biotas in which free niche space is presumably scarce. Geological and climatic changes may create ecological opportunities, but competition for the occupation of the new niches may be intense. Key innovations, on the other hand, can create new empty niches for particular clades, or can determine which of the existing clades can exploit the ecological opportunities created by geological or climatic changes. Either way, key innovations may have a more important role in adaptive radiations in continents than in islands.

**Morphological Innovations in Furnariidae**

According to simple models of cladogenesis, the Furnariidae has diversified at a higher rate when compared to its closest relatives (Chapter 2). This increase in rate has not affected all furnariids because the Sclerurinae seem to be evolving at the same slow background rate of closely related families (Figure 2.5). Here I explore this phenomenon in more detail. First, using a complete phylogeny I reevaluate the existence of shifts in diversification rate and their placement in the tree. Second, I investigate whether changes in diversification rates in Furnariidae can be explained by morphological key innovations. In particular, I investigated furnariid features that are unique or rare among other passerine birds. To facilitate the interpretation of the functional and ecological significance of these morphologies, I grouped traits into three main functional syndromes: adaptations for climbing, spiny-tail specialization, and cranial kinesis.
• Climbing Adaptations. Few groups of passerine birds present highly specialized climbing adaptations. Usually, species that forage on thick branches have longer hind toes and more curved claws than perching birds (Richardson 1942, Bock & Miller 1959, Osterhaus 1962, Feduccia 1993, Pike & Maitland 2004). However, more specialized trunk-climbers that use the tail for support present a suite of adaptations in the lower body musculoskeletal system (Richardson 1942, Bock & Miller 1959, Norberg 1986, Moreno 1991, Raikow 1994a). Furnariids show a wide spectrum of climbing specializations. Species in the genus *Xenops*, for example, forage acrobatically on dead branches and vines of varying diameters (Skutch 1969, Remsen 2003); although they possess strongly curved claws and long hind toes, they have a normal passerine tail. Species in the genera *Margarornis*, *Premnoplex*, *Roraimia*, and to a lesser extent, *Cranioleuca*, use their tails as a brace when climbing vertical branches and trunks (Feduccia 1970, Remsen 2003, Areta 2007). Tail feathers in these species present slightly stiffened and protruding rachises. At the most specialized end of the spectrum are the woodcreepers, which show a degree of climbing specialization rivaling that of woodpeckers (Richardson 1942). Many aspects of the woodcreeper anatomy are modified for climbing, including hindlimb proportions, relative toe length, claw curvature, tail feather structure, and several components of the hindlimb-tail musculoskeletal apparatus (Richardson 1942, Feduccia 1973, Bledsoe et al. 1993, Raikow 1993, 1994a, Tubaro et al. 2002). This suite of adaptations allows woodcreepers to forage on trunks and major branches of the forest, places that are less accessible to other passerines. Therefore, climbing adaptations acted as a key innovation by putting some furnariid lineages in a new adaptive zone (Raikow & Bledsoe 2000).

• Spiny-tail Morphology. Furnariids present a wide variety of tail morphologies, of which tails adapted for climbing are only a fraction (Remsen 2003, Fjeldså et al. 2005). In particular, a diverse group of furnariids in the traditional subfamily Synallaxinae are known as 'spinetails'
because of the particular structure of their tails. Their tails are long and highly graduated, with a reduced number of feathers in some cases, and with loosely integrated vanes that end in a tapered or pointed tip. In some species, feather wear erodes the distal barbs easily and nude rachises protrude beyond the vanes like spines. The function of these tails during locomotion has not been studied in detail. From an aerodynamic point of view, tails with short outer rectrices are inferior for lift, maneuverability, and agility, even for birds that fly in cluttered habitats (Thomas & Balmford 1996). Therefore, flight enhancement does not seem to be responsible for the spiny-tail morphology. Field observations as well as patterns of wear indicate that these tails are usually in contact with the vegetation during locomotion. The species that show the most extreme spiny-tail morphologies forage in dense vegetation such as thickets, bushes, and bunch grasses in forest borders or open habitats. The tail seems be used as a prop to stabilize the body during acrobatic movement among the vegetation. In this regard, they may play a role in body support and stability, as in climbing birds. However, the mode and frequency of use as well as the nature of the substrate make the spiny-tail a different adaptation, which is also evident in their distinct morphology. In addition to direct support during perching, spiny-tails may provide stability during jumping from perch to perch as in lizards (Gill et al. 2009). Interestingly, Anolis lizards that live in cluttered low vegetation including grasses or bushes have longer tails (Losos 2009). The few other passerine genera that show tails similar to the spinetails also live in dense thickets or tall grass: Megalurus, Bradypterus, Sphenoeacus, Bowdleria (Sylviidae), Stipturus (Maluridae), and Emberizoides (Thraupidae). Acute to acuminate tail feathers are common among birds that live in tall grasslands such as Ammodramus, Donacospiza, Coryphaspiza (Emberizidae), and Dolichonyx (Icteridae). Among non-passerines, mousebirds (Coliiformes) are well known for using their long and strongly graduated tails for support during acrobatic maneuvers and postures among bush twigs. Irestedt et al. (2009) found that Synallaxinae
spinetails have diversified at a higher rate and hypothesized that the expansion to open habitats facilitated this diversification. If the spiny-tail morphology enhances locomotion in cluttered vegetation, then it may represent a key innovation that helped Synallaxinae lineages to expand and diversify in South American non-forested habitats.

- Skull Kinetics. Modern birds present two main types of skull kinesis (Bock 1964, Zusi 1984). In prokinetic birds the rostrum is rigid and articulates with the cranium in a single bending axis at the craniofacial junction (Figure 4.1). In rhynchokinetic birds, in contrast, there are multiple bending zones along the rostrum. Although most birds are prokinetic, rhynchokinesis is the dominant condition in many diverse groups such as Charadriiformes, Columbiformes, and Trochilidae (Zusi 1984). In Passeriformes in particular, rhynchokinesis is present in only two families: Acanthisittidae (New Zealand wrens) and Furnariidae. The functional significance of rhynchokinesis is well known in shorebirds: bending zones along the bill allow precise movement of the tip of the bill that help birds capture prey in the sediment or other constricted spaces (Zusi 1984). However, in the Furnariidae the bending zones are close to the skull: a condition called 'proximal rhynchokinesis' (Zusi 1984). In proximally rhynchokinetic birds the pattern of bill movement is similar to that of prokinetic skulls. For this reason, Zusi (1984) proposed that proximal rhynchokinesis is a derived condition that originated from the need to strengthen the rostrum in clades in which rhynchokinesis is the ancestral condition. On the other hand, Fjeldså et al. (2005) hypothesized that rhynchokinesis was one of the most important innovations in Furnariidae because it allowed ancestral furnariids to feed on hidden prey. According to this hypothesis a more flexible bill facilitates probing difficult substrates such as masses of epiphytes, suspended plant debris, and bromeliads. Although the exact mechanism needs to be investigated, it is possible that rhynchokinesis opened many feeding niches in Furnariidae.
METHODS

Morphology

I examined study skins of 290 of the 293 currently recognized species of Furnariidae. Most specimens were examined at Louisiana State University Museum of Natural Science (LSUMZ), and the majority of additional specimens were examined at the American Museum of Natural History and the Field Museum of Natural History (see Acknowledgments for a complete list of institutions from which specimens were examined). I also obtained morphometric data for all these species, as described in Chapters 1 and 2. In addition, details of bill, tail, and foot morphology were recorded as discrete characters.

• Climbing Adaptations. Representing climbing adaptations, I used seven characters of the tail and one character of the foot that can be readily evaluated in study skin and have clear functional significance (Table 4.1). For each character, states were coded in such a way that 0 represent no specialization for climbing (the dominant states among passerines), and the other states represent
an increasing degree of specialization (Table 4.1). Then, I calculated a composite index of climbing adaptations for each species as the sum of the eight character states divided by the theoretical maximum (i.e. the sum of all higher states = 15). Claw curvature, which is greater in climbing birds and has a clear functional role (Richardson 1942, Feduccia 1993, Pike & Maitland 2004), was not considered in the present analysis. Claw curvature is high in climbing birds regardless of whether they use their tails or not (Richardson 1942). In this study, however, because I am specifically interested in the evolution of tail-supported climbing, the lack of information on claw curvature is not particularly detrimental.

• Spiny-tail Morphology. The spiny-tail adaptation was represented by five characters (Table 4.2). The functional significance of these characters has not been investigated empirically, and here I advance some hypotheses. One aspect of the spiny-tail syndrome is a disproportionate increase in the development of the central rectrices and a correlated reduction of the outer rectrices. This is evident in two complementary aspects: the degree of tail graduation and the number of rectrices (Table 4.2). I hypothesize that an emphasis on the central rectrices may be advantageous for the use of the tail as a staff during perching and hoping in dense vegetation. Because the central feathers are adjacent to the keel of the pygostyle, they can transmit forces directly to the axial skeleton. The external rectrices, on the other hand, are held in place by the rectricial bulb, which is a fibro-adipose body into which the base of the rectrices is inserted (Baumel et al. 1993). If the outer feathers were as long or longer than the central rectrices, then they would be the ones more likely to contact the substrate, providing a weaker support and reduced stability as compared to the central rectrices. This is probably the reason the central feathers in climbing birds are also the strongest. The forces acting on climbing tails, however, are more predictable, acting parallel to the rachis of the feathers, whereas in spinetails the substrate (branches, leaves, grass) may contact the tail from many directions. In addition to this
mechanical advantage, elongation of central rectrices and reduction of outer rectrices produces an increase in tail length without increasing tail mass. Therefore, strongly graduated tails may be more economic in terms of both metabolic investments during tail development and molt, and metabolic costs during locomotion.

Two other characters may be related to protection of barbs from abrasion. One, as in climbing tails, is the tapering of the vanes towards the tips for increasing exposure of the rachis to prevent damage of the distal barbs. The other is an increase in the asymmetry of the vanes by a decrease in the proportion of the vane lateral to the rachis. I hypothesize that this is another way of protecting the vanes from abrasion because the rachis protects the inner portion of the vane from being damaged by the vegetation.

The fifth character is the degree of integration of the vanes (Table 4.2). In many spinetails the barbs seem to be in lower density and are loose (not interlocked), resulting in a somewhat transparent vane. This condition may affect the entire feather or, more often, the distal portions only. Surprisingly, the vanes that are more exposed to the vegetation are not reinforced but weakened. I propose that this barb rarefaction is an adaptation to reduce water absorption or reduce drying times. Feathers that are in contact with the vegetation are exposed to water in the form of raindrops or dew. A dense, well-integrated vane can absorb more water whereas a lighter vane with loose barbs can retain less water and facilitate the drying process. As a first approximation to test this hypothesis I compared pairs of sister spinetail species that inhabit
Table 4.1 External characters that represent adaptations for tail-supported trunk climbing in Furnariidae.

<table>
<thead>
<tr>
<th>Character</th>
<th>States</th>
<th>Functional Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tail rachis curvature</td>
<td>0 straight</td>
<td>Rachis curvature increases the angle with which the tip touches the substrate (Richardson 1942). A uniformly decurved rachis is the most basic way of attaining this. Decurving only the tip has the advantage of maintaining a flat, streamlined tail for flight (Figure 4.2b). A logistic shape is considered here the most specialized in the sense that it involves and additional change in curvature direction during feather development. It is associated with the use of short stiff barbs for support instead of the tip; the distal straightening increases the contact of these barbs with the substrate (Figure 4.2c).</td>
</tr>
<tr>
<td></td>
<td>1 uniformly decurved</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2 decurved distally</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3 logistic</td>
<td></td>
</tr>
<tr>
<td>Rachises of central rectrices (dorsal</td>
<td>0 parallel</td>
<td>In all woodcreepers and a few other furnariids with specialized tails the rachises of the central feathers are not completely parallel but diverge distally. I hypothesize that this results in a more stable support because these rachises can 'absorb' some lateral forces that otherwise would produce bending stresses.</td>
</tr>
<tr>
<td>view)</td>
<td>1 divergent distally</td>
<td></td>
</tr>
<tr>
<td>Rectrix I, barbs in rachis tip</td>
<td>0 rachis tip with barbs</td>
<td>When the rachis tip plays a major role in support, a reduction in density of barbs towards the tip enhances contact of the tip with the substrate (Figure 4.3b). It also prevents barb abrasion if distal barbs are soft.</td>
</tr>
<tr>
<td></td>
<td>1 semi-nude</td>
<td></td>
</tr>
<tr>
<td>Rectrix I, rachis tip stiffness</td>
<td>0 soft</td>
<td>Provides a stronger and more stable support for the tail, especially when the rachis tip plays a major role in support</td>
</tr>
<tr>
<td></td>
<td>1 semi-rigid (still flexible to the touch)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2 rigid</td>
<td></td>
</tr>
<tr>
<td>Rectrix I, apex shape</td>
<td>0 rounded or obtuse</td>
<td>Decreasing barb length towards the tip maximizes rachis exposure and minimizes barb abrasion (Richardson 1942). I divided a more detailed classification of rectrix tip shapes (Figure 4.4) into three categories representing an increasing degree of shortening of distal barbs. Asymmetrical forms are considered highly specialized because they show a considerable reduction in barb length in the lateral side of the vane, which is more exposed to abrasion.</td>
</tr>
<tr>
<td></td>
<td>1 acute, acuminate, short</td>
<td></td>
</tr>
<tr>
<td></td>
<td>attenuate, short cuspidate, or bilobate</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2 long attenuate, long cuspidate, or asymmetrical forms</td>
<td></td>
</tr>
<tr>
<td>Rectrix I, apex barb specializations</td>
<td>0 unspecialized</td>
<td>Stiff barbs near the tip can contribute to mechanical support and are more resistant to abrasion (Richardson 1942). Stiffened barbs can be long and flexible (Figure 4.3a) or short (Figure 4.3c).</td>
</tr>
<tr>
<td></td>
<td>1 long semi-stiff barbs</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2 short stiff barbs</td>
<td></td>
</tr>
<tr>
<td>Rectrix I, apex barbs orientation</td>
<td>0 lateral</td>
<td>Facilitates the contact of stiffened barbs with the substrate.</td>
</tr>
<tr>
<td></td>
<td>1 lateroventral</td>
<td></td>
</tr>
</tbody>
</table>
Relative length of toe IV
0 equal to II
1 slightly longer than toe II
2 slightly shorter than toe III
3 roughly equal to III

Elongation of the outer toe improves ability to grasp around trunks and branches (Richardson 1942, Bock & Miller 1959), which counteracts the forces that tend to pull the bird apart from the trunk (Norberg 1986).

Table 4.2 External characters in Furnariidae that contribute to the spiny-tail morphology.

<table>
<thead>
<tr>
<th>Character</th>
<th>States</th>
<th>Functional Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tail graduation</td>
<td>Continuous: the ratio between the length of the central rectrices and the length of the outer rectrices.</td>
<td>Emphasis on the central axis of the tail (Figure 4.5).</td>
</tr>
<tr>
<td>Number of rectrices</td>
<td>0 six pairs</td>
<td>Emphasis on the central axis of the tail.</td>
</tr>
<tr>
<td></td>
<td>1 five pairs</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2 four pairs</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3 three pairs</td>
<td></td>
</tr>
<tr>
<td>Rectrix I, shape of apex</td>
<td>0 rounded or obtuse</td>
<td>Elongation of the central axis of the feather and reducing exposure of distal barbs to abrasion (Figure 4.4).</td>
</tr>
<tr>
<td></td>
<td>1 acute, acuminate, short attenuate, short cuspidate, bilobate, asymmetrical acute or asymmetrical round-cuspidate.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2 long attenuate, long cuspidate, or asymmetrical cuspidate</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3 linear (Sylviorthorhynchus)</td>
<td></td>
</tr>
<tr>
<td>Rectrix I, vane symmetry</td>
<td>0 lateral vane wider than medial vane</td>
<td>Reduced exposure of barbs to abrasion or deformation while maintaining vane area.</td>
</tr>
<tr>
<td></td>
<td>1 symmetrical vanes</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2 medial vane slightly wider than lateral vane</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3 medial vane nearly two times wider than lateral vane</td>
<td></td>
</tr>
<tr>
<td>Vane integration</td>
<td>0 completely integrated</td>
<td>Reduce vane volume or increase barb spacing to reduce moisture retention (Figure 4.6).</td>
</tr>
<tr>
<td></td>
<td>1 disintegrated at the tip</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2 disintegrated distal half</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3 all disintegrated</td>
<td></td>
</tr>
</tbody>
</table>

Figure 4.3 Climbing specializations at the tip of the tail feathers. a - Long semi-stiff barbs (*Lepidocolaptes angustirostris* LSUMZ 54403). b – Semi-nude rachis tip (*Dendrocincla tyrannina* LSUMZ 128400). c – Short stiff barbs (*Deconychura longicauda* LSUMZ 108272).
regions with drastically different levels of humidity. I determined relative habitat humidity from information on geographic distribution and habitat (Stotz et al. 1996, Remsen 2003).

I used all five characters to construct an index that represents the spiny-tail syndrome. I first scaled the tail graduation ratio so it varies between 0 and 3. Then, I added the values of the five characters and divided the result by eleven, which produced an index that varies between 0.02 and 1.
Figure 4.5 Four examples of tail graduation in Furnariidae. a – Forked tail (*Geositta tenuirostris* LSUMZ 114108). b – Slightly graduated (*Anabacerthia variegaticeps* LSUMZ 24435). c – Moderately graduated tail (*Synallaxis albilora* LSUMZ 124013). d – Strongly graduated tail (*Leptasthenura fuliginiceps* LSUMZ 123969).

Figure 4.6 Four levels of vane integration. a - Completely integrated (*Synallaxis albilora* LSUMZ 124013). b - Disintegrated at the tip (*Leptasthenura yanacensis* LSUMZ 95946). c - Disintegrated distal half (* SYNALLAXIS UNIRUFA* LSUMZ 81914). d - All disintegrated (*Schizoeaca palpebralis* LSUMZ 64141).
• Skull Kinesis. I inferred kinesis modes from characteristics of the skull (Zusi 1984, Claramunt & Rinderknecht 2005) using skeletal specimens deposited principally at LSUMZ and the AMNH. In some cases, kinesis type was corroborated by direct manipulation of completely clean and disarticulated skulls, but the difference between prokinesis and proximal rhynchokinesis is subtle and cannot be appreciated by direct observation of movements. Proximally rhynchokinetic skulls have four bending zones in the rostrum (Figure 4.7). One is the original craniofacial hinge between the skull and the dorsal bar of the rostrum. A second axis of bending is developed dorsocaudally to the craniofacial hinge involving the lateral bars of the rostrum. These two bending zones are separated physically by the caudal extension of the bony nares. Therefore, I recorded the caudal extension of the nares as one component of the development of the rhynchokinetic skull. Two additional bending zones in the rostrum are necessary for allowing movement. In the Furnariidae, flattened ventral bars, and slits at the junction of the lateral bars with the ventral bar constitute the two additional pairs of bending zones in the rostrum (Feduccia 1973, Zusi 1984, Claramunt & Rinderknecht 2005). Finally, complete ossification of the nasal or

![Diagram of skull showing hinges and bending zones](image)

**Figure 4.7** Hinges and bending zones in the skull of *Cinclodes taczanowskii* (LSUMZ 65376), a typical rhynchokinetic furnariid.
the alinasal walls would impede rhynchokinesis by securing the dorsal and ventral bars together (Figure 4.8).

![Diagram of nasal and alinasal walls]

**Figure 4.8** Ossification of nasal and alinasal walls in *Nasica longirostris* (LSUMZ 118574).

Even after examining these anatomical details, I could not determine kinesis types unequivocally in all cases. Some furnariids show intermediate morphologies for which is difficult to evaluate kinetic type (see also Feduccia 1973). For example, it is difficult to assess whether a minuscule slit at the base of the lateral bar or a ventral bar of intermediate thickness are sufficient to allow bending. In other cases, the bending zone of the lateral bars is absent, but kinesis is maintained (Zusi 1984). In addition, some furnariids have the additional bending zones in the rostrum but are prokinetic judging from the configuration of the nares, which end rostrally to the craniofacial hinge and therefore do not permit independent movement of the dorsal and lateral bars. For these reasons, instead of forcing the data to a dichotomy between prokinesis and rhynchokinesis, I constructed an index of kinetic mode that is the sum of rhynchokinetic traits across the five characters in Table 4.3. The index varies from 0 (a solid constructed prokinetic rostrum) to 9 (a fully rhynchokinetic rostrum).
Table 4.3 Characters of the skull that determine skull kinesis.

<table>
<thead>
<tr>
<th>Character</th>
<th>States</th>
<th>Functional Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nares extension: Extension of the caudal</td>
<td>0 clearly rostral</td>
<td>Only when the nasal openings surpass the craniofacial hinge the bending zone of the</td>
</tr>
<tr>
<td>border of the nasal openings in relation</td>
<td>1 slightly rostral</td>
<td>lateral bars can be displaced dorsocaudally and form a secondary hinge (hinge A in Zusi</td>
</tr>
<tr>
<td>to the craniofacial hinge</td>
<td>2 at the same level</td>
<td>1984 fig. 6).</td>
</tr>
<tr>
<td></td>
<td>3 dorsocaudally</td>
<td></td>
</tr>
<tr>
<td>Ven tral bar: flattened ventral bar near</td>
<td>0 absent, thick bar</td>
<td>Allow articulation between the ventral bar and the premaxillary rostrum (Figure 4.7,</td>
</tr>
<tr>
<td>the premaxillary rostrum</td>
<td>1 intermediate bar</td>
<td>hinge D in Zusi 1984 fig. 6).</td>
</tr>
<tr>
<td>Slits between lateral and ventral bars</td>
<td>0 absent</td>
<td>Allow articulation between the lateral and ventral bars (Figure 4.7, hinge E in Zusi</td>
</tr>
<tr>
<td></td>
<td>1 small slit</td>
<td>1984 fig. 6).</td>
</tr>
<tr>
<td></td>
<td>2 large slit</td>
<td></td>
</tr>
<tr>
<td>Alinasal wall</td>
<td>0 ossified</td>
<td>The ossification of the alinasal wall forms the sheet of bone that covers the caudal</td>
</tr>
<tr>
<td></td>
<td>1 unossified</td>
<td>portion of the bony nares in some birds (Parker 1877 plate lvii.10) and produces the</td>
</tr>
<tr>
<td></td>
<td></td>
<td>amphirhinal condition in others (von Ihering 1915, Feduccia 1967). Ossification of the</td>
</tr>
<tr>
<td></td>
<td></td>
<td>alinasal wall precludes rhynchokinesis because it secures the ventral and dorsal bars</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(Figure 4.8).</td>
</tr>
<tr>
<td>Nasal wall</td>
<td>0 ossified</td>
<td>The ossification of the nasal wall produces the sheet of bone that encircles the nares</td>
</tr>
<tr>
<td></td>
<td>1 unossified</td>
<td>in some birds (Parker 1877 plate lx.4). Ossification of the nasal wall precludes</td>
</tr>
<tr>
<td></td>
<td></td>
<td>rhynchokinesis because it secures the ventral and dorsal bars (Figure 4.8).</td>
</tr>
</tbody>
</table>

Statistical Analysis

During the past twenty years there has been continuous progress towards the development of statistical techniques to test the influence of traits on diversification. Most recent methods use phylogenies to estimate ancestral states and rates of diversification (Paradis 2005, Ree 2005, Maddison et al. 2007). Because of the high number of discrete states (Tables 4.1 and 4.2), I chose not to take a hypothesis-testing approach for each one at a time. Instead, I first investigated whether discrete shifts were detectable in diversification rates across the phylogeny. If such shifts are present, then I investigated whether they coincide with discrete evolutionary changes. As an alternative approach, I investigated gradual changes in diversification rate by evaluating
the effect of adaptive syndromes on diversification in a simultaneous analysis that combines all traits.

To investigate whether there were shifts in diversification rates within Furnariidae I used the MEDUSA (Modeling Evolutionary Diversification Using Stepwise AIC) approach (Alfaro et al. 2009a). MEDUSA uses a calibrated phylogeny to fit birth-death models of cladogenesis using likelihood methods (Rabosky et al. 2007). First, a model with single speciation and extinction rates across the tree is fitted. Then, models with two sets of rates are evaluated across the tree, assuming that a change from one set of rates to the other occurred on a particular branch. The best two-rates model is the one associated with the branch that maximizes the likelihood. With this rate shift fixed, a new round of models is evaluated consisting on an additional rate shift on the remaining branches. The model that maximizes the likelihood becomes the best three-rates model. In this way, models with an increasing number of rate shifts can be evaluated. As the number of rate shifts increases, so does the likelihood of the model but also the number of parameters that need to be estimated. Therefore, Akaike's information criterion (AIC) is used to select the best models regarding a balance between model fit and number of parameters. In this way, MEDUSA determines a set of branches in which a significant shift in diversification rates occurred.

The main advantage of the MEDUSA approach is that it evaluates all the nodes in the tree. A statistical test on a single branch associated with a trait change (like the BiSSE approach of Maddison et al. 2007) may be misleading if, for example, the shift in rates occurred not in that particular branch but in a nearby branch or in any descendant branch because diversification shifts may have a trickle-down effect (Alfaro et al. 2009b).

To explore whether particular morphological changes coincided with shifts in rates of diversification, I reconstructed ancestral states for both individual characters and the composite
indices. For individual traits, I reconstructed ancestral states using parsimony in Mesquite (Maddison & Maddison 2009). Multistate characters were treated as ordered. Usually, there are not only one but multiple equally parsimonious reconstructions. I examined all maximum parsimony reconstructions for the relevant branches. In addition to examining specific branches in which a shift in diversification occurred, I looked for state changes in two adjacent ancestral branches and the two descendant branches. Finally, as a measure of overall change, I computed the number of state changes along each branch of the phylogeny using PAUP* (Swofford 2003). I computed branch lengths using both accelerated and delayed transformation algorithms.

To reconstruct ancestral states for the composite indices, I used maximum-likelihood methods (Schluter et al. 1997). Because the indices are not unconstrained continuous variables, a strict Brownian motion model may not be appropriate. Therefore, I did not use branch length information for ancestral reconstructions. Ancestral states were estimated using function getAncStates() in the GEIGER library (Harmon et al. 2008) after setting all branch lengths equal to one using function kappaTree(). This method yields unweighted squared-change parsimony reconstructions (Maddison 1991).

To test the effect of adaptive syndromes on diversification, I used a Yule model with covariates approach (Paradis 2005). This approach models the diversification rate associated with each node in a phylogeny with a linear model of the form

\[ \ln \frac{\lambda}{1 - \lambda} = x_1 \beta_1 + x_2 \beta_2 + \ldots + x_p \beta_p + \alpha \]  

(4.1)

in which the logit transformation of the diversification rate \( \lambda \) is a linear function of the values of \( p \) variables. The model uses not only values at the terminal nodes (the observed values of the species) but also reconstructed values at each internal node. Parameters \( \beta \) and \( \alpha \) are estimated using maximum likelihood methods, specifically, by minimizing the deviance (equal to -2
log[likelihood]) using nonlinear minimization functions in R (see Paradis 2005 for further details). The great advantage of the Yule with covariates approach is that more than one variable can be analyzed simultaneously. Therefore, the question of the effect of a trait on diversification becomes analogous to a multiple regression problem. To test the effect adaptive syndromes on diversification, I fitted a separate model for each adaptive syndrome and then a model combining both syndromes. Using the likelihood of each model, I calculated AICs to guide model selection. When possible, statistical significance of the effect of a variable was evaluated by comparing models with and without the variable using a likelihood ratio test (Paradis 2005). Otherwise, I used the estimated standard errors of the coefficients to calculate \( P \)-values based on the Student's \( t \)-distribution (Faraway 2005).

I investigated the effect of climbing and spiny-tail morphological syndromes on diversification. Syndrome indices were log transformed to improve normality, and standardized (mean = 0, standard deviation = 1) to conform to the distributional requirement of the analysis (Paradis 2005). Then, I estimated ancestral states using maximum likelihood (Schluter et al. 1997). Skull kinesis could not be analyzed using this method because of the incomplete taxon sampling due to the dependence on skeletal material. Finally, the effect of a trait on diversification may vary from clade to clade (de Queiroz 2002, Paradis 2005, Donohue 2005). This scenario can be investigated using the Yule model with covariates in a straightforward fashion because clade identity can be included in the models as a categorical variable. Evaluating the significance of interaction terms, as in standard linear model approaches, can test clade-specific effect. In particular I investigated whether climbing adaptations had a differential effect in woodcreepers vs. other groups, for which I included in the models a categorical variable indicating whether a species or an internal node belongs to the Dendrocolaptini or not.
RESULTS

Ecological Correlates of the Spiny-tail Morphology

Functional significance of the spiny-tail morphology. In this preliminary analysis I found ten pairs of sister species that live in regions with marked differences in humidity (Table 4.4). Although some of these pairs are parapatric and may be in the same environment in the contact zone, they are exposed to different climates in most of their ranges. In five of these cases the species that inhabit the humid environment also have a higher degree of barb disintegration but in two cases the species that inhabit the driest environment had a more disintegrated tail. Even after discarding pairs that did not show differences in vane integration, the pattern is not statistically significant (Binomial test: 5 out of 7, \( P = 0.45 \)). None of the other discrete traits show a distinguishable tendency towards a difference between humid and dry habitat. On the other hand, tail graduation showed a strong relation with humidity (Table 4.4). In all 10 comparisons the species from the most humid environment had a more strongly graduated tail (Binomial test: 10 out of 10, \( P = 0.002 \)). Similarly, for the spiny-tail syndrome Index, nine out of ten comparisons showed a higher index in humid environments (Binomial test: \( P = 0.02 \)).

Major Shifts in Diversification Rates

The MEDUSA analysis revealed three major discrete shifts in diversification rates in the Furnariidae (Table 4.5, Figure 4.9). Although the models included both speciation and extinction, estimated extinction fractions (extinction rate/speciation rate) were negligible (> 0.001); therefore, the estimated diversification rates can be interpreted as speciation rates. The shift that maximized the likelihood was an increase in the speciation rate at the base of Cranioleuca spinetails (a monophyletic Cranioleuca including Thripophaga berlepschi but not Cranioleuca gutturata or C. sulphurifera). The second major improvement in likelihood was produced by an increase in the speciation rate at the base of a clade composed of the three
Table 4.4 Comparison of spiny-tail characteristics of ten sister species pairs that live in regions with markedly different levels of humidity.

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>Graduation</th>
<th>Number of rectrices</th>
<th>Vane symmetry</th>
<th>Apex shape</th>
<th>Vane integration</th>
<th>Spiny-tail Index</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Synallaxis albilora</em></td>
<td>dry</td>
<td>2.38</td>
<td>10</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0.39</td>
</tr>
<tr>
<td><em>Synallaxis gujanensis</em></td>
<td>humid</td>
<td>3.08</td>
<td>10</td>
<td>2</td>
<td>1</td>
<td>3</td>
<td>0.68</td>
</tr>
<tr>
<td><em>Synallaxis scutata</em></td>
<td>dry</td>
<td>2.99</td>
<td>10</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>0.587</td>
</tr>
<tr>
<td><em>Synallaxis cinerascens</em></td>
<td>humid</td>
<td>3.06</td>
<td>10</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>0.588</td>
</tr>
<tr>
<td><em>Synallaxis candei</em></td>
<td>dry</td>
<td>2.82</td>
<td>10</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0.40</td>
</tr>
<tr>
<td><em>Synallaxis erythrothorax</em></td>
<td>humid</td>
<td>3.30</td>
<td>10</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>0.59</td>
</tr>
<tr>
<td><em>Cranioleuca antisiensis</em></td>
<td>dry</td>
<td>1.90</td>
<td>12</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>0.47</td>
</tr>
<tr>
<td><em>Cranioleuca curtata</em></td>
<td>humid</td>
<td>2.05</td>
<td>12</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>0.48</td>
</tr>
<tr>
<td><em>Cranioleuca pyrrphodia</em></td>
<td>dry</td>
<td>1.69</td>
<td>12</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>0.47</td>
</tr>
<tr>
<td><em>Cranioleuca pallida</em></td>
<td>humid</td>
<td>2.05</td>
<td>12</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>0.39</td>
</tr>
<tr>
<td><em>Asthenes ottonis</em></td>
<td>dry</td>
<td>2.96</td>
<td>12</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>0.50</td>
</tr>
<tr>
<td><em>Schizoeaca palpebralis</em></td>
<td>humid</td>
<td>3.58</td>
<td>10</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>0.78</td>
</tr>
<tr>
<td><em>Asthenes pudibunda</em></td>
<td>dry</td>
<td>1.84</td>
<td>12</td>
<td>3</td>
<td>0</td>
<td>1</td>
<td>0.38</td>
</tr>
<tr>
<td><em>Schizoeaca vilcabambae</em></td>
<td>humid</td>
<td>3.58</td>
<td>10</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>0.87</td>
</tr>
<tr>
<td><em>Asthenes pyrrholecua</em></td>
<td>dry</td>
<td>1.95</td>
<td>12</td>
<td>3</td>
<td>0</td>
<td>1</td>
<td>0.38</td>
</tr>
<tr>
<td><em>Oreophylax moreirae</em></td>
<td>humid</td>
<td>2.97</td>
<td>10</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>0.77</td>
</tr>
<tr>
<td><em>Asthenes anthoides</em></td>
<td>dry</td>
<td>1.66</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0.29</td>
</tr>
<tr>
<td><em>Asthenes hudsoni</em></td>
<td>humid</td>
<td>1.70</td>
<td>0</td>
<td>3</td>
<td>2</td>
<td>0</td>
<td>0.47</td>
</tr>
<tr>
<td><em>Coryphistera alaudina</em></td>
<td>dry</td>
<td>1.27</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0.10</td>
</tr>
<tr>
<td><em>Anumbius annumbi</em></td>
<td>humid</td>
<td>1.63</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>0.38</td>
</tr>
</tbody>
</table>

*a* Indicates which one of the habitats of a given pair is drier or wetter in relation to the other. Does not imply absolute humid or dry conditions from climatic classification.

*b* Original values of graduation ratio and number of rectrices are given. Definitions for the other characters are provided in Table 3.2.
traditional major subgroups within Furnariinae: Furnariini, Synallaxini, and Philydorini (ranked here as tribes within the subfamily). Excluded from this group, and evolving at the background rate, are the 'basal' furnariids *Xenops, Berlepschia*, and the Pygarrhichini (sensu Moyle et al. 2009). A third increase in speciation rates occurred at the base of the "strong-billed" woodcreepers as defined by Feduccia (1973, i.e. all the large woodcreepers, plus *Xiphorhynchus* and the "curve-billed" clade sensu Claramunt et al. 2010). A model with four rate shifts was optimal according to the AIC criterion, although not significantly better than a model with three shifts (ΔAIC = 1.81, models within 2 ΔAIC units from the optimal model have substantial support). The fourth shift occurred at the base of the genus *Cinclodes* after the splitting of *C. pabsti*. Models with additional shifts did not improve AIC values (Table 4.5).

<table>
<thead>
<tr>
<th>Shifts</th>
<th>Clade</th>
<th>Likelihood</th>
<th>p</th>
<th>r</th>
<th>AIC</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td></td>
<td>-808.2</td>
<td>2</td>
<td>0.076</td>
<td>1620.50</td>
<td>32.37</td>
</tr>
<tr>
<td>1</td>
<td><em>Cranioleuca</em>&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-796.6</td>
<td>5</td>
<td>0.61</td>
<td>1603.15</td>
<td>15.03</td>
</tr>
<tr>
<td>2</td>
<td>Furnariinae&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-789.9</td>
<td>8</td>
<td>0.17</td>
<td>1595.82</td>
<td>7.69</td>
</tr>
<tr>
<td>3</td>
<td>&quot;strong-billed&quot; woodcreepers&lt;sup&gt;c&lt;/sup&gt;</td>
<td>-784.0</td>
<td>11</td>
<td>0.17</td>
<td>1589.94</td>
<td>1.81</td>
</tr>
<tr>
<td>4</td>
<td><em>Cinclodes</em>&lt;sup&gt;d&lt;/sup&gt;</td>
<td>-780.0</td>
<td>14</td>
<td>0.41</td>
<td>1588.12</td>
<td>0.00</td>
</tr>
<tr>
<td>5</td>
<td>&quot;Asthenes&quot;&lt;sup&gt;e&lt;/sup&gt;</td>
<td>-777.1</td>
<td>17</td>
<td>-</td>
<td>1588.14</td>
<td>0.01</td>
</tr>
<tr>
<td>6</td>
<td><em>Synallaxis</em>&lt;sup&gt;f&lt;/sup&gt;</td>
<td>-774.3</td>
<td>20</td>
<td>-</td>
<td>1588.51</td>
<td>0.39</td>
</tr>
</tbody>
</table>

<sup>a</sup> including *Thripophaga berlepschi* but not *Cranioleuca gutturata* or *C. sulphurifera*.
<sup>b</sup> excluding the basal groups *Xenops, Berlepschia, Pygarrhichas*, and allies (Moyle et al. 2009)
<sup>c</sup> as defined by Feduccia (1973)
<sup>d</sup> except for the basal *C. pabsti*.
<sup>e</sup> except for the basal *A. dorbignyi, A. baeri*, and the *A. patagonica* clade (*Pseudasthenes*)
<sup>f</sup> a monophyletic *Synallaxis* including *Gyalophylax, Poecilurus, Siptornopsis* but excluding *Synallaxis propinqua*.
<sup>g</sup> background rate of diversification under the optimal model with four shifts.
Figure 4.9 Calibrated phylogeny of Furnariidae with colors indicating clades identified by the MEDUSA procedure that diversified at higher rates respect to the background rate (black). Time before the present in millions of years (Ma).
Ancestral Character Reconstruction

Branches in which increases in diversification rate occurred are not associated with an excess of morphological change (Figure 4.10). In particular, very few changes seem correlated with the Furnariinae and Cinclodes transitions. In Cranioleuca, only a reduction in toe IV length occurred at the relevant branch, and an increase in vane asymmetry occurred in the immediately ancestral branch (Figure 4.11). A change in rectrix apex shape is also implied for those branches, but its exact position is ambiguous.

At the base of the Furnariinae, there are ambiguous transitions to more pointed rectrices, changes in nares extension, and an origin of mild tail curvature at the base of the Synallaxini (Figure 4.12). In addition, the origin of slits is unambiguous in the branch immediately ancestral to the focal branch. At the base of the strong-billed woodcreepers there is a reduction in nares extension, thus implying two consecutive changes starting from state 2 (at the level of the craniofacial hinge) to state 0 (clearly rostral to the craniofacial hinge) (Figure 4.13). The first transition (2 to 1) is ambiguous but the establishment of short nares (0) coincides unambiguously with the shift in diversification rate. Other transitions that occurred before and after this branch are also related to an increase in ossification and strengthening of the rostrum. Finally, at the base of Cinclodes the only reconstructed transition is a reduction in toe IV length at one of the branches that precede the increase in diversification rate (Figure 4.14).

The index of climbing adaptations showed no pronounced changes that coincided with shifts in speciation rate (Figure 4.15). In woodcreepers, the shift was correlated with a slight increase in climbing adaptations. On the other hand, at the base of the genera Cranioleuca and Cinclodes the trend in climbing adaptations decreased. Several groups with relatively intermediate values, such as Sclerurus (climbing index range: 0.23-0.27), Pygarrhichas (0.73), and the Margarornis
Figure 4.10 Tree with branch lengths proportional to the estimated number of character changes based on maximum parsimony. Lengths are averages of the result of accelerated and delayed optimization methods. Diamonds mark the most recent common ancestor of clades that experienced and increase in diversification rates. Colors like in Figure 4.9. Scale in number of changes.
Figure 4.11 Inferred morphological transitions based on parsimony ancestral state reconstructions for *Cranioleuca* and allies. Transitions are presented for the branches in black only. Dots flank the branch where a shift in diversification rate was detected by the diversification analysis. Branches in which changes occurred are numbered, and inferred state transitions at each branch are indicated in the legend. Note that because all possible most parsimonious reconstructions were considered, the same transitions may appear in more than one branch, and even in consecutive branches.
Figure 4.12 Inferred morphological transitions based on parsimony ancestral state reconstructions of morphological traits for the basal nodes in the Furnariinae. See Figure 4.11 for further details. The transition marked with an asterisk in the legend was unequivocal (a unique most-parsimonious reconstruction) within the clade.

clade (0.33-0.47), have few species and are relatively basal in the tree, suggesting a negative effect of climbing on diversification.

The spiny-tail syndrome does not change significantly in branches where major diversification rates occurred (Figure 4.16). The phylogeny confirms that the spiny-tail morphology evolved exclusively in the Synallaxini. However, rather than a single event or a trend, highly developed spiny-tail morphologies evolved multiple times within the Synallaxini,
Figure 4.13 Inferred morphological transitions based on parsimony ancestral state reconstructions of morphological traits for the basal nodes in the Dendrocolaptinae. See Figure 4.11 for further details. The transition marked with an asterisk in the legend was unequivocal (a unique most-parsimonious reconstruction) within the clade.
and most subclades contain species with high and low values of the spiny-tail index. The *Cranioleuca* clade, however, seems to be more conservative. Most species within this clade have intermediate values of the index, and no significant changes in the index occurred at basal branches of the clade (Figure 4.16).
Figure 4.15 Squared-change parsimony ancestral reconstruction of the composite index of climbing adaptations, which was rescaled to vary from 0 (yellow) to 100 (red). Major groups and some genera mentioned in the text are indicated (O.G = outgroup). Values are provided for relevant nodes, and values in bold flank branches where a significant increase in speciation rate occurred (MEDUSA analysis). Time before the present in millions of years (Ma).
Figure 4.16 Squared-change parsimony ancestral reconstruction of the spiny-tail morphology. The spiny-tail index was rescaled to vary from 0 (yellow) to 100 (red). Major groups and some genera mentioned in the text are indicated (O.G = outgroup). Values are provided for relevant nodes, and values in bold flank branches where a significant increase in speciation rate occurred (MEDUSA analysis). Time before the present in millions of years (Ma).
Effect of Adaptive Syndromes on Diversification Rates

The best model for explaining changes in diversification rates included climbing adaptations, the spiny-tail syndrome, and the clade effect (Table 3.6), and had an overall highly significant effect on diversification rates (model deviance: -1040; null deviance: -1013; Chi-square = 26.3, d. f. = 3, P < 0.001). The effect of the spiny-tail morphology was positive (β = 0.36, SE = 0.063) and highly significant (Chi-square = 17.1, d. f. = 1, P < 0.001). The effect of climbing adaptations depended on clade identity. For furnariids other than woodcreepers the effect was negative (β = -0.56, SE = 0.094) and marginally nonsignificant (t = 5.99, d. f. = 1, P = 0.053). The effect for woodcreepers was positive but not significant (β = 0.13, SE = 0.094, t = 1.4, d. f. = 1, P = 0.2).

If the clade effect is excluded, then the overall effect of climbing adaptations is significantly negative (β = -0.23, SE = 0.058; Chi-square = 7.8, d. f. = 1, P < 0.005). These trends can be seen in a plot of predicted speciation rates as a function of adaptive syndromes (Figure 4.17).

Table 4.6 Comparison of five models of the effect of climbing adaptations and spiny-tails on diversification. The semicolon indicates interaction.

<table>
<thead>
<tr>
<th>Model</th>
<th>log-Lik</th>
<th>parameters</th>
<th>AIC</th>
<th>dAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>climb:clade + spiny-tail</td>
<td>519.8</td>
<td>4</td>
<td>-1032</td>
<td>0.0</td>
</tr>
<tr>
<td>climb + spiny-tail</td>
<td>514.4</td>
<td>3</td>
<td>-1023</td>
<td>8.8</td>
</tr>
<tr>
<td>spiny-tail</td>
<td>510.5</td>
<td>2</td>
<td>-1017</td>
<td>14.6</td>
</tr>
<tr>
<td>climb:clade</td>
<td>511.2</td>
<td>3</td>
<td>-1016</td>
<td>15.1</td>
</tr>
<tr>
<td>climb</td>
<td>510.0</td>
<td>2</td>
<td>-1016</td>
<td>15.6</td>
</tr>
</tbody>
</table>
Figure 4.17 Predicted speciation rates derived from a Yule model with the effects of climbing adaptations (a) and the spiny-tail morphology (b). The effect of climbing adaptations was conditioned on clade identity (woodcreeper or not).
DISCUSSION

Shifts in Rates of Diversification and Phenotypic Innovations

The analysis of cladogenesis suggests that furnariids experienced four shifts in diversification rates. From an ancestral rate of 0.076 species/Ma, the rate increased to 0.17 species/Ma independently in the Furnariinae and the strong-billed woodcreepers. Then, two clades within Furnariinae (*Cranioloeuca* and *Cinclodes*) experienced a further increase in speciation rates (Figure 4.9). In this section I will discuss aspects concerning the small radiations (*Cranioloeuca* and *Cinclodes*), and in the following sections I will explore factors affecting the other two shifts and the influence of traits on diversification across the entire tree.

Evidence for rapid diversification in *Cranioloeuca* spinetails has been accumulating for some time. Remsen (1984b), for example, found differences in the color of the crown between specimen samples taken 50 years apart in *Cranioloeuca albiceps*, suggesting that plumage evolution can take place in short historical times. Plumage diversity across the genus high substantial, not only in color and patterns but also in the morphology of the rectrices. In addition, several of these plumage characters appear to vary independently from each other (Maijer & Fjeldså 1997, Claramunt 1999) and show leapfrog patterns of geographic variation (Remsen 1984a, Maijer & Fjeldså 1997). A molecular phylogeny revealed low levels of generic divergence across *Cranioloeuca* spinetails, providing the first strong evidence of accelerated or nearly simultaneous cladogenesis (Garcia-Moreno et al. 1999). That many plumage traits can evolve fast and independently from each other may explain the phenotypic diversity in *Cranioloeuca*. However, how this variation is related to cladogenesis is not evident. If plumage traits are used in mate choice and species recognition, then plumage evolution may stimulate speciation (Price 2008). *Cranioloeuca* spinetails are rather homogeneous in vocalizations (Maijer & Fjeldså 1997), and thus they may rely more on plumage for species recognition. On the other
hand, reproductive isolation may not to be complete in some cases, given the existence of a hybridize zone with introgression between two species with distinctive plumages (Belton 1984, Claramunt 2002). High plumage variation is also evident in other diverse spinetail genera such as Synallaxis and Asthenes, which also have specialized color patches used in behavioral displays (Remsen 2003). The role of plumage traits in species recognition and diversification in spinetails deserve further investigation.

Although none of the morphological traits analyzed seems to constitute a key innovation for the Cinclodes radiation, some lineages within the genus acquired a notable evolutionary innovation. Some Cinclodes species live at the oceanic coast and feed primarily on marine invertebrates (Sabat 2000, Sabat & Martinez del Río 2002, 2005, Remsen 2003). Such feeding habits require high osmoregulatory capacity, which in Cinclodes is attained by increasing the volume and performance of the kidneys (Sabat 2002, Sabat et al. 2006a). Therefore, an evolutionary innovation allowed some Cinclodes lineages to occupy a new niche. In this sense, increased kidney function may be viewed as a key innovation that triggered an adaptive radiation (Sabat et al. 2006b). However, increased osmoregulatory capacity and occupation of marine habitats evolved relatively recently and independently in two Cinclodes (Chesser 2004, Sabat et al. 2006b); therefore, these changes occurred well after the basal increase in diversification rates found in this study. Alternatively, not a change in state but a change in osmoregulatory plasticity may have occurred at the base of the Cinclodes radiation. This may explain why marine specialization evolved twice within Cinclodes (Chesser 2004), whereas it is extremely rare among passerines in general because they lack salt glands found in all other marine birds. The next challenge is to identify the evolutionary changes that allowed such versatility in osmoregulation.
Climbing and Diversification in Furnariidae

The hypothesis that climbing adaptations acted as a key innovation in Furnariidae was not supported. Ancestral character reconstructions indicate that the increase in diversification rates in woodcreepers occurred well after the evolution of advanced climbing adaptations. The MEDUSA analysis suggested that only the strong-billed woodcreepers experienced higher rates of diversification. The remaining woodcreepers, called 'intermediates' by Feduccia (1973) because of their phenotypic intermediacy with some philydorines, seem to have evolved at the slower background rate of basal furnariids (Figure 4.9). The phenotypic intermediacy does not involve external climbing adaptations but characteristics of the skull (Feduccia 1973). Some species of *Dendrocincla* show a lesser degree of development of climbing adaptations in both external traits (climbing index: 0.73-0.80) and myological traits (Bledsoe et al. 1997) in agreement with a less active tree-trunk foraging behavior (Skutch 1969, Willis 1972, Chapman & Rosenberg 1991). The genera *Sittasomus*, *Glyphorynchus*, and *Deconychura*, on the other hand, are professional trunk foragers (Marantz et al. 2003) and show climbing index values well in the range of the strong-billed woodcreepers (all 0.93). Moreover, the apparent intermediate nature of the most recent common ancestor of all woodcreepers in the analysis of continuous trait evolution may be an averaging artifact intrinsic to the analysis of continuous data. Reconstruction of discrete traits for the ancestor resulted in unambiguous assignment of the eight climbing traits producing an index of climbing adaptations equal to 0.93; this suggests that the most recent common ancestor of all woodcreepers was a highly specialized climber.

Myological and integumentary data are in agreement with the notion that specialized woodcreeper adaptations evolved well before the origin of strong-billed woodcreepers. Two major muscles responsible for hind limb adduction, and thus responsible to maintain the bird against a vertical tree trunk, are the *M. iliotibialis cranialis* and the *M. flexor cruris lateralis*.
The M. iliobibialis cranialis in woodcreepers is wider than in most passerines (Raikow 1994a). However, this condition is also present in other furnariids (Raikow 1994a), suggesting that its origin predates the woodcreeper radiation. Woodcreepers do show a greater degree of development of the M. flexor cruris lateralis than other furnariids. However, as inferred from character state distribution and parsimony reconstruction (Raikow 1994b), changes in this muscle either predate or postdate the origin of strong-billed woodcreepers. Other significant changes in woodcreepers musculature are related to reduction in abductor muscles (Raikow 1994a). The particular pattern of body pterylosis found in woodcreepers is shared by all examined species, including the intermediates (Clench 1995).

The overall effect of the climbing syndrome on diversification was negative. This is in agreement with a general tendency among passerine birds in that clades specialized in climbing and tree-trunk foraging tend to have few species: Climacteridae (7 species), Sittidae (25), Certhiidae (8), Rhabdornithidae (2) (Dickinson 2003). However, a negative effect of climbing on diversification seems to be at odds with the fact that woodcreepers stand out as a diverse group (Raikow & Bledsoe 2000, Chapter 2). The best Yule model suggested a differential effect of climbing on diversification in which the effect was negative in all furnariids except for woodcreepers, which showed a mild positive effect. Two scenarios may explain this differential effect of climbing. The first scenario is related the fact that only the first lineage that enters a new niche may experience the stimulating effect of ecological opportunities (Losos et al. 1998). The Dendrocolaptinae was the first clade within Furnariidae that evolved advanced climbing adaptations about 23 Ma ago (Figure 4.15). Lineages that acquired climbing adaptations later found that niche already occupied and faced competition with woodcreepers. Pygarrhichas, however, inhabit the Patagonian temperate forest, where there are not woodcreepers. A second possibility is that lineages with intermediate climbing capabilities cannot take full advantage of
the new niche, yet they have lost an optimal generalized perching morphology; only highly specialized lineages experienced a stimulating effect of climbing on diversification. In any case, however, the positive effect of climbing on woodcreeper diversification was not statistically significant. Therefore, there is still no evidence of any stimulating effect of climbing on diversification.

**Cranial Kinesis and Diversification in Furnariidae**

Changes in cranial morphology occurred at the base of two of the four clades that experienced an increase in diversification. However, those changes imply evolution in opposing functional strategies. Morphological changes at the base of the strong-billed clade are not related to climbing but to skull morphology (Figure 4.13). All changes involved an increase in ossification, with the functional effect of strengthening of the rostrum. All woodcreepers have prokinetic skulls and so did their most recent common ancestor as inferred from the lack of bending zones in the rostrum and the caudal end of the nares. The intermediates have elongated nares that end slightly rostral to or at the level (only in *Glyphorynchus*) of the craniofacial hinge. The ancestor of the strong-billed woodcreepers acquired a more ossified rostrum in which the nares are shorter, and this change coincides unequivocally with an increase in the diversification rate (Figure 4.13). This condition is actually similar to the one observed in the outgroup and most passerine birds, so it represents a reversion to the ancestral passerine morphology. Some genera evolved even more ossified rostrums by ossifying nasal and alinasal walls. This strengthening of the rostrum is related to the large and in some cases extremely long and decurved bills showed by the strong-billed woodcreepers (Feduccia 1973). The bills are used in the capture and killing of large invertebrates and even small vertebrates (Chapman & Rosenberg 1991, Marantz et al. 2003, Lopes et al. 2005). The evolution of strong bills may have been a key innovation that allowed woodcreepers to exploit these types of prey in trunks and branches.
At the base of the Furnariinae, changes in the bony rostrum were in the opposite direction: elongation of nares and an increase in bending zones (Figure 4.12). The most recent common ancestor of all furnariids is reconstructed as having elongated nares but not surpassing the craniofacial hinge (states 1 and 2); therefore, it is inferred to have been prokinetic. It also lacked the slits that allow independent movement of the lateral and ventral bars. However, the ventral bars are inferred to have been intermediate to flattened, implying a light construction and perhaps some flexibility. Complete rhynchokinesis with the full set of bending zones appeared more recently and independently in the Pygarrhichini, the Furnariini, and the Synallaxini. One potentially important innovation, the slits that allow bending between the lateral and ventral bars, appeared in the branch immediately ancestral to the increase in the rate of diversification in the Furnariinae (Figure 4.12). This evolutionary novelty is unequivocal, but it is not unique, because it appeared independently in Geositta (Sclerurinae). This trend towards rhynchokinesis at the base of the Furnariinae was reversed in the tribe Philydorini, most of which are prokinetic.

Given the functional similarity between prokinesis and proximal rhynchokinesis, Zusi (1984) concluded that the evolution from prokinesis to proximal rhynchokinesis was unlikely, and that proximal rhynchokinetic birds probably evolved from ancestors that had more flexible rostrum with other functional capabilities such as independent movement of the bill tip to capture prey inside tunnels. Proximal rhynchokinesis in Furnariidae, however, seem to have evolved from prokinetic ancestors. The trend towards rhynchokinesis at the base of furnariid clades is puzzling because it implies the evolution of features related to rhynchokinesis but without acquiring a fully functional rhynchokinetic bill. Fjeldså et al. (2005) postulated that bill flexibility is advantageous for capturing hidden prey. Although this seems to be the case of distal and double rhynchokinesis (Zusi 1984), how proximal rhynchokinesis is advantageous for capturing hidden prey is not clear. Given the uncertainties in ancestral reconstructions, the lack
of definite evidence of an adaptive advantage, and the possible idiosyncratic effect on
diversification, key innovations related to cranial kinesis and rostrum configuration remain
hypothetical.

**Spiny-tail Morphology and Diversification in Furnariidae**

The comparison of ten sister species pairs exposed to environments with markedly different
levels of humidity did not support the hypothesis of a relationship between vane disintegration
and habitat humidity. However, with only ten comparisons and coarse categories of vane
integration, the power of the test is low. On the other hand, the test revealed a strong relationship
between tail graduation and habitat humidity. It is possible that the emphasis on the central tail
feathers is a mechanism to avoid excessive accumulation of moisture in the tail. When the tail is
closed, the feathers on each side are approximately stacked one over the other. Therefore, if the
feathers are of the same length, every part of the tails would have six layers. In a strongly
graduated tail, however, only the proximal part of the tails would have six layers, and the number
of layers will diminish towards the tip, making it easier to dry out. On the other hand, the function
of graduation may be strictly mechanical as hypothesized before if vegetation structure differs
between dry and humid habitats. Further studies on the adaptive significance of the spiny-tail are
warranted, including improvement in the characterization of the spiny-tail morphology
(quantification of traits, study of barb microstructure), detailed phylogenetic comparative studies
of its ecological correlates, and experimental evaluations of its biomechanical and functional
properties.

The origin of the spiny-tail morphology could not be determined with certainty. Spiny-tails
occur only within the Synallaxini, but within this clade there are multiple origins of well-
developed spiny-tails. Concomitantly, ancestral state reconstructions for traits involved in the
spiny-tail morphology are ambiguous. Changes in apex shape and vane symmetry occurred at the
base of *Cranioleuca* and Furnariinae (Figures 4.11, 4.12). However, the placement of these changes is ambiguous, and parallel changes and reversions occurred throughout the three. Therefore, pinpointing a specific event that can be considered a key innovation was not possible.

Rather than a definite establishment of a spiny-tail morphology, the Synallaxini acquired the ability of evolving spiny-tails, i.e. they acquired evolutionary versatility or increased evolvability in tail morphology (Vermeij 1973, Kirschner & Gerhart 1998, Klingenberg 2008). This versatility presumably evolved in the most recent common ancestor of the Synallaxini; however, tails in the two most basal clades, the *Margarornis* group and *Aphrastura*, show more characteristics of climbing tails than spiny-tails (Figures 4.15 and 4.16). In any case, this increase in versatility seems not to be associated with an increase in speciation rates, which occurred earlier (the basal Furnariinae shift) and later (the *Cranioleuca* shift).

Irestedt et al. (2009) concluded that the Synallaxini has experienced unusually high rates of diversification. However, they used Magallón and Sanderson's (2001) method, which is based on information on clade age and number of species. Methods that use the complete phylogeny, such as those used in the present study, are more powerful in pinpointing shifts across the entire tree. By lumping lineages in clades, shifts that occurred within a clade may be assigned to the entire clade. The MEDUSA analysis identified no increases in diversification at the base of the Synallaxini but an increase at the base of *Cranioleuca*. Similarly, the higher rate of diversification inferred for woodcreepers in Chapter 2 is also an artifact of lumping lineages because the shift occurred only for the strong-billed clade.

Despite the absence of discrete increases in diversification rates at the base of the Synallaxini, the Yule model with covariates revealed a correlation between the degree of development of the spiny-tail morphology and speciation rates. An alternative hypothesis for the diversification of the Synallaxini hinges in its ability to build domed nests. Remsen (2003)
hypothesized that the ability of some furnariid lineages to construct domed nests may represent a key innovation by protecting eggs and nestlings from harsh climatic conditions without the dependence on cavities or other specialized nest placements that are usually scarce (see also Collias 1997, Irestedt et al. 2006). Using nest information from Zyskowski & Prum (1999) and Remsen (2003), Irestedt et al. (2006) estimated the origin of domed nest architecture near the base of the Synallaxini. However, taxon sampling in Irestedt et al. (2006) was incomplete, and some relevant relationships, such as the placement of the *Margarornis* group, differed from the present analysis. Further analysis of nest architecture evolution in Furnariidae and the functional role of the spiny-tail morphology and its ecological correlates are warranted. In particular, an explicit statistical evaluation of the relative effect of nest architecture and the spine-tail morphology on diversification will be critical to gain an insight on the factors that has promoted diversification in the Furnariidae.
CHAPTER 5

CONCLUSIONS

By providing a historical framework for information on extant species, phylogenies allow new ways to study the process of biological diversification (Felsenstein 1985, Harvey & Pagel 1991, Nee et al. 1994, Schluter et al. 1997, Hansen & Martins 1996, Pagel 1999, Nee 2006, Ricklefs 2007). In this dissertation I used some of these tools, and helped develop new ones, to explore the processes that generated high species diversity in a continental group of passerine birds, the family Furnariidae.

I first investigated whether the Furnariidae constitutes a case of rapid diversification (Chapter 2). I compared levels of species richness and morphometric diversity between Furnariidae and all other six closely related families in the infraorder Furnariides (Moyle et al 2009). Using simple models of cladogenesis, I found that the Furnariidae and the Thamnophilidae have significantly more species than expected, assuming a common diversification rate for all Furnariides. For comparing levels of phenotypic diversity, I developed a novel measure of phenotypic diversity that is a new multivariate extension of the variance. Because a phylogeny of most species in the group is not yet available, I could not use intensive phylogenetic methods. However, instead of ignoring phylogeny, I developed a simulation protocol for comparing phenotypic diversity that takes into account some of the effect of the phylogenetic structure of the data. Using these new methods, I demonstrated that both the Furnariidae and the Thamnophilidae show significantly higher morphometric diversity than other families in the Furnariides. However, significantly high morphometric diversity in the Thamnophilidae involves only body size, whereas in the Furnariidae shape is involved. Moreover, all shape variables are related to feeding behavior and locomotion. Accelerated rates of cladogenesis in an ecomorphologically diverse group are associated with the concept of
adaptive radiation (Simpson 1953, Givnish 1997, Schluter 2000). However, a consensus is lacking on what exactly an adaptive radiation is. The concept has changed over time (see Givnish 1997 for a review), and even today, markedly different definitions coexist (e.g. Schluter 2000 versus Losos & Miles 2003). This situation provoked Olson & Arroyo-Santos (2009) into questioning the usefulness of 'adaptive radiations' as a scientific concept. Ultimately, adaptive, non-adaptive, and other types of radiations are better considered parts of a continuum generated by differences in rates of cladogenesis and anagenesis (Olson & Arroyo-Santos 2009) and the relative contribution of drift, natural, and sexual selection (Schluter 2000). By being at the upper end of this continuum in both species proliferation and ecomorphological differentiation, the Furnariidae may be considered an adaptive radiation.

Why are furnariids so diverse? To answer this question I embarked on the study of processes that influenced furnariid diversification. In this dissertation, I considered two main general models: 1) a simple model of gradual evolution in which speciation is triggered by geographic isolation, and 2) a model of adaptive radiation driven by ecological speciation and ecological opportunities. These two models make contrasting predictions regarding the influence of dispersal. If speciation is primarily driven by geographic isolation, then all else being equal, lineages with low dispersal ability are more likely to speciate. On the other hand, if speciation is driven by ecological opportunities and divergent natural selection, lineages with high dispersal ability should experience more speciation (Price 2008). In Chapter 2, I tested these predictions in the Furnariidae. First, I quantified the relative potential dispersal ability of each furnariid species. I provided theoretical and empirical evidence suggesting that a simple index of wing shape, related to flight performance (Kipp 1957), can be a useful surrogate for dispersal ability in birds. To evaluate an effect of flying ability on diversification, I used wing shape data and a calibrated phylogeny of 97% of the species in the Furnariidae. Using a new statistical technique for
evaluating the effect of traits on diversification (Paradis 2005) I found a negative effect of dispersal on diversification, suggesting that geographic isolation was an influential factor in furnariid diversification. The idea that dispersal stimulates diversification was not supported. However, a positive relationship between dispersal and diversification has been found in other organisms.

When the effect of dispersal on range size and colonization is taken into account, it is evident that even in a purely geographic model, extremely low level of dispersal should inhibit diversification. Therefore, speciation rates should be highest at intermediate levels of dispersal (Mayr & Diamond 2001, Price & Wagner 2004), a phenomenon that can be called "the intermediate dispersal hypothesis". Whether the relationship between dispersal and diversification is positive or negative depends on the clade's dispersal ability and the geographical setting. Diversification in archipelagos or at planetary scales may be stimulated by dispersal, but diversification within continents may be inhibited by dispersal. Given that even moderate dispersal abilities have inhibited diversification in furnariids, I predict that a negative relationship between dispersal and diversification will be the dominant pattern among continental avifaunas in general.

The ecological theory of adaptive radiation predicts that key innovations can promote speciation because they create ecological opportunities (Simpson 1953, Schluter 2000). Moreover, key innovations may be particularly important for creating ecological opportunities in continents. In Chapter 5, I investigated key innovations in Furnariidae and evaluated their effect on diversification. I concentrated on morphological adaptations for climbing, the unusual spiny-tail morphology, and cranial kinesis. All these innovations are related to locomotion or feeding, and are extremely rare among passerine birds other than furnariids.
Adaptations for climbing are a clear example of key innovations in the Furnariidae (Raikow & Bledsoe 2000). A suite of functionally related morphological innovations allowed some furnariid lineages to forage effectively on trunks and large branches (Richardson 1942, Feduccia 1973, Raikow 1994a, Tubaro et al. 2002). No other passerines in the Neotropics forage on vertical trunks. Trunk-foraging woodpeckers (Picidae) specialize on excavating and drilling into the bark and wood for insect larvae and seldom glean insects from the trunk surface as woodcreepers do; therefore, they are not likely to compete for food resources with furnariids. Moreover, a new calibrated phylogeny of woodpeckers suggests that they arrived in South America within the last 10 million years (Fuchs et al. 2006), whereas our calibrated phylogeny indicates that the most recent common ancestor of woodcreepers is older than 20 million years. Comparison of these two chronograms also suggests that tail-assisted trunk climbing evolved in woodcreepers about 10 million years before than in woodpeckers. Therefore, furnariid lineages that first acquired climbing adaptations likely encountered an unoccupied niche and entered a new adaptive-zone. However, contrary to the prediction of the ecological theory, this innovation did not increase speciation rates: early woodcreepers diversified at a relatively slow rate of cladogenesis like basal furnariids. A clade of strong-billed woodcreepers experienced an acceleration in rates of cladogenesis but the acceleration occurred well after the origin of specialized trunk climbing.

Whether the spiny-tail morphology and rhynchokinesis constitute key innovations is difficult to determine because the functional and ecological consequences of these innovations are not well understood. Nevertheless, I found a positive relationship between the degree of development of the spiny-tail morphology and rates of cladogenesis. If the spiny-tail morphology increases performance of locomotion among cluttered vegetation with grasses and shrubs, then it may have contributed to the success of synallaxines in non-forested habitats throughout the
continent. The functional properties of the spiny-tail morphology could be investigated with carefully designed experiments with living birds.

Discrete evolutionary changes coincident with shifts in diversification do not seem to be of great functional significance, except perhaps the increase in rostrum ossification at the base of the strong-billed woodcreepers. In addition to an increase in rates of cladogenesis, an increase in rates of bill evolution likely occurred at the base of the strong-billed woodcreepers, given their astonishing diversity in bill shape (Raikow & Bledsoe 2000). Shifts at the base of *Cranioleuca* and *Cinclodes* may be more related to an increase in phenotypic versatility rather than to a discrete ecological innovations (plumage variability in the former, osmoregulatory physiology plasticity in the later). All these phenomena warrant further investigation.

Key innovations may influence diversification in multiple ways, and the effect of a key trait on species proliferation may not be evident until other changes in the phenotype or the environment take place. Therefore, the effect of key innovations may be highly contingent and extremely difficult to evaluate analytically (Cracraft 1990, Jensen 1990, de Queiroz 2002, Donoghue 2005). My overall assessment of this primary search for key innovations in the Furnariidae echoes Jonathan Losos' conclusions regarding his research on key innovations in anoles: "...the ideas are interesting, the data somewhat persuasive, but the ability to strongly test the hypotheses limited." (Losos 2009: 337).

In summary, I found support for a role of geographic isolation on diversification in the Furnariidae but mixed support for a role of ecological opportunities. This does not mean that ecological opportunities or niche processes were not important during the evolution of the clade. First, I only explored a handful of traits. Ecological opportunities, however, can be manifested in multiple ways, and the search for ecological influences in furnariid diversification needs to be expanded. Second, adaptations to particular niches and ecological roles have evidently had a
pervasive influence in morphological evolution in this family, as revealed by the wide variety of adaptations and extreme cases of ecomorphological specialization (Remsen 2003). My results suggest, however, that morphological adaptation and species proliferation may be decoupled in this continental radiation. Decoupled anagenesis and cladogenesis has been found in other diverse clades such as dipsacales plants (Moore & Donoghue 2007), geckos of western Indian Ocean archipelagos (Harmon et al. 2008), and plethodontid salamanders (Adams et al. 2009), and is consistent with classic models of evolution in which phenotypic change occur gradually along lineages and independently of speciation. Given that niche-filing processes and ecological limits are hypothesized to have a pervasive effect on clade diversification in general and in adaptive radiations in particular (Price 2008, Gavrilets & Losos 2009, Rabosky 2009a, 2009b, Ricklefs 2009), the lack of a strong signal of niche processes in furnariid cladogenesis is fascinating and call for careful consideration of neutral and geographic factors in highly diverse continental radiations.
LITERATURE CITED


APPENDIX A

EVALUATION OF THE ESTIMATOR OF THE MULTIVARIATE BROWNIAN RATE

To evaluate equation (2.4) as an estimator of the Brownian rate matrix using phenotypic diversity I assessed whether rate matrices estimated using equation (2.4) generate simulated trait matrices with levels of phenotypic diversity close to the observed phenotypic diversity of each Furnariides family. For each family, I generated 500 trees with the same species richness and age of the corresponding family using geiger's function birthdeath.tree() (Harmon et al. 2008), and a new tree-scaling function (Appendix B). For each tree, I used equation (2.4) to estimate a corresponding rate matrix $\mathbf{R}$ using the crown age and the covariance matrix $\mathbf{V}$ of the corresponding family. Then, for each tree I created a matrix of traits using function geiger's function sim.char() (Harmon et al. 2008) and then I computed the proper variance of each trait matrix. The mean phenotypic diversity of the 500 simulated clades lies close to the observed values (Figure A.1). Deviations of means from observed values are small compared to the stochasticity generated by the simulations of trees and traits.
Figure A.1 Density curves of the distribution of 500 simulated clades generated with an estimate of the Brownian rate matrix from equation (4). Dashed lines are means of the distribution of simulated clades. Solid lines are the observed proper variances.
APPENDIX B

R CODE FOR CHAPTER 2

New functions and example code in the R language (R Development Core Team 2008) used for computing phenotypic diversity and the Monte Carlo simulations of Chapter 2 and Appendix A.

In addition to the basic R package, the libraries CORPCOR (Schäfer and Strimmer 2005), APE (Paradis et al. 2004), and GEIGER (Harmon et al. 2008) are required.

# PHENOTYPIC DIVERSITY INDICES
# M is the data matrix of N species by p variables
# Total Variance
TV <- function(M) {
  if(class(M)=="numeric") {var(M)}
  else {sum(diag(var(M)))}}

# Proper Variance
PV1 <- function(M) {
  E <- eigen(var(M), only.values=TRUE)$values
  (sum(sqrt(E[E>0])))^2}

# Proper Variance using the shrinkage estimator of the covariance matrix
PV2 <- function(M) {
  E <- eigen(cov.shrink(M, verbose=F), only.values=TRUE)$values
  (sum(sqrt(E[E>0])))^2}

# MOSIMANN'S SIZE AND SHAPE PARTITION
# M is a matrix of log-transformed variables
# Function for obtaining the Log-size vector
Lsize <- function(M){as.vector(t(mean(as.data.frame(t(M)))))}

# Function for obtaining the Log-shape matrix
Lshape <- function(M) {M-mean(as.data.frame(t(M)))}

# RESAMPLING RAREFACTION FUNCTION
# This function computes the data for creating rarefaction curves using resampling. M: data matrix of N species by p traits. F: function to be applied to the resampled data (e.g. any of the indices of phenotypic diversity). nreps: number of replicates
Rarefaction <- function(M, F, nreps=500, to=nrow(M), by=1) {
  Svalues <- seq(from=2, to=to, by=by) #1
  R <- matrix(nrow=nreps, ncol=length(Svalues))
  for (i in 1:length(Svalues)) {for (j in 1:nreps) R[j,i] <- (F(M[sample(nrow(M), Svalues[i], replace=FALSE),]))} #2
Raresult <- cbind(Svalues, mean(as.data.frame(R)), sd(as.data.frame(R))) #3
colnames(Raresult) <- c("Svalues", "E", "SD")
write.table(Raresult, file= paste("Rare", deparse(substitute(M)),
deparse(substitute(F)), sep="")) Raresult}

#Notes:
#1 - The default is to generate pseudoreplicates for each the entire range of
species numbers (1, 2, 3... N). Alternatively, only a sequence of values
(Svalues) is used (e.g. 1, 2, 4,... N).
#2 - Function sample() generates n integers from 1 to nrow(M) (the total
number of species); sample size n is determined by Svalues[i]. The list of
integers are used as row indexes to select a subset of the original matrix.
#3. Calculates de mean and standard deviation for each S value; first, matrix
R is converted to a data frame so the means and standard deviations are
calculated for each column of R.

#FUNCTION FOR REScALING PHyLOGENETIC TREES
scale.phylo <- function(phy, depth=1)
{if (class(phy) != "phylo")
   stop("object "phy" is not of class "phylo"")
   t1 <- max(branching.times(phy))
   phy$edge.length <- depth*phy$edge.length/t1
   phy}

#EXAMPLE CODE FOR CREATING SIMULATED CLADES AND TRAIT MATRICES

#SIMULATION OF A LIST OF TREES WITH A GIVEN AGE (t) AND NUMBER OF SPECIES (N)
RtreesNt <- list()
for(i in 1:500){RtreesNt[[i]] <- scale.phylo(birthdeath.tree(b=1, d=0,
taxa.stop=N, seed=0), depth=t)}

#LIST OF AVERAGE RELATEDNESS - mean(C) - VALUES
meanC <- numeric(length=500)
for(i in 1:500) {meanC[i] <- mean(vcv.phylo(RtreesNt[[i]], cor=F))}

#SIMULATION OF A LIST OF TRAIT MATRICES USING EQUATION (2.4) TO ESTIMATE THE
BROWNIAN MODEL MATRIX
Rtraits <- list()
for(i in 1:500) {Rtraits[[i]] <- sim.char(RtreesNt[[i]],
model.matrix=SD%*%Cor%*%SD/(t-meanC[i]), nsims=1, model="brownian")[,1]}

#in which
Cor <- (cor(M)+ cor.shrink(M))/2
# observed correlation matrix of a clade (log data matrix m) computed as the
average of the ordinary and shrinkage estimates
#and
SD <- diag(sqrt(diag(var(M)))) # diagonal matrix of standard deviations
APPENDIX C

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Santiago Javier Claramunt Tammaro was born in June 1975 in Montevideo, Uruguay, to Roberto Claramunt and Amalia Tammaro. He developed his interest in animals and nature early in his life, probably influenced by spending summer vacations at his grandmother's estancia in the countryside or at the beach house, or by watching nature and science documentaries during the cold winters. His early interest in science was highly influenced by his brother Gabriel, who was always engaging him in conversations or games about outer space, computers, and robots. In 1992 he joined a group of young naturalists in the NGO Centro de Estudios de Ciencias Naturales, with whom he participated in field trips doing biological inventories and collecting small vertebrates. His interest in birds crystallized during these trips. In 1997 he began to work at the National Museum of Natural History of Uruguay thanks to an assistantship from the Ministry of Education and Culture. He worked in the museum first as a guide in the exhibit hall, and then as the assistant of the bird collection under the guidance of Juan Cuello. He attended Universidad de la República, earning his degree of Licenciado en Ciencias Biológicas in 1999 with an orientation in evolution. One of the most influential professors during his undergraduate studies was Dr. Enrique P. Lessa, who introduced Santiago to the forefront of evolutionary biology, including molecular techniques and phylogenetic thinking. Between 1999 and 2003 he continued working at the museum and worked also in a project on speciation in freshwater fishes in the laboratory of Dr. Graciela García. In 2003 he moved to Baton Rouge to begin his doctoral studies at LSU under the advice of Drs. J. V. Remsen and R. T. Brumfield. In this period he met Adriana Bravo, a doctoral student from Peru. They became best friends immediately, sweethearts shortly after, and spouses in 2007. Santiago defended his doctoral dissertation in March 2010.