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Biogeography of *Buarremon* brush-finches (Aves, Emberizinae): Integrating Ecology, Evolution, and Systematics

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Department of Biology
Graduate Program in Ecology, Evolution, and Systematics

Biogeography of *Buarremon* brush-finches (Aves, Emberizinae): Integrating Ecology, Evolution, and Systematics

A Dissertation Submitted to The Graduate School of the University of Missouri – St. Louis in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy in Biology

by

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ABSTRACT

Ecological and historical approaches to studying species' geographic ranges have yet to be unified. Ideal scenarios for integrating ecology with evolutionary biology in biogeography are those where contemporary ecological interactions may have influenced species' distributions historically, driving the evolution of ecological niches. I focused on understanding the origin of elevational distributions of species, and specifically on the role of interspecific competition in the origin of complementary elevational ranges. To test hypotheses about the origin of elevational distributions, I followed a combined approach involving molecular phylogenetics, phylogeography, population genetics, and ecological niche modeling. I focused on *Buarremon torquatus* and *B. brunneinucha* (Aves, Emberizinae), whose elevational distributions appear to be influenced by interspecific competition.

The hypothesis that elevational distributions in *Buarremon* changed in opposite directions as a result of competition is untenable because: (1) a historical expansion of the range of *B. brunneinucha* into areas occupied by *B. torquatus* was not accompanied by a shift in the elevational range of the former species, (2) when *B. brunneinucha* colonized the range of *B. torquatus*, lineages with disparate elevational distributions had already diverged, and (3) historical trends in effective population size do not suggest populations with elevational ranges abutting those of putative competitors have declined as would be expected if competition caused range contractions. In addition, explicit analyses relating elevation to environmental variables that limit distributions directly indicate some distribution patterns can be more parsimoniously explained by hypotheses alternative to competition. The role of competition in elevational zonation may be to act as a sorting mechanism that allows the coexistence along mountain slopes only of ecologically similar species that differ in elevational distributions prior to attaining sympatry.

A comprehensive assessment of species limits within *B. torquatus* based on phylogenetic, vocal, morphological, and ecological data indicates that *B. torquatus* comprises multiple species. Although examining the origin of the contrasting elevational ranges of different species is still sensible because the *B. torquatus* complex is a clade, when viewed in comparison to those of genera with multiple species, the patterns of elevational distribution of "*B. torquatus*" do not appear as unique as traditionally thought.

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CHAPTER 1

Molecular Phylogenetics and Phylogeography of *Buarremon* brush-finches (Aves, Emberizinae)

Introduction

Recent years have seen much progress in the development of comprehensive phylogeographic studies of various groups of Neotropical organisms. This new body of work has led to important insights on the history of biotic diversification in the Neotropics that substantially improves our understanding of the degree to which populations are genetically structured, the timing of population differentiation, the relationships among areas of endemism, and the role of features of the landscape such as rivers, mountains, or geological arcs as barriers to gene flow (reviewed by Moritz et al. 2000; see also Marks et al. 2002, Aleixo 2004, Dick et al. 2003, Dick et al. 2004, Cheviron et al. 2005, Weigt et al. 2005). Much of this work, however, has focused exclusively on lineages occurring in the Neotropical lowlands.

A recent review of molecular phylogenies of birds revealed important differences in the history of diversification between lowland and highland regions of the Neotropics (Weir 2006). Lineage-through-time plots indicate that, in contrast to lowland areas, where diversification rates were highest in the late Miocene and appear to have decreased towards the present, rates of species production in highland areas have increased substantially in recent times following the onset of Pleistocene glacial cycles in the Andes. Therefore, Weir (2006) concluded that Neotropical organisms occurring in lowland and highland regions were affected differently by climatic fluctuations and other recent events within the region. This implies that patterns of population differentiation that appear to have some generality in lowland taxa (e.g. strong genetic structuring and Pre-Pleistocene population differentiation in birds) may not reflect the extent and timing of population differentiation in montane areas. However, to date, few comprehensive phylogeographic studies of Neotropical montane taxa have been conducted, and most of those available have focused on relatively narrow geographic regions.

In this study we present a detailed assessment of evolutionary relationships and patterns of genetic differentiation in *Buarremon* brush-finches (Aves: Emberizidae), a group of passerine birds widely distributed in montane areas of the New World from Mexico through Argentina. We begin by reconstructing phylogenetic relationships among *Buarremon* and related genera, among species of

Buarremon, and among lineages of each species occurring in different regions based on sequences of several mitochondrial and nuclear genes. Guided by this phylogenetic framework, we use gene genealogies inferred from mtDNA data to examine the evolutionary relationships of population lineages in more detail, to describe the geographic distribution of genetic variation, and to assess the extent of migration between some populations separated by potential barriers to gene flow. To our knowledge, this study represents the most comprehensive analysis of population genetic differentiation conducted for a widespread group of Neotropical montane organisms. In addition to furthering our general understanding of the history of biotic diversification in the tropical and subtropical mountains of Central and South America, our results provide a framework for forthcoming studies on the evolution of phenotypic diversity, species limits, and the role of interspecific interactions in the origin of elevational distributions in *Buarremon.*

Materials and methods

Study system

As currently defined, the genus *Buarremon* includes three species: *B. torquatus* (Stripe-headed Brush-finch), which ranges from central Costa Rica to northern Argentina, *B. brunneinucha* (Chestnut-capped Brush-finch), occurring from central Mexico to southern Peru, and *B. virenticeps* (Green-striped Brush-finch), endemic to western and central Mexico (A.O.U. 1998, Remsen et al. 2006). Both *B. torquatus* and *B. brunneinucha* were originally described in the genus *Embernagra*, but they were placed in *Buarremon* by Bonaparte (1850), who, without a clear rationale, erected the genus including not only these two taxa, but also several other species of emberizines, most of which are now placed in the genus *Atlapetes*. *Buarremon virenticeps* was described a few years later by Bonaparte himself as a new member of the genus. Based only on similarities in bill shape, Hellmayr (1938) merged *Buarremon* with the large genus *Atlapetes,* a treatment followed without question by all subsequent authors until mitochondrial DNA and allozyme evidence indicated that *Buarremon* (i.e., *B. brunneinucha* and *B. torquatus*) and *Atlapetes* are not each other’s closest relatives (Hackett 1992). This prompted the resurrection of *Buarremon* for *brunneinucha, torquatus,* and *virenticeps*, now widely accepted (Remsen and Graves 1995, A.O.U. 1998). Our ongoing phylogenetic studies with broader taxon sampling support this rearrangement, and strongly suggest that together with the genera *Arremon* and *Lysurus*, the three species of *Buarremon* form one of six major clades within the Emberizini (J. Klicka et al., unpubl. data). However, relationships among these three genera are uncertain, and the long-held assumption of the monophyly of *Buarremon* has not been rigorously tested. As is typical for nine-primaried oscines in general, unambiguous morphological synapomorphies that would aid in establishing the affinities among members of this clade are lacking.

At a lower level, relationships among *Buarremon* taxa are not well established. Based on the morphological similarity between juvenile *B. torquatus* and adult *B. virenticeps*, Paynter (1970) considered these taxa to be conspecific but later regarded them as distinct sister species (Paynter 1978), which has been the more common position of systematists notwithstanding the lack of a phylogenetic appraisal. Species delimitation has been especially contentious within what is currently treated as a single species, *B. torquatus* (see Remsen and Graves 1995b for a review). Different authors have argued this taxon may comprise as many as three species-level taxa, yet there is disagreement over how these species should be circumscribed. Part of this uncertainty is a result of the remarkable phenotypic diversity of the group, which consists of 14 allopatrically distributed subspecies among which plumage characters vary rather chaotically, with no clear correspondence between the geographic proximity of populations and their phenotypic similarity (Chapman 1923, Paynter 1978). There has also been some discussion regarding species limits in *B. brunneinucha,* with some authors favoring the treatment of the subspecies *apertus* of the Sierra de los Tuxtlas, Mexico, as a separate species based on its distinct plumage (Navarro-Sigüenza and Peterson 2004).

Taxon and geographic sampling

We followed a variety of taxon sampling and DNA sequencing strategies to reconstruct evolutionary relationships and to examine patterns of population differentiation at various hierarchical levels in *Buarremon* and near relatives. In total, we generated sequence data for 235 samples, including 138 individuals representing eight of the nine subspecies of *B. brunneinucha,* 78 representing 13 of the 14 subspecies of *B. torquatus*, eight *B. virenticeps*, and one for each of four species of *Arremon*, the two species of *Lysurus,* and outgroup taxa in the genera *Atlapetes*, *Pezopetes*, *Pselliophorus*, *Pipilo, Ammodramus*, *Junco*, *Zonotrichia,* and *Melospiza.* Our choice of outgroups was guided by analyses based on sequences of multiple genes for nearly all genera in the Emberizini (J. Klicka *et al*., unpubl. data).

To obtain a general overview of relationships of major groups and a detailed picture of patterns of differentiation in *Buarremon*, we sequenced the second subunit of the NADH dehydrogenase mitochondrial gene (ND2) for all available samples of all taxa. Based on results of preliminary analyses of this data set, we selected a few individuals from each major lineage of *B. torquatus* and *B.*

brunneinucha for more data-intensive analyses. For this subset, and for all individuals of other taxa, we sequenced the cytochrome *b* (cyt *b*), ATP-synthase 6 (ATPase 6), and ATP-synthase 8 (ATPase 8) mitochondrial genes. In addition, for a subset of these, we sequenced fragments of introns of two nuclear genes linked to the *Z* chromosome: intron 10 of aconitase 1 (ACO1) and intron 3 of muscle-specific kinase (MUSK). In sum, we used three data sets for analyses: (1) 1026 bp of ND2 for 235 individuals, (2) 2871 bp of ND2, cyt b, ATPase 6, and ATPase 8 for 43 individuals, and (3) 4208 bp of ND2, cyt b, ATPase 6, ATPase 8, ACO1, and MUSK for 22 individuals. Whenever possible, we used samples collected with voucher museum specimens; for a few cases in which we used non-vouchered material, subspecies identifications rely on the localities where samples were obtained. Appendix 1 presents localities and information on vouchers for all sequenced samples. Fig. 1 shows the localities where samples of *Buarremon* included in analyses were obtained.

Laboratory procedures

We extracted DNA from liver or pectoral muscle tissues, blood samples, feathers, or skin from toe pads of museum specimens using the DNeasy Tissue Kit (Qiagen) following the manufacturer's instructions, except for the addition of 30μl of 10% dithiothreitol (DTT) solution to the digestion buffer, and for final elution in only 60μl of AE buffer heated to 70°C when working with feather and toe pad samples. We amplified the ND2 gene for most individuals using combinations of primers L5216, H5766, L5758, and H6313 (Sorenson et al. 1999, M. Sorenson pers. comm.). Whenever possible, the whole gene (1041 bp) was amplified as a single fragment to reduce the likelihood of amplifying nuclear pseudogenes, but this was not always feasible due to degradation of some of the samples. To work with samples yielding low-quality DNA, we designed six internal primers that, in combination with others, allowed us to amplify and sequence fragments of 300-350 bp (Table 1). For amplification and sequencing of cyt *b*, we employed primers L14996, H15646, L15413, and H16064 (Sorenson et al. 1999), and for ATPase6 and ATPase8 primers CO2GQL and CO3HMH (G. Seutin and E. Bermingham, http://nmg.si.edu/bermlab/bermlab.htm). To amplify and sequence the nuclear introns ACO1 and MUSK we used unpublished primers designed by F. K. Barker.

PCR amplifications, conducted in a PTC-200 Thermal Cycler (MJ Research), typically consisted of an initial denaturation at 94°C for 2 min, followed by 35 cycles of denaturation at 94°C for 45 s, annealing at 52°C for 30 s and extension at 72°C for 60 s, occasionally finishing with an additional extension at 72°C for 10 minutes. Amounts of PCR constituents were: 1–2 μl of template DNA, 0.625U of *Taq* polymerase (Promega), 10mM Tris–HCl (pH 9.0), 50mM KCl, 1.5mM $MgCl_2$, 0.48

μM of each primer, and 80 μM dNTP's, in a total volume of 25μl. For poor-quality extracts that could not be amplified as indicated above, we prepared 25 or 50μl reactions using HotStar Taq DNA polymerase (Qiagen) with the concentration of constituents indicated by the manufacturer; in order to activate the enzyme, the PCR protocol included an initial phase of heating at 95°C for 15 minutes. When amplifications yielded a single product of the expected size, we purified them directly using the QiaQuick PCR Kit (Qiagen). If multiple products were obtained, we excised the appropriate bands from agarose gels and purified them using the GeneClean III protocol (BIO 101), a Gel Extraction Kit (Qiagen), or by incubating them overnight with GELase (Epicentre). Clean products were used as templates for sequencing both light and heavy DNA strands employing the same primers used for amplification and the Big Dye Terminator kit (ABI). Products were treated with ethanol and sodium acetate to remove unincorporated dyes, and run on an ABI 377 sequencer or an ABI 3730XL analyzer.

Alignment and exploration of sequence data

We assembled and edited sequence chromatograms in the program SeqMan (DNAstar), and aligned sequences manually using a text editor. All mitochondrial sequences lacked conflict between complementary light and heavy strands, their base composition and patterns of substitution were typical of protein-coding mtDNA (e.g., most substitutions were transitions at third codon positions), and indels and stop or nonsense codons were lacking, suggesting they were in fact of mitochondrial origin and not nuclear pseudogenes. This was further corroborated by the large number of haplotypes observed relative to the number of individuals assayed (see Results). Insertions and deletions in nuclear sequences were rare, which allowed us to align them manually in a straightforward fashion.

The incongruence length difference test (Farris et al. 1995) implemented in the program PAUP* version 4.0b10 (Swofford 2002) did not reveal any instance of significant conflict in the phylogenetic signal of different genes or data partitions (e.g. mitochondrial *vs.* nuclear genes). Thus, we conducted analyses combining sequences of all genes in single matrices, but also analyzed partitions independently to assess the degree of support for relationships afforded by different character sets.

To assess the possibility of substitutional saturation of mtDNA sequences, we plotted pairwise comparisons of uncorrected *p*-distances based on different substitution types (transitions, transversions) as a function of maximum-likelihood distances estimated under a best-fit model of nucleotide substitution (see below). Plots indicated evidence of saturation for transitions in the third position of codons in cyt *b* and the ATPase genes above model-corrected distances of ca. 0.10. We assessed the effect of saturation on phylogenetic inference by employing different character weighting schemes in parsimony analyses (see below).

Phylogenetic analyses

We conducted analyses aimed at resolving relationships among *Buarremon* and related genera and among species and major lineages of *Buarremon* using maximum likelihood, Bayesian, and maximum parsimony methods of phylogenetic inference. These analyses were based on the 42-individual, 4-gene mitochondrial data set and the 21-individual, six-gene mitochondrial-nuclear data set. For maximum likelihood analyses of both data sets we implemented the GTR+I+G model of nucleotide substitution, which was selected as the best fit to the data according to the Akaike Information Criterion (AIC) in ModelTest version 3.7 (Posada and Crandall 1998). We conducted heuristic searches under the maximum-likelihood criterion in PAUP*, each consisting of ten replicates with random taxon addition and tree-bisection reconnection (TBR) branch swapping. We assessed support for nodes under maximum likelihood via bootstrap resampling (200 and 500 pseudoreplicates for the mitochondrial and nuclear-mitochondrial data sets, respectively). We conducted Bayesian analyses using the parallel implementation of MrBayes version 3.0 (Ronquist et al. 2003, Altekar et al. 2004). To ensure proper examination of tree and parameter space, we employed Metropolis-coupled Markov Chain Monte Carlo (MCMC) sampling with one cold and three incrementally heated chains ran for 25 million generations. To further ensure that results did not depend on starting conditions, we conducted four independent analyses initiated from random trees on each data set. Results of each run were examined for convergence by plotting the posterior probabilities of clades as a function of generation number using AWTY (Wilgenbusch et al. 2004); convergence across runs was evaluated by examining the standard deviation of the split frequencies reported by MrBayes and by plotting the correlation of clade frequencies obtained in different analyses in AWTY. We did not observe changes in the posterior probabilities of clades after c. 5 million generations of sampling in any run; thus, we conservatively discarded the first ten million generations of each run as the burn-in. Indicating convergence to the posterior distributions, results of the independent runs were remarkably similar to each other, so we combined them and constructed a majority rule consensus of 60,000 trees for each data set (trees sampled every 1000 generations were saved for each run). Results of Bayesian analyses in which separate partitions were specified (e.g. mitochondrial vs. nuclear genes) did not differ appreciably from those based on unpartitioned data and are not reported here. For parsimony analyses, we employed heuristic searches with tree-bisection-reconnection (TBR) branch swapping and 100 random stepwise addition replicates in PAUP*. To assess nodal support, we conducted bootstrap analyses with 1000 replicates. To explore the effect of substitutional saturation on the outcome of parsimony reconstructions, we examined bootstrap support for clades in analyses in which transitions in third codon positions of cyt *b* and ATPase 6 & 8 were excluded or downweighted with respect to other substitution types by factors of 2, 5, and 20.

We reconstructed genealogical relationships among ND2 haplotypes in *Buarremon* using maximum likelihood and maximum parsimony. Separate analyses were conducted for (1) *B. brunneinucha* and *B. virenticeps*, which were shown to be closely related taxa by the comprehensive multigene analyses (see below) and (2), the *B. torquatus* complex. Based on the AIC calculated using ModelTest we selected the GTR+I+G model of nucleotide substitution as the best fit to both data sets and implemented it in maximum-likelihood analyses, which were run as described above. Maximum parsimony analyses of the ND2 data were similar to those described above for the multigene data sets, except that the number of trees retained per random addition replicate was set to 100.

Assessment of statistical conflict between taxonomy and phylogeny

Some hypotheses of relationship revealed by our phylogenetic analyses are contrary to those implied by traditional taxonomic classifications. We assessed the significance of these conflicts from frequentist and Bayesian perspectives. First, we conducted hypothesis testing in a maximum-likelihood framework to determine whether observed topologies were statistically more likely than hypotheses of relationships implied by taxonomic treatments available in the literature. We calculated the likelihood of constraint trees in which genera were forced to be monophyletic and contrasted these likelihoods with that of the unconstrained maximum-likelihood trees using Shimodaira-Hasegawa tests with resampling estimated log-likelihood (RELL) optimization and 1000 bootstrap replicates. This test evaluates the null hypothesis that all topologies are equally good explanations of the data (Shimodaira and Hasegawa 1999, Goldman et al. 2000). From a Bayesian perspective, the posterior probability of a node in a phylogenetic tree indicates the probability that the relationships indicated by the node are correct, conditional on the data and the model of nucleotide substitution (Huelsenbeck and Rannala 2004). Thus, to determine whether the data provided any support for the monophyly of clades defined by traditional taxonomy that were not recovered in the majority rule consensus of the MCMC samples of trees, we determined their posterior probabilities by excluding from the sample all trees that did not include these clades and determining the proportion of the total sample represented by the remaining trees.

Population genetic analyses in Buarremon

Guided by the gene genealogies inferred by phylogenetic analyses, we used the program DNAsp (Rozas et al. 2003) to calculate nucleotide diversity (the average number of nucleotide differences per site between two sequences; Nei 1987) and its standard deviation for selected clades and for populations occurring in distinct geographic regions. Nucleotide diversity is typically reduced in areas that have been more recently colonized (reviewed by Zink 2002), which allowed us to make inferences regarding the directionality of range expansions. We also used DNAsp to conduct Tajima's (1989) test to assess whether departure from neutral evolution could compromise the use of mtDNA data to make inferences about population history.

To obtain estimates of gene flow between selected pairs of populations occurring in geographical proximity, we used the coalescent method implemented in the program MDIV (Nielsen and Wakeley 2001). For these analyses, we focused on populations occurring in lower Central America and South America, where our sampling was most intensive. The specific pairs of populations were selected based on the existence of potential barriers to gene flow and patterns observed in genealogies, which seemed to suggest isolation between some of them, but distinct, isolated clades were not always well-supported by phylogenetic analyses. The implementation of the coalescent approach allowed us to estimate the extent of gene flow between populations independently of the uncertainty inherent to the reconstruction of gene genealogies. MDIV uses MCMC sampling of genealogies to obtain joint estimates of migration rates and divergence times between pairs of populations assuming no further population subdivision and selective neutrality (Nielsen and Wakeley 2001). Each run consisted of 5,000,000 generations of MCMC sampling, of which the first 500,000 were discarded as burn-in; based on estimates obtained in preliminary test runs, we set the maximum values for the scaled migration rates and divergence times in all analyses to 10 and 5, respectively. To ensure that results did not depend on starting conditions, we conducted each analysis three times starting from different random seeds; all runs employed the HKY substitution model (Palsbøll et al. 2004).

Results

Phylogenetics – Mitochondrial data

Phylogenetic relationships among genera, among species of *Buarremon*, and among major lineages of *B. torquatus* and *B. brunneinucha* inferred from sequences of the four mitochondrial genes are shown in Fig. 2. Results obtained using different methods of phylogenetic inference were congruent with each other except for a few nodes that were not strongly supported in any analysis.

Although the mitochondrial data strongly support the monophyly of *Arremon* and *Lysurus*, they suggest that *Buarremon* as currently defined is not a monophyletic group. All analyses placed the *Arremon* clade as sister to the *B. torquatus* complex, a result strongly supported in Bayesian analyses (0.96 posterior probability), but less so in maximum-likelihood (64% bootstrap), or parsimony (53% bootstrap) analyses. In all analyses, *B. brunneinucha* appeared to be closest to the clade formed by species in the genus *Lysurus*, but this hypothesis of relationship was never strongly supported. Inferences from parsimony bootstrap analyses in which transitions at third codon positions in cyt *b* and the ATPase genes were excluded or downweighted (results not shown) were generally consistent with the unweighted analysis. Support for deep relationships (i.e., those among genera, whose recovery could have been obscured by saturation) was low, as in the unweighted analysis.

In stark contrast with traditional taxonomy, we found that *B. virenticeps* is clearly sister (100% maximum-likelihood and maximum parsimony bootstrap and 1.00 posterior probability) to *B. brunneinucha*, not to *B. torquatus*. Moreover, some reconstructions suggested *B. brunneinucha* may be paraphyletic with respect to *B. virenticeps*, a result strongly supported in the Bayesian and maximum likelihood analyses, in which a posterior probability of 0.99 and bootstrap value of 78% was obtained for a clade formed by *B. virenticeps* and a representative of the nominate subspecies of *B. brunneinucha*, to the exclusion of other Mexican and Central and South American populations of the latter. Based on this data set, populations of *B. brunneinucha* from Central and South America form a clearly distinct clade with respect to those from Mexico, a pattern we will discuss at length below.

Support for the monophyly of the phenotypically variable *B. torquatus* complex was strong in all analyses (100% bootstrap and 1.00 posterior probability). Within the complex, a well-supported basal division separates the Central American taxon *costaricensis* from the rest of the group. Within the latter clade, however, basal relationships among major groups (several of which were well-supported) could not be resolved with certainty owing to the collapse in a polytomy of several long branches connected by short internodes. Relationships within this group are discussed in detail below based on more comprehensive sampling of populations.

Phylogenetics – Nuclear data

Sequence variation in the two nuclear introns was limited. Considering only ingroup taxa (i.e., *Buarremon, Arremon, Lysurus*) only 54 and 48 variable characters were observed in ACO1 and MUSK, respectively, of which only 27 and 26 were informative from a parsimony standpoint. Therefore, the number of characters supporting relationships inferred only from nuclear data (Fig. 3) was always small, and we emphasize that results should be viewed with care (the unexpected position of *Melospiza* in the MUSK tree immediately calls for caution). Nonetheless, it is noteworthy that despite their limited information content, both nuclear genes recovered some of the relationships obtained with the mitochondrial data with good support (Fig. 3). These include the monophyly of the *B. torquatus* complex, of *Arremon,* and of *Lysurus,* and the close relationship of *B. virenticeps* and Mexican *B. brunneinucha*. However, the two introns offered contrasting information regarding relationships among genera*:* while inferences from MUSK were consistent with the mitochondrial data in placing *B. torquatus* and *Arremon* as sister clades, ACO1 recovered a clade that included all *Buarremon* and *Lysurus,* with moderate support for *Arremon* as its sister group.

Phylogenetics – Combined data

The topology obtained from the combined analyses including mitochondrial and nuclear sequences (Fig. 4) is entirely consistent with the mitochondrial trees, which is not surprising considering the much higher information content in the mitochondrial data. However, although informative substitutions in the nuclear sequences were limited, when analyzed in combination with mitochondrial data they increased support for some relationships. These include the sister relationship of *B. torquatus* and *Arremon* (supported by a posterior probability of 1.00, 80% maximum-likelihood bootstrap and 62% parsimony bootstrap) and the relationship of *B. brunneinucha-B. virenticeps* to *Lysurus,* which increased to 0.94 posterior probability, though bootstrap support remained low (61% in maximum-likelihood and less than 50% in parsimony).

Statistical assessment of Buarremon *monophyly*

Shimodaira-Hasegawa likelihood tests indicated that trees in which the monophyly of *Buarremon* was enforced are not significantly worse explanations of the mitochondrial and combined mitochondrial and nuclear sequence data than the optimal trees we recovered, in which *Buarremon* was not monophyletic (Table 2). In contrast, not a single tree of the combined total of 120,000 that were sampled in Bayesian analyses of mitochondrial and combined data showed *B. torquatus, B. brunneinucha* and *B. virenticeps* forming a clade, implying that the posterior probability of the monophyly of *Buarremon* is zero.

Phylogeography of B. brunneinucha

We obtained complete sequences of the ND2 gene for a total of 135 individuals of *B. brunneinucha* and 8 individuals of *B. virenticeps*, which represented 98 and 6 different haplotypes, respectively. The deep branching structure of the tree indicating genealogical relationships among haplotypes in the *B. brunneinucha – B. virenticeps* clade (Fig. 5) was not well supported as indicated by low bootstrap values, and by discrepancies in resolution of branching patterns between the maximum-likelihood and maximum parsimony trees (not shown). Despite these discrepancies, reconstructions under both criteria indicated that Mexican populations from west of the Isthmus of Tehuantepec constitute a paraphyletic assemblage composed of several early branching lineages. Due to the lack of support for relationships among deep branches, however, we cannot rule out the hypothesis that lineages from west of Tehuantepec form a clade. Based on this larger sample of individuals, *B. brunneinucha* still appears to be paraphyletic with respect to *B. virenticeps,* which in turn was recovered as monophyletic. However, support for the paraphyly of *B. brunneinucha* is not compelling, which implies that the hypothesis that *B. brunneinucha* and *B. virenticeps* are sister species cannot be rejected.

Independently of the uncertainty in resolving the deeper branches of the tree, all analyses recovered a well-supported "southern" *B. brunneinucha* clade consisting of all samples collected throughout Mesoamerica east of Tehuantepec and South America. Haplotypes from Chiapas, Mexico, are not shown in the tree because DNA from the available samples (old study skins) was degraded, and we could only sequence c. 300 base pairs; however, analyses based on that short fragment unambiguously indicated these are closely allied to populations from Guatemala rather than those from Mexico west of Tehuantepec, which is consistent with their subspecific designation. Relationships among some of the major lineages in the southern *B. brunneinucha* clade were not well supported, probably as a result of a rapid population expansion through Central America.

A phylogeographic break in *B. brunneinucha* appears to exist between western and central-eastern Panama, with most individuals from each region forming a reciprocally monophyletic group; individuals from central and eastern Panama are more closely allied to populations occurring in South America. Reciprocal monophyly is not complete owing to the placement of one individual from Chiriquí Province (western Panama) in the central-eastern clade and of one individual from Veraguas Province (central Panama) in the eastern clade; these may reflect ongoing gene flow or incomplete lineage sorting in isolated populations (see below).

Further south, it appears clear that a recent major split took place between populations from central Panama and South America (including the Panamanian Darién region). The derived position of South American populations with respect to Mexican and Central American ones suggests that *B. brunneinucha* had a northern origin and expanded its range southward to colonize South America. This hypothesis is further supported by a marked decline in nucleotide diversity from Mexico south (Table 3).

Within South America, two distinct clades can be identified: one comprises haplotypes from the Cordillera Oriental of Colombia, montane areas of Venezuela, and the Amazonian slope of the Andes of Ecuador and Peru, whereas the other includes haplotypes from the Cordillera Central and Cordillera Occidental of Colombia and the Pacific slope of the Ecuadorian Andes. Within the latter clade, individuals from the Coastal Cordillera of Ecuador (subspecies *inornatus*) form a monophyletic group together with a single individual from the Pacific Andean slope. Ecuadorian populations from the west slope of the Andes do not form a clade with respect to those of Central and Western Colombia. Within the eastern South America clade geographic structure was limited. The four individuals sampled from the isolated population (*allinornatus*) from the Sierra de San Luis in Venezuela shared a single haplotype, which was most similar to other haplotypes from Venezuela.

Gene flow in B. brunneinucha

Tajima's tests conducted for several clades and geographic regions where *B. brunneinucha* occurs were never significant ($P > 0.1$ in all cases), indicating that patterns of genetic variation are consistent with selective neutrality. Estimates of migration from coalescent analyses revealed that different populations of *B. brunneinucha* separated by lowland areas are genetically isolated to varying degrees (Fig. 6). Perhaps the most striking pattern is the apparently complete lack of gene flow between populations occurring in eastern (Cordillera Oriental) and central-western (Cordillera Central and Cordillera Occidental) Colombia: the posterior probability distribution estimated by MDIV was concentrated at or very near values of zero female migrants per generation. In contrast, the posterior distribution estimated for migration between the Cordillera Central and the Cordillera Occidental of Colombia is essentially flat, with equivalent probabilities extending up to remarkably high levels of migration. Although strong inferences cannot be made owing to the enormous credibility interval around the modal estimate of migration, the data suggest that these two populations are panmictic. Movement of individuals between western and central Panama appears to be higher than between eastern and central-west Colombia, but still somewhat limited. In western Ecuador, the probability distribution was more evenly spread over values of migration in the range up to c. 1.5 female migrants per generation between the Coastal Cordillera and the Pacific slope of the Andes.

Phylogeography of B. torquatus

We obtained sequence data for a total of 78 individuals of *B. torquatus,* which represented 68 different ND2 haplotypes. Phylogenetic analyses (Fig. 7) revealed a well-supported basal split between the taxon *costaricensis* of Costa Rica and western Panama and a clade comprising populations occurring through central and eastern Panama and all of South America. The Panamanian taxon *tacarcunae* is nested within the clade formed by the South American members of the group, which suggests eastern and central Panama may have been colonized from South America. However, the geographic origin of *B. torquatus* as a whole is uncertain, as the sister group of the complex is the genus *Arremon*, which also has both Central and South American members. At any rate, the long branches and distinct clades present within South America indicate that this group has been in that continent for a substantial period of time; uncorrected sequence divergence (*p* distance) among South American members of the complex reaches 8%.

As mentioned above for the four-gene mitochondrial data set, resolution of relationships among South American lineages of *B. torquatus* was quite limited, with several long branches collapsing in a polytomy. These branches of unresolved affinities correspond to populations occurring in (1) the Sierra Nevada de Santa Marta of Colombia (subspecies *basilicus*), (2) the Serranía de Perijá in the Venezuela-Colombia border (*perijanus*), (3) east Venezuela (*phygas*), (4) extreme southern Peru, Bolivia, and northern Argentina (*torquatus, fimbriatus,* and *borelli*), (5) high elevation areas of the Colombian Andes, Ecuador, and Peru (*assimilis*, *nigrifrons*, and *poliophrys*) and northeast Colombia and west Venezuela (*larensis*), and (6) foothill to mid-elevation areas of the Andes of Colombia and eastern and central Panama (*atricapillus* and *tacarcunae*). Within lineage 4, *borelli* and *fimbriatus* were not reciprocally monophyletic and formed a clade sister to the monophyletic nominate *torquatus.* In lineage 5, *larensis* was sister to the *assimilis-nigrifrons-poliophrys* clade, within which *poliophrys* was sister to the closely allied *assimilis* and *nigrifrons,* which were not reciprocally monophyletic. Note that in contrast to monographic work on *B. torquatus* that treated populations occurring in the northern sector of the Cordillera Oriental of Colombia (Depto. Norte de Santander) as referable to subspecies *perijanus* (Paynter 1978), here we consider birds from this area as belonging to the taxon *larensis* (formerly thought to occur only in Venezuela) based on their very close affinity indicated by the mtDNA data and general similarity in plumage (see further details in Chapter 4).

Discussion

Phylogenetics

Unexpectedly, we found that *B. virenticeps* is not sister to B. *torquatus* as had always been assumed based on the close resemblance in plumage of adult *B. virenticeps* and juvenile *B. torquatus* (Paynter 1970, 1978). Rather, *B. virenticeps* is more closely allied to *B. brunneinucha*, a result strongly supported in all analyses, and independently by mitochondrial and nuclear data. Furthermore, although support is not compelling, mtDNA data suggest that *B. virenticeps* may be nested within *B. brunneinucha,* making the latter species paraphyletic. Such a striking apparent decoupling of phenotypic and genetic variation must be interpreted cautiously because several factors can affect the ability of mitochondrial genealogies to accurately reflect species relationships (Nichols 2001); more data are necessary to address this intriguing possibility. At any rate, the close relationship between *B. virenticeps* and *B. brunneinucha* demonstrates that external appearance (i.e., plumage) is not a reliable indicator of phylogenetic relationships in *Buarremon*, mirroring the situation documented for the allied genus *Atlapetes* (García-Moreno and Fjeldså 1999).

The monophyly of the genus *Buarremon* as currently defined is dubious. Although support for relationships among major groups in the clade formed by *Buarremon, Arremon,* and *Lysurus* was variable in analyses conducted using different methods (e.g., Bayesian inference vs. maximum parsimony) and employing different data (i.e., mitochondrial vs. nuclear sequences), perhaps the most telling fact is that we never recovered a monophyletic *Buarremon* in any analysis of mitochondrial, nuclear, or combined data. Indeed, an exclusive clade formed by *B. torquatus*, *B. brunneinucha,* and

B. virenticeps was not observed in a single tree of the combined total of 120,000 sampled in Bayesian analyses of mitochondrial and combined data. This implies that, conditional on our data and the models of nucleotide substitution, the probability that these three taxa form a clade is zero (Huelsenbeck and Rannala 2004). However, according to Shimodaira-Hasegawa (S-H) tests, the hypothesis of a monophyletic *Buarremon* is not a significantly less likely explanation of the sequence data than the optimal topologies we obtained. This discrepancy in the statistical conclusions reached by Bayesian and maximum-likelihood tests of topologies may be attributable to the tendency for Bayesian MCMC analyses to place excessive confidence on relatively short branches owing to how prior probabilities of branch lengths are set (Lewis et al. 2005, Yang and Rannala 2005), or to the conservative nature of the S-H test (Goldman et al. 2000, Shi et al. 2005). The former possibility appears less likely because the branches receiving high posterior probability support did not exhibit low bootstrap values under maximum-likelihood, which is typical for cases in which high posteriors on short branches may be artifactual (Lewis et al. 2005).

Mitochondrial data suggest that *B. torquatus* is more closely related to the genus *Arremon* than to *B. brunneinucha* and *B. virenticeps*, a result consistently recovered in all analyses and supported strongly by Bayesian posterior probability (0.96). However, this result was only moderately to weakly supported by bootstrap values (64% in maximum likelihood and 53% in parsimony). One of the nuclear genes (MUSK) was consistent with this sister relationship, whereas the other (ACO1) placed *Arremon* outside a clade formed by *Lysurus* and *Buarremon.* In retrospect, that *B. torquatus* and *Arremon* may be sister groups is not altogether surprising, because some *Arremon* taxa (e.g., *A. taciturnus*) are strikingly similar in plumage to members of the *B. torquatus* complex. Perhaps the only marked difference between *B. torquatus* and species of *Arremon* is the smaller body size of the latter, which might reflect their occurrence at lower, warmer elevations (i.e., Bergmann’s ecogeographic “rule”, see Zink and Remsen 1986). The hypothesis that the *B. torquatus* complex and *Arremon* are two distinct, probably sister, groups is robust to denser sampling within *Arremon*: ongoing studies involving all species in this genus support its monophyly (J. Klicka, C. D. Cadena and J. Pérez-Emán, unpubl. data). On the other hand, *B. brunneinucha* and *B. virenticeps* may be more closely allied to the genus *Lysurus* than to *B. torquatus*, but support for this relationship in the mitochondrial data set was not compelling, and it was not recovered by any of the nuclear genes. Our findings seemingly contrast with allozyme variation documented by Hackett (1992), who found that *B. brunneinucha* and *B. torquatus* formed a monophyletic group with respect to *Lysurus castaneiceps.* However, her data set lacked representatives of *Arremon*, and bootstrap support for the monophyly of *Buarremon* was not reported.

In sum, although one statistical test suggested that the hypothesis of a monophyletic *Buarremon* cannot be rejected as an explanation of the sequence data, the evidence we have presented points more strongly away from *Buarremon* being a monophyletic group. Therefore, we suggest that the classification of this group should be revised to be consistent with the recognition of monophyletic supraspecific taxa. Even if the sister relationship between *B. torquatus* and *Arremon* to the exclusion of *B. brunneinucha* and *B. virenticeps* turns out not to be supported by additional data, which we consider unlikely, genetic differentiation between the two clades of *Buarremon* is clearly at least as great as the differentiation that exists between *Arremon* and *Lysurus*, and between these and the two *Buarremon* clades. Considering this, and especially the strong similarities among all *Buarremon*, *Arremon*, and *Lysurus* taxa in plumage, voices, behavior, and microhabitat, we believe the best course is to treat all of them as members of an expanded genus *Arremon* (this name has priority over *Buarremon* and *Lysurus;* Paynter 1970). To retain the information conveyed by traditional classification regarding the existence of distinct clades within this expanded genus, *Lysurus* and *Arremon* (*sensu stricto*), but not *Buarremon*, could be recognized at the subgenus level. For consistency, however, and until this proposed change in nomenclature is accepted by taxonomic authorities (i.e., Remsen et al. 2006), in the following we continue to refer to the established genus names to avoid confusion.

Phylogeography

Variation in mtDNA sequences strongly supports the scenario that *B. brunneinucha* originated in northern Mesoamerica (presumably in montane areas of Mexico), an area from which populations expanded across Central America and into South America. That populations have had more time to differentiate in the northern sector of the range provides a reasonable explanation for patterns of phenotypic variation: several morphologically distinctive forms of *B. brunneinucha* occur in Mexico and northern Mesoamerica, whereas variation in plumage across lower Central America and South America is quite limited (Parkes 1954, Paynter 1978). Probably as a result of rapid differentiation, relationships among Mexican populations (including *B. virenticeps*) could not be established with certainty, but it is clear that following their rapid divergence these have had a long history of isolation (see also Peterson et al. 1992). Although additional data are necessary to resolve relationships among Mexican lineages and to determine whether some of them (e.g. *apertus*) should be treated as distinct species (see Navarro-Sigüenza and Peterson 2004), mitochondrial data clearly demonstrate the existence of a marked phylogeographic break within Mexico that separates populations from the western and eastern sides of the Isthmus of Tehuantepec. This pattern is consistent with genetic differentiation in other montane taxa (e.g. Sullivan et al. 2000, Pérez-Emán 2002, García-Moreno et al. 2004, García-Moreno et al. 2006), highlighting the importance of the low-elevation Isthmus as a barrier to dispersal.

The short internodes separating mitochondrial lineages of *B. brunneinucha* occurring through much of Central America is suggestive of rapid expansion of populations across the region. A similar pattern of rapid north to south expansion across Central America has been documented for the Slate-colored Redstart *Myioborus miniatus* (Pérez-Emán 2002), and, in fact, assuming that rates of nucleotide substitution are similar in *Buarremon* and *Myioborus*, population expansions in both groups appear to have occurred concurrently on the basis of mtDNA divergence levels.

Further south, another phylogeographic break in *B. brunneinucha* appears between western and central-eastern Panama, with most individuals from each region forming a reciprocally monophyletic group. Isolation of these areas is not complete, however, as coalescent analyses give some support for the existence of limited gene flow. From central-southern Costa Rica south, the ranges of *B. brunneinucha* and *B. torquatus* begin to overlap. Although no samples of *B. torquatus* from western Panama were available for this study, populations from Chiriquí Province are referable to the taxon *costaricensis* and thus are probably closest to those from adjacent Costa Rica. Since *costaricensis* is sister to all other members of the *B. torquatus* complex, populations in western and central-eastern Panama are also likely differentiated in this complex. Other phylogeographic studies on montane taxa (e.g. Solórzano et al. 2004) do not have comparable sampling to ours across Panama, and so we cannot determine the generality of this pattern of differentiation. Clearly, further analyses of montane species are necessary to better understand the history of diversification across lower Central America, especially because varied phylogeographic patterns among lowland taxa highlight the historical complexity of this region (Bermingham and Martin 1998, Brumfield and Braun 2001, Marks et al. 2002, Perdices et al. 2002, Cortés-Ortiz et al. 2003, Dick et al. 2003, 2004, González et al. 2003, Witt 2004, Weigt et al. 2005).

Divergence between central Panamanian and South American populations of *B. brunneinucha* is relatively modest, with mean uncorrected *p* distances reaching only 2-3%. Therefore, the available estimates of nucleotide substitution rates for avian protein-coding mitochondrial genes (reviewed by Lovette 2004a; Arbogast et al. 2006) imply that the colonization of South America by *B. brunneinucha* took place after the completion of the Isthmus of Panama, dated at c. 3 million years before present (Coates and Obando 1996). The direction of colonization of *B. torquatus* cannot be established with certainty by polarizing ancestral areas on the phylogeny, but the divergence between Central American (*costaricensis*) and South American populations appears to have occurred earlier than in *B. brunneinucha.* The timing of population divergence in both species is explored in more detail elsewhere (Chapter 2). Although data on other taxa are still quite limited, studies of avifaunal interchange across the Central American land bridge have documented range expansions both north to south (Pérez-Emán 2002, 2005; Barker 2006; this study) and south to north (Hackett 1995, Burns and Naoki 2004, Witt 2004), with some of these events occurring prior to the completion of a terrestrial connection (Witt 2004, Barker 2006). As with the expansion across Central America, genetic distances suggest that colonization of South America by *B. brunneinucha* may have occurred simultaneously with that of *M. miniatus* (Pérez-Emán 2002), highlighting once again that these co-distributed taxa appear to have had remarkably congruent histories. It is also noteworthy that patterns of geographic variation in plumage are similar in *B. brunneinucha* and *M. miniatus*, with both species showing minimal variation in South America relative to Middle America. Accumulating similar phylogeographic information for additional taxa will be of great interest to determine whether consistent patterns are observed in multiple lineages; ultimately, this will allow a better understanding of the role of trans-Isthmian colonization events on the historical assembly of communities in both North and South America (Ricklefs 2002).

The existence of distinct western and eastern South American clades of *B. brunneinucha* haplotypes is remarkable. Although they were not always strongly supported, both lineages were recovered in all analyses, and coalescent estimates of migration indicate negligible levels of gene flow between eastern and central-western Colombia. The documentation of these two distinct haplotype clades suggests that range expansion by *B. brunneinucha* across South America following a single colonization event proceeded through two independent routes, one through the west and one through the east of the continent. Members of the two phylogroups probably come quite close to each other in areas of the Ecuadorian Andes, but they are likely isolated by unsuitable high-elevation habitat. That populations from the Cordillera Oriental of Colombia are genetically isolated from those from the Cordillera Central and Cordillera Occidental represents evidence of the long-suspected effect of the complex geography of the Colombian Andes on patterns of population genetic differentiation, and specifically on the role of the Río Magdalena Valley as a barrier to gene flow for montane organisms. Indeed, of the three pairs of populations among which we documented restricted to moderate migration, the ones occurring in closest geographic proximity to one another are those from eastern and central-western Colombia, where migration appears most restricted. Because the elevations of the lowland areas separating these pairs of populations differ little, the more restricted migration in Colombia may reflect the additional barrier to dispersal imposed by the Río Magdalena. Although detailed studies on population differentiation of Andean birds are lacking, these results are consistent with those of studies conducted in other montane regions that show an effect of lowland areas as barriers to gene flow (Bowie et al. 2006), and in the Neotropical lowlands demonstrating an effect of large rivers restricting genetic exchange (Aleixo 2004, Bates et al. 2004, Cheviron et al. 2005). In contrast, however, populations separated by the Río Cauca Valley (i.e., those occurring in the Cordillera Central and Cordillera Occidental of Colombia) are less differentiated, have not attained reciprocal monophyly, and maintain gene flow as indicated by coalescent analysis. This probably reflects the very close proximity of these cordilleras, the fact that they are connected at their southern ends, and the higher elevation of the Cauca Valley in comparison to the Magdalena, which may have allowed for increased historical connectivity between mountain ranges during cool periods when vegetation zones were displaced downslope (Hooghiemstra and van der Hammen 2004). Other studies have documented close affinities between montane taxa from the Cordillera Central and Cordillera Occidental of Colombia (see Cuervo et al. 2005), suggesting this pattern may have some generality.

In contrast to signatures of restricted gene flow across some lowland areas in *B. brunneinucha,* differentiation along broad latitudinal expanses of the Andes appears to be limited in the two South American lineages of *B. brunneinucha* and in the *assimilis*-*nigrifrons* clade of *B. torquatus*. This lack of clear population genetic structuring with respect to latitude is somewhat surprising, considering that the linear distributions of Andean taxa are thought to be especially prone to fragmentation and subsequent allopatric divergence (Graves 1988). However, processes of this sort may be responsible for the differentiation between *assimilis*-*nigrifrons* and *poliophrys,* which despite their relatively close proximity in the Peruvian Andes are reciprocally monophyletic, ca. 4 % different in mtDNA, and phenotypically distinct (see also Chapter 4). Another instance of differentiation along the Andes in *B. torquatus* occurs between the clade formed by *larensis, assimilis, nigrifrons,* and *poliophrys* and the one comprising nominate *torquatus, fimbriatus,* and *borelli.* Although members of these clades have been collected within 50 km of one another in southern Peru (Chapter 4), mtDNA suggests a long history of isolation, with the minimum uncorrected sequence divergence between the nearly abutting *poliophrys* and *torquatus* being 6.6%. This zone may represent an area of secondary contact. Finally, differentiation along the Andes is also apparent from the recovery of distinct clades in northern-central Bolivia (*torquatus*) and southern Bolivia and Argentina (*fimbriatus* and *borelli*), although we cannot rule out the possibility that these two clades are in fact the extremes of a cline in genetic variation that we did not observe due to sparse sampling (see Brumfield 2005).

The *B. torquatus* complex comprises a suite of relatively old lineages, which according to the widely applied rate of nucleotide substitution of 1.6-2% divergence per million years (Lovette 2004a, Weir 2006), would appear to have last shared a common ancestor more than 3 million years ago. Even assuming that ND2 evolves at a faster rate (Arbogast et al. 2006), the divergence among these lineages would date back to at least 1.5 million years before present. Regardless of whether these phylogroups represent different species or variants of a single species (Chapter 4), these levels of divergence are comparatively high for Neotropical montane birds, many of which diversified within the last million years as inferred from the 2% per million years rate calibration (Weir 2006). In fact, the patterns of mtDNA differentiation observed in *B. torquatus* resemble those documented for several passerine birds of the Neotropical lowlands (e.g., Bates et al. 1999, Marks et al. 2002, Lovette 2004b, Cheviron et al. 2005) in terms of the existence of highly distinct phylogroups of pre-Pleistocene age. There are however, some cases of Pre-Pleistocene differentiation in Andean taxa (García-Moreno and Fjeldså 2000, Pérez-Emán 2005).

Relationships among major phylogroups of South American *B. torquatus* are unresolved. Because mitochondrial data could recover relationships at deeper and shallower levels of divergence with good support, we consider this to be a hard polytomy resulting from differentiation within a brief period. Similar patterns of rapid diversification of distinct lineages have been described for Neotropical warblers in the genera *Phaeothlypis* and *Myioborus* (Lovette 2004b, Pérez-Emán 2005). The apparently explosive differentiation of *B. torquatus* in South America precludes strong inference about the geographic context of differentiation in the group. It is striking, however, that lineages occurring in the same general area (e.g., *assimilis* and *atricapillus*, which are found segregating elevationally on the same mountain slopes in the three Colombian cordilleras) are approximately equally divergent from each other as they are from groups occurring in distant locations (e.g. the clade occurring through Bolivia and Argentina). Moreover, although phylogenetic relationships among lineages at this level are tentative, tree topologies suggest that lineages occurring in allopatry and separated by thousands of kilometers may be each other's closest relatives. If this were correct, then *B. torquatus* would have a complex history of diversification, probably involving multiple events of vicariance, dispersal, and lineage extinction over broad spatial scales (see also Dingle et al. 2006). This suggests that processes of avian diversification in the Andes likely involve complex large scale processes in addition to the rather simple, small-scale vicariant events that are thought to prevail

(Remsen 1984, García-Moreno and Fjeldså 2000).

Due to various reasons, including political instability in the region, researchers working on population genetics, phylogeography, and molecular phylogenetics of Neotropical organisms have largely ignored Colombian populations. Studies on Andean birds have either focused on taxa distributed in the Central and Southern Andes (reviewed by García-Moreno and Fjeldså 2000, Weir 2006), or have described patterns of differentiation in widespread groups without including material from Colombia (e.g. Dingle et al. 2006; but see Witt 2004, Pérez-Emán 2005). Without sampling in Colombia, our analyses would have resulted in a woefully incomplete picture of the history of *Buarremon*, missing the crucial but unexpected affinities of populations of *B. brunneinucha* from the Cordillera Oriental to those of Venezuela and the Amazonian slope of the Andes of Ecuador and Peru, and of populations from the Cordillera Central and Cordillera Occidental to those from the Pacific slope of Ecuador, in addition to the occurrence of five divergent lineages of *B. torquatus* that are not each other's closest relatives within the country. Due to its geographic position at the crossroads between Central and South America and the expected effects of its complex geography on population structure, it comes as no surprise that the results of this study imply that analyses of patterns of differentiation involving detailed sampling in Colombia should be considered essential to understanding the biogeographic history of many Neotropical taxa.

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Table 1. Primers designed for PCR amplification of fragments of the ND2 gene from degraded DNA samples. Primers are named according to their position in comparison to the first nucleotide in the ND2 gene and on whether they are located on the light (L) or heavy (H) strand.

Primer	**Sequence (5' to 3')**
L301	GCAGTAGCAATAAAACTYGGAYTAG
H330	TTCTGGGAATCAGAAGTGGAAT
L515	ARACACAAATCCGAAAAATCYTAG
H590	GTTRAGGAGAGTGAGTTTRGGGT
L697	ACATGAAGCAAAGYYCCA
H850	AARAAYAGGCTTAGTAGTGAGAGGAG

Table 2. Results of Shimodaira-Hasegawa tests comparing the likelihoods of maximum-likelihood estimates of phylogeny obtained for mitochondrial and combined mitochondrial and nuclear data with those of trees recovered in maximum-likelihood analyses in which the monophyly of *Buarremon* was enforced. Tests were one-tailed, based on 1000 RELL bootstrap replicates.

Data Set	**ML tree -ln L**	**Constrained tree -ln L**	**p-value**
Mitochondrial (four genes)	19856.741	19861.797	0.216
Mitochondrial – nuclear (six genes)	19217.315	19226.091	0.134

Table 3. Estimates of nucleotide diversity and its standard deviation calculated for different areas and regions where *B. brunneinucha* occurs, indicating declining genetic diversity from north to south.

Region	***n***	**Nucleotide Diversity ± S. D.**
Mexico (excluding *virenticeps)*	12	0.0459 ± 0.0041
Mexico (including *virenticeps*)	20	0.0445 ± 0.0031
Central America (Guatemala – Panama)	30	0.0249 ± 0.0024
Guatemala – West Panama	24	0.0206 ± 0.0029
Central Panama	6	0.0148 ± 0.0073
South America (East Panama – Peru)	93	0.0168 ± 0.0005
Western Clade	32	0.0134 ± 0.0008
Eastern Clade	59	0.0131 ± 0.0008

FIGURE LEGENDS

Figure 1. Geographic distribution of samples of *Buarremon brunneinucha* and *B. virenticeps* (A) and *B. torquatus* (B) included in phylogenetic and phylogeographic analyses. Localities are numbered by species following the locality codes indicated in the Appendix.

Figure 2. Phylogenetic hypothesis for relationships of 43 individuals of *Buarremon, Lysurus, Arremon,* and outgroup taxa based on combined analyses of 2871 aligned base pairs of four mitochondrial genes. The phylogram shown is the maximum-likelihood tree. Numbers on branches indicate Bayesian posterior probabilities and bootstrap values obtained under maximum-likelihood and maximum parsimony, respectively. Support values for relationships of taxa in the outgroup are not shown.

Figure 3. Phylogenies inferred for 22 individuals using sequences of two nuclear loci, ACO1 (top), and MUSK (bottom). The phylograms shown are the maximum-likelihood trees obtained for each data set. Numbers above and below nodes are bootstrap values obtained under maximum-likelihood and maximum parsimony, respectively, whenever these are greater than 50%.

Figure 4. Phylogenetic hypothesis for relationships of *Buarremon, Lysurus,* and *Arremon* taxa based on combined analyses of 4208 aligned base pairs of four mitochondrial and two nuclear genes. The phylogram shown is the maximum-likelihood tree. Numbers on branches indicate Bayesian posterior probabilities and bootstrap values obtained under maximum-likelihood and maximum parsimony, respectively. Outgroup not shown.

Figure 5. Maximum-likelihood tree showing relationships among haplotypes of *B. brunneinucha* and *B. virenticeps.* Localities are named as in Figure 1a and in the Appendix. The number of individuals sharing a given haplotype is indicated in parentheses following each locality, when applicable. Brackets on the right group haplotypes by region, but note that for Mexico and Central America these do not correspond to clades. For selected clades discussed in the text, bootstrap values obtained under maximum-likelihood and maximum parsimony are shown above and below branches, respectively. Other clades receiving high support under both criteria are indicated with asterisks. Support for relationships near terminal branches is not shown for clarity; deep nodes without boostrap values or asterisks were not strongly supported. The tree was rooted with sequences of *Lysurus castaneiceps* and *L. crassirostris* (not shown).

Figure 6. Posterior probability distributions of estimates of migration between selected pairs of populations of *B. brunneinucha* obtained using coalescent analyses in MDIV. (A) Cordillera Oriental vs. Cordilleras Central and Occidental, Colombia. (B) Cordillera Central vs Cordillera Occidental, Colombia. (C) Coastal Cordilleras vs. West Andean Slope, Ecuador. (D). East Panama vs. Central Panama.

Figure 7. Maximum-likelihood tree showing relationships among haplotypes of *B. torquatus.* Localities are named as in Figure 1b and in the Appendix. The number of individuals sharing a given haplotype is indicated in parentheses following each locality, when applicable. Bootstrap values exceeding 70% obtained under maximum-likelihood and maximum parsimony are shown above and below branches, respectively; support values are omitted from terminal branches for clarity.

FIGURE 1A

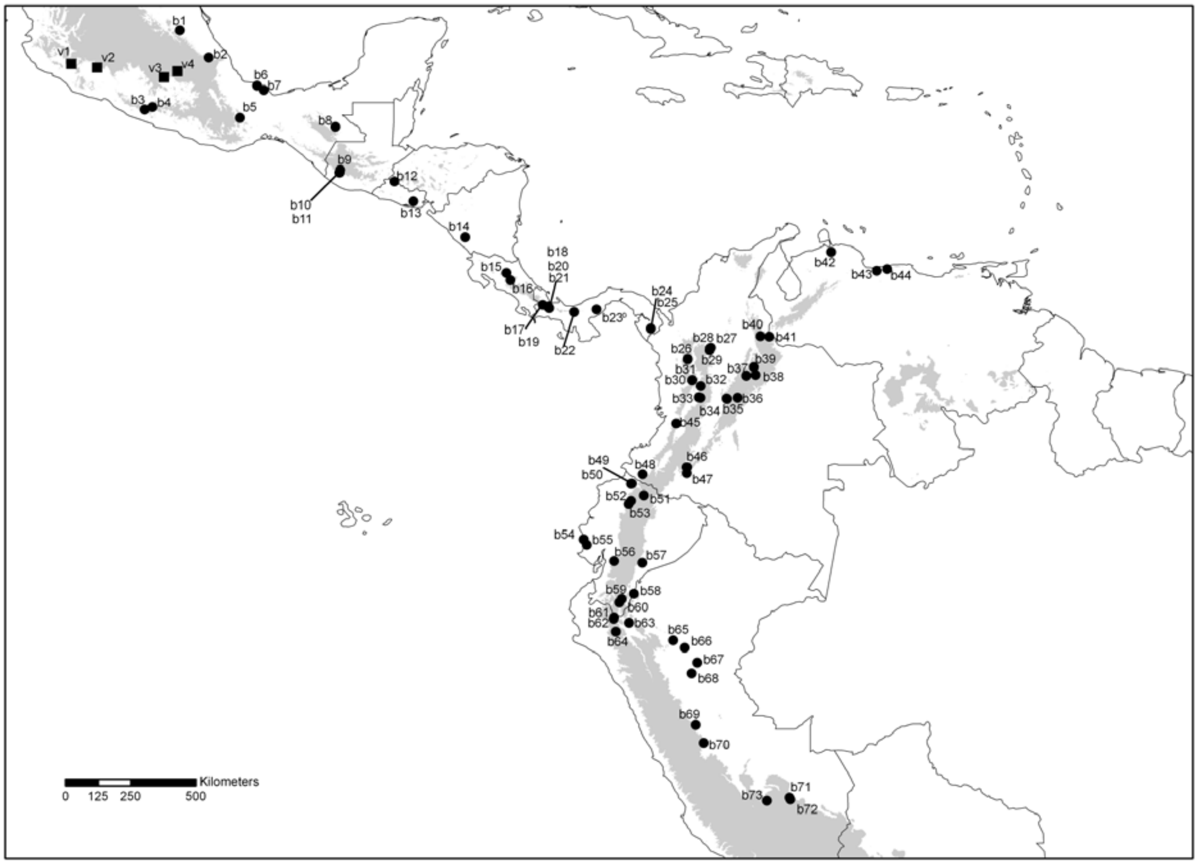
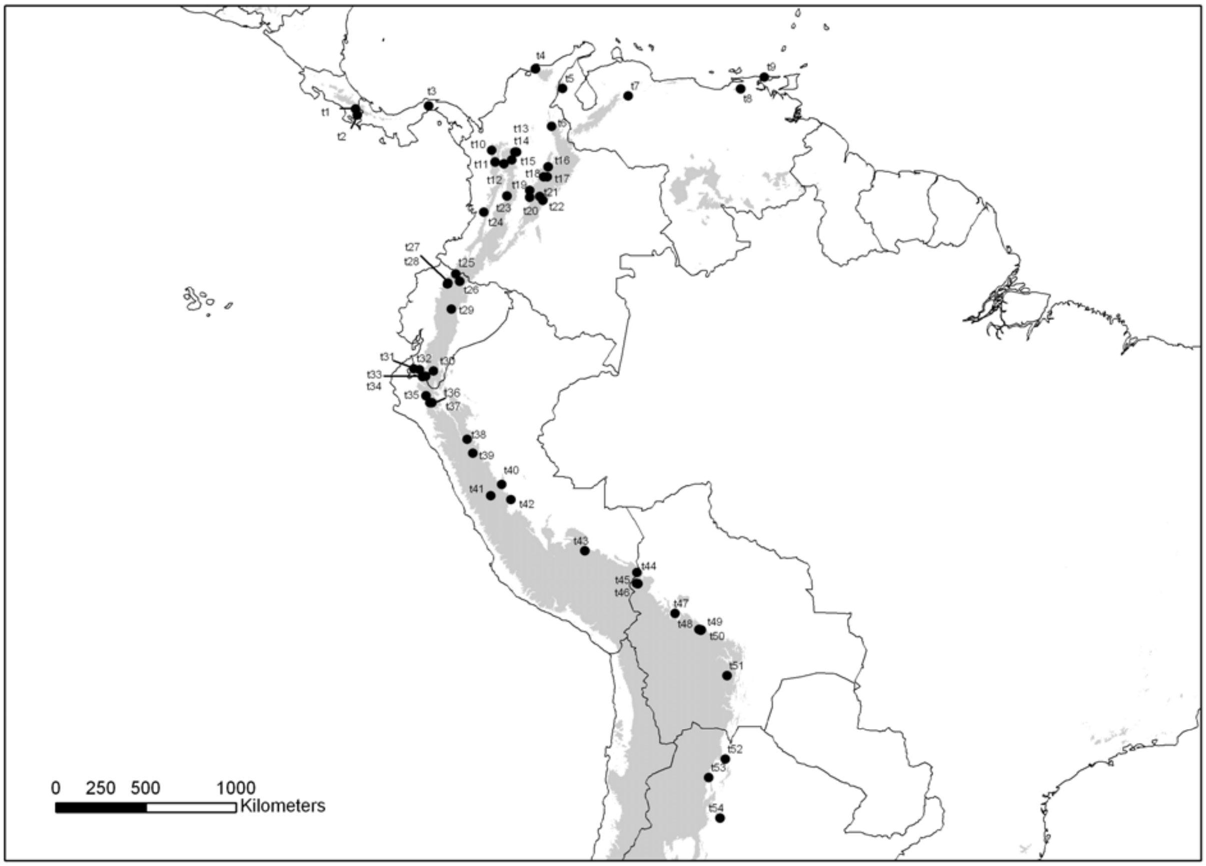

b1
v1
v2
v3
v4
b2
b3
b4
b5
b6
b7
b8
b9
b10
b11
b12
b13
b14
b15
b16
b17
b18
b19
b20
b21
b22
b23
b24
b25
b26
b27
b28
b29
b30
b31
b32
b33
b34
b35
b36
b37
b38
b39
b40
b41
b42
b43
b44
b45
b46
b47
b48
b49
b50
b51
b52
b53
b54
b55
b56
b57
b58
b59
b60
b61
b62
b63
b64
b65
b66
b67
b68
b69
b70
b71
b72
b73
Kilometers
0
125
250
500

FIGURE 1B


t1
t2
t3
t4
t5
t6
t7
t8
t9
t10
t11
t12
t13
t14
t15
t16
t17
t18
t19
t20
t21
t22
t23
t24
t25
t26
t27
t28
t29
t30
t31
t32
t33
t34
t35
t36
t37
t38
t39
t40
t41
t42
t43
t44
t45
t46
t47
t48
t49
t50
t51
t52
t53
t54
0
250
500
1000
Kilometers

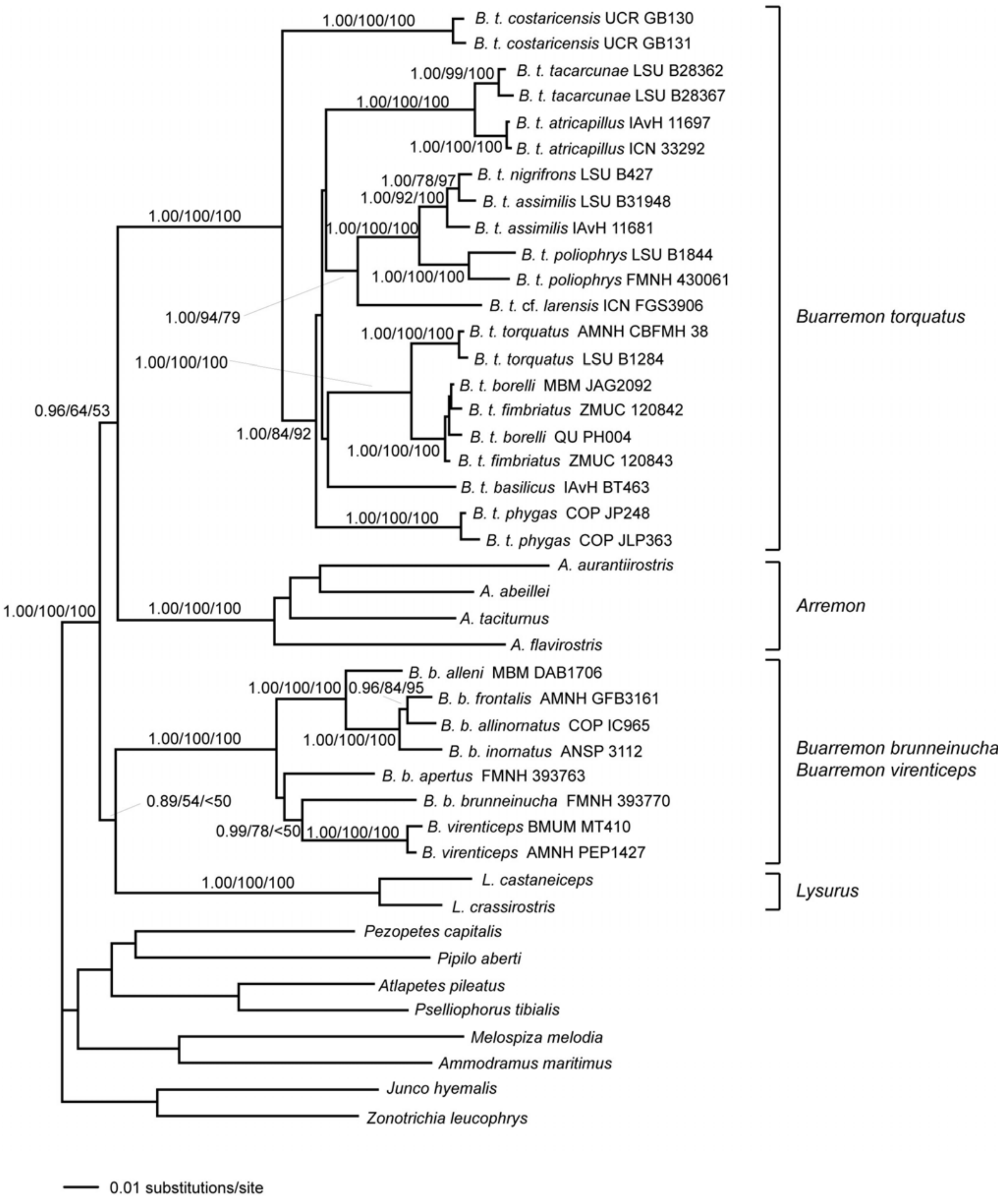
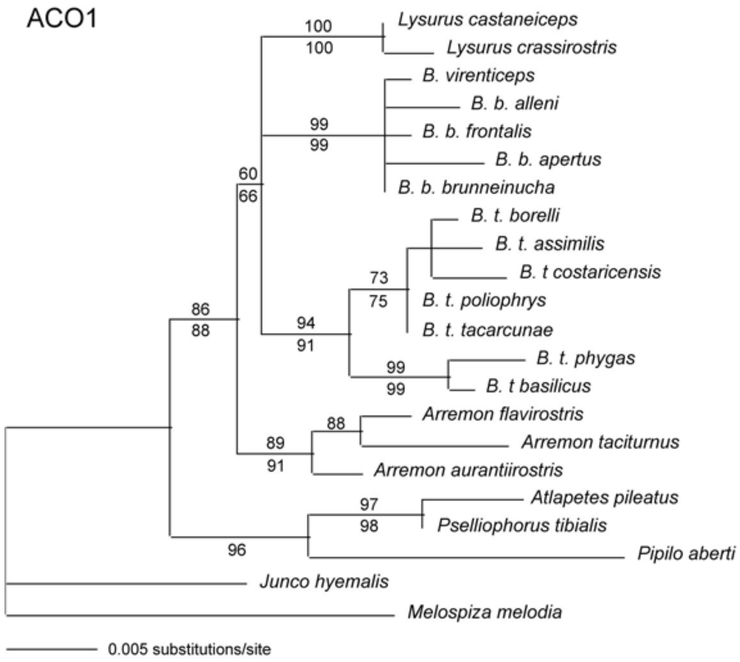

1.00/100/100
B. t. costaricensis UCR GB130
B. t. costaricensis UCR GB131
1.00/99/100
B. t. tacarcunae LSU B28362
B. t. tacarcunae LSU B28367
1.00/100/100
B. t. atricapillus IAvH 11697
1.00/100/100
B. t. atricapillus ICN 33292
1.00/78/97
B. t. nigrifrons LSU B427
1.00/92/100
B. t. assimilis LSU B31948
1.00/100/100
B. t. assimilis IAvH 11681
1.00/100/100
B. t. poliophrys LSU B1844
1.00/100/100
B. t. poliophrys FMNH 430061
1.00/94/79
B. t. cf. larensis ICN FGS3906
1.00/100/100
B. t. torquatus AMNH CBFMH 38
1.00/100/100
B. t. torquatus LSU B1284
B. t. borelli MBM JAG2092
0.96/64/53
B. t. fimbriatus ZMUC 120842
1.00/84/92
B. t. borelli QU PH004
1.00/100/100
B. t. fimbriatus ZMUC 120843
B. t. basilicus IAvH BT463
1.00/100/100
B. t. phygas COP JP248
B. t. phygas COP JLP363
Buarremon torquatus
A. aurantiirostris
A. abeillei
1.00/100/100
1.00/100/100
A. taciturnus
A. flavirostris
Arremon
B. b. alleni MBM DAB1706
1.00/100/100
0.96/84/95
B. b. frontalis AMNH GFB3161
B. b. allinornatus COP IC965
1.00/100/100
1.00/100/100
B. b. inornatus ANSP 3112
B. b. apertus FMNH 393763
0.89/54/<50
B. b. brunneinucha FMNH 393770
0.99/78/<50
1.00/100/100
B. virenticeps BMUM MT410
B. virenticeps AMNH PEP1427
Buarremon brunneinucha
Buarremon virenticeps
1.00/100/100
L. castaneiceps
L. crassirostris
Lysurus
Pezopetes capitalis
Pipilo aberti
Atlapetes pileatus
Pselliophorus tibialis
Melospiza melodia
Ammodramus maritimus
Junco hyemalis
Zonotrichia leucophrys
0.01 substitutions/site

FIGURE 3


ACO1
100
100
Lysurus castaneiceps
Lysurus crassirostris
B. virenticeps
B. b. alleni
99
99
B. b. frontalis
B. b. apertus
60
66
B. b. brunneinucha
B. t. borelli
B. t. assimilis
B. t costaricensis
73
75
B. t. poliophrys
86
88
94
91
B. t. tacarcunae
99
99
B. t. phygas
B. t basilicus
88
Arremon flavirostris
89
91
Arremon taciturnus
Arremon aurantiirostris
97
98
Atlapetes pileatus
Pselliophorus tibialis
96
Pipilo aberti
Junco hyemalis
Melospiza melodia
0.005 substitutions/site

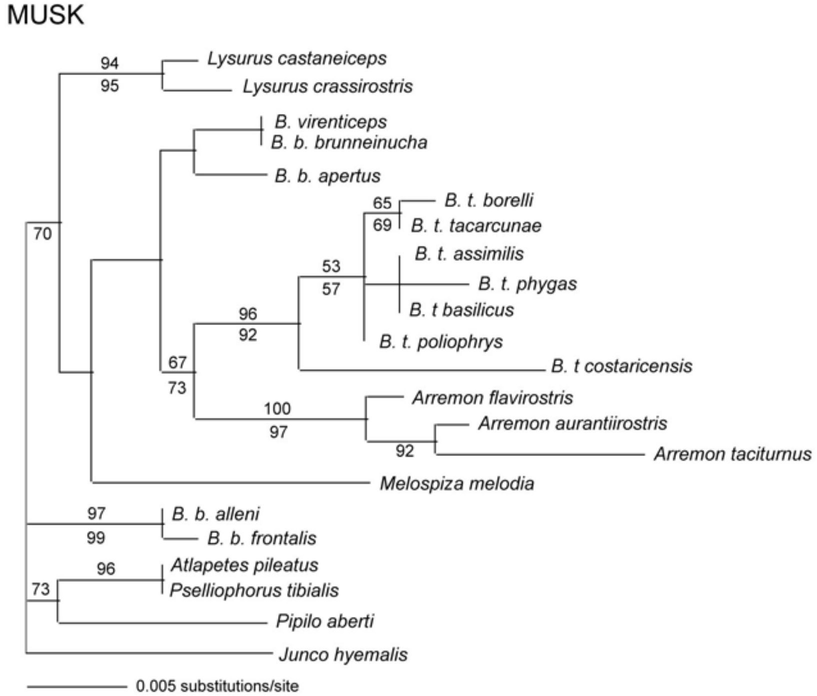

MUSK
94
95
Lysurus castaneiceps
Lysurus crassirostris
B. virenticeps
B. b. brunneinucha
B. b. apertus
65
69
B. t. borelli
B. t. tacarcunae
70
B. t. assimilis
53
57
B. t. phygas
B. t basilicus
96
92
B. t. poliophrys
67
73
B. t costaricensis
Arremon flavirostris
100
97
Arremon aurantiirostris
92
Arremon taciturnus
Melospiza melodia
97
99
B. b. alleni
B. b. frontalis
96
Atlapetes pileatus
73
Pselliophorus tibialis
Pipilo aberti
Junco hyemalis
0.005 substitutions/site

FIGURE 4

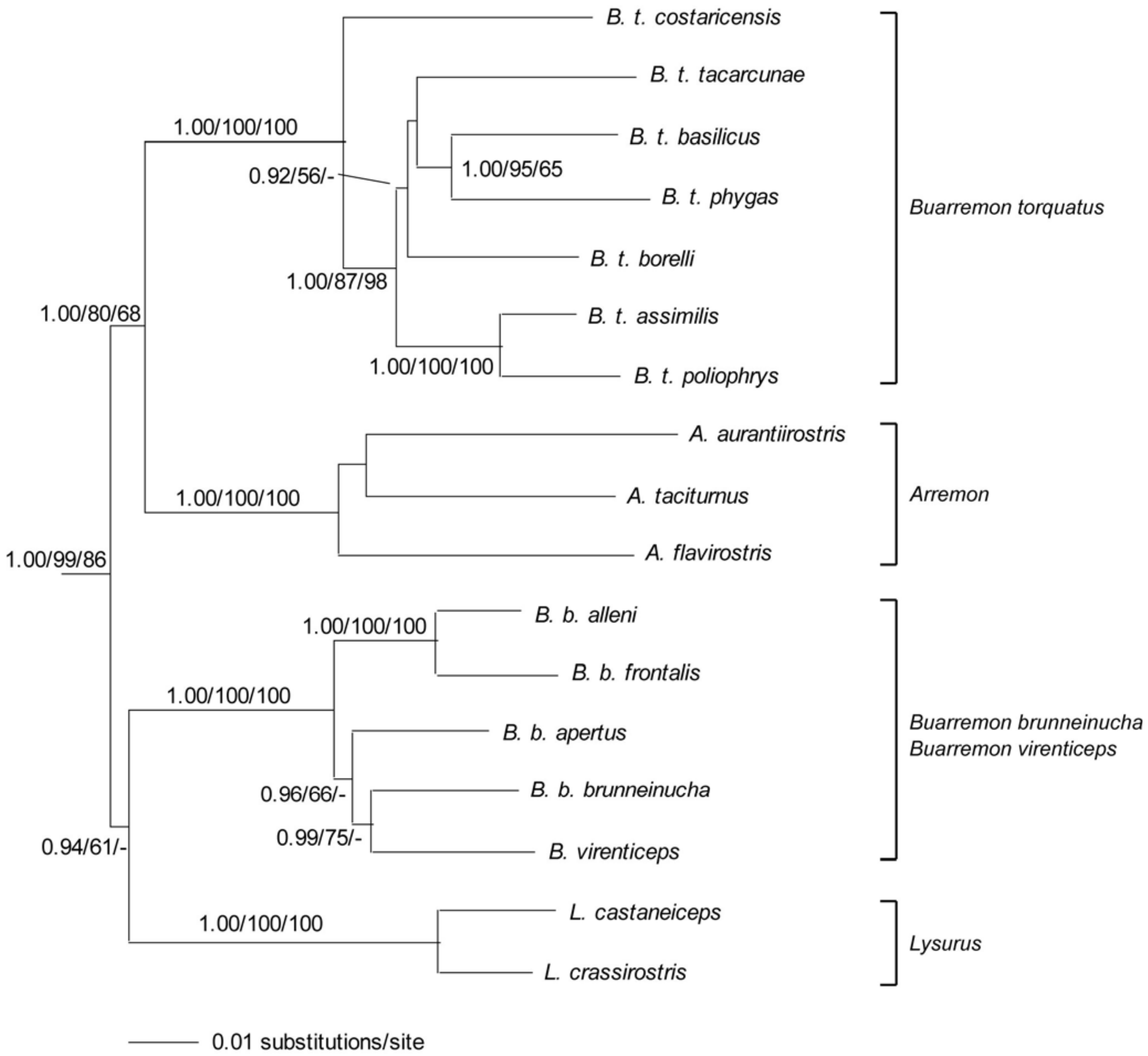

B. t. costaricensis
B. t. tacarcunae
B. t. basilicus
B. t. phygas
B. t. borelli
B. t. assimilis
B. t. poliophrys
Buarremon torquatus
A. aurantiirostris
A. taciturnus
A. flavirostris
Arremon
B. b. alleni
B. b. frontalis
B. b. apertus
B. b. brunneinucha
B. virenticeps
Buarremon brunneinucha
Buarremon virenticeps
L. castaneiceps
L. crassirostris
Lysurus
1.00/100/100
0.92/56/-
1.00/95/65
1.00/87/98
1.00/80/68
1.00/100/100
1.00/100/100
1.00/99/86
1.00/100/100
1.00/100/100
0.96/66/-
0.99/75/-
0.94/61/-
1.00/100/100
0.01 substitutions/site

FIGURE 5

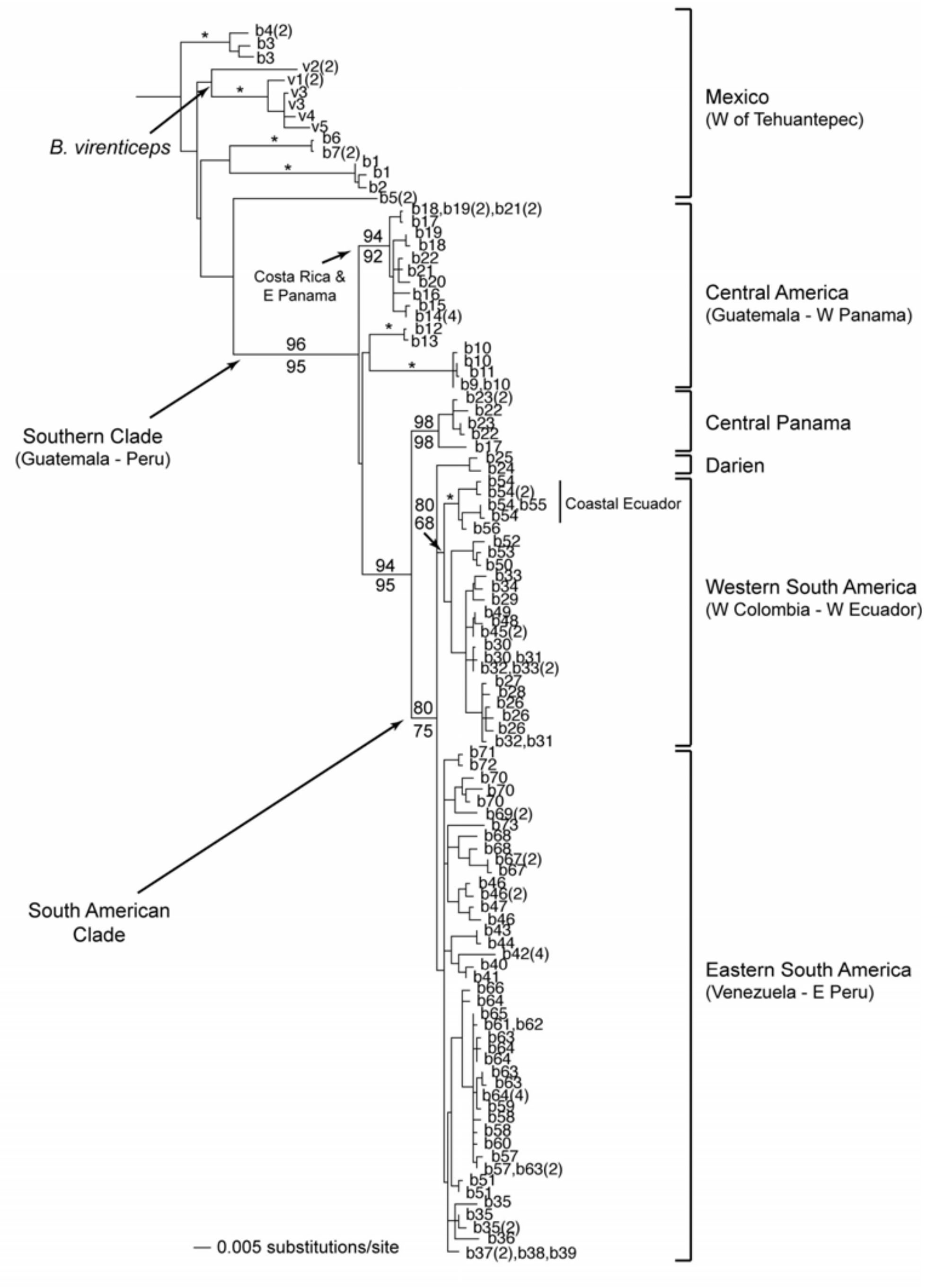

*
b4(2)
b3
b3
v2(2)
v1(2)
*
v3
v3
v4
v5
B. virenticeps
*
b6
b7(2)
*
b1
b1
b2
b5(2)
b18,b19(2),b21(2)
b17
94
92
b19
b18
Costa Rica & E Panama
b22
b21
b20
b16
b15
b14(4)
*
b12
b13
96
95
*
b10
b10
b11
b9,b10
b23(2)
b22
98
98
b23
b22
b17
Southern Clade
(Guatemala - Peru)
b25
b24
*
b54
b54(2)
b54,b55
b54
b56
Coastal Ecuador
80
68
b52
b53
b50
94
95
b33
b34
b29
b49
b48
b45(2)
b30
b30,b31
b32,b33(2)
b27
b28
b26
b26
b26
b32,b31
80
75
South American Clade
b71
b72
b70
b70
b70
b69(2)
b73
b68
b68
b67(2)
b67
b46
b46(2)
b47
b46
b43
b44
b42(4)
b40
b41
b66
b64
b65
b61,b62
b63
b64
b64
b63
b63
b64(4)
b59
b58
b58
b60
b57
b57,b63(2)
b51
b51
b35
b35
b35(2)
b36
b37(2),b38,b39
0.005 substitutions/site
Mexico
(W of Tehuantepec)
Central America
(Guatemala - W Panama)
Central Panama
Darien
Western South America
(W Colombia - W Ecuador)
Eastern South America
(Venezuela - E Peru)

FIGURE 6

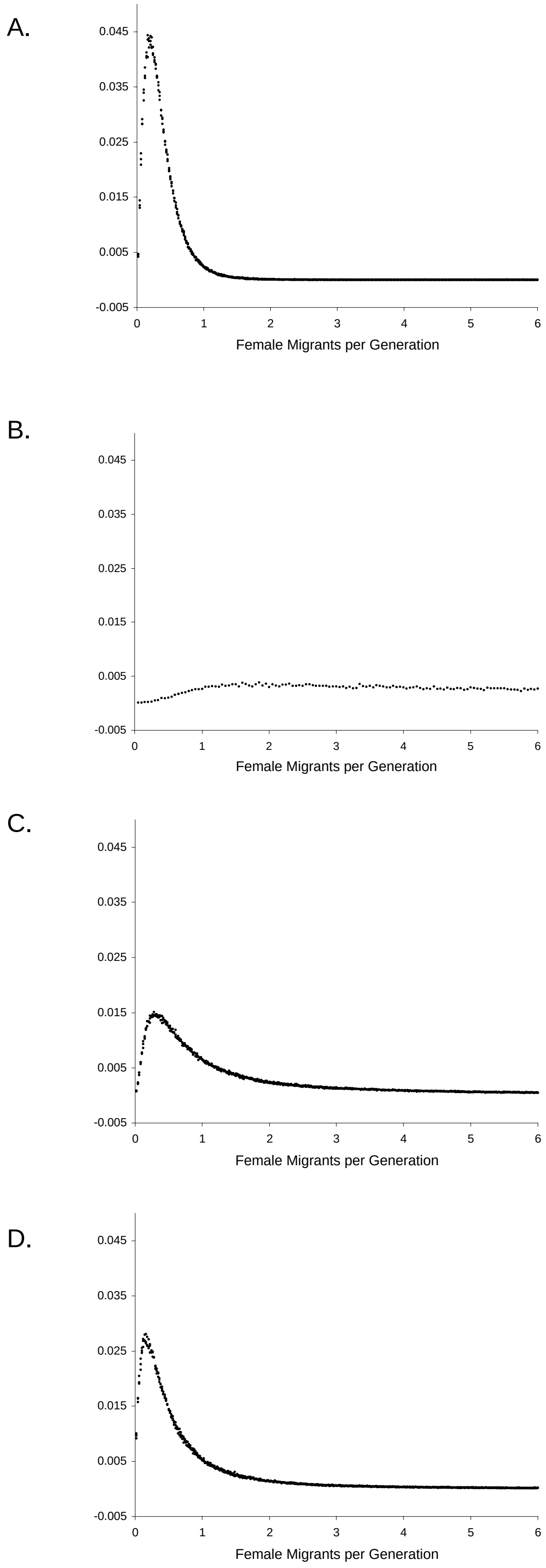
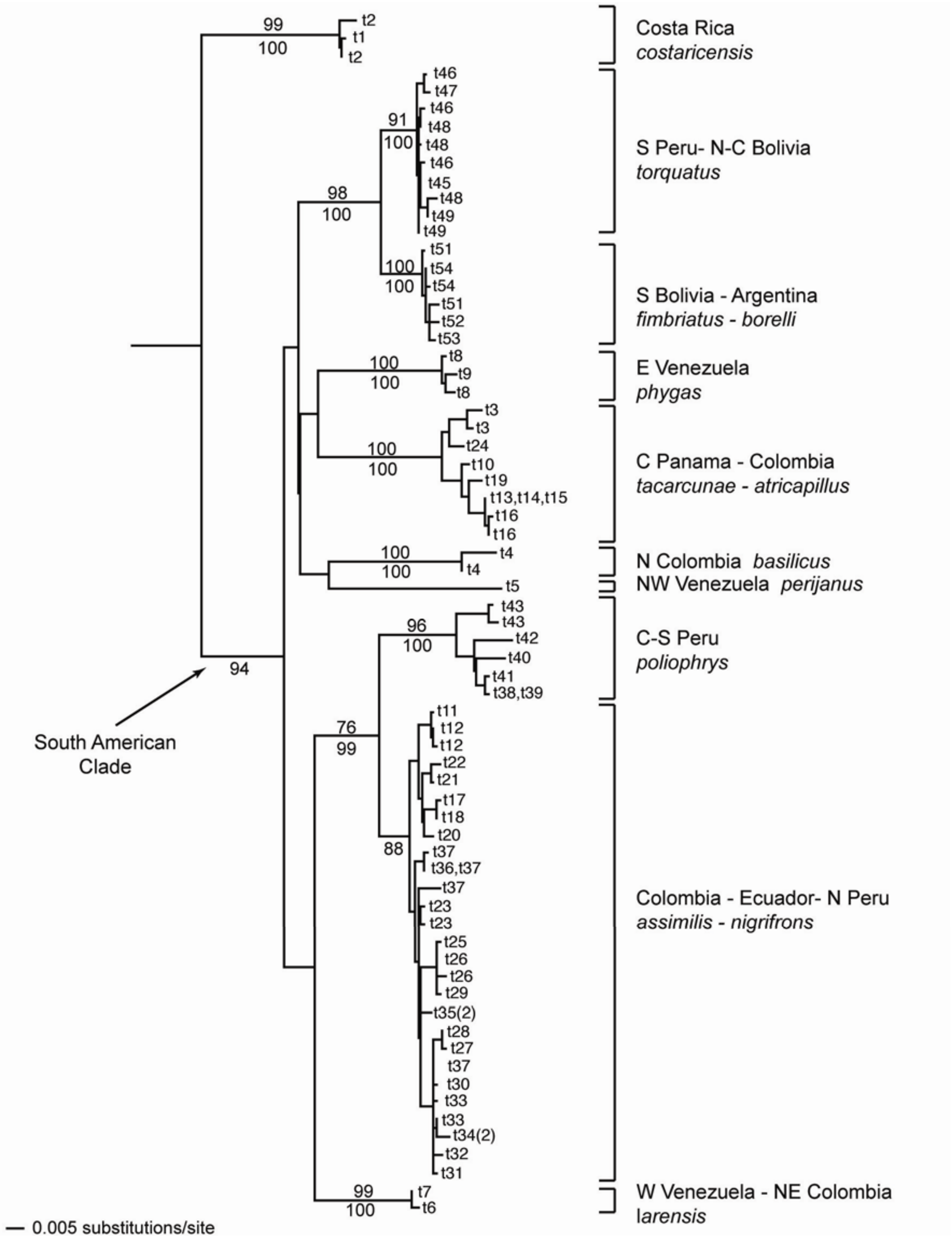

A.
B.
C.
D.
0.045
0.035
0.025
0.015
0.005
-0.005
0
1
2
3
4
5
6
Female Migrants per Generation

FIGURE 7


99
100
t2
t1
t2
Costa Rica
costaricensis
t46
t47
t46
t48
t48
t46
t45
t48
t49
t49
91
100
98
100
S Peru- N-C Bolivia
torquatus
t51
t54
t54
t51
t52
t53
100
100
S Bolivia - Argentina
fimbriatus - borelli
100
100
t8
t9
t8
E Venezuela
phygas
t3
t3
t24
t10
t19
t13,t14,t15
t16
t16
100
100
C Panama - Colombia
tacarcunae - atricapillus
100
100
t4
t4
t5
N Colombia *basilicus*
NW Venezuela *perijanus*
t43
t43
t42
t40
t41
t38,t39
96
100
C-S Peru
poliophrys
94
South American Clade
76
99
88
t11
t12
t12
t22
t21
t17
t18
t20
t37
t36,t37
t37
t23
t23
t25
t26
t26
t29
t35(2)
t28
t27
t37
t30
t33
t33
t34(2)
t32
t31
Colombia - Ecuador- N Peru
assimilis - nigrifrons
99
100
t7
t6
W Venezuela - NE Colombia
larensis
0.005 substitutions/site

Appendix. Information on localities and museum catalogue numbers for samples of *Buarremon* brush-finches included in phylogenetic and phylogeographic analyses. The ID field indicates localities as shown in Figures 1, 5, and 7. Sequences of the ND2 gene were obtained for all samples**;** samples with an asterisk after the ID were included in analyses of ND2, cyt b, ATPase 6 and ATPase 8; those with two asterisks were included in analyses of the four mitochondrial genes and the ACO1 and MUSK nuclear introns.

Id	**Taxon**	**Country**	**Locality**	**Catalogue No. ***	**Lat.**	**Lon.**
	Buarremon brunneinucha					
b1	*Buarremon brunneinucha brunneinucha*	Mexico	Hidalgo, 5 km E Tlanchinol	FMNH 394029	21.013	-98.646
b1	*Buarremon brunneinucha brunneinucha*	Mexico	Hidalgo, 5 km E Tlanchinol	FMNH 394035	21.013	-98.646
b2	*Buarremon brunneinucha brunneinucha*	Mexico	Puebla, 2 km W Teziutlan	LSUMZ B44	19.821	-97.379
b3	*Buarremon brunneinucha suttoni*	Mexico	Guerrero, El Iris, Sierra de Atoyac	FMNH 393757	17.504	-100.212
b3	*Buarremon brunneinucha suttoni*	Mexico	Guerrero, El Iris, Sierra de Atoyac	FMNH 394152	17.504	-100.212
b4	*Buarremon brunneinucha suttoni*	Mexico	Guerrero, Carrizal de Bravo, Sierra Madre del Sur	MBM MM 907	17.613	-99.871
b4	*Buarremon brunneinucha suttoni*	Mexico	Guerrero, Carrizal de Bravo, Sierra Madre del Sur	MBM GMS 905	17.613	-99.871
b5	*Buarremon brunneinucha brunneinucha*	Mexico	Oaxaca, Cerro Zempoaltéptl, Totontepec	FMNH 393766	17.133	-95.983
b5**	*Buarremon brunneinucha brunneinucha*	Mexico	Oaxaca, Cerro Zempoaltéptl, Totontepec	FMNH 393770	17.133	-95.983
b6	*Buarremon brunneinucha apertus*	Mexico	Veracruz, Volcan San Martin, 21 km N San Andres Tuxtla	MBM 4989	18.560	-95.220
b7**	*Buarremon brunneinucha apertus*	Mexico	Veracruz, [Catemaco] El Bastonal, 3 km S, 3 km E, Sierra de Santa Martha	FMNH 393763	18.371	-94.921
b7	*Buarremon brunneinucha apertus*	Mexico	Veracruz, [Catemaco] El Bastonal, 3 km S, 3 km E, Sierra de Santa Martha	FMNH 393870	18.371	-94.921
b8	*Buarremon brunneinucha macrourus*	Mexico	Chiapas, Las Margaritas, approx. 33 mi NE; Finca Patichuiz	WFVZ 1190	16.739	-91.737
b9	*Buarremon brunneinucha macrourus*	Guatemala	Quetzaltenango, Xela, El Baul	MBM DHB 4405	14.821	-91.521
b10	*Buarremon brunneinucha macrourus*	Guatemala	Quetzaltenango, Santa Maria de Jesus 5km SSW, Fca de Sta. Maria	MBM DHB 4429	14.713	-91.563
b10	*Buarremon brunneinucha macrourus*	Guatemala	Quetzaltenango, Santa Maria de Jesus 5km SSW, Fca de Sta. Maria	MBM DHB 4434	14.713	-91.563
b10	*Buarremon brunneinucha macrourus*	Guatemala	Quetzaltenango, Santa Maria de Jesus 5km SSW, Fca de Sta. Maria	MBM DHB 4440	14.713	-91.563
b11	*Buarremon brunneinucha macrourus*	Guatemala	Quetzaltenango, Santa Maria de Jesus 2km E	MBM GAV 2372	14.713	-91.538
b12	*Buarremon brunneinucha alleni*	El Salvador	Chalatenango, Cerro El Pital	KU 5072	14.313	-89.113
b13	*Buarremon brunneinucha alleni*	El Salvador	San Miguel	KU 4903	13.421	-88.279
b14	*Buarremon brunneinucha alleni*	Nicaragua	Nicaragua, Chocoyero, Volcan Mombacho, 48 km SE Managua	MBM DAB 960	11.829	-85.963
b14	*Buarremon brunneinucha alleni*	Nicaragua	Nicaragua, Chocoyero, Volcan Mombacho, 48 km SE Managua	MBM DAB 1751	11.829	-85.963
b14**	*Buarremon brunneinucha alleni*	Nicaragua	Nicaragua, Chocoyero, Volcan Mombacho, 48 km SE Managua	MBM DAB 1706	11.829	-85.963
b14	*Buarremon brunneinucha alleni*	Nicaragua	Nicaragua, Chocoyero, Volcan Mombacho, 48 km SE Managua	MBM DAB 1834	11.829	-85.963
b15	*Buarremon brunneinucha elsae*	Costa Rica	Heredia, Finca La Fortuna, 4 km SE Virgen del Socorro	LSUMZ B16053	10.246	-84.129
b16	*Buarremon brunneinucha elsae*	Costa Rica	Cartago, near Fca. Pizote, Tres Rios, 4.5 km NE	FMNH 393081	9.929	-83.963
b17	*Buarremon brunneinucha elsae*	Panama	Chiriqui, Boquete, Paso de Respingo on Cerro Punta-Boquete trail	LSUMZ B28316	8.838	-82.521

Id	Taxon	Country	Locality	Catalogue No. *	Lat.	Lon.
b17	*Buarremon brunneinucha elsae*	Panama	Chiriqui, Boquete, Paso de Respingo on Cerro Punta-Boquete trail	LSUMZ B28322	8.838	-82.521
b18	*Buarremon brunneinucha elsae*	Panama	Chiriqui, Gualaca-Chiriqui Grande Road, at continental divide	USNM B05407	8.763	-82.271
b18	*Buarremon brunneinucha elsae*	Panama	Chiriqui, Gualaca-Chiriqui Grande Road, at continental divide	USNM B05408	8.763	-82.271
b19	*Buarremon brunneinucha elsae*	Panama	Chiriqui, Los Planes, 10 km N Fortuna Field Station	USNM B05300	8.736	-82.273
b19	*Buarremon brunneinucha elsae*	Panama	Chiriqui, Los Planes, 10 km N Fortuna Field Station	USNM B05329	8.736	-82.273
b19	*Buarremon brunneinucha elsae*	Panama	Chiriqui, Los Planes, 10 km N Fortuna Field Station	USNM B05474	8.736	-82.273
b20	*Buarremon brunneinucha elsae*	Panama	Chiriqui, Gualaca, Cordillera Central, 4.3 km by road S Lago Fortuna dam	LSUMZ B26947	8.729	-82.246
b21	*Buarremon brunneinucha elsae*	Panama	Chiriqui, 12.6-23.3 road km N Los Planes, Gualaca-Chiriqui Grande Road	USNM B01436	8.688	-82.229
b21	*Buarremon brunneinucha elsae*	Panama	Chiriqui, 12.6-23.3 road km N Los Planes, Gualaca-Chiriqui Grande Road	USNM B01492	8.688	-82.229
b21	*Buarremon brunneinucha elsae*	Panama	Chiriqui, 12.6-23.3 road km N Los Planes, Gualaca-Chiriqui Grande Road	USNM B01542	8.688	-82.229
b22	*Buarremon brunneinucha elsae*	Panama	Veraguas, Santa Fe 3km WSW hacia Alto de Piedra Road	MBM JMD 126	8.513	-81.121
b22	*Buarremon brunneinucha elsae*	Panama	Veraguas, Santa Fe 3km WSW hacia Alto de Piedra Road	MBM JMD 145	8.513	-81.121
b22	*Buarremon brunneinucha elsae*	Panama	Veraguas, Santa Fe 3km WSW hacia Alto de Piedra Road	MBM JMD 146	8.513	-81.121
b23	*Buarremon brunneinucha elsae*	Panama	Cocle, El Valle, foothills NE of town	MBM JK 04209	8.629	-80.129
b23	*Buarremon brunneinucha elsae*	Panama	Cocle, El Valle, foothills NE of town	MBM JK 04210	8.629	-80.129
b23	*Buarremon brunneinucha elsae*	Panama	Cocle, El Valle, foothills NE of town	MBM JK 04211	8.629	-80.129
b24	*Buarremon brunneinucha frontalis*	Panama	Darien, ca. 9km NW Cana on slopes of Cerro Pirre	LSUMZ B1371	7.788	-77.721
b25	*Buarremon brunneinucha frontalis*	Panama	Darien, ca. 6 km NW Cana	LSUMZ B2102	7.771	-77.721
b26	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Páramo de Frontino	ZMUC 134985	6.413	-76.079
b26	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Páramo de Frontino	ZMUC 134994	6.413	-76.079
b26	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Páramo de Frontino	ZMUC 134963	6.429	-76.079
b27	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Amalfi, Vda. Las Animas, Bosque Las Animas	AMC 160	6.929	-75.038
b28	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Amalfi, Vda. Salazar, Finca Bodega Vieja	IAvH BT-1165	6.902	-75.088
b29	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Amalfi, Vda. Cajamarca, Fca. Canales	IAvH BT-2137	6.818	-75.104
b30	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Jardin, Vda. Dojurgo, Finca Las Mercedes	ICN 34716	5.504	-75.871
b30	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Jardin, Vda. Dojurgo, Finca Las Mercedes	ICN 34717	5.504	-75.871
b31	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Jardin, La Mesenia	ZMUC 134844	5.496	-75.888
b31	*Buarremon brunneinucha frontalis*	Colombia	Antioquia, Jardin, La Mesenia	ZMUC 134852	5.496	-75.888
b32	*Buarremon brunneinucha frontalis*	Colombia	Caldas, Aranzazu, Vda. El Laurel, Hda. Termopilas	IAvH 11906	5.229	-75.496
b32	*Buarremon brunneinucha frontalis*	Colombia	Caldas, Aranzazu, Vda. El Laurel, Hda. Termopilas	IAvH 11925	5.229	-75.496
b33	*Buarremon brunneinucha frontalis*	Colombia	Risaralda, Pereira, Vda. La Suiza, SFF Otun Quimbaya	IAvH 11691	4.721	-75.579
b33	*Buarremon brunneinucha frontalis*	Colombia	Risaralda, Pereira, Vda. La Suiza, SFF Otun Quimbaya	IAvH 11692	4.721	-75.579
b33	*Buarremon brunneinucha frontalis*	Colombia	Risaralda, Pereira, Vda. La Suiza, SFF Otun Quimbaya	CDC 056	4.721	-75.579
b34	*Buarremon brunneinucha frontalis*	Colombia	Risaralda, Pereira, Parque Ucumari, La Pastora	IAvH 11693	4.701	-75.504
b35	*Buarremon brunneinucha frontalis*	Colombia	Cundinamarca, Mpio. Bojaca, Finca Macanal	IAvH 11679	4.663	-74.346
b35	*Buarremon brunneinucha frontalis*	Colombia	Cundinamarca, Mpio. Bojaca, Finca Macanal	IAvH 11686	4.654	-74.329

Id	Taxon	Country	Locality	Catalogue No. *	Lat.	Lon.
b35	*Buarremon brunneinucha frontalis*	Colombia	Cundinamarca, Mpio. Bojaca, Finca Macanal	CDC 010	4.654	-74.329
b35	*Buarremon brunneinucha frontalis*	Colombia	Cundinamarca, Mpio. Bojaca, Finca Macanal	CDC 011	4.654	-74.329
b36	*Buarremon brunneinucha frontalis*	Colombia	Cundinamarca, Parque Nacional Chingaza, Rio Blanco	IAvH 12676	4.696	-73.854
b37	*Buarremon brunneinucha frontalis*	Colombia	Boyacá, Mpio. Villa de Leyva, S.F.F. Iguaque	IAvH 11661	5.685	-73.470
b37	*Buarremon brunneinucha frontalis*	Colombia	Boyacá, Mpio. Villa de Leyva, S.F.F. Iguaque	IAvH 11667	5.696	-73.471
b38	*Buarremon brunneinucha frontalis*	Colombia	Boyaca, alrededores de SFF Iguaque	IAvH 12562	5.729	-73.054
b39	*Buarremon brunneinucha frontalis*	Colombia	Santander, Encino, Reserva Cachalú	IAvH 11690	6.071	-73.129
b40	*Buarremon brunneinucha frontalis*	Colombia	Norte de Santander, Mpio de Cucutilla, Vda. Carrizal, Sector Sisavita	IAvH 12104	7.446	-72.838
b41	*Buarremon brunneinucha frontalis*	Colombia	Norte de Santander, PNN Tamá. Sector Orocué	IAvH 10650	7.429	-72.446
b42	*Buarremon brunneinucha allinornatus*	Venezuela	Falcón, Sierra de San Luis, Cerro Galicia	COP IC 963	11.180	-69.704
b42*	*Buarremon brunneinucha allinornatus*	Venezuela	Falcón, Sierra de San Luis, Cerro Galicia	COP IC 965	11.180	-69.704
b42	*Buarremon brunneinucha allinornatus*	Venezuela	Falcón, Sierra de San Luis, Cerro Galicia	COP IC 981	11.180	-69.704
b42	*Buarremon brunneinucha allinornatus*	Venezuela	Falcón, Sierra de San Luis, Cerro Galicia	COP IC 991	11.180	-69.704
b43	*Buarremon brunneinucha frontalis*	Venezuela	Aragua, Paso Portachuelo, Rancho Grande, PN Henry Pitier	COP IC 742	10.346	-67.671
b44**	*Buarremon brunneinucha frontalis*	Venezuela	Aragua, Km 40 on El Junquito/Col. Tovar Road	AMNH GFB3161	10.421	-67.213
b45	*Buarremon brunneinucha frontalis*	Colombia	Valle del Cauca, La Cumbre, Chicoral	IAvH 12455	3.568	-76.588
b45	*Buarremon brunneinucha frontalis*	Colombia	Valle del Cauca, La Cumbre, Chicoral	IAvH 12461	3.568	-76.588
b46	*Buarremon brunneinucha frontalis*	Colombia	Huila, sendero entre Centro de Visitantes Andaqui y Cueva de los Guacharos	IAvH 11738	1.629	-76.121
b46	*Buarremon brunneinucha frontalis*	Colombia	Huila, sendero entre Centro de Visitantes Andaqui y Cueva de los Guacharos	IAvH 11769	1.629	-76.121
b46	*Buarremon brunneinucha frontalis*	Colombia	Huila, sendero entre Centro de Visitantes Andaqui y Cueva de los Guacharos	IAvH 11806	1.629	-76.121
b46	*Buarremon brunneinucha frontalis*	Colombia	Huila, Cueva de los Guacharos, Puente Nuevo , cuenca del rio Suaza	IAvH 11790	1.629	-76.096
b47	*Buarremon brunneinucha frontalis*	Colombia	Caquetá. Mpio. San José de Fragua. Vda. La Esmeralda, Alto río Yurayaco	IAvH 11406	1.346	-76.113
b48	*Buarremon brunneinucha frontalis*	Colombia	Nariño, Altaquer, Rio Ñambí	JCDC 01	1.300	-78.083
b49	*Buarremon brunneinucha frontalis*	Ecuador	Esmeraldas, El Placer	LSUMZ B11931	0.879	-78.596
b50	*Buarremon brunneinucha frontalis*	Ecuador	Esmeraldas, ca. 2 km E Alto Tambo	LSUMZ B30013	0.883	-78.555
b51	*Buarremon brunneinucha frontalis*	Ecuador	Napo, Rio Maspa Chico	ZMUC 120268	0.371	-78.029
b51	*Buarremon brunneinucha frontalis*	Ecuador	Napo, Rio Maspa Chico	ZMUC 120271	0.371	-78.029
b52	*Buarremon brunneinucha frontalis*	Ecuador	Pichincha, Maquipucuna	ZMUC 121333	0.129	-78.596
b53	*Buarremon brunneinucha frontalis*	Ecuador	Bellavista Cloud Forest Reserve (c. 60 km NW Quito)	DB 309	-0.011	-78.705
b54	*Buarremon brunneinucha inornatus*	Ecuador	Manabi, Cerro San Sebastian, PN Machalilla	ANSP 2945	-1.584	-80.689
b54	*Buarremon brunneinucha inornatus*	Ecuador	Manabi, Cerro San Sebastian, PN Machalilla	ANSP 2953	-1.584	-80.689
b54*	*Buarremon brunneinucha inornatus*	Ecuador	Manabi, Cerro San Sebastian, PN Machalilla	ANSP 3112	-1.584	-80.689
b54	*Buarremon brunneinucha inornatus*	Ecuador	Manabi, Cerro San Sebastian, PN Machalilla	ANSP 3149	-1.584	-80.689
b54	*Buarremon brunneinucha inornatus*	Ecuador	Manabi, Cerro San Sebastian, PN Machalilla	ANSP 3384	-1.584	-80.689
b54	*Buarremon brunneinucha inornatus*	Ecuador	Manabi, Cerro San Sebastian, PN Machalilla	DB 289	-1.584	-80.689
b54	*Buarremon brunneinucha inornatus*	Ecuador	Manabi, Cerro San Sebastian, PN Machalilla	DB 450	-1.584	-80.689

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b55	*Buarremon brunneinucha inornatus*	Ecuador	Guayas, Loma Alta, Cerro La Torre, 35 km S PN Machalilla	DB 525	-1.829	-80.563
b56	*Buarremon brunneinucha inornatus*	Ecuador	Azuay, Manta Real, ca. 6 km S Zhucay (near Naranjal)	ANSP 3529	-2.554	-79.346
b57	*Buarremon brunneinucha frontalis*	Ecuador	Morona-Santiago, Cordillera de Cutucu, trail Logrono to Yaupi-Yapitya	LSUMZ B6124	-2.629	-78.096
b57	*Buarremon brunneinucha frontalis*	Ecuador	Morona-Santiago, Cordillera de Cutucu, trail Logrono to Yaupi-Yapitya	LSUMZ B6126	-2.629	-78.096
b58	*Buarremon brunneinucha frontalis*	Ecuador	Zamora-Chinchipe, below Chinapinza	ZMUC 116150	-4.001	-78.472
b58	*Buarremon brunneinucha frontalis*	Ecuador	Zamora-Chinchipe, below Chinapinza	ZMUC 116151	-4.001	-78.472
b59	*Buarremon brunneinucha frontalis*	Ecuador	Zamora-Chinchipe, S Romerillos	ZMUC 119146	-4.238	-79.013
b60	*Buarremon brunneinucha frontalis*	Ecuador	Zamora-Chinchipe, Cerro Toledo	ZMUC 122261	-4.384	-79.122
b61	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Machete on Sapalache-Carmen trail	LSUMZ B224	-5.050	-79.350
b62	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, E slope Cerro Chinguela, 8 km NE Sapalache	LSUMZ B316	-5.113	-79.371
b63	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Nuevo Peru, 16 km NE junction Rios Tabacomas and Chinchipe	LSUMZ B33491	-5.285	-78.685
b63	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Nuevo Peru, 16 km NE junction Rios Tabacomas and Chinchipe	LSUMZ B33497	-5.285	-78.685
b63	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Nuevo Peru, 16 km NE junction Rios Tabacomas and Chinchipe	LSUMZ B33667	-5.285	-78.685
b63	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Nuevo Peru, 16 km NE junction Rios Tabacomas and Chinchipe	LSUMZ B33725	-5.285	-78.685
b63	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Nuevo Peru, 16 km NE junction Rios Tabacomas and Chinchipe	LSUMZ B33400	-5.285	-78.685
b64	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B31704	-5.688	-79.272
b64	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B31855	-5.688	-79.272
b64	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B31944	-5.688	-79.272
b64	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B31987	-5.688	-79.272
b64	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B32207	-5.688	-79.272
b64	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B32349	-5.688	-79.272
b64	*Buarremon brunneinucha frontalis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B32532	-5.688	-79.272
b65	*Buarremon brunneinucha frontalis*	Peru	San Martin, 15 km by trail NE Jirillo on trail to Balsapuerto	LSUMZ B5541	-6.071	-76.721
b66	*Buarremon brunneinucha frontalis*	Peru	San Martin, 20 km by road NE Tarapoto on road to Yurimaguas	LSUMZ B5462	-6.396	-76.213
b67	*Buarremon brunneinucha frontalis*	Peru	Loreto, 77 km WNW Contamana	LSUMZ B27755	-7.054	-75.654
b67	*Buarremon brunneinucha frontalis*	Peru	Loreto, 77 km WNW Contamana	LSUMZ B27816	-7.054	-75.654
b67	*Buarremon brunneinucha frontalis*	Peru	Loreto, 77 km WNW Contamana	LSUMZ B27856	-7.054	-75.654
b68	*Buarremon brunneinucha frontalis*	Peru	Loreto, ca. 86 km SE Juanjui on E bank upper Rio Pauya	LSUMZ B39863	-7.538	-75.904
b68	*Buarremon brunneinucha frontalis*	Peru	Loreto, ca. 86 km SE Juanjui on E bank upper Rio Pauya	LSUMZ B40009	-7.538	-75.904
b69	*Buarremon brunneinucha frontalis*	Peru	Pasco, Playa Pampa, ca. 8 km NW Cushi on trail to Chaglla	LSUMZ B7990	-9.829	-75.721
b69	*Buarremon brunneinucha frontalis*	Peru	Pasco, Playa Pampa, ca. 8 km NW Cushi on trail to Chaglla	LSUMZ B8095	-9.829	-75.721
b70	*Buarremon brunneinucha frontalis*	Peru	Pasco, Santa Cruz, ca. 9 km SSE Oxapampa	LSUMZ B1626	-10.621	-75.363
b70	*Buarremon brunneinucha frontalis*	Peru	Pasco, Santa Cruz, ca. 9 km SSE Oxapampa	LSUMZ B1645	-10.621	-75.363
b70	*Buarremon brunneinucha frontalis*	Peru	Pasco, Santa Cruz, ca. 9 km SSE Oxapampa	LSUMZ B1688	-10.621	-75.363
b71	*Buarremon brunneinucha frontalis*	Peru	Cusco, Paucartambo, San Pedro	FMNH 430059	-13.056	-71.548
b72	*Buarremon brunneinucha frontalis*	Peru	Cusco, Paucartambo, Suecia, km 138.5 on Cusco-Shintuya Highway	FMNH 398360	-13.129	-71.504

Id	Taxon	Country	Locality	Catalogue No. *	Lat.	Lon.
b73	*Buarremon brunneinucha frontalis*	Peru	Cusco, Machu Picchu, Intipata ruins	MUSM 24327	-13.188	-72.546
	Buarremon virenticeps					
v1	*Buarremon virenticeps*	Mexico	Jalisco, Puerto Los Mazos, Sierra de Manantlán	FMNH 343338	19.538	-103.479
v1	*Buarremon virenticeps*	Mexico	Jalisco, Puerto Los Mazos, Sierra de Manantlán	FMNH 343351	19.538	-103.479
v2	*Buarremon virenticeps*	Mexico	Michoacan, 3 km N Zirimondiro, Pico de Tancítaro	FMNH 394040	19.371	-102.334
v2	*Buarremon virenticeps*	Mexico	Michoacan, 3 km N Zirimondiro, Pico de Tancítaro	FMNH 394041	19.371	-102.334
v2	*Buarremon virenticeps*	Mexico	Michoacan, 3 km N Zirimondiro, Pico de Tancítaro	FMNH 394043	19.371	-102.334
v3	*Buarremon virenticeps*	Mexico	Ocuilon-Cuernavaca Hwy, Km 14	FMNH 394044	18.938	-99.354
v3	*Buarremon virenticeps*	Mexico	Ocuilon-Cuernavaca Hwy, Km 14	FMNH 395825	18.938	-99.354
v4**	*Buarremon virenticeps*	Mexico	Mexico, 2 km E San Rafael, hacia Cañada de los Diamantes, Iztaccihuatl	AMNH PEP 1427	19.209	-98.758
v5*	*Buarremon virenticeps*	Mexico	Mexico, undetermined locality	BMUM MT410	-	-
	Buarremon torquatus					
t1	*Buarremon torquatus costaricensis*	Costa Rica	Puntarenas, Potrero Grande, 12 km NE; Finca Los Helechales	WFVZ 26697	9.096	-83.063
t2**	*Buarremon torquatus costaricensis*	Costa Rica	Puntarenas, Coto Brus, Estación Biológica Las Cruces	UCR GB 130	8.786	-82.973
t2*	*Buarremon torquatus costaricensis*	Costa Rica	Puntarenas, Coto Brus, Estación Biológica Las Cruces	UCR GB 131	8.786	-82.973
t3**	*Buarremon torquatus tacarcunae*	Panama	Panama, NW slope Cerro Jefe	LSUMZ B28362	9.254	-79.413
t3*	*Buarremon torquatus tacarcunae*	Panama	Panama, NW slope Cerro Jefe	LSUMZ B28367	9.254	-79.413
t4**	*Buarremon torquatus basilicus*	Colombia	Magdalena, Sierra Nevada de Santa Marta, Estación San Lorenzo	IAvH BT-463	11.104	-74.063
t4	*Buarremon torquatus basilicus*	Colombia	Magdalena, Sierra Nevada de Santa Marta, Estación San Lorenzo	ICN 23517	11.104	-74.063
t5	*Buarremon torquatus perijanus*	Venezuela	Zulia, Sierra del Perijá, Barranquilla Rancheria Julian	COP 58258	10.121	-72.713
t6*	*Buarremon torquatus* cf *larensis*	Colombia	Norte de Santander, Agua de la Virgen	ICN FGS 3906	8.229	-73.254
t7	*Buarremon torquatus larensis*	Venezuela	Lara, 40 km S Cabudare	COP 72251	9.746	-69.429
t8	*Buarremon torquatus phygas*	Venezuela	Sucre, Piedra de Moler, San Antonio, Serrania del Turimiquire	COP JLP 358	10.103	-63.815
t8*	*Buarremon torquatus phygas*	Venezuela	Sucre, Piedra de Moler, San Antonio, Serrania del Turimiquire	COP JLP 363	10.103	-63.815
t9**	*Buarremon torquatus phygas*	Venezuela	Sucre, PN Peninsula de Paria, Subida al Cerro Humo desde Las Melenas	COP JLP 248	10.704	-62.629
t10	*Buarremon torquatus atricapillus*	Colombia	Antioquia, Dabeiba, Río Amparradó, campamento Pantano Ingeominas	ICN 27218	7.017	-76.267
t11	*Buarremon torquatus assimilis*	Colombia	Antioquia, Páramo de Frontino	ZMUC 134956	6.429	-76.079
t11	*Buarremon torquatus assimilis*	Colombia	Antioquia, Páramo de Frontino	ZMUC 134979	6.429	-76.079
t12	*Buarremon torquatus assimilis*	Colombia	Antioquia, Bello, Cgto. San Felix, Cuchilla de Las Baldias, "Las Antenas"	IAvH 11698	6.338	-75.654
t12	*Buarremon torquatus assimilis*	Colombia	Antioquia, Bello, Cgto. San Felix, Cuchilla de Las Baldias, "Las Antenas"	IAvH 11700	6.338	-75.654
t13	*Buarremon torquatus atricapillus*	Colombia	Antioquia, Amalfi, Vda. Salazar, Finca Bodega Vieja	ICN AMC 658	6.929	-75.096
t14	*Buarremon torquatus atricapillus*	Colombia	Antioquia, Amalfi, Vda. Las Animas, Bosque La Escuela	ICN AMC 634	6.929	-75.004

Id	**Taxon**	**Country**	**Locality**	**Catalogue No. ***	**Lat.**	**Lon.**
t15*	*Buarremon torquatus atricapillus*	Colombia	Antioquia, Mpio. Don Matías, Estación Pradera	IAvH 11697	6.529	-75.263
t16	*Buarremon torquatus atricapillus*	Colombia	Santander, Suaita, 3 km ENE San José de Suaita	ICN 33290	6.188	-73.429
t16*	*Buarremon torquatus atricapillus*	Colombia	Santander, Suaita, 3 km ENE San José de Suaita	ICN 33292	6.188	-73.429
t17	*Buarremon torquatus assimilis*	Colombia	Boyacá, Santuario de Fauna y Flora de Iguaque	IAvH 12207	5.696	-73.471
t18	*Buarremon torquatus assimilis*	Colombia	Boyaca, Sutamarchán, Serranía de Merchan	IAvH 12271	5.679	-73.663
t19	*Buarremon torquatus atricapillus*	Colombia	Cundinamarca, La Vega, Finca El Encanto	ICN 16248	5.000	-74.350
t20**	*Buarremon torquatus assimilis*	Colombia	Cundinamarca, Bojacá, Via Bogotá - La Mesa	IAvH 11681	4.663	-74.346
t21	*Buarremon torquatus assimilis*	Colombia	Cundinamarca, Parque Nacional Chingaza, Río Blanco	IAvH 12680	4.696	-73.854
t22	*Buarremon torquatus assimilis*	Colombia	Meta, Parque Nacional Chingaza, San José	IAvH 12632	4.494	-73.693
t23	*Buarremon torquatus assimilis*	Colombia	Risaralda, Parque Regional Ucumarí, Camino Peña Bonita a Peñas Blancas	IAvH 11695	4.718	-75.488
t23	*Buarremon torquatus assimilis*	Colombia	Risaralda, Parque Regional Ucumarí, Camino Peña Bonita a Peñas Blancas	IAvH 11696	4.718	-75.488
t24	*Buarremon torquatus atricapillus*	Colombia	Valle del Cauca, Rio Bravo, Embalse Rio Calima	ICN 28442	3.921	-76.646
t25	*Buarremon torquatus assimilis*	Ecuador	Carchi, W slope, near road Maldonado-Tulcán along Río La Plata	ANSP 631	0.804	-78.054
t26	*Buarremon torquatus assimilis*	Ecuador	Carchi, ca. 3k SE Impueran, Cerro Mongus	ANSP 3955	0.438	-77.854
t26	*Buarremon torquatus assimilis*	Ecuador	Carchi, ca. 3k SE Impueran, Cerro Mongus	ANSP 4001	0.438	-77.854
t27	*Buarremon torquatus assimilis*	Ecuador	Imbabura, Apuela road	ZMUC 116213	0.346	-78.438
t28	*Buarremon torquatus assimilis*	Ecuador	Imbabura, Loma Taminanga	ZMUC 116216	0.271	-78.471
t29	*Buarremon torquatus assimilis*	Ecuador	Napo, Rio Azul	ZMUC 122189	-0.979	-78.271
t30	*Buarremon torquatus nigrifrons*	Ecuador	Loja, Cajanuma	ZMUC 121538	-4.101	-79.172
t31	*Buarremon torquatus nigrifrons*	Ecuador	Loja, 10 km E El Limo	ANSP 5164	-3.988	-80.163
t32	*Buarremon torquatus nigrifrons*	Ecuador	Loja, Celica Mts.	ZMUC 116214	-4.029	-79.879
t33	*Buarremon torquatus nigrifrons*	Ecuador	Loja, Utuana	ZMUC 116219	-4.371	-79.721
t33	*Buarremon torquatus nigrifrons*	Ecuador	Loja, Utuana	ZMUC 116220	-4.371	-79.721
t34	*Buarremon torquatus nigrifrons*	Ecuador	Loja, 1 km SE Carimanga	ZMUC 116217	-4.354	-79.563
t34	*Buarremon torquatus nigrifrons*	Ecuador	Loja, 1 km SE Carimanga	ZMUC 116218	-4.354	-79.563
t35	*Buarremon torquatus nigrifrons*	Peru	Piura, Cruz Blanca, 33 rd km SW Huancabamba	LSUMZ B405	-5.338	-79.546
t35*	*Buarremon torquatus nigrifrons*	Peru	Piura, Cruz Blanca, 33 rd km SW Huancabamba	LSUMZ B427	-5.338	-79.546
t36	*Buarremon torquatus assimilis*	Peru	Cajamarca, El Espino	LSUMZ B31669	-5.688	-79.338
t37*	*Buarremon torquatus assimilis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B31948	-5.688	-79.254
t37	*Buarremon torquatus assimilis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B31970	-5.688	-79.254
t37	*Buarremon torquatus assimilis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B32429	-5.688	-79.254
t37	*Buarremon torquatus assimilis*	Peru	Cajamarca, Quebrada Lanchal, ca. 8 km ESE Sallique	LSUMZ B32460	-5.688	-79.254
t38	*Buarremon torquatus poliophrys*	Peru	San Martin, Puerta del Monte, 30 km NE Los Alisos	LSUMZ B51279	-7.538	-77.479
t39	*Buarremon torquatus poliophrys*	Peru	La Libertad, Masua, E Tayabamba, on trail to Ongon	LSUMZ B51355	-8.221	-77.196
t40	*Buarremon torquatus poliophrys*	Peru	Pasco, Playa Pampa, ca. 8 km NW Cushi on trail to Chaglla	LSUMZ B8129	-9.796	-75.746
t41	*Buarremon torquatus poliophrys*	Peru	Pasco, Millpo, E Tambo de Vacas on Pozuzo-Chaglla Trail	LSUMZ B8240	-10.371	-76.304

Id	Taxon	Country	Locality	Catalogue No. *	Lat.	Lon.
t42*	*Buarremon torquatus poliophrys*	Peru	Pasco, Cumbre de Ollon, ca. 12 km E Oxapampa	LSUMZ B1844	-10.579	-75.296
t43	*Buarremon torquatus poliophrys*	Peru	Cusco, Paucartambo, Pillahuata	FMNH 430060	-13.164	-71.595
t43*	*Buarremon torquatus poliophrys*	Peru	Cusco, Paucartambo, Pillahuata	FMNH 430061	-13.164	-71.595
t44	*Buarremon torquatus torquatus*	Peru	Puno, Abra de Maruncunca, 10 km SW San Juan del Oro	LSUMZ B51275	-14.246	-69.004
t45*	*Buarremon torquatus torquatus*	Bolivia	La Paz, Piara, near Pelechuco	AMNH CBF 38	-14.787	-69.019
t46	*Buarremon torquatus torquatus*	Bolivia	Franz Tamayo, Parque Nacional Apolobamba	AMNH CJV 379	-14.821	-68.952
t46	*Buarremon torquatus torquatus*	Bolivia	Franz Tamayo, Parque Nacional Apolobamba	AMNH CJV 384	-14.821	-68.952
t46	*Buarremon torquatus torquatus*	Bolivia	Franz Tamayo, Parque Nacional Apolobamba	AMNH OMZ 102	-14.821	-68.952
t46	*Buarremon torquatus torquatus*	Bolivia	Franz Tamayo, Parque Nacional Apolobamba	AMNH OMZ 129	-14.821	-68.952
t47*	*Buarremon torquatus torquatus*	Bolivia	La Paz, ca. 1 km S Chuspipata	LSUMZ B1284	-16.296	-67.084
t48	*Buarremon torquatus torquatus*	Bolivia	Cochabamba, Tablas Montes, Tunari	ZMUC 122899	-17.104	-65.888
t48	*Buarremon torquatus torquatus*	Bolivia	Cochabamba, Tablas Montes, Tunari	ZMUC 122904	-17.104	-65.888
t48	*Buarremon torquatus torquatus*	Bolivia	Cochabamba, Tablas Montes, Tunari	ZMUC 122925	-17.104	-65.888
t49	*Buarremon torquatus torquatus*	Bolivia	Cochabamba, Chapare, San Onofre, ca. 43 km W Villa Tunari	LSUMZ B38932	-17.138	-65.785
t49	*Buarremon torquatus torquatus*	Bolivia	Cochabamba, Chapare, San Onofre, ca. 43 km W Villa Tunari	LSUMZ B39032	-17.138	-65.785
t50	*Buarremon torquatus torquatus*	Bolivia	Cochabamba, Villa Tunari	UWBM RIS 114	-17.163	-65.796
t51*	*Buarremon torquatus fimbriatus*	Bolivia	Chuquisaca, 7 km N Sopachuy	ZMUC 120842	-19.438	-64.479
t51*	*Buarremon torquatus fimbriatus*	Bolivia	Chuquisaca, 7 km N Sopachuy	ZMUC 120843	-19.438	-64.479
t52	*Buarremon torquatus borelli*	Argentina	Jujuy, Yuto	WFVZ 37050	-23.638	-64.571
t53**	*Buarremon torquatus borelli*	Argentina	Salta, 30 km N, 5 km E Salta	MBM 5489	-24.554	-65.404
t54	*Buarremon torquatus borelli*	Argentina	Tucumán, Rio Tajamar, a few kilometers from Taruca towards Rio Nio	PH 003 (1992)	-26.574	-64.834
t54*	*Buarremon torquatus borelli*	Argentina	Tucumán, Rio Tajamar, a few kilometers from Taruca towards Rio Nio	PH 004 (1992)	-26.574	-64.834

* Museum acronyms: AMNH (American Museum of Natural History), ANSP (Academy of Natural Sciences of Philadelphia), BMUM (Bell Museum of Natural History, University of Minnesota), COP (Colección Ornitológica Phelps), FMNH (Field Museum of Natural History), IAvH (Instituto Alexander von Humboldt), ICN (Instituto de Ciencias Naturales, Universidad Nacional de Colombia), KU (University of Kansas Natural History Museum), LSUMZ (Louisiana State University Museum of Natural Science), MBM (Marjorie Barrick Musem, University of Nevada-Las Vegas), MUSM (Museo de la Universidad de San Marcos), UCR (Universidad de Costa Rica), USNM (United States National Museum, Smithsonian Institution), UWBM (University of Washington Burke Museum), WFVZ (Western Foundation of Vertebrate Zoology), ZMUC (Zoological Museum, University of Copenhagen)

* Collections of blood or feather samples: AMC (Andrés M. Cuervo), CDC (Carlos Daniel Cadena), DB (Dusti Becker, University of New Mexico), JCDC (Juan Carlos de las Casas), PH (Paul Handford – Steven Lougheed, Queens University)

CHAPTER 2

Testing the Role of Interspecific Competition in the Evolutionary Origin of Elevational Zonation

Introduction

Species' ranges result from the interplay of processes that act across many scales of time, so understanding the current distributions of species depends on the integration of various core concepts of ecological and evolutionary theory (Kirkpatrick and Barton 1997, Pulliam 2000, Gaston 2003, Holt 2003, Holt and Keitt 2005). Nevertheless, ecological and historical approaches to studying geographic ranges have yet to be unified (Wiens and Donoghue 2004). The ecological biogeographic perspective (e.g., MacArthur 1972) emphasizes the role of environmental conditions, the distribution and abundance of resources, and species interactions as determinants of geographic ranges. In contrast, historical biogeography (e.g., Crisci et al. 2003) focuses on the role of events that have taken place in Earth history and their impact on processes that affect distributions, such as vicariance, dispersal, and extinction. Although these two approaches are valid in their own right, both are limited in scope because the dichotomy between "ecology" and "history" is artificial. Ecological processes observable in contemporary time influence species' ranges over evolutionary time scales (Jackson and Overpeck 2000, Holt 2003), and current ecology is contingent upon the history of the region and organisms involved (Webb et al. 2002; Ackerly 2003; Ricklefs 2004, 2005). Thus, a critical challenge for ecological and historical biogeographers alike is integrating processes that affect geographic ranges across a broad continuum of timescales (Donoghue and Moore 2003, Jackson 2004, Fjeldså and Rahbek 2006).

Parapatric distributions, in which pairs of taxa have separate but abutting ranges, occur widely and have provided a focus for many analyses of geographic ranges (Bull 1991). In particular, since Humboldt's (1807) time, researchers have been interested in the replacement of species along elevational gradients, often referred to as elevational zonation. Factors influencing elevational ranges can be distinguished according to the ecological versus historical (or shallow-time versus deep-time) apparent dichotomy outlined above (see also Vuilleumier and Simberloff 1980). On the ecological side of the continuum, hypotheses to explain elevational zonation invoke local determinism, and focus on individual tolerances to environmental conditions, distribution of resources and habitats, and interactions such as predation, parasitism, or competition, that change with elevation (Terborgh 1971, Repasky and Schluter 1994, Carothers et al. 2001, Navas 2003, Buckley and Roughgarden 2005). The hypothesis that interspecific competition underlies elevational replacements is supported by observations of pairs of species with restricted and complementary distributions where they co-occur, but broader elevational ranges where one or the other is absent (Lack and Southern 1949; Diamond 1970, 1973; Terborgh and Weske 1975; Mayr and Diamond 1976; Remsen and Cardiff 1990; Remsen and Graves 1995; Hall et al. 2005; but see Prodon et al. 2002).

At the other end of the spectrum, purely historical hypotheses have also been advanced to explain vertical zonation of species and geographic variation in the positions of species along elevational gradients. For instance, it has been proposed that the uplift of mountains or the subsidence of plates in marine environments might stratify species along vertical gradients of elevation or depth, respectively (Heads 1989, 2005). Indeed, examples of geographic variation in elevational ranges used to illustrate the role of interspecific competition in elevational zonation (Diamond 1986) have also been attributed to tectonic processes (Heads 2001). Similarly, vicariance resulting from mountain uplift, or from fragmentation of habitats driven by climate change, could cause the differentiation of lowland and highland clades (e.g. Patton and Smith 1992, Schulte et al. 2000). Other “historical” explanations for elevational zonation include parapatric speciation along elevational gradients (Endler 1982, Hall et al. 2005) and the colonization of newly formed high-elevation areas by taxa from other regions tracking their favored environments (Chapman 1917).

Hypotheses that attribute a protracted role in time for ecological processes affecting geographic ranges lie somewhere in between. Although ecological interactions such as interspecific competition are often viewed as proximate mechanisms that maintain patterns of elevational zonation ultimately generated by some other process (Remsen and Cardiff 1990), competition might also play a role in generating such patterns. Foremost, Diamond (1970, 1973) described several stages in a hypothetical process leading to pairs of species with exclusive elevational ranges. He proposed that when allopatric, ecologically similar species with broadly overlapping elevational distributions expand their ranges and come into contact, competition causes them to segregate with respect to elevation, with each species “giving up” the section of its range in which it is an inferior competitor. This partitioning of the elevational range allows the species to coexist at the landscape scale. Diamond argued that this process of elevational displacement need not entail evolutionary modifications of species’ fundamental niches (sensu Hutchinson 1957); he believed it often involves only compression of realized niches through plastic behavioral responses (Diamond and Marshall 1977). However, Diamond (1973) also entertained the possibility that species’ fundamental niches can evolve via adaptation to different elevational ranges following competitive segregation, which would lead to fixed elevational distributions. This idea is equivalent to the hypothesis of ecological character displacement (Brown and Wilson 1956; reviewed by Schluter 2000, Dayan and Simberloff 2005).

Whether the concept of character displacement can be applied to elevational distributions depends on whether they reflect phenotypic traits amenable to evolution by natural selection. Although elevational distributions are population rather than organismal attributes, they do represent evolved functional traits that allow individuals to survive and reproduce within the range of environmental conditions encountered over a range of elevation (Porter et al. 2002, Navas 2003, Altshuler and Dudley 2006). Accordingly, the concept of character displacement applied to elevational ranges is sensible and amenable to testing (see Schluter 2000). Indeed, recent theoretical work has demonstrated that interspecific competition can lead to character displacement in the positions of species along environmental gradients, and may result in stable parapatric range margins (Case and Taper 2000, Case et al. 2005). Moreover, specific elements of the character displacement scenario proposed by Diamond (1973) have been identified, including shifts in competitive superiority in pairs of species with elevation (Altshuler 2006), and inability of species that segregate altitudinally to expand their elevational ranges as a consequence of evolved niche differences (Angert and Schemske 2005). However, the fundamental assumption that competition is responsible for the origin of altitudinally exclusive ranges remains untested.

Distinguishing among alternative explanations for distributional patterns is made challenging in many cases by the absence of clearly articulated, falsifiable predictions. For example, responding to criticism of his competition hypothesis for the origin of elevational replacements, Diamond (1978) acknowledged: "“Proof” that the correlation with the competitor’s presence was causal is neither available nor possible”. However, tools that were for the most part unavailable at the time of Diamond’s writings now offer insights into the role of competition relative to other explanations for the origin of elevational zonation. In particular, as with the evolution of ecological interactions, such as host-parasite associations (articles in Page 2003), the origin of presumed competitive interactions and their role in the historical development of elevational ranges can be assessed from a phylogenetic perspective.

Molecular phylogenies provide information on patterns of relationship and timing of historical events that can be brought to bear on the origin of elevational replacements. Specifically, they can reveal the evolutionary lability or conservation of elevational ranges, and can show whether inferred changes in elevational distributions occurred at times and places when competition could have been causally involved with their origin (see Losos 1990). In addition, the study of within-species genetic variation in a geographical context using gene trees (phylogeography), combined with population genetic analyses grounded in coalescent theory, offers insights into the biogeographic history of species and the events that have played a role structuring their geographic ranges (Avise 2000, Wakeley 2005). In particular, recently developed methods use DNA sequence data to estimate population divergence times and to infer the occurrence of historical events, including range expansions and changes in population size (reviewed by Knowles 2004). When these methods are applied to study the history of species that occur in the same geographical setting and interact ecologically, valuable information can be gained on how these interactions arose through space and time, and on the influence that species may have had on each other (Arbogast and Kenagy 2001, Flanagan et al. 2004).

In this study, I develop predictions based on possible effects of interspecific competition resulting in elevationally exclusive ranges, describe how these can be tested using phylogenetic and population genetic methods, and apply this framework to study the origin of elevational replacements in a group of Neotropical birds whose ranges are thought to be strongly influenced by competition. My analyses illustrate how the factors underlying geographic ranges can be better understood if ecological processes that are thought to operate at present are viewed retrospectively in the context of population histories, an approach that has seldom been taken to explain features of species' distributions (e.g., Bernardi 2005).

Study System

Understanding distributions of birds along elevational gradients in the Neotropical region has been a subject of keen interest ever since the early explorations of montane areas of South America (e.g., Chapman 1917, Todd and Carriker 1922). In general, montane bird species occupy relatively consistent elevation ranges throughout their distributions (Graves 1988), with some remarkable exceptions, such as the brush-finches in the genus *Buarremon* (Emberizini). Consistent with Diamond's (1973) hypothesis, the stripe-headed (*Buarremon torquatus*) and chestnut-capped (*B. brunneinucha*) brush-finches replace each other along elevational gradients in areas where both occur, but *B. torquatus* occupies most of the montane gradient in areas of allopatry in South America. This suggests that interspecific competition is an important determinant of distributions (Remsen and Graves 1995). Competition-mediated elevational replacements have been argued to be pervasive in Andean birds (Terborgh and Weske 1975; but see Remsen and Graves 1995), yet the case of

Buarremon is anomalous because the relative elevational positions of the putative competitors vary geographically (Remsen and Graves 1995). In regions where both taxa occur along the Peruvian, Ecuadorian, and most of the Colombian Andes, *B. brunneinucha* consistently occupies the lower part of the gradient, whereas *B. torquatus* occurs at high elevations. In some regions of northern South America and Central America the pattern is reversed, and *B. torquatus* is found at lower elevations; in other areas, mid-montane populations of *B. brunneinucha* are puzzlingly sandwiched between high and low elevation populations of *B. torquatus*. Although I have argued elsewhere that the currently defined *B. torquatus* comprises more than one species-level taxon, and specifically that the populations that sandwich *B. brunneinucha* in the Colombian Andes must be treated as different species, all the taxa that have been considered part of the *B. torquatus* complex by recent authors constitute a strongly supported monophyletic group (Chapter 1, Chapter 4). This implies it is sensible to investigate the causes of geographic variation in elevational distribution of this clade, irrespective of whether its members represent different species, different subspecies, or different populations. Thus, for simplicity, in the following I refer to the group formed by all members of this species complex as *B. torquatus* and refer to distinct populations with their subspecific epithets. I also note that the genus *Buarremon* is unlikely to be monophyletic with respect to the genera *Arremon* and *Lysurus* (Chapter 1); however, because a change in nomenclature merging these three genera into an expanded *Arremon* has yet to be broadly accepted (Remsen et al. 2006), here, to avoid confusion, I continue to use *Buarremon* to refer to *torquatus* and *brunneinucha*.

How did the unusual patterns of elevational distribution of *Buarremon* brush-finches arise? Remsen and Graves (1995) did not present information on elevational distributions from Central America and Mexico, where *B. brunneinucha* occurs mostly in the absence of *B. torquatus*. Therefore, documenting the elevational ranges of *B. brunneinucha* in areas with and without *B. torquatus* remains a crucial missing step towards testing the hypothesis that the elevational ranges of the two species may have evolved in opposite directions as a consequence of competition (Diamond 1973). In addition, previous analyses did not consider distribution patterns in the context of the biogeographic history of species and the ages of different lineages. Therefore, the origin of the differences in elevational distributions of populations of *B. torquatus* and *B. brunneinucha* that replace each other along montane gradients may have predated the co-occurrence of these species (see Losos 1990).

Predictions

The hypothesis that interspecific competition caused the elevational ranges of *B. torquatus* and *B. brunneinucha* to change in opposite directions (cf. Diamond 1973) predicts that (1) elevational distributions of both species differ between areas of allopatry and areas of sympatry, and (2) that historical changes in elevational ranges occurred within geographical areas and periods of time during which these species could have interacted. Likewise, if the varying elevational distributions of different populations in the *B. torquatus* complex, specifically the occurrence of members of the group only at the two extremes of the elevational gradient in the Northern Andes, were caused by competition with *B. brunneinucha*, (1) splits among these populations must have occurred at times and places when interacting with this species was possible, and (2) populations replacing *B. brunneinucha* at low and high elevations along the same mountain slope should be sister taxa. Alternatively, even if competition was not involved directly with the divergence of these populations, competition might still have been responsible for the origin of observed distributions if it caused their elevational ranges to contract after they diverged. Accordingly, members of the *B. torquatus* complex with limited elevational distributions should show evidence of historical population declines. Specific tests of these predictions are described in detail below.

Materials and Methods

Data on elevational distributions. I characterized the elevational distributions of *B. brunneinucha* and *B. torquatus* throughout their geographic ranges based on c. 350 georeferenced locality records for each species obtained from museum specimens, publications, and field data gathered by myself or provided by several researchers. Elevations were obtained from the primary data (specimen labels, field notes) whenever possible, or by overlaying the geographic coordinates of localities onto a 1 km by 1 km digital elevation model (Shuttle Radar Topography Mission; http://www.jpl.nasa.gov/srtm) using a geographic information system (GIS; ArcGIS 9.1, ESRI, Inc.). Details on this procedure, data sources, and protocols followed to verify the accuracy of georeferenced data are presented elsewhere (Chapter 3).

Phylogenetic and population genetic data. In an earlier study (Chapter 1), I reconstructed phylogenetic relationships among members of the *B. torquatus* complex, among species of *Buarremon*, and among *Buarremon* and related genera on the basis of sequences from several mitochondrial and nuclear genes. In addition, based on thorough sampling of variation in mitochondrial DNA, I presented a general picture of the biogeographic history of *B. torquatus* and *B. brunneinucha*. Here, I use the inferences about phylogenetic relationships and population history as a framework to guide the development and testing of predictions related to the role of interspecific competition in the origin of elevational distributions in *Buarremon.* I also capitalize on the available sequence data to conduct new analyses on the timing of lineage differentiation and on the demographic history of populations.

The Effect of *B. torquatus* on the Elevational Range of *B. brunneinucha*

The hypothesis of character displacement predicts that coexistence along mountain slopes with elevational replacement follows secondary sympatry, and that elevational distributions of derived lineages occurring in sympatry with competitors should be shifted in comparison to those of early branching lineages that occur in allopatry. I was able to test this prediction for *B. brunneinucha* because populations from the southern sector of its range, where it co-occurs with *B. torquatus*, are of recent origin with respect to those of the northern sector, from where *B. torquatus* is absent (Chapter 1). Testing for character displacement requires that environments are similar enough in sympatry and allopatry that differences in species' ecology cannot be accounted for by tracking of varying environmental factors (Grant 1972, 1975; Schluter and McPhail 1992). Therefore, I compared the slopes and intercepts of the relationship between elevation and mean annual temperature measured in areas of allopatry and sympatry. In contrast to elevation, which only limits distributions indirectly through its correlation with other factors, temperature affects organisms directly. This comparison allowed me to assess whether the documented differences in the elevation-temperature relationship between lower and higher latitudes (Janzen 1967, Ghalambor et al. 2006) are observable within the study region. If they were, then elevational ranges in different areas would not be readily comparable because, on average, *B. brunneinucha* occurs at higher latitudes in allopatry than in sympatry. To set up this analysis, I used GIS to randomly place 1500 points in the area of allopatry and 1500 in sympatry, with the constraint that they should fall within the elevation range encompassed by all *B. brunneinucha* localities. At each point, I recorded elevation based on the digital elevation model and temperature from an interpolated surface with a 1 km x 1 km resolution (Hijmans et al. 2005).

Because randomly placed points sample different elevations in proportion to their area, I used these data to account for differences in the abundance of sites at different elevations when testing for differences in the mean of the elevational range of *B. brunneinucha* in sympatry and allopatry. That is, the variation in the elevational distribution of the random points in allopatry and sympatry can be taken as a null expectation against which actual differences in elevational distributions can be compared. I conducted a two-way ANOVA with geographic context (i.e., allopatry or sympatry) and elevation data source (i.e., locality records or randomly placed points) as main factors, and elevation as response variable. A significant interaction term would indicate the difference in mean elevational distributions of *B. brunneinucha* between regions deviated from the difference that would be expected as a consequence of varying abundance of sites at different elevations. This could result from interspecific competition. I also examined elevational distributions in areas where populations of *B. brunneinucha* were either sandwiched, replaced at high elevations, or replaced at low elevations by *B. torquatus*. If displacement in elevational ranges occurred, then populations replaced at low elevations should be shifted towards higher altitudes in comparison to those being replaced at high elevations.

The Effect of *B. brunneinucha* on the Elevational Range of *B. torquatus*

Timing of Differentiation. The hypothesis that competition with *B. brunneinucha* is responsible for the disparate elevational distributions of populations of *B. torquatus* predicts these populations diverged at times when *B. brunneinucha* and *B. torquatus* could have been in sympatry. To test this prediction, I used a relaxed molecular clock approach to compare the ages of South American lineages of *B. torquatus* with the estimated time at which *B. brunneinucha* colonized South America. Based on results of phylogenetic analyses that included multiple individuals of the three species of *Buarremon* and a variety of related genera (Chapter 1), I selected a few representatives of major groups and inferred their relationships using sequences of the mitochondrial ND2 gene. Relationships inferred from ND2 sequences do not conflict significantly with those inferred with more data from other mitochondrial and nuclear genes, and restricting analyses to ND2 allowed me to sample lineages for which sequences of other genes are not available.

To root the phylogeny of the clade formed by *Buarremon, Arremon,* and *Lysurus*, I used sequences of *Atlapetes* and *Pipilo* as outgroups. I conducted maximum-likelihood phylogenetic analyses in PAUP* (Swofford 2002), using procedures described in Chapter 1. A likelihood ratio test comparing the scores of the maximum-likelihood tree and of a tree with a molecular clock enforced rejected the null hypothesis of clock-like sequence evolution. Therefore, I used the penalized likelihood method (Sanderson 2002) implemented in the program r8s version 1.70 (Sanderson 2003) to convert branch lengths to comparable estimates of divergence times. This method allows for rate variation across the tree, but applies a roughness penalty to discourage departures from rate constancy among close relatives. I determined the optimal level of rate smoothing using the cross-validation procedure available in r8s. Because neither fossil nor biogeographic calibrations are available for *Buarremon* and its near relatives, I did not attempt to infer the absolute timing of historical events, but rely on relative timing. For this purpose, I fixed the node representing the most recent common ancestor of the ingroup (i.e., the *Buarremon-Arremon-Lysurus* clade) to have an age of 1.0 and scaled branch lengths relative to this value. Based on the resulting chronogram, I estimated the relative ages of nodes indicating the colonization of South America by *B. brunneinucha* or the divergence of populations of *B. torquatus* with contrasting elevational ranges. To assess the uncertainty of estimates of node ages resulting from data sampling error, I estimated these ages for 100 bootstrap pseudoreplicate data sets (Sanderson and Doyle 2001). Because a few nodes in the phylogeny were not well supported, phylogenetic uncertainty introduces additional error in node age estimation. To evaluate the influence of this source of error, I repeated the analysis for trees in which branches receiving less than 70% maximum-likelihood bootstrap support were resolved in alternative ways. Because all the poorly supported branches are short, alternative topologies did not influence the main conclusions of this analysis. Therefore, I only report results based on the maximum-likelihood phylogeny.

Inferences about the divergence time between populations of a species can be confounded by ancestral polymorphism (Edwards and Beerli 2000). However, I did not employ methods to distinguish between the time of gene divergence and the time of population divergence (e.g., Nielsen and Wakeley 2001) because the data did not meet the assumption of no population structure within the diverging groups. This assumption was particularly unsuited for *B. torquatus*, which comprises several distinct, reciprocally monophyletic, and geographically isolated groups (Chapter 1). I address the effect of possible biases in the estimation of population divergence times in the discussion.

Historical Demography. Methods that reconstruct ancestral character states for nodes on phylogenies are not well suited for the study of historical changes in elevational distributions. Consider the hypothetical situation that all extant members of a clade occur over a narrow elevational range: ancestral state reconstructions will typically indicate the range of their ancestor was similarly narrow (see Hardy and Linder 2005). This scenario overlooks the possibility that the elevational distributions of all members of the clade may have been compressed in concert since they last shared a common ancestor, which would be what one would expect if competitive displacement occurred relatively recently in evolutionary history. Although one could accommodate this possibility by employing a model of trait evolution that allows high rates of change along branches in the phylogeny, ancestral states estimated under such a model would be imprecise. Therefore, I did not attempt to infer the evolutionary pathways by which current elevational distributions arose. Instead, I use historical patterns of change in population size to determine the plausibility of the occurrence of elevational range contractions because the restriction of a widespread population to a narrow elevational range cannot occur unless there is a reduction in its size, especially if it occurs at or near its carrying capacity. Population genetic theory provides a framework that allows assessing historical demographic trends: alleles sampled from historically stable, shrinking, and expanding populations exhibit different distributions of coalescence times because lineages coalesce back to their common ancestor more rapidly when populations are small and more slowly when they are large (Kingman 1982). If a population has declined as a consequence of a contraction in its elevational range, this should be detectable in gene genealogies inferred from series of randomly sampled haplotypes (reviewed by Emerson et al. 2001, Knowles 2004). I applied this framework to test the hypothesis that competition with *B. brunneinucha* caused the elevational ranges of populations of *B. torquatus* to contract.

I used two different coalescent approaches to examine historical trends in population size using ND2 sequence data for *assimilis* and *atricapillus*, two members of the *B. torquatus* complex that could have experienced elevational range contractions as a result of competition with *B. brunneinucha,* and that presently sandwich that species in areas of the Colombian Andes. First, I estimated historical population growth rates using LAMARC version 1.2.2 (Kuhner et al. 2004). This package samples genealogies using a Markov chain Monte Carlo (MCMC) method, and assuming a model of exponential change in population size and no selection, migration, or recombination, it calculates maximum-likelihood estimates of θ, a measure of genetic diversity that reflects female effective population size and mutation rate per site ($\theta = N_e\mu$ for the haploid and maternally-inherited mtDNA), and its exponential growth parameter g ($\theta_t = \theta_{now} exp\text{-}\ [gt]$, where t is some time in the past). Positive values of g indicate population growth, whereas negative values indicate population decline. I analyzed data for *assimilis* and *atricapillus* independently using 10 short-chain runs of 1,000 steps, followed by two long-chain runs of 100,000 steps; chains were sampled every 20 steps, with the first 1000 discarded as burn-in. I also assessed trends in effective population size using the Bayesian skyline plot method (Drummond et al. 2005), a nonparametric approach implemented in BEAST version 1.2 (Drummond and Rambaut 2003) that estimates a posterior distribution of effective population size through time on the basis of a set of plausible genealogies sampled using MCMC. I used the TrN+I and TrN models of nucleotide substitution (selected based on the AIC using ModelTest 3.7; Posada and Crandall 1998) to analyze data for *assimilis* and *atricapillus,* respectively. Chains were run for 50,000,000 iterations with genealogies and model parameters sampled every 1000 iterations; the first 1% of iterations was discarded as burn-in. The number of groups (m) was set to 10 for analyses involving *assimilis* and to 5 for those involving *atricapillus* due to varying sample sizes. I imported the output of each run into Tracer version 1.2 (Rambaut and Drummond 2003) and examined results to verify that parameter estimates were based on acceptable effective sample sizes and that trace plots indicated appropriate mixing. Finally, I generated skyline plots in Tracer showing the median estimates of population size and their associated credibility intervals (95% highest posterior density) from present time back to the most recent common ancestor of the samples.

These approaches to assessing historical demography assume that sequences are sampled from a single panmictic population. Estimates of migration between Colombian and Ecuadorian-Peruvian highland populations of *B. torquatus* indicate that, on average, one female individual is exchanged between the two regions approximately every five generations (C. D. Cadena, unpubl. data; see Chapter 1 for methods). Although simulations suggest migration would need to be much lower to bias the estimation of *g* (P. Beerli, unpublished data), the credible interval for this estimate of gene flow is wide, and cannot distinguish complete isolation from relatively frequent interchange of migrants. Thus, I tested for the sensitivity of the models to population structure by conducting independent analyses with: (1) only sequences of *assimilis* from Colombia, (2) sequences of *assimilis* and *nigrifrons* from Ecuador and Peru, and (3) all sequences of *assimilis* and *nigrifrons* from Colombia, Ecuador, and Peru. Because geographic structure is limited within Colombia and in Ecuador-Peru (Chapter 1), consistent results across analyses with these different sampling schemes would suggest that the models were robust to the possible violation of the assumption of panmixia (Shapiro et al. 2004). Sequences of *nigrifrons* were included in the analyses because this taxon and *assimilis* are not reciprocally monophyletic. Although this taxon only replaces *B. brunneinucha* at high elevations in part of its range (see below), not considering it would likely have resulted in gene genealogies with longer coalescent times near the base, which would have biased analyses towards inferring population declines. The sample size for *atricapillus* was too limited to allow for sensitivity analyses, so I considered all available sequences as a single group, except for the fact that I conducted analyses with and without sequences of *tacarcunae,* a closely related taxon. Although the sample size precluded examining the possible effect of violating the assumption of no population subdivision in *atricapillus,* it was probably sufficient to capture the general structure of gene genealogies, and thereby reach the level of accuracy that can be achieved estimating population genetic parameters from single-locus data (Felsenstein 2006).

Forces other than interspecific competition with *B. brunneinucha* might have influenced population sizes throughout the history of *B. torquatus*, especially because the areas it inhabits have experienced mountain uplifting and vertical displacement of ecological zones as a consequence of climate change

(Gregory-Wodzicki et al. 2000, Hooghiemstra and Van der Hammen 2004). Therefore, even if interspecific competition caused ranges to contract, these contractions might be difficult to detect from the background of all other events that influenced population sizes over time. This caveat applies particularly to the estimation of *g* because LAMARC assumes constant exponential growth or decline, and, thus, reveals only an overall trend in population size. It is less likely that fluctuations unrelated to competition would obscure a strong pattern of competition-driven decline in skyline plots, which can recover distinct episodes of growth and decline throughout a population's history (Drummond et al. 2005). Nonetheless, I sought to address the possible confounding effect of demographic changes unrelated to competition on the outcome of coalescent analyses by assessing trends in population size in "control" taxa.

An ideal control would be a population of similar age and distribution to the one that may have been displaced by competition; this control population would be expected to have been affected by the same historical processes resulting in population growth and decline, except competition. I used two controls: (1) the population of *B. torquatus* (subspecies t*orquatus*) that extends from the Peru-Bolivia border south to central Bolivia, and (2) the lineage formed by *Myioborus ornatus* and *M. melanocephalus* (Parulidae) that extends from the Venezuela-Colombia border through Colombia into northern Peru (Pérez-Emán 2005). The Bolivian *B. torquatus* are close relatives of *assimilis-nigrifrons* and *atricapillus-tacarcunae,* constitute a lineage of comparable age that may have been similarly affected by large-scale historical changes in climate, and occur in areas where *B. brunneinucha* does not occur (with the exception of a single locality in southernmost Peru). Although the *M. ornatus-M. melanocephalus* complex belongs to a different family, it occurs in similar environments to *assimilis-nigrifrons,* the distribution and elevational ranges of the two groups are remarkably consistent, and sequence data for the same genes indicate similar age (Chapter 1, Pérez-Emán 2005, J. L. Pérez-Emán and C. D. Cadena, unpublished data).

RESULTS

History of populations and elevational ranges in **B. brunneinucha**

Southern Costa Rican, Panamanian, and South American populations of *B. brunneinucha* that occur in sympatry at the landscape scale with members of the *B. torquatus* complex are of recent origin with respect to populations from Mexico and northern Mesoamerica that occur in allopatry (Chapter 1). This allowed me to test the prediction of the character displacement hypothesis that derived populations occurring in sympatry should exhibit shifted elevational ranges with respect to populations free of competition from areas of allopatry. Although the relationship between elevation and climate varies with latitude, differences are minor within the range of *Buarremon:* the slopes and intercepts of regressions between elevation and temperature do not differ between regions (data not shown). This suggests that the elevational distributions of *B. brunneinucha* in sympatry and allopatry can be compared to one another.

Elevational distributions of *B. brunneinucha* in sympatry and allopatry differ significantly (Kolmogorov-Smirnov two-sample test, $p=0.0034$, Fig. 1a), and the mean elevation of records of this species is significantly higher in sympatry than in allopatry (ANOVA, $P < 0.0001$, Fig. 1b). However, this can hardly be interpreted as evidence of displacement resulting from interspecific competition with *B. torquatus*. First, the magnitude of differences in mean elevation of records between areas does not exceed that of differences that would be expected by chance as a result of the varying abundance of sites at different elevations in each area, as indicated by the lack of a significant interaction term in the ANOVA that involved a comparison of the mean elevation of randomly placed points in allopatry and sympatry ($P = 0.42$, Fig. 1b). Second, distributions in sympatry are shifted towards higher elevations in comparison to allopatry independently of whether *B. brunneinucha* is replaced at low elevations, replaced at high elevations, or sandwiched by *B. torquatus* (Fig. 1c). This is inconsistent with the prediction from competitive displacement that distributions would be shifted towards those elevations not occupied by the putative competitors. Finally, the elevational range of *B. brunneinucha* has similar standard deviations in areas of allopatry ($s = 569 \pm 36$ m SE), and areas where replaced at low elevations ($s = 599 \pm 68.7$ m), replaced at high elevations ($s = 555 \pm 38$ m), and sandwiched ($s = 544 \pm 48$ m) by *B. torquatus,* indicating that ranges are not more compressed in sympatry.

***History of populations and elevational ranges in B.* torquatus**

As described in Chapter 1, relationships among major South American lineages of *B. torquatus* are generally poorly supported, but there are several distinct and strongly supported clades, some of which comprise lineages occupying similar positions along elevational gradients (Fig. 2). In particular, the populations that replace *B. brunneinucha* at high elevations form a well-supported monophyletic group that in turn comprises two distinct clades, one including forms from Colombia, Ecuador, and northern Peru (*assimilis* and *nigrifrons*), the other a form ranging from central to southern Peru (*poliophrys*). Low-elevation taxa do not form a single monophyletic group, but *atricapillus*, *tacarcunae,* which replace *B. brunneinucha* at low elevations appear to constitute a clade, with the low-elevation and allopatric *phygas*, although support is weak. The other low-elevation taxa are sister to all other members of the complex (*costaricensis*), to the high-elevation clade (*larensis*), or to the elevationally widespread *basilicus* (*perijanus*), but the latter relationship is not strongly supported. Finally, the three taxa that occur in allopatry from *B. brunneinucha* in Bolivia and Argentina (nominate *torquatus*, *fimbriatus*, and *borelli*) formed a well-supported group (*fimbriatus* is not shown in the figure; this taxon and *borelli* are not reciprocally monophyletic with respect to each other; Chapter 1).

Penalized likelihood analyses of timing of diversification indicate the colonization of South America by *B. brunneinucha* occurred substantially more recently than the origin of most South American lineages of *B. torquatus* that presently have disparate elevational distributions (Fig. 2). This result is robust to error introduced by substitutional noise in the mtDNA data, as indicated by the entirely non-overlapping bootstrap estimates of ages of relevant nodes (Fig. 3). Specifically, estimates of the crown ages of groups of *B. torquatus* that replace *B. brunneinucha* at high or low-elevation areas (nodes 4 and 5 in Fig. 2) have confidence intervals that do not overlap with the confidence interval around the crown age of South American *B. brunneinucha* (node 1; Fig. 3a). Differences are more striking when the ages of stem groups (i.e., nodes 2 and 3) are compared (Fig. 3b). Likewise, the divergence between the low-elevation taxon *perijanus* and the wide-ranging *basilicus* (node 7) clearly predates the colonization of South America by *B. brunneinucha* (Fig. 3c). In sum, interspecific competition with *B. brunneinucha* in South America is not a parsimonious explanation of the differentiation of *B. torquatus* into distinct lineages that currently replace *B. brunneinucha* at particular elevational zones: these lineages last shared common ancestors well before the onset of sympatry with *B. brunneinucha* in South America. However, it is important to note that the taxon *nigrifrons* only replaces *B. brunneinucha* at high elevations in the northern extreme of its range; through much of southern Ecuador and northern Peru, it occurs in allopatry and extends to low elevation areas. The divergence of *assimilis* and *nigrifrons* is recent (they are not reciprocally monophyletic, Chapter 1) and penalized likelihood cannot reject the hypothesis that they diverged after the colonization of South America by *B. brunneinucha* (Fig. 2). This raises the possibility that the elevational range of *assimilis* and *poliophrys*, but not of *nigrifrons*, may have been compressed as a consequence of competition (see below).

Historical Demography

Maximum-likelihood estimates of the exponential growth parameter (*g*) were greater than zero for all populations (Table 1), suggesting histories of demographic growth. However, the MCMC method implemented in LAMARC tends to produce upwardly biased estimates of *g* (Kuhner et al. 1998, Felsenstein et al. 1999). The fact that the 95% confidence intervals of *g* did not include zero or negative values in some analyses (Table 1) argues more strongly against population decline than for population expansion. The confidence intervals around *g* estimated for *atricapillus-tacarcunae* are too large to reach definitive conclusions, other than that there is no compelling evidence that these populations have declined. Likewise, Bayesian credibility intervals in skyline plots were wide, particularly for *atricapillus-tacarcunae* (Fig. 4), yet the median estimates of population size in these analyses showed trends that indicate either growth or stable population sizes. The value of *g* for one of the control populations (Bolivian *torquatus*) was an order of magnitude greater than those estimated for *assimilis-nigrifrons* and *atricapillus-tacarcunae,* but the estimate of θ for this population had an extremely large confidence interval, spanning four orders of magnitude (Table 3). Because the extent of population growth or decline can only be interpreted with reference to θ, making inferences about the demographic history of this taxon is difficult. For comparison, patterns in *Myioborus ornatus-melanocephalus* appear indistinguishable from those of the populations of *B. torquatus* that might have been affected by competition with *B. brunneinucha* (Table 3). Note that the results of analyses did not vary qualitatively with different sampling schemes, indicating that inferences are unlikely to be affected by possible violations of the assumption of panmixia.

DISCUSSION

Biogeographers have long been interested in determining what factors underlie the replacement of species along elevational gradients, a question that is arguably central to explaining macroecological patterns such as the turnover of species composition and the changes in species diversity with elevation (reviewed by Rahbek 2005). This issue is especially relevant in the tropical Andes, where elevational turnover is a major component of high regional species richness in many groups of organisms. In this study I set out to evaluate the hypothesis that abutting elevational distributions result from interspecific competition by testing predictions involving historical scenarios with phylogenetic and population genetic analyses in a group of Neotropical birds. Although some conclusions depend on the assumption that the history of mitochondrial lineages reflects the history of populations, my results reject some potential historical roles for interspecific competition in elevational zonation in *Buarremon*. Although the results of this study might not be generalizable across other taxa and regions, of all Neotropical birds, *Buarremon* is the group in which elevational distribution patterns seemed to be most consistent with the hypothesis that competition may have been causally involved with their origin (see Remsen and Graves 1995 for a review of problems with other cases in which elevational zonation had been suggested to be determined by competition).

Historical Effect of Interspecific Competition on the Elevational Range of B. brunneinucha

Mitochondrial DNA variation in *B. brunneinucha* suggests that this species colonized the southern portion of its present distribution from northern Central America (Chapter 1). Because members of the *B. torquatus* complex do not occur north of central Costa Rica (and presumably did not extend much further north historically), the biogeographic history of *B. brunneinucha* is well suited to test the hypothesis that its elevational range was modified by interspecific competition once it expanded into the range of *B. torquatus* (Diamond 1973). Although the mean of the elevational distribution of *B. brunneinucha* differs between the region of sympatry and the region of allopatry, the area available at different elevations also differs between regions in parallel, obviating the need to invoke competition. Moreover, a shift towards higher elevations in areas of sympatry is observed regardless of whether *B. brunneinucha* is replaced at high elevations, replaced at low elevations, or sandwiched by its putative competitor, and this shift is not accompanied by a compression in the elevational range. Thus, I can reject the hypothesis that the elevational distribution of *B. brunneinucha* has been influenced by competition with *B. torquatus.* The more restrictive scenario of ecological character displacement, which also requires niche evolution beyond the alternative of ecological plasticity (Schluter 2000, but see Pfennig et al. 2006), must also be rejected.

Although character displacement is typically tested only on the basis of mean differences in traits, the mean and the variation around it are not the only descriptors of elevational ranges that merit consideration. The distributions of *B. brunneinucha* in allopatry and sympatry are not only significantly different in their means, but also according to a Kolmogorov-Smirnov test, which is sensitive to differences in location, dispersion, and skewness. Also, elevational distributions in allopatry and sympatry appear to differ in terms of their relationship to the relative abundance of sites at different elevations in their respective areas (data not shown). It is improbable, however, that these patterns may reflect an effect of *B. torquatus* on elevational distributions because the relationships between proportional use and abundance are similar in areas of replacement at low elevations and at high elevations. Although at a coarse level the relationship between elevation and some environmental variables that may limit species' distributions directly is similar in sympatry and allopatry, it is possible that a finer examination of environmental variation between regions could explain these regional differences in elevational distributions in more detail. I present such an examination based on multivariate analyses and modeling of species ecological niches (Carpenter et al. 1993) based on a broad suite of environmental variables in Chapter 3.

Effect of Interspecific Competition on the Diversification of Lineages in B. torquatus

Distinct lineages of *B. torquatus* currently associated with different elevational zones in South America last shared common ancestors well before the colonization of the continent by *B. brunneinucha*. Thus, although divergence in elevational ranges might have occurred more recently in response to competition with *B. brunneinucha* (see below), the origin of these lineages predated sympatry. Furthermore, the populations of *B. torquatus* that sandwich *B. brunneinucha* in the Colombian Andes (*assimilis* and *atricapillus*) are not each other's closest relatives, which implies there is no support for a scenario in which competition displaced members of a single lineage to the extremes of the elevational gradient, a pattern that has been described in systems involving other kinds of gradients and by theoretical models of character displacement (Austin et al. 1990, Austin 1999, Doebeli and Dieckmann 2000).

Conclusions involving estimates of divergence times are robust to bias introduced by failing to account for the discrepancy between the time of gene divergence and the time of population divergence. As noted by Edwards and Beerli (2000), equating gene divergence with population divergence will almost invariably result in overestimation of divergence times, a bias that is most acute for cases of recent separation of lineages. Therefore, if divergence times are overestimates, the bias is likely strongest for *B. brunneinucha*, which would argue even more compellingly in favor of the idea that its colonization of South America occurred after the differentiation of major lineages of *B. torquatus*. Also, as shown by analyses reported elsewhere (Chapter 1), the shallow differentiation between Central American and South American populations of *B. brunneinucha* is not a consequence of recurrent migration, and contrasting patterns of mtDNA variation in *B. brunneinucha* and *B. torquatus* cannot be explained by varying effects of selection.

Historical Effect of Interspecific Competition on the Elevational Range of B. torquatus

The plausibility of the hypothesis that competition with *B. brunneinucha* led to contractions in the elevational distributions of lineages of *B. torquatus* (cf. Diamond 1973) remains somewhat uncertain. If ecological niches are conserved, that lineages of *B. torquatus* replacing *B. brunneinucha* at high or low elevations originated prior to sympatry would imply lack of support for this hypothesis. To some extent, the assumption of elevational niche conservatism is tenable because distinct clades associated with particular elevational zones have been documented in multiple organisms and geographic regions (Patton and Smith 1992, Arctander and Fjeldså 1994, García-Moreno et al. 1999, Renner and Won 2001, Moyle et al. 2005, Pérez-Emán 2005). More generally, theory argues for niche conservatism (Holt and Gaines 1992, Holt 2003), and numerous empirical studies support this idea (Ricklefs and Latham 1992, Peterson et al. 1999, Hugall et al. 2002, Ackerly 2003, Martínez-Meyer et al. 2004, Qian and Ricklefs 2004). Also, it could be argued that if all members of a clade have similar elevational distributions, it is most parsimonious to assume they inherited those distributions unchanged from their most recent common ancestor. This line of reasoning would imply rejecting the hypothesis that competition with *B. brunneinucha* caused changes in the elevational distributions of *B. torquatus* lineages.

The arguments in favor of niche conservatism and the principle of parsimony notwithstanding, elevational distributions evidently differ between lineages, implying they do change over time, and they have done so in *B. torquatus*. Therefore, the relevant issue is not whether elevational niches are conserved, but rather when and under what circumstances niche conservatism breaks down (see Wiens and Graham 2005). I addressed the possibility of recent changes in elevational ranges using coalescent models to examine historical trends in population size for *B. torquatus* taxa that replace *B. brunneinucha* along elevational gradients. The analyses did not provide strong evidence that these populations have experienced substantial declines as would have been expected if competition-driven range displacement occurred, and demographic trends appear quite similar to those observed in a co-distributed lineage that presumably was not affected by competition. Thus, the null hypothesis that populations have been stable or even growing cannot be rejected in favor of the hypothesis that they have declined. However, support for scenarios of constant size or growth is not compelling either. Both coalescent methods rendered reconstructions of the demographic history of populations with a substantial amount of uncertainty (i.e., wide confidence limits and credibility intervals). Part of this uncertainty likely reflects the limitations inherent to employing information from a single locus to infer population history; simulations suggest that multilocus data increase the accuracy and precision in the estimation of population genetic parameters (Felsenstein 2006). Because results appear more suggestive of growing or stable than of declining populations, incorporating sequence data from additional loci in the analyses may allow rejecting the prediction of population declines with some confidence. However, the only study that has tested the effect of the number of loci on the estimation of ancestral population sizes empirically did not demonstrate a consistent decline in variance with increasing numbers of loci (Jennings and Edwards 2005).

What is the historical role of competition in elevational replacements?

Although I have shown that it is unlikely that elevational distributions in *Buarremon* arose through a process of reciprocal range contraction in both *B. brunneinucha* and *B. torquatus* as envisioned by Diamond (1973) in his hypothesis for the origin of elevational replacements, interspecific competition might still have been of historical importance in this system and in others involving parapatric elevational distributions in alternative ways, some of which are not mutually exclusive. First, my analyses suggest that interspecific competition with *B. torquatus* does not seem to have modified the elevational distribution of *B. brunneinucha*, but it is not entirely clear that the reverse did not occur because of the wide confidence intervals in coalescent inferences of historical demography. If the latter were to be confirmed, it could imply the occurrence of asymmetric character displacement (i.e., only one of two interacting species experiences a response to interspecific competition). Asymmetric displacement appears to be more of a rule than an exception (Schluter 2002), and probably reflects the varying competitive abilities of species, with inferior competitors being the ones that become displaced and experience reduced fitness as a consequence of trade-offs resulting from selection to reduce competition (Pfennig and Pfennig 2005). Hence, one could speculate that *B. brunneinucha* may be competitively superior to *B. torquatus*, a hypothesis that can be tested using distributional data and information on spatial variation in species' abundances (Anderson et al. 2002), or by measuring the effects of release from competition in the field (Martin and Martin 2001). This novel hypothesis regarding the contemporary ecology of these species can be formulated based on the historical information offered by their phylogeographies, which highlights the value of developing ecological studies in light of an understanding of species' histories.

Second, bi-directional interspecific competition may have not been involved with the origin of patterns of elevational replacement, but may play a pivotal role in their maintenance (Remsen and Cardiff 1990). Testing this hypothesis experimentally by manipulating the occurrence of species and examining changes in fitness components or in the boundaries of elevational ranges would be challenging for *Buarremon*, but assessing the potential for interference competition through interspecific territoriality in areas of parapatry could shed some light on its plausibility (Robinson and Terborgh 1995). I have conducted a limited number of playback experiments in the Colombian Andes that indicate that *B. torquatus* and *B. brunneinucha* at least occasionally respond to each other's vocalizations, which suggests that interspecific territoriality between them is possible. This hypothesis deserves further scrutiny.

Third, because I tested only for the historical signals of one-to-one competition between *B. brunneinucha* and *B. torquatus,* I cannot rule out the possibility that their elevational ranges could have been shaped by competition with other species individually (e.g., members of the closely allied genus *Arremon*), or through diffuse competition at the community level (Terborgh and Weske 1975, Mayr and Diamond 1976). Addressing these hypotheses in detail is beyond the scope of this study, but I note that the absence of *Buarremon* species from particular geographical areas in some cases correlates with the absence of other taxa, suggesting it is possible that compressed elevational ranges in sympatry may partly reflect competition with a suite of species, not only with each other. For instance, Remsen and Graves (1995) demonstrated a marked expansion of the elevational range of *B. torquatus* south of northern Bolivia; since *B. brunneinucha* does not occur in this region, a sensible explanation for the expanded range of *B. torquatus* was release from competition with *B. brunneinucha*. However, the absence of *B. brunneinucha* from this region correlates with a conspicuous decline in avian species richness along the eastern slope of the Andes from central Bolivia to the south (Rahbek and Graves 2001).

Finally, there might be a role for interspecific competition in the origin of elevational zonation that would imply turning Diamond’s (1973) original argument on its head: coexistence with elevational segregation may be possible only if the elevational distributions of species that colonize any given mountain slope are different enough at the outset that they do not compete (cf. Losos 1990, Pfennig and Murphy 2003). In other words, the role of interspecific competition may be to act as a sorting mechanism that allows co-occurrence along mountain slopes only of ecologically similar species with pre-existing differences in elevational distributions that minimize the potential for competition. The idea that ecological sorting enables the coexistence of species with contrasting niches evolved prior to community assembly has gained ample support from studies combining data on community structure with phylogenetic analyses of the evolution of ecological traits (reviewed by Webb et al. 2002; see also Kozak et al. 2005, Vitt and Pianka 2005). The patterns of elevational replacement in *Buarremon* may thus be the result of a process in which upon colonizing the range of *B. torquatus*, *B. brunneinucha* established populations at elevations that matched its ecological requirements, without any modifications of elevational ranges in either species. This scenario would be consistent with the idea that elevational niches are evolutionarily conserved. In addition, it would imply that at some point in the past, members of the *B. torquatus* complex could have had disjunct distributions along the northern Andean slopes, and that colonizing individuals of *B. brunneinucha* established populations at “vacant” intermediate elevations, leading to the present-day sandwich pattern of elevational replacements in the Colombian cordilleras. This would not be entirely atypical, as some avian taxa belonging to the same species or species complex have disjunct elevational distributions at present (Vuilleumier 1986).

Biogeographic history and the origin of elevational distributions

Although this hypothesis could not be rejected firmly in this study, it appears unlikely that competition with *B. brunneinucha* was involved with the origin of the contrasting elevational distributions of different lineages in the *B. torquatus* complex, a phenomenon ornithologists have long been interested in explaining (Paynter 1978, Fjeldså and Krabbe 1990, Remsen and Graves 1995). More generally, the origin of elevational replacements in this group and others may not be related to interspecific competition, which leaves open for discussion the question of how patterns of abrupt turnover of congeners along elevational transects arise.

The hypothesis that populations may be displaced vertically as mountains uplift (Heads 1989) would predict that the separation of lineages associated with elevational zones occurred during periods of tectonic activity. The Cordillera Oriental of the Colombian Andes was fairly low (40% of its current elevation) up until the early Pliocene and elevations increased rapidly between 5 and 2 million years before present, achieving its modern altitudes by around 2.7 Ma (Gregory-Wodzicki 2000). If branch lengths are transformed to approximate divergence times based on existing calibrations of nucleotide substitution rates in avian protein-coding mtDNA (reviewed by Lovette 2004, see also Weir 2006, Arbogast et al. 2006), then the divergence among Northern Andean lineages of *B. torquatus* would appear to have taken place concurrently with events of mountain uplifting in this region (i.e., more than 1.5-3 million years ago). Thus, the hypothesis that orogenic processes were involved with the differentiation of lineages with distinct elevational distributions appears plausible. An additional prediction of this hypothesis that would allow for a much more robust test is that consistent patterns in phylogenetic relationships and timing of differentiation of lineages with similar elevational distributions should be observed in other organisms. Owing to the current lack of comprehensive phylogenetic and phylogeographic studies on other North Andean taxa, this prediction is not yet testable.

In contrast to the idea that species may be stratified along elevational gradients as a result of limited dispersal abilities that "trap" populations in vertical geological movements, elevational zonation can also be explained on the basis of dispersal scenarios. It has long been hypothesized (e.g. Chapman 1917; reviewed by Vuilleumier 1986) that species replacing others in high-elevation areas may have colonized these environments from temperate latitudes tracking their favored environmental conditions. This hypothesis is supported by phylogenetic evidence that taxa occurring at high elevations in the Northern Andes had their origin in alpine temperate areas (Chesser 2000, von Hagen and Kadereit 2003, Chesser 2004, Bell and Donoghue 2005). Although basal relationships among major South American lineages of *B. torquatus* are not well supported, it is intriguing that phylogenetic analyses suggest affinities between populations occurring in quite distant geographical areas (Chapter 1). Because they may reflect extinction of intervening populations of formerly widespread lineages, these disjunct patterns need not involve scenarios of long-distance dispersal, but do illustrate the potential for complex historical changes in the geographic distributions of montane taxa (see also Dingle et al. 2006). If species' niches remain conserved despite range expansions and shifts, colonization processes coupled with "niche tracking" may be an important determinant of patterns of elevational zonation, particularly in light of the hypothesis that interspecific competition may act as a sorting mechanism in community assembly along elevational gradients (Stephens and Wiens 2004).

Finally, although this hypothesis does not apply to *Buarremon* brush-finches, speciation along elevational gradients can result in closely related species with abutting elevational ranges. Speciation may occur as a consequence of varying selective pressures along the elevational gradient that lead to differentiation of continuously distributed populations into pairs of daughter species (i.e., the divergence with gene flow model; reviewed by Smith et al. 2005), or as a result of allopatric differentiation following dispersal across elevations, with parapatry resulting from subsequent range expansions. Although they cannot distinguish between these two scenarios, phylogenetic studies on Andean taxa provide evidence of speciation into the highlands, with successively sister taxa distributed parapatrically and the most recently diverged species occurring at the highest elevations (Bates and Zink 1994, Hall et al. 2005).

Conclusion

This study demonstrates that two taxa that were thought to have potentially influenced the limits of their geographic ranges mutually have had quite contrasting histories of differentiation in the continent where distributions led ecologists to suspect they might have had closely interconnected histories. *Buarremon brunneinucha* appears to have colonized the range of *B. torquatus* only recently, and this colonization does not seem to have involved a modification of its elevational range in response to the possible onset of interspecific competition. Although the possibility that the elevational distributions of lineages of *B. torquatus* were shaped by competition with *B. brunneinucha* cannot be entirely ruled out by coalescent analyses, if this happened it must have occurred relatively recently in the history of these taxa. This insight adds to mounting evidence that, regardless of their pervasiveness in present time, ecological interactions may have played out over only short snapshots of the evolutionary history of lineages (e.g., Sorenson et al. 2003, Flanagan et al. 2004), which underscores the importance of framing hypotheses related to the effect of current species interactions on geographic ranges and on the evolution of ecological niches in an explicitly historical context.

The results of this study also highlight a challenge for researchers testing hypotheses of character displacement using phylogenetic comparative methods. Phylogenetic tests of character displacement (Losos 1990, Butler and Losos 1997, Radtkey et al. 1997, Giannasi et al. 2000) attempt to distinguish whether exaggerated differences between species in sympatry reflect evolution of derived character states taken place *in situ*, or the retention of plesiomorphic states acquired elsewhere prior to the potential onset of interspecific competition. Although this approach has provided much valuable insights, under some circumstances it may be misleading as a consequence of the dynamic nature of geographic ranges. As illustrated by the history of *Buarremon* brush-finches, although two species may now co-occur with ecological segregation in a particular geographical setting, it is possible that these species have had quite different residence times in such setting, implying that ecological differences that allow them to coexist may have evolved *in situ* but effectively in allopatry in areas where they are currently sympatric. This scenario cannot be distinguished from evolution in real sympatry only on the basis of phylogenetic relationships, species distributions, and geographic variation in ecological traits. It follows that an additional prediction of character displacement is that differences between species evolved within a time period in which they could have been sympatric. In other words, ideally, one would like to determine not only where but also precisely *when* did ecological differences arise, especially in studies with little or no replication of areas of sympatry and allopatry. Unfortunately, however, the difficulty of obtaining precise and accurate reconstructions of trait evolution (Webster and Purvis 2002) represents a major obstacle to implementing robust tests of predictions about the timing of ecological differentiation. As probabilistic approaches for inferring the evolution of organismal traits (e.g. Huelsenbeck et al. 2003) and geographic ranges (Ree et al. 2005) continue to be developed, the current hurdles may be overcome in the not too distant future**.**

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Table 1. Estimates of the exponential growth parameter (*g*) and population size (Θ) for different sets of populations belonging to the *B. torquatus* complex and control taxa obtained using LAMARC. Values are the maximum-likelihood estimates and 95% confidence intervals (in parentheses). All estimates of *g* are greater than 0 and confidence intervals do not include 0 or negative values in some analyses, indicating that population growth or stasis cannot be rejected in favor of population declines, as predicted by the hypothesis that competition caused the ranges of populations to contract.

Taxa and Region	***n***	***g***	**Θ**
assimilis Colombia	11	348.5 (-34.4 – 879.5)	0.035 (0.011 – 0.160)
assimilis and *nigrifrons* Ecuador & Peru	19	437.5 (60.9 – 984.8)	0.041 (0.016 – 0.130)
assimilis and *nigrifrons* Colombia, Ecuador & Peru	30	411.7 (167.3 – 757.5)	0.077 (0.038 – 0.174)
atricapillus Colombia	8	96.5 (-292.5 – 507.4)	0.014 (0.004 – 0.065)
atricapillus and *tacarcunae* Colombia & Panama	10	157.1 (-124.6 – 467.1)	0.027 (0.009 – 0.102)
Control Taxa			
torquatus Bolivia	13	2158.6 (622.2 – 8876.6)	0.059 (0.007 – 120.9)
Myioborus ornatus – melanocephalus	16	483.5 (-109.4 – 1530.0)	0.017 (0.006 – 0.067)

FIGURE LEGENDS

Figure 1. (A). Frequency distribution of elevations obtained from locality records of *B. brunneinucha* from areas where it occurs in allopatry from *B. torquatus* (black bars) and areas where it occurs with it in sympatry at the landscape scale (white bars). Note the shift in the distribution towards higher elevations in sympatry. (B) Mean elevation (± 2 standard errors) of locality records (open dots) of *B. brunneinucha* and randomly placed points (black dots) in areas of allopatry and sympatry with *B. torquatus*. The magnitude of the differences between allopatry and sympatry is not significantly different for locality data and random data, as indicated by the slopes of the lines connecting mean values. (C) Elevational distributions of *B. brunneinucha* in areas where it co-occurs with *B. torquatus* and areas of allopatry. Box plots show the 5th, 10th, 25th, 50, 75th, and 90th, and 95th percentiles. The horizontal dotted line indicates the mean of the elevational range in allopatry, which shows that ranges are displaced towards higher elevations in sympatry, regardless of the relative position along mountain slopes of putative competitors. Sample sizes are shown above each box plot.

Figure 2. Maximum-likelihood tree showing relationships of major lineages of *B. brunneinucha*, *B. torquatus*, and related taxa inferred based on mitochondrial DNA sequences. Branches have been scaled to reflect time using penalized likelihood, setting the age of the deepest node to 1 (see scale). The ages of numbered nodes are discussed in the text and the confidence intervals of some are shown in Figure 3. Box plots to the right of taxon names in *B. torquatus* indicate the elevational distribution of each lineage, and whether they replace *B. brunneinucha* at low elevations (grey) or high elevations (black), or if they occur in allopatry (white). Taxon *nigrifrons* is shown in black because where it co-occurs with *B. brunneinucha* it replaces it at high elevation, but through much of this range this taxon occurs in allopatry (see text). The number of locality points on which elevational distributions are based, and the geographic distribution of each lineage, are shown to the right of box plots. The 5th and 95th percentiles (black dots) are shown only when more than 20 records are available. Data on elevational distributions of the closely allied *atricapillus* and *tacarcunae* are shown in a single plot. Note that the diversification of most South American lineages of *B. torquatus* with disparate altitudinal ranges predates the divergence between Central and South American populations of *B. brunneinucha* (an indication of its colonization time).

Figure 3. Frequency distributions of the ages of nodes estimated using penalized likelihood based on 100 bootstrap replicate data sets. Ages of nodes relevant to the colonization of South America by *B. brunneinucha* are shown in black bars and those indicating the divergence of *B. torquatus* lineages in grey. Note that none of the distributions are overlapping. However, confidence intervals are not shown for node 5 in Figure 2 (i.e., divergence between *assimilis* and *nigrifrons*), the age of which is very consistent with the timing of colonization of South America by *B. brunneinucha* (see text).

Figure 4. Two examples of Bayesian skyline plots showing population size as a function of time for members of the *Buarremon torquatus* complex inferred using the program BEAST. (a) *assimilis* + *nigrifrons* (Colombia, Ecuador, and Peru); (b) *atricapillus* (Colombia). The solid lines indicate the median estimates of population size and the shaded areas its Bayesian credibility intervals (i.e., 95% highest posterior densities). Time zero is the present, with increasing values representing time into the past. Both axes are scaled by the mutation rate. Although credible intervals are large, these plots do not suggest the population declines that would be expected if competition with *B. brunneinucha* had caused the elevational ranges of these populations to contract.

FIGURE 1

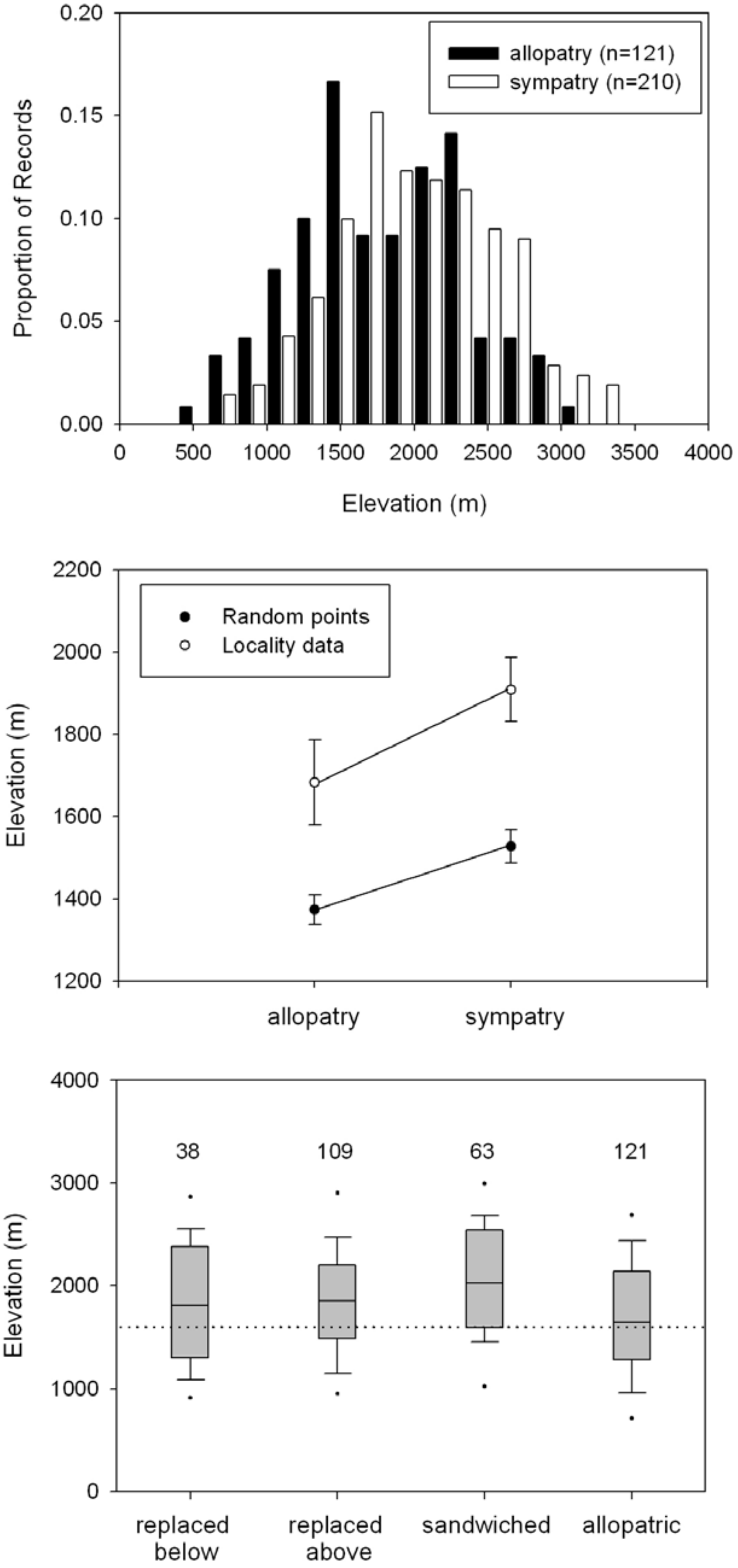

allopatry (n=121)
sympatry (n=210)
Proportion of Records
0.20
0.15
0.10
0.05
0.00
0
500
1000
1500
2000
2500
3000
3500
4000
Elevation (m)
Random points
Locality data
Elevation (m)
2200
2000
1800
1600
1400
1200
allopatry
sympatry
Elevation (m)
4000
3000
2000
1000
0
38
109
63
121
replaced below
replaced above
sandwiched
allopatric

FIGURE 2


South America
1
2
Central Panama
Mexico - West Panama
Buarremon brunneinucha
Lysurus
Arremon
Buarremon torquatus
costaricensis
14 Costa Rica - W Panama
larensis
14 W Venezuela, NE Colombia
3
poliophrys
34 C-S Peru
4
assimilis
94 Colombia - N Peru
nigrifrons
5
38 SW Ecuador - NW Peru
torquatus
26 S Peru - C Bolivia
borelli
35 S Bolivia - Argentina
phygas
10 E Venezuela
6
atricapillus
25 C Panama - Colombia
tacarcunae
basilicus
18 N Colombia
perijanus
7
11 NW Venezuela, N Colombia
1
0
0
1000
2000
3000
4000
Elevation (m)

FIGURE 3

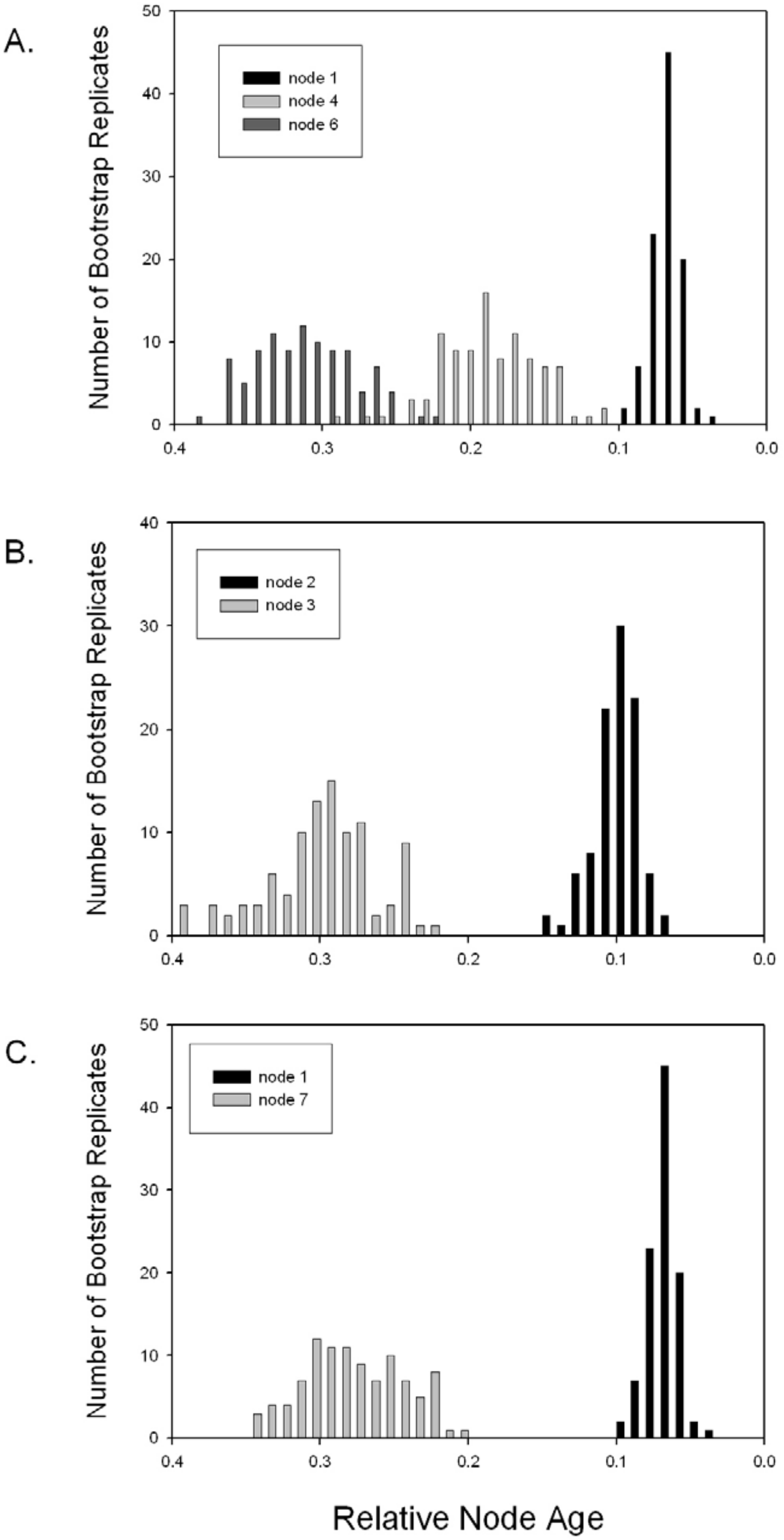
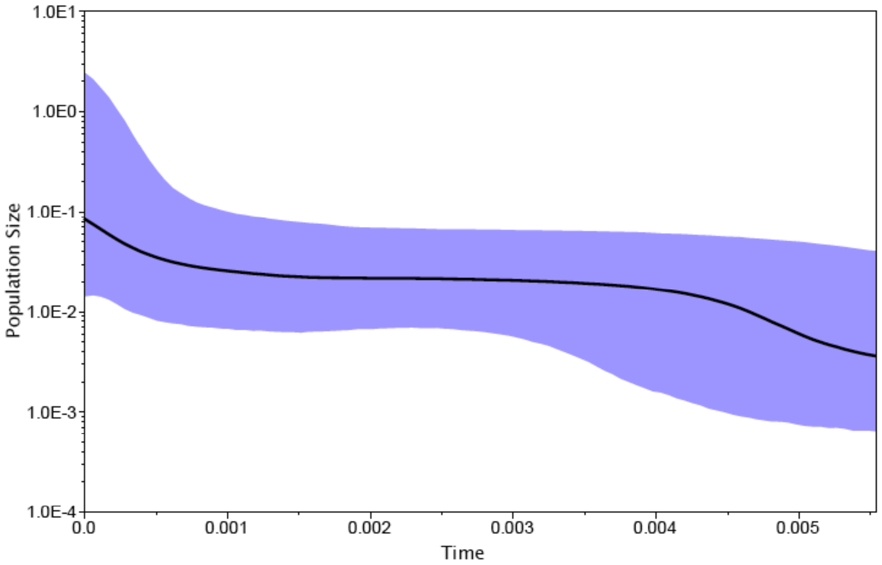
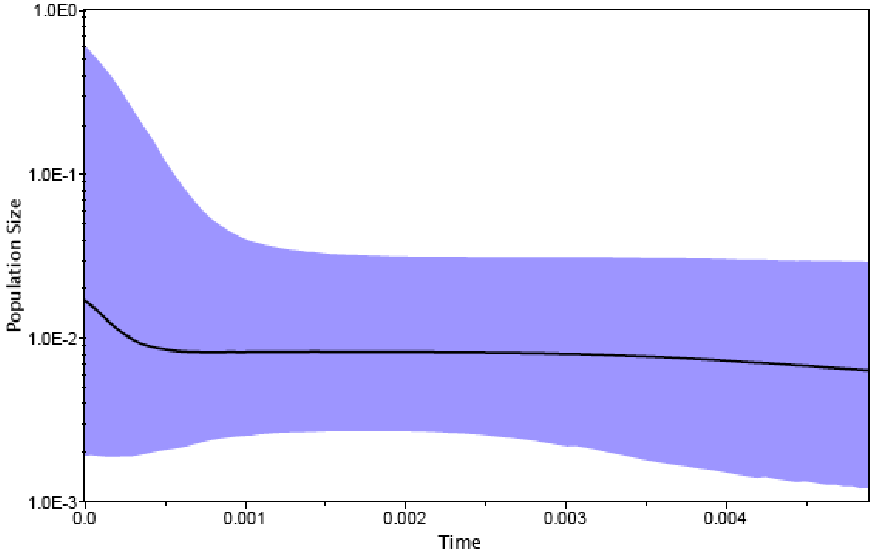

A.
Number of Bootrstrap Replicates
node 1
node 4
node 6
50
40
30
20
10
0
0.4
0.3
0.2
0.1
0.0
B.
Number of Bootstrap Replicates
node 2
node 3
40
30
20
10
0
0.4
0.3
0.2
0.1
0.0
C.
Number of Bootstrap Replicates
node 1
node 7
50
40
30
20
10
0
0.4
0.3
0.2
0.1
0.0
Relative Node Age

FIGURE 4


1.0E1
1.0E0
1.0E-1
1.0E-2
1.0E-3
1.0E-4
Population Size
0.0
0.001
0.002
0.003
0.004
0.005
Time


1.0E0
1.0E-1
1.0E-2
1.0E-3
Population Size
0.0
0.001
0.002
0.003
0.004
Time

CHAPTER 3

Limits to Elevational Distributions: Disentangling the Role of Interspecific Competition, Autoecology, and Geographic Variation in the Environment

"The only conclusion that one can draw at present from the observations is that although animal communities appear qualitatively to be constructed as if competition were regulating their structure, even in the best studied cases there are nearly always difficulties and unexplored possibilities"

G. E. Hutchinson, Concluding Remarks, p. 419.

INTRODUCTION

The idea that interspecific interactions impose limits to the spatial distribution of organisms, from patterns of habitat use at local scales to geographic ranges at the scale of large regions, is pervasive in ecology (MacArthur 1972). In particular, the influence of interspecific competition on distributions is explicitly embodied in some definitions of the ecological niche (Pulliam 2000), one of the central concepts of ecological theory (Chase and Leibold 2003). According to niche theory, competitive interactions constrain species to occupy a limited portion—the realized niche—of the full spectrum of conditions under which they could maintain populations without immigration—the fundamental niche (Hutchinson 1957).

Testing the role of interspecific competition in limiting the geographic ranges of species is challenging because experiments cannot be conducted over landscape to regional scales. Thus, researchers have traditionally relied on "natural experiments", in which distributions of species are compared in the presence and absence of putative competitors. When species' distributions along ecological gradients are narrower in the presence of competitors, ecologists have inferred competitive displacement in sympatry or competitive release in allopatry. Results of many studies of distributions over elevation gradients indicate that species often occur over wider ranges where potential competitors are absent, which suggests that interspecific competition is an important factor that creates or maintains parapatric distributions along elevational gradients (Lack and Southern 1949; Diamond 1970, 1973; Terborgh and Weske 1975; Mayr and Diamond 1976; Remsen and Cardiff 1990; Remsen and Graves 1995).

Many studies on the role of interspecific competition in limiting geographic ranges compare the position of species along gradients of a single variable selected from among all those that may impose constraints on their distributions in sympatry and allopatry. This narrow focus may be misleading, particularly when the variables examined are not the factors that directly limit species' ranges, but rather surrogates for other factors that may covary with them in complex ways. An example of one such surrogate is elevation, which in itself is not the factor that directly limits species' ranges along montane gradients. Instead, these are governed by regulators or resources (sensu Austin and Smith 1989) that covary with elevation (e.g. temperature, partial oxygen pressure, availability of particular food types) and impose limits to the fitness of organisms directly according to their physiological tolerances and ecological requirements. As is typical for indirect gradients as defined by niche theory (Austin and Smith 1989; Huston 1994; Austin 1999, 2002), the relationship between many of these factors and elevation is context-dependent. For example, although temperature declines with increasing elevation, this relationship varies with latitude, the mass of mountains, and the orientation of mountains with respect to prevailing winds. Therefore, "elevation" may pose different challenges to the performance of organisms and thus to the persistence of populations in different areas (Janzen 1967, Ghalambor et al. 2006). Consequently, the inference that expanded elevational ranges in areas of allopatry reflect a release from competition relies on the critical assumption that environments located at the same elevations in sympatry and allopatry are comparable in terms of the factors that affect organisms directly. Because previous studies have not tested this important assumption explicitly, one cannot rule out the hypothesis that expanded elevational ranges in allopatry or contracted ranges in sympatry reflect the response of organisms to geographic variation in the way in which elevation covaries with environmental conditions rather than competitive release.

In this study we present a refined approach to study the role of interspecific competition in elevational replacements that considers niche differentiation not only with reference to elevation, but also to a suite of climatic variables that likely impose limits to geographic ranges along montane slopes directly. We focus on the Neotropical brush-finches in the genus *Buarremon* (Aves, Emberizinae), whose patterns of geographic variation in elevational distributions present a compelling case for the influence of interspecific competition in limiting elevational ranges (Remsen and Graves 1995). We assess patterns of niche differentiation in *Buarremon* using ecological niche modeling (sensu Peterson 2001), an approach that characterizes species niches based on environmental variables at localities within the known range, and then projects these models onto geographic space (reviewed by Guisan and Zimmerman 2000, Elith et al. 2006). In addition, we conduct multivariate analyses that allow us to distinguish potentially limiting environmental variables that vary with elevation from others that do not. Although we have not examined all relevant niche axes, our analyses confirm that some patterns of variation in elevational distributions are consistent with predictions of the hypothesis of ecological release in allopatry. However, we also find that some patterns of ecological differentiation consistent with the hypothesis that expanded elevational ranges in allopatry are a result of competitive release have alternative, more parsimonious, explanations.

Natural history of study species

The Chestnut-capped (*Buarremon brunneinucha*) and Stripe-headed (*B. torquatus*) brush-finches are common passerine birds that inhabit the undergrowth of Neotropical montane forests. *Buarremon brunneinucha* is widely distributed from Mexico through southern Peru, whereas *B. torquatus* ranges from central Costa Rica south to northern Argentina. Based on museum specimen locality data, Remsen and Graves (1995) showed that *B. brunneinucha* and *B. torquatus* have complementary elevational distributions in areas of South America where they co-occur, and that *B. torquatus* expands its range to encompass much of the montane gradient in areas where *B. brunneinucha* is naturally absent. Cadena (Chapter 2) further compared the elevational distributions of *B. brunneinucha* between areas where it co-occurs with *B. torquatus* (i.e., central Costa Rica south through southern Peru) and areas where it occurs in allopatry (i.e., Mexico through central Costa Rica). In contrast to the patterns of elevational range expansion documented for *B. torquatus,* the elevational ranges of *B. brunneinucha* are not wider in allopatry, yet, on average, populations of this species occur at higher elevations in sympatry. Because the range shift to higher elevations by *B. brunneinucha* is consistent across areas where this species is replaced at high elevations, replaced at low elevations, and sandwiched by populations of *B. torquatus,* Cadena (Chapter 2) reasoned that the shift was not likely a consequence of competitive displacement. Instead, regional differences in elevational distributions might be better explained by an increased abundance of sites that occur at higher elevations in South America. If populations have equivalent niches, their establishment in regions that differ in the distribution of sites at different elevations would naturally lead to ranges being shifted upslope in areas where sites at higher elevations that meet niche requirements are disproportionately abundant (Chapter 2).

Although both Remsen and Graves (1995) and Cadena (Chapter 2) presented arguments that suggest elevational distributions in different areas may be considered roughly comparable to each other in terms of conditions that likely affect the distributions of *Buarremon* brush-finches directly, they did not formally address this assumption based on a broad suite of environmental variables. In fact, there are also compelling reasons why one may think elevational ranges may not be readily comparable in across different areas as a result of varying environmental conditions. Consider the three regions where populations of *B. torquatus* have remarkably expanded elevational ranges in the absence of *B. brunneinucha*. These regions correspond to (1) an ocean-facing slope of an isolated mountain massif that rises from dry lowlands in very close proximity to the Caribbean Ocean (the northern slope of the Sierra Nevada de Santa Marta in northern Colombia), (2) an area where climate is affected strongly by the Pacific Ocean, from which it is separated by a narrow stretch of xeric lowlands (the western slope of the Andes in southwestern Ecuador and northwestern Peru), and (3) the most southerly latitudes at which *B. torquatus* occurs (the Andes of Bolivia and Argentina). Environmental conditions, such as temperature and precipitation, may differ markedly between mountain slopes in these geographical settings and other slopes, such as those on the eastern versant of the Andes. Likewise, on average, the populations of *B. brunneinucha* occurring in the absence of *B. torquatus* are located at higher (i.e., more northerly) latitudes than those occurring in sympatry. In addition, all populations of *B. brunneinucha* in allopatry occur in the northern hemisphere and many of those in sympatry in the southern hemisphere, and climate is known to differ substantially between hemispheres with increasing distances from the Equator (Chown et al. 2004).

Hypotheses and Predictions

Two hypotheses may account for situations in which species have wider elevational ranges where potential competitors are absent. First, range expansions may simply reflect that the environmental conditions over which species can maintain populations occur over a broader range of elevations in areas of allopatry. We refer to this hypothesis as that of autoecology because it implies species tend to occur in similar environments throughout their ranges, tracking areas where their fundamental niches intersect with the combinations of environmental conditions that actually exist in geographic space (Jackson and Overpeck 2000, Soberón and Peterson 2005). Alternatively, expanded distributions in allopatry may reflect ecological release resulting from the absence of competitors. The predictions of these hypotheses are testable by examining the environmental conditions under which species occur in sympatry and allopatry (see also Anderson et al. 2002). If wider elevational ranges in allopatry reflect autoecology, the environmental conditions of sites occupied in these areas should be readily predictable based on those from sites located in areas where closely allied populations co-occur with potential competitors. In contrast, the hypothesis of ecological release predicts that the environmental space occupied should be wider in allopatric populations in comparison to populations potentially constrained by competition in sympatry. Furthermore, ecological release predicts that the expansion in environmental space should result from the occupation of niche space that the putative competitor occupies in sympatry. We describe specific tests of these predictions in relation to the elevational ranges of *Buarremon* brush-finches below.

MATERIALS AND METHODS

Primary Occurrence Data

We compiled primary occurrence data for *B. torquatus* and *B. brunneinucha* based on museum specimens, published reports, field records provided by several ornithologists, and observations we collected in the field. We entered data into Geographical Information Systems (GIS; ArcView 3.2, ArcGIS 9.0, ESRI) by georeferencing all available point localities using published (e.g., Paynter 1997) and internet-based (e.g., GEOnet Names Server: http://earth-info.nga.mil/gns/html/index.html) gazetteers. As a first step to verify the accuracy of georeferences, we relocated points that mapped to obviously incorrect areas (i.e., incorrect countries, provinces, or geographic regions). Following this initial screening, we cross-checked each point individually for correspondence between the elevation recorded in specimen labels or measured in the field and the elevation indicated by a digital elevation model with a 1 km by 1 km resolution (Shuttle Radar Topography Mission; http://www.jpl.nasa.gov/srtm). Georeferences for which both sources of elevation data differed by 100 m or less were left unchanged. Cases revealing discrepancies were either corrected by moving points to the nearest site matching the elevation on the specimen label or the field data if this site was within 2-3 km of the original georeference, georeferenced again and re-checked, or discarded if accurate coordinates could not be obtained. For localities lacking data on elevation, most of which were located in Mexico, we extracted the elevation for each point based on the digital elevation model and excluded from the database all those that extended beyond the known elevation range of each taxon in the region (e.g. Howell and Webb 1995). Although this approach does not guarantee records will always be mapped with maximum accuracy, it is conservative in that localities representing conditions that extend beyond those known to be part of the realized niche of populations are not considered. Finally, we randomly excluded records of the same taxon located within 1 km of one another. The final database consisted of 342 and 350 point localities for *B. brunneinucha* and *B. torquatus*, respectively. For each locality, we recorded whether it was located in areas of sympatry or areas of allopatry based on existing maps of species' distributions (Ridgely et al. 2005) and on compilations of locality data (Remsen and Graves 1995; this study). The areas from where one or the other of the species appears to be absent have been extensively sampled by ornithologists using techniques likely to lead to their detection or collection as revealed by the existence of multiple records of the other species. This suggests absences over broad areas are real and not artifacts of incomplete sampling (Anderson 2003).

Ecological Niche Modeling

We examined ecological differentiation on climatic niche space across the range of *B. torquatus* and *B. brunneinucha* based on 19 climate surfaces on a 30 arc-second resolution grid (ca. 1 km, or 0.00833 decimal degrees on the side) obtained from WorldClim version 1.2 (Hijmans et al. 2005). These surfaces reflect annual trends (e.g. mean annual temperature), seasonality (e.g. annual range in rainfall), and extreme conditions (e.g. temperature of the coldest month) in variables thought to be important in limiting species' distributions, and thus represent a closer approximation to ecological niches than elevation, which only influences distributions indirectly.

We used principal components analysis (PCA) to reduce the 19 environmental variables to a set of uncorrelated axes that we then employed as independent variables to construct ecological niche models. Recording climate data at every 1 km^2 grid cell from Mexico through Argentina would have resulted in a very large database that would have been difficult to manipulate. Instead, we sampled environmental variation across the study region (i.e., all countries where *Buarremon* species occur) by recording the values of each bioclimatic variable at 100,000 points placed at random locations. We standardized the data by transforming each climatic variable to have a mean of zero and a standard deviation of one to control for differences in the variances among variables and allow measurements made in different units to contribute equally to the analysis. We then conducted PCA on the standardized data using the FACTOR procedure in SAS version 9.1 (SAS Institute, Cary, NC). Using the eigenvector coefficients obtained in PCA, we created GIS layers that covered the whole study region for different principal component axes using the raster calculator in ArcMap. Four of these layers were then used to construct ecological niche models and predict potential distributions because they had eigenvalues that exceeded those predicted by a broken-stick model (Peres-Neto et al. 2003) and encompassed most (i.e., 91%) of the climatic variation across the study region. In addition, because locality data for some populations modeled were limited (i.e., less than 20 records), including more variables would likely have resulted in model over-fitting.

We modeled ecological niches for different taxa and populations using the DOMAIN algorithm (Carpenter et al. 1993) implemented in the program DIVA-GIS version 5.2 (http://www.diva-gis.org).

DOMAIN assigns each grid cell in the output layer the distance in environmental space (measured by the Gower [1971] metric) to the closest site in which the taxon being modeled is known to occur (Carpenter et al., 1993). Thus, the output of this algorithm can be readily interpreted as a measurement of overall environmental similarity to sites of known occurrence, and is thus consistent with niche theory (Hill and Binford 2002). Many studies employing DOMAIN to predict potential distributions consider sites to be ecologically suitable when receiving scores ≥ 95 (i.e., points not more than 5% outside the range of occupied sites). Because we do not focus on predicting potential distributions but rather on describing ecological similarity, here we follow this convention only when presenting maps of the geographic projection of niche models or for display purposes in graphs, but treat DOMAIN scores as a continuous variable that measures ecological similarity to sites of known occurrence.

We used ecological niche modeling to test the predictions of autoecology and ecological release for the four cases of elevational range expansions or shifts in allopatry mentioned above, namely those involving populations of B. *torquatus* in the Sierra Nevada de Santa Marta, the Pacific Andean slope, and the Andes of Bolivia and Argentina, and populations of *B. brunneinucha* occurring from Mexico to central Costa Rica. For each of these “target” populations, we constructed two different ecological niche models that served to evaluate the predictions of each hypothesis, one based on localities of conspecific populations occurring in sympatry with the putative competitor, and one based on localities of the putative competitor from areas of sympatry (see Table 1). We projected models onto geographic space, and then recorded the DOMAIN score on each model at all the points of occurrence of the target populations. This resulted in data sets in which all localities of the target allopatric populations (e.g. *B. torquatus* in Bolivia and Argentina) were associated with two DOMAIN scores, one indicating environmental similarity to sites occupied by a population of the same species occurring in sympatry with the putative competitor (e.g. *B. torquatus* populations occurring in sympatry with *B. brunneinucha* along the East Andes) and one indicating environmental similarity to sites occupied by the putative competitor (e.g. *B. brunneinucha* in areas of sympatry). We compared these scores for each target population using paired t-tests: significantly higher scores on the model constructed for the conspecific population would support the hypothesis of autoecology and significantly higher scores for the heterospecific one would support ecological release. This test was somewhat inconclusive for the case involving populations of *B. brunneinucha* in sympatry and allopatry (see below). Therefore, we also projected the model based on data from localities in allopatry onto the area of sympatry, where we recorded the score at each locality of occurrence. This allowed us to further evaluate the two competing hypotheses by examining the scores of sites in sympatry based on the model constructed with data from allopatry and vice versa. If the shifted range towards higher elevations in sympatry reflects competitive displacement, sites at higher elevations in sympatry should receive lower scores in the model based on data from allopatry (i.e., a regression between elevation and model scores would have a negative slope), and sites at lower elevations in allopatry should receive lower scores in the model based on data from sympatry (i.e., a regression between elevation and model scores would have a positive slope). Alternatively, if the shift reflects autoecology, there should be no relation between elevation and model scores (i.e., slopes should not differ from zero).

Principal Components Analysis

The projection of ecological niche models onto geographic space allows one to determine whether environments where allopatric populations occur resemble more closely those occupied by individuals of the same species elsewhere or those occupied by the species that is a putative competitor, thereby allowing one to tease apart the role of autoecology and ecological release in creating expanded elevational distributions in allopatry. However, models do not readily indicate which climatic variables contribute most to overall assessments of differences and similarities in the environments populations experience in different areas. We pursued this question examining climatic variation using PCA. Instead of using the principal component GIS layers we created for ecological niche modeling, we conducted a new PCA with varimax rotation in which we included only climatic data for all the localities where *B. torquatus* and *B. brunneinucha* are known to occur. This focused PCA allowed us to visualize variation in climatic niches more clearly by plotting the scores of each of the point localities along different axes of environmental variation.

RESULTS

Buarremon torquatus in the Sierra Nevada de Santa Marta

The elevational range of the population of *B. torquatus* occurring in the Sierra Nevada de Santa Marta (*B. t. basilicus*) is one of the widest among all taxa that comprise the *B. torquatus* complex, ranging from c. 500 m to 3000 m. Ecological niche modeling shows that all of the localities where *B. t. basilicus* is known to occur are climatically similar to sites where *B. brunneinucha* is found elsewhere. All localities of *B. t. basilicus* received higher DOMAIN scores on the model constructed for *B. brunneinucha* (mean score ± SD: 98.3 ± 1.9) than on the model based on localities of *B. t. perijanus* and *B. t. larensis* (79.4 ± 15.1) despite the fact that the latter populations occur in close proximity to the Sierra Nevada. Mean scores on the *B. brunneinucha* model were significantly higher (t=5.62, 17 df, P < 0.0001), and were always greater than 95%, whereas none of the scores on the *B. torquatus* model reached this value (Figure 1). These results are consistent with the hypothesis that *B. t. basilicus* occurs over a broad elevational range by filling ecological space occupied elsewhere by *B. brunneinucha,* not by tracking conditions under which conspecific populations occur elsewhere.

Buarremon torquatus **on the Pacific Andean Slope**

On the Pacific slope of the Andes of southern Ecuador and northwestern Peru, *B. torquatus nigrifrons* occurs over a wide range of elevations, and extends to lowland areas that its sister taxon (*B. t. assimilis*) never occupies. DOMAIN scores recorded at the localities of occurrence of *B. t. nigrifrons* were significantly higher (t=5.4, 36 df, P < 0.0001) on the model constructed based on *B. brunneinucha* locality data (96.2 ± 4.0) than on the model based on records of *B. t. assimilis* from Colombia, Ecuador, and Peru (88.9 ± 9.2). Moreover, the environmental conditions at all eight localities of *B. t. nigrifrons* below the lower elevational limit of *B. t. assimilis* were more similar to those of sites occupied by *B. brunneinucha* where it co-occurs with *B. torquatus* than to sites occupied by *B. t. assimilis* (Figure 2). Again, these data indicate that the expanded elevational range of *B. t. nigrifrons* may in fact reflect release from interspecific competition with *B. brunneinucha.*

Buarremon torquatus **in Bolivia and Argentina**

Ecological niche models indicate that localities of occurrence of *B. torquatus* in the Andes of Bolivia and Argentina are environmentally more similar to sites occupied elsewhere by *B. brunneinucha* (90.1± 7.1) than to sites occupied by *B. torquatus* along the eastern slope of the Andes in areas where it co-occurs with *B. brunneinucha* (83.1 ± 11.4). Although mean DOMAIN scores differed significantly between models (t=10.7, 83 df, P < 0.001), scores on both models in this region were generally low in comparison to those obtained in analyses of other target populations. This suggested the possibility that neither hypothesis (i.e., autoecology nor ecological release) might be the best explanation for the expanded elevational range of *B. torquatus* in the region, which prompted us to examine the data in more detail.

Plotting the elevation of occurrence records of *B. torquatus* along the eastern slope of the Andes with respect to latitude confirms the pattern documented by Remsen and Graves (1995) based on a partly non-overlapping data base (Figure 3a). *Buarremon torquatus* ranges to substantially lower elevations south of the Peru-Bolivia border (ca. 15° S), and this elevational range expansion coincides with the absence of *B. brunneinucha,* which replaces it at lower elevations from Colombia through southern Peru along this slope, but is absent from Bolivia and Argentina. However, niche models indicate that the environments to which *B. torquatus* expands in Bolivia and Argentina are distinct from those that are occupied by *B. brunneinucha* in areas where both species co-occur with elevational segregation. Of a total of 32 localities in which *B. torquatus* occurs at elevations that are below those known from areas where it co-occurs with *B. brunneinucha,* only 4 correspond to sites that DOMAIN classified as climatically suitable for the latter species (i.e., sites receiving scores ≥ 95%), all of which are located at elevations that are within 100 m of the lowest record of *B. torquatus* in areas of sympatry (Figure 3a). This result is insensitive to the cutoff value applied to discriminate between suitable and unsuitable sites for *B. brunneinucha* in the DOMAIN model: a strong correlation between latitude and DOMAIN model scores is readily apparent (Figure 3b). Similar patterns (i.e., decreased environmental similarity to sites of known occurrence with increasing latitude) are observed based on the niche model constructed with data from the range of *B. torquatus* (not shown). These data suggest that the expansion of the elevational range of *B. torquatus* in Bolivia and Argentina to lower elevations cannot be explained satisfactorily based on the hypotheses of autoecology or ecological release because the environments to which the species expands at these latitudes are not similar to those occupied by either *B. brunneinucha* or *B. torquatus* in areas of sympatry.

Buarremon brunneinucha **in allopatry and sympatry**

Sites where *B. brunneinucha* occurs in allopatry from *B. torquatus* are significantly more similar (t=6.84, 115 df, P < 0.0001) to sites occupied by this species in areas where it is sympatric with *B. torquatus* (95.8 ± 3.7) than to the sites that *B. torquatus* occupies in areas of sympatry (93.9 ± 4.6). However, differences in scores between the two models are not as marked as in other cases and biologically do not seem very compelling. Thus, we believe that this comparison is insufficient to favor the hypothesis of autoecology, which we explore further below.

The vast majority of localities in areas of allopatry were classified as environmentally suitable (DOMAIN scores ≥95%) by the model constructed based on data from sympatry, and vice versa (Figure 4a) indicating the species occurs in very similar environments in both parts of its range. Although the model from allopatry performed less well in characterizing the environmental characteristics under which the species occurs in sympatry (scores under 90% were more frequent in this model), all localities from sympatry receiving low scores on the model from allopatry occur at rather low elevations (Figure 4b), which is contrary to what would have been expected if the shift to higher elevations in sympatry were the result of competition. Moreover, the slopes of regressions between elevation and DOMAIN scores are not different from zero in either sympatry (slope ± SE = 0.002 ± 0.001) or allopatry (0.001 ± 0.001), which implies that the shift to higher elevations in sympatry is fully consistent with the hypothesis of autoecology.

Principal Components Analysis

PCA reduced the variation in climate that *Buarremon* brush-finches experience across their ranges to a small set of independent axes of environmental variation, and allowed us to distinguish sets of potentially limiting climatic variables that correlate with elevation from sets that do not. Indeed, although elevation was not included in the analyses, scores along the first principal component, which accounted for 38% of the climatic variation, correlate tightly with elevation (Figure 5a). High scores along this axis indicate high values for annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, and mean temperatures of the wettest, driest, warmest, and coldest quarters. The second axis accounted for 33% of the variation, and has a remarkable correspondence with latitude (Figure 5b). High scores reflect high values of mean diurnal range in temperature, temperature seasonality, and temperature annual range, and low values of isothermality. The third axis accounted for 13% of the variation; high values reflect high annual precipitation, precipitation during the wettest month, and precipitation during the wettest and warmest quarters. Finally, the fourth axis explained 7% of the variation; scores correlate positively with precipitation during the driest month, driest quarter, and coldest quarter, and negatively with precipitation seasonality.

Examining the positions of populations along axes of climatic variation allows us to interpret the results from ecological niche modeling. Based on scores along the first principal component, populations of *B. torquatus* occurring in Bolivia and Argentina indeed appear to occupy environments that are intermediate between those occupied by lowland and highland populations of *B. torquatus* and resemble closely those occupied by *B. brunneinucha* (Figures 6a, 6c). However, the positions along the second principal component clearly indicate that sites in the region occupied by *B. torquatus* are characterized by environmental conditions that are not experienced by *B. brunneinucha* anywhere on the part of its range where it co-occurs with *B. torquatus* (Figure 6c). It is also worth noting that the range of variation in climatic variables that correlate with elevation (i.e., principal component 1) over which Bolivian and Argentinean populations occur is not nearly as wide in comparison to that of other populations as a cursory examination of elevational distributions would suggest (contrast elevation range and PC1 range in Figures 6e and 6f). Also, the range of environmental conditions in which these populations occur is rather limited compared to others in other dimensions of climatic space (i.e., principal components 3 and 4, Figure 6b).

Patterns of variation in environmental space occupied by populations of *B. brunneinucha* have similar interpretations. First, the discrepancy in the mean elevational distributions in sympatry and allopatry becomes less pronounced when these populations are plotted along the first principal component of climatic variation (Figure 6e, 6f). Second, the reduced ability of the model from allopatry to establish environmental suitability in sympatry very likely results from the changing climatic conditions with latitude; the localities receiving lower scores on the DOMAIN model (Figure 4b) are those with higher values along the second principal component (Figure 6c).

DISCUSSION

Ecological niche modeling and multivariate analyses of the climatic conditions under which different populations of *Buarremon* brush-finches occur support the predictions of competitive release for some populations occurring in allopatry from competitors but not for others. In the Sierra Nevada de Santa Marta and the Pacific slope of the Andes of southern Ecuador and Peru, the elevational expansion of the range of *B. torquatus* indeed results in the occupation of areas of niche space that *B. brunneinucha* occupies in areas of coexistence, and is not consistent with the hypothesis that range expansion is a result of tracking geographic variation in the elevations at which favored conditions occur. On the other hand, attributing the wide elevational range of *B. torquatus* in areas of Bolivia and Argentina to release from competition with *B. brunneinucha* is untenable because the environments to which the species expands are not equivalent to those occupied by its potential competitor in areas of sympatry. Finally, the shift towards higher elevations of populations of *B. brunneinucha* occurring in sympatry with *B. torquatus* is not likely to be a consequence of the presence of the competitor, but is consistent with tracking environmental suitability. This pattern, in combination with the apparent differences in the availability of sites at different elevations between areas of sympatry and areas of allopatry (Chapter 2), suggests that the elevational range of *B. brunneinucha* was most likely not influenced by competition with *B. torquatus* as it encountered this species following its southward range expansion from areas of northern Central America (Chapter 2). This implies that there is no support for the hypothesis that elevational replacements in this group arose as a consequence of reciprocal contractions in the ranges of both species resulting from interspecific competition (Diamond 1973).

Examining geographic variation in the elevational distributions of species is relatively straightforward, which explains why this has been one of the dimensions of geographic ranges on which researchers have placed most emphasis when addressing the role that interspecific interactions may play in constraining species' niches and spatial distributions. That elevation is an indirect gradient that affects organisms only through its influence on regulators and resources with which it covaries in different ways in different areas (Austin and Smith 1989, Huston 1994) implies that some of the studies that assumed elevational distributions are comparable across geographic regions may have reached spurious conclusions. Some readers may interpret our results as showing this is not necessarily true because much of the climatic variation is captured by a linear combination of climatic variables that correlate tightly with elevation. However, concluding that elevation is a good surrogate for variation in several climatic variables that likely affect organisms directly from our data has two rather serious caveats. First, the reasoning that the correlation of many climatic variables and elevation implies the latter is a proper surrogate for climatic variation is circular because the climate surfaces we employed are the result of interpolations based on a digital elevation model (Hijmans et al. 2005); thus, such reasoning can only be made rigorously on the basis of non interpolated climate data. Second, because the correlation between elevation and climatic variables is not perfect (i.e., r^2 does not equal 1.0, Figure 5a), the slopes of the relationship between elevation and climatic axes (e.g. principal component 1) may differ substantially among different geographic areas.

Of course, the correlation between elevation and some climatic variables is not at all surprising. More importantly, our results illustrate patterns related to the interaction between elevation, climatic variation, and species' distributions that are not as widely appreciated. Foremost, our analyses show clearly that from the perspective of some environmental variables that likely limit species' distributions directly, elevation may mean very different things in different areas. The most striking effect in this regard we observed was that of latitude. Clearly, ecologists have long been aware that the relationship between elevation and climate varies with latitude (e.g., Janzen 1967), but we emphasize that the lack of consistent "meaning" for elevation does not only manifest itself over broad spatial scales and need not involve variation in latitude. For example, ecological niche modeling shows that environments in the Sierra Nevada de Santa Marta are quite distinct from those in the adjacent Serranía de Perijá and the Andes of northeast Colombia and west Venezuela (Figure 1b). Although there are many sites at the same elevations in both areas, the conditions at these sites are rather different, as shown by the rather limited areas of potential habitat identified for *B. t. perijanus* and *B. t. larensis* in Santa Marta. That elevation may mean different things in different areas even over relatively small geographic scales implies that some of the classic examples of competitive displacement and competitive release along elevational gradients (e.g. Diamond 1973, Terborgh and Weske 1975) may need to be re-evaluated.

A related issue is that the occurrence of a population over a wide elevational range does not necessarily imply that it occurs over a broader range of environmental conditions than a population with a more restricted elevational range. For example, although the elevational range of populations of *B. torquatus* in Bolivia and Argentina as a whole is certainly much wider than that of populations occurring in sympatry at the landscape scale with *B. brunneinucha,* the differences in ecological amplitude among regions do not appear nearly as large when they are considered in terms of the climatic variables that correlate with elevation (i.e., principal component 1, Figure 6e, f). In this particular case, this pattern most likely reflects that the elevational distribution of *B. torquatus* is not consistent through Bolivia and Argentina: with increasing latitudes, the species' range as a whole is displaced to lower elevations (Figure 3a). Indeed, at any given latitude, the elevational range of *B. torquatus* does not appear to be any wider than that of populations occurring in sympatry with *B. brunneinucha.* This suggests that the rationale for proposing that populations in Bolivia and Argentina encompass a wider range of elevations as a result of competitive release (Remsen and Graves 1995) was incorrect to begin with.

More generally, our analyses show that niche breadth along one axis of ecological differentiation may say very little about niche breadth along other axes (e.g. contrast the large range of environmental conditions occupied by Bolivian-Argentinean populations along principal components 1 and 2 and the narrow ranges along principal components 3 and 4; Figure 6). Therefore, although elevation is indeed a valid surrogate for important ecological variation, this variable may be uninformative about differentiation along other niche axes that may be just as important descriptors of the ecology of different populations. The implications are twofold. On one hand, examining elevational ranges by themselves will often be insufficient to ascertain whether the expansion of elevational ranges of populations in allopatry represents an expansion to occupy the same environmental space that populations of competitors occupy in areas of sympatry. On the other, the observation that populations occurring with and without competitors have similar elevational distributions does not imply that the two species do not impose limits to each other's geographic ranges in areas where their distributions come into contact. Elevation is perhaps the easiest dimension of niche space to examine, but there is no reason why ecological displacement and ecological release cannot occur along direct climatic gradients that are uncorrelated with elevation (e.g. Melville et al. 2002).

In describing the hypotheses that could account for expanded elevational ranges in the absence of competitors we only mentioned those of ecological release and autoecology. Our analyses reveal the importance of a third hypothesis that we suspect is likely to apply in many other similar situations: geographic variation in the realized environment (sensu Jackson and Overpeck 2000, see also Ackerly 2003, Peterson and Holt 2003). For example, populations of *B. torquatus* occur over a wide elevational range in Bolivia and Argentina, an apparent niche expansion that entails the occupation of areas of environmental space that simply do not exist throughout the rest of the distribution range of this species. Thus, the wide elevational range of *B. torquatus* in the region cannot be explained on the basis of the hypotheses of autoecology or ecological release. Patterns such as this may reflect either adaptive evolution of fundamental niches as populations encounter varying environmental conditions across their ranges (see Holt 2003), or simply a more complete expression of the realized niche that is not possible anywhere else owing to patterns of geographic variation in the environment; distinguishing these two alternatives requires experimental work (Kearney and Porter 2004). It follows that contrary to claims repeatedly made in the literature (e.g. Peterson et al. 1999, reviewed by Soberón and Peterson 2005), ecological niche models are unlikely to approximate species' fundamental niches. In addition, we suggest that the use of ecological niche modeling or multivariate analyses of climatic data to test ecological and evolutionary hypotheses about ecological niches across geography (e.g. Peterson et al. 1999, Anderson et al. 2002, Peterson and Holt 2003, Rice et al. 2003, Hoffmann 2005) should involve a characterization of the combinations of environmental conditions that actually exist in different geographic regions. For instance, in a novel study integrating ecological niche modeling with phylogenetics to study modes of speciation, Graham et al. (2004) concluded that most speciation events involve both geographic isolation and ecological differentiation because sister species are typically allopatric and occur in climatically different environments. Without information on whether climatically similar environments in fact exist in sympatry and allopatry, it is unclear whether the correlation between ecological divergence and speciation is causal, or rather a fortuitous byproduct of a correlation between geographic distance and environmental dissimilarity.

Finally, our analyses assume that the climatic variables we considered act as direct gradients (sensu Austin and Smith 1989) that affect the distributions of populations along elevational transects through direct effects on the performance of organisms. This assumption has been well-established by functional studies (e.g. Porter et. al 2002, Navas 2003, Altshuler and Dudley 2006), implying that our approach is closer to characterizing ecological niches than that of studies that only consider elevation, a variable that affects organisms only indirectly. However, climatic variables influence elevational distributions indirectly as well. For example, variables such as temperature, precipitation, and evapotranspiration influence vegetation structure (see Holdridge 1967), which in turn is often an important proximate correlate of species' distributions. Just as the relationship between elevation and climate is context-dependent, the relationship between elevation, climate, and vegetation is unlikely to be the same everywhere. Therefore, it is important to bear in mind that geographic variation in elevational distributions may arise if organisms track relevant attributes of niche dimensions that cannot be predicted precisely only based on climatic data, a possibility that our analyses do not address. Nevertheless, this further illustrates the importance of distinguishing variables that affect species' distributions directly from those that do not, and cautions against using elevation uncritically as a dimension of ecological niches.

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Table 1. Populations of *Buarremon* with expanded or shifted elevational ranges in areas where competitors are absent and populations used to construct models that allowed testing the hypotheses of autoecology and ecological release in each case.

	Population or taxa modeled	
Target populations with expanded or shifted elevational range in allopatry	**Autoecology hypothesis**	**Ecological release hypothesis**
B. torquatus basilicus Sierra Nevada de Santa Marta (N Colombia)	*B. t. perijanus* and *B. t. larensis*[1] (NE Colombia – NW Venezuela)	*B. brunneinucha* in sympatry with *B. torquatus* (central Costa Rica – Peru)
B. torquatus nigrifrons Pacific Slope of the Andes (Ecuador – Peru)	*B. t. assimilis*[2] (Ecuador – Peru)	*B. brunneinucha* in sympatry with *B. torquatus* (central Costa Rica – Peru)
B. t. torquatus, B. t. fimbriatus, and *B. t borelli* (Bolivia – Argentina)	*B. torquatus* East slope (Colombia – Peru)	*B. brunneinucha* in sympatry with *B. torquatus* (central Costa Rica – Peru)
B. brunneinucha, several subspecies (Mexico – central Costa Rica)	*B. brunneinucha* in sympatry with *B. torquatus* (central Costa Rica – Peru)	*B. torquatus* in sympatry with *B. brunneinucha*[3] (central Costa Rica – Peru)

(1) These populations occur in sympatry with *B. brunneinucha* and are those in closest geographic proximity to the Sierra Nevada de Santa Marta. Also, mitochondrial sequence data (Chapter 2) indicates *B. t. perijanus* is the sister taxon of *B. t. basilicus.*

(2) This taxon is very closely allied to *B. t. nigrifrons* (i.e., they are each others closest relatives and have not attained reciprocal monophyly in mtDNA; Chapter 2) and occurs in sympatry with *B. brunneinucha.*

(3) The populations of *B. torquatus* considered are only those that occur in sympatry with *B. brunneinucha* in the region: *costaricensis, tacarcunae, atricapillus, assimilis, larensis, perijanus, phaeopleurus,* and *poliophrys* (*basilicus, phygas, nigrifrons, torquatus, fimbriatus* and *borelli* are not included).

FIGURE LEGENDS

Figure 1. Geographic projections onto the Sierra Nevada de Santa Marta of ecological niche models constructed for (A) *B. brunneinucha* and (B) populations of *B. torquatus* occurring in the Serranía de Perijá and the Eastern Andes of northeast Colombia and west Venezuela. Points are the localities of known occurrence of *B. torquatus* in the region and shaded areas indicate grid cells receiving DOMAIN scores ≥95%. Models classify extensive areas as suitable for *B. brunneinucha*, but only limited areas for the *B. torquatus* taxa, and all localities match sites of predicted presence of *B. brunneinucha*, not of *B. torquatus.*

Figure 2. Scores obtained by overlaying localities of known occurrence of *B. torquatus nigrifrons* on the Pacific slope of the Andes of southern Ecuador and northern Peru onto ecological niche models constructed based on locality data for *B. brunneinucha* (black dots) and *B. torquatus assimilis*, its sister taxon occurring through Colombia, Ecuador, and northern Peru (white dots). The vertical dotted line shows the lower elevational limit of *B. t. assimilis* where it co-occurs with *B. brunneinucha*, and the horizontal line indicates the 95% threshold of environmental similarity. Note that DOMAIN scores for all localities of *B. t. nigrifrons* under the lower elevational limit of *B. t. assimilis* in sympatry are higher on the model based on locality data from *B. brunneinucha.* Some localities at higher elevations received equal scores on both models; in these cases points overlap, but only those on the *B. t. assimilis* model are shown.

Figure 3. (A) Elevational distribution of *B. torquatus* with respect to latitude along the eastern slope of the Andes, from Colombia to northern Argentina. The vertical line indicates the approximate latitude marking the southern limit of the distribution of *B. brunneinucha* and the horizontal line the lowest elevation at which *B. torquatus* is known to occur in this slope in areas where it co-occurs with *B. brunneinucha.* Dots are colored according to whether they are above (white) or below (black) the 95% environmental similarity threshold according to the ecological niche model constructed based on locality data for *B. brunneinucha*. Note that all sites at which *B. torquatus* occurs at high latitudes and low elevations are classified as unsuitable for *B. brunneinucha* by the model. (B) Positive relationship between elevation and environmental similarity to sites where *B. brunneinucha* occurs for records of *B. torquatus* from the eastern slope of the Andes, indicating its expansion to lower elevations does not reflect the occupation of environments occupied by its potential competitor in areas of sympatry.

Figure 4. (A) Frequency distribution of similarity scores of records of *B. brunneinucha* from areas of sympatry to models constructed based on data from allopatry (white bars) and vice versa (black bars). Note that in both cases the majority of records are at or above 95%, indicating the environments occupied by the species in sympatry and allopatry are similar. However, sites receiving scores ≤ 90% are more common for localities in sympatry. (B) Lack of relationship between elevation and the environmental similarity of records of *B. brunneinucha* from areas of sympatry to models constructed based on data from allopatry (white dots) and vice versa (black dots). Box plots show the shift in distribution to higher elevations in sympatry.

Figure 5. Relationships between the first two principal components of climatic variation observed at localities of occurrence of *B. torquatus* and *B. brunneinucha* and elevation (A) and latitude (B).

Figure 6. Results of principal components analyses of climatic variation observed at localities of occurrence of *B. torquatus* and *B. brunneinucha.* Panes (A) through (D) show the positions in environmental space along the first four principal components of different populations (note that the scale of the first component has been inverted to indicate increasing elevations from left to right). In (A) and (B), grey circles correspond to localities of *B. torquatus* in Bolivia and Argentina, and white

and black circles to localities of this species from areas where it replaces *B. brunneinucha* at low and high elevations, respectively. White and black squares in (C) and (D) are localities where *B. brunneinucha* occurs in allopatry and sympatry with *B. torquatus*, respectively. Panes (E) and (F) illustrate that differences among populations in elevational ranges are more pronounced than differences in the actual range of climatic conditions that correlate with elevation (i.e. principal component 1) under which these populations occur.

FIGURE 1

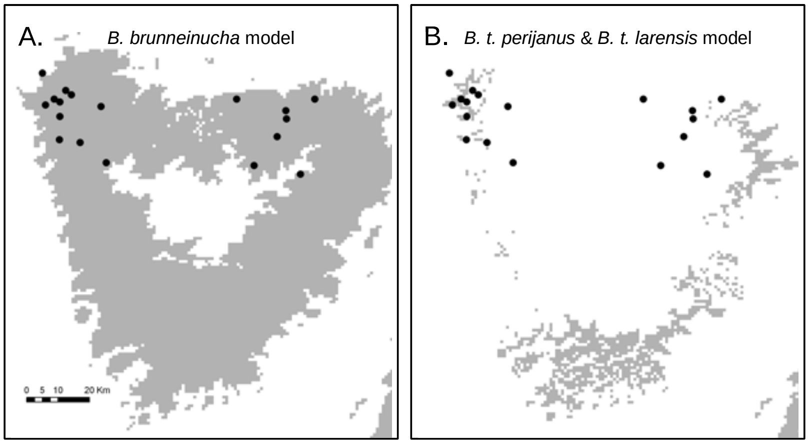

A.
B. brunneinucha model
0 5 10 20 Km
B.
B. t. perijanus & *B. t. larensis* model

FIGURE 2

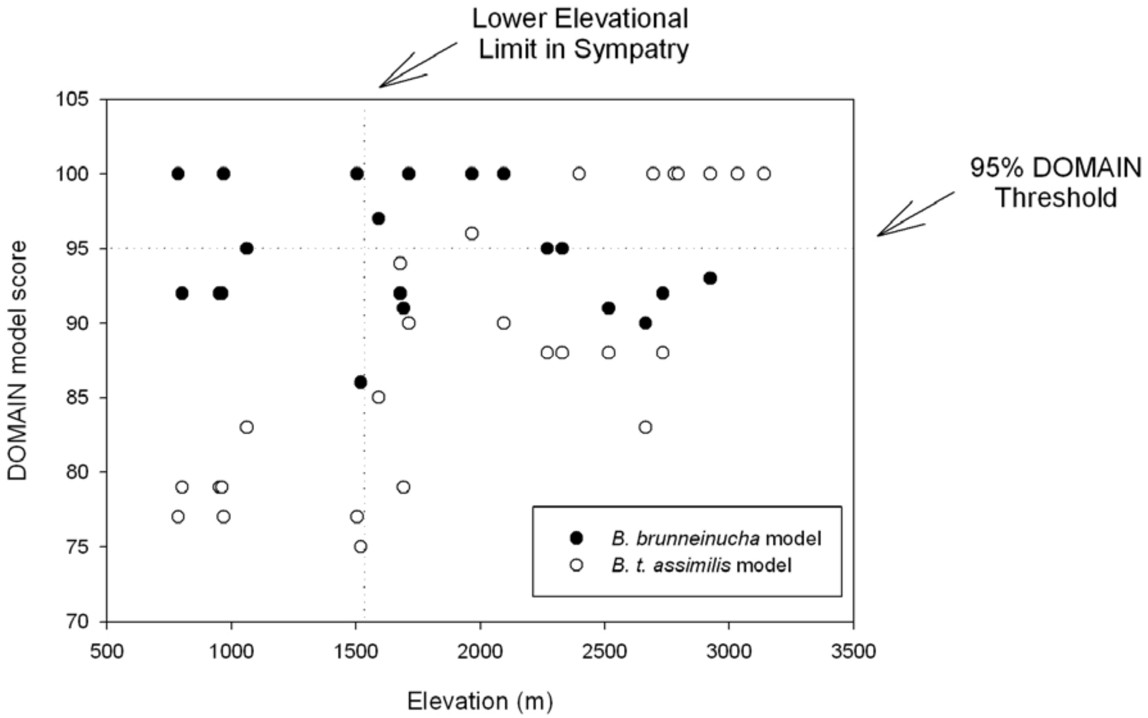

Lower Elevational Limit in Sympatry
95% DOMAIN Threshold
DOMAIN model score
105
100
95
90
85
80
75
70
Elevation (m)
500
1000
1500
2000
2500
3000
3500
● *B. brunneinucha* model
○ *B. t. assimilis* model

FIGURE 3

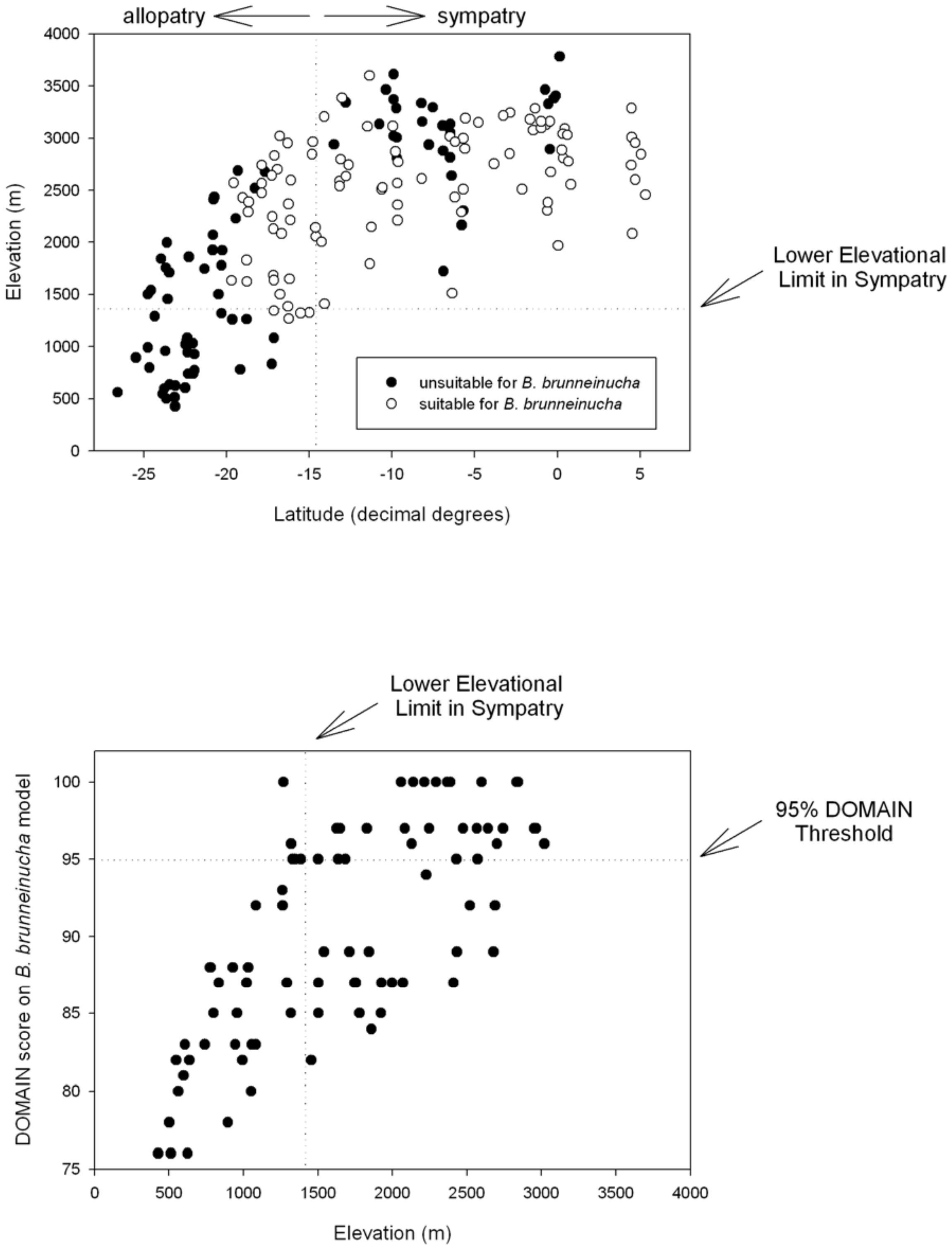

allopatry
sympatry
Elevation (m)
4000
3500
3000
2500
2000
1500
1000
500
0
-25
-20
-15
-10
-5
0
5
Latitude (decimal degrees)
unsuitable for *B. brunneinucha*
suitable for *B. brunneinucha*
Lower Elevational Limit in Sympatry
Lower Elevational Limit in Sympatry
95% DOMAIN Threshold
DOMAIN score on *B. brunneinucha* model
100
95
90
85
80
75
0
500
1000
1500
2000
2500
3000
3500
4000
Elevation (m)

FIGURE 4

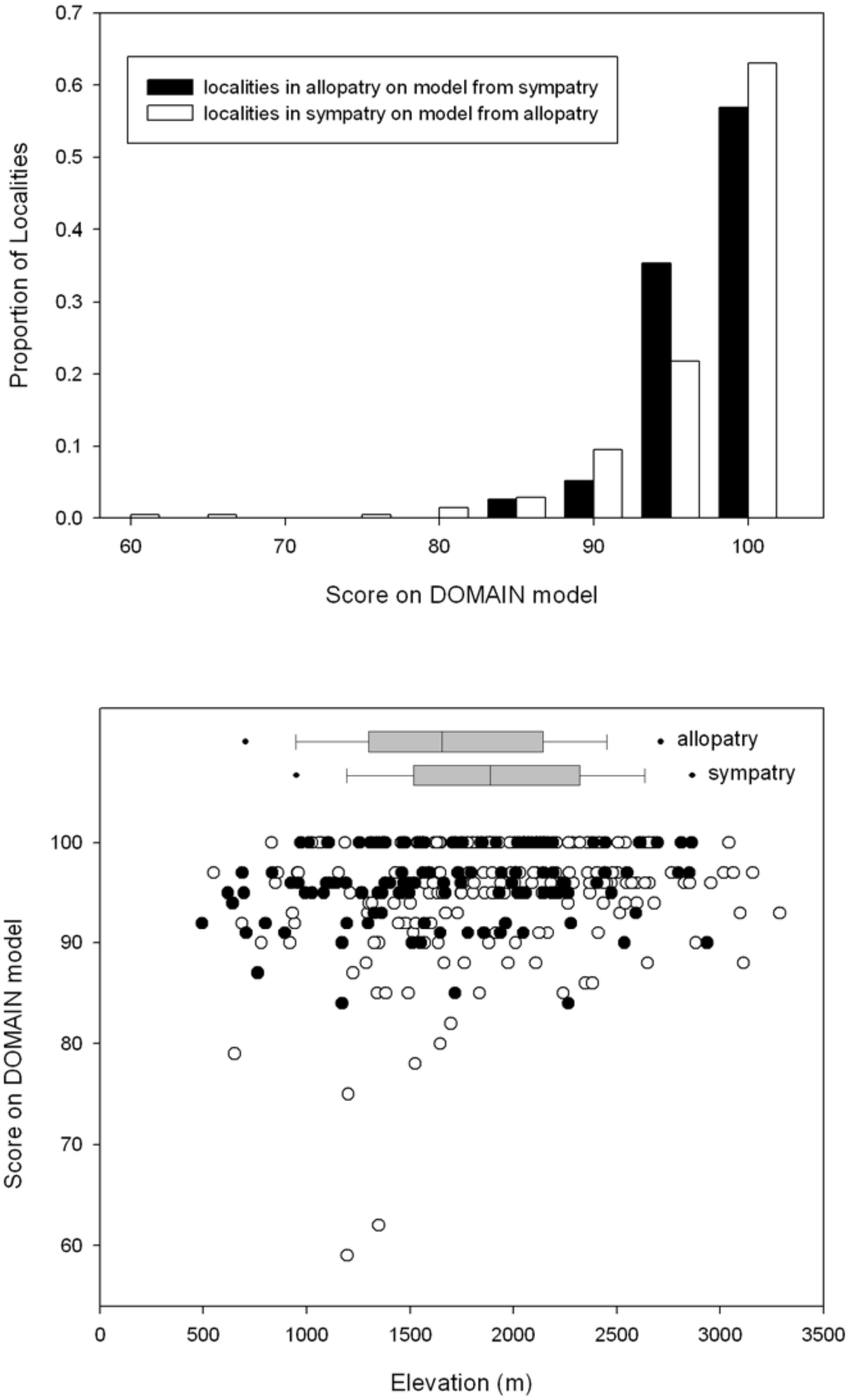

0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Proportion of Localities
localities in allopatry on model from sympatry
localities in sympatry on model from allopatry
60
70
80
90
100
Score on DOMAIN model
allopatry
sympatry
100
90
80
70
60
Score on DOMAIN model
0
500
1000
1500
2000
2500
3000
3500
Elevation (m)

FIGURE 5

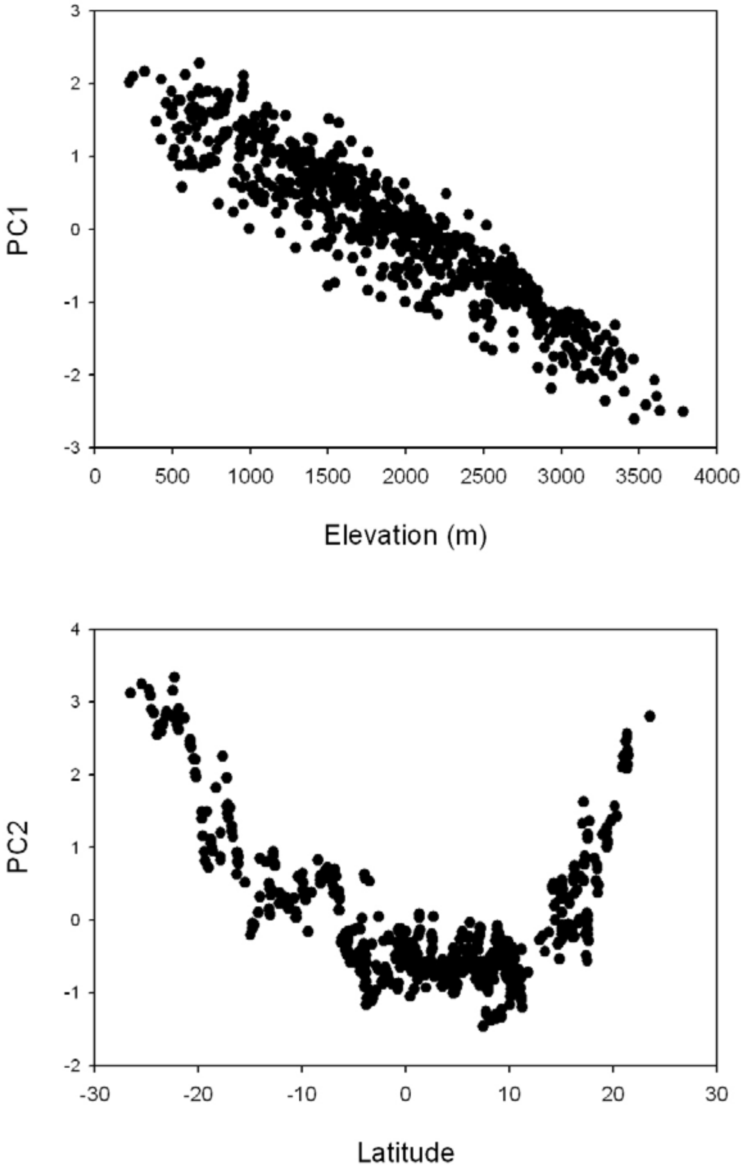
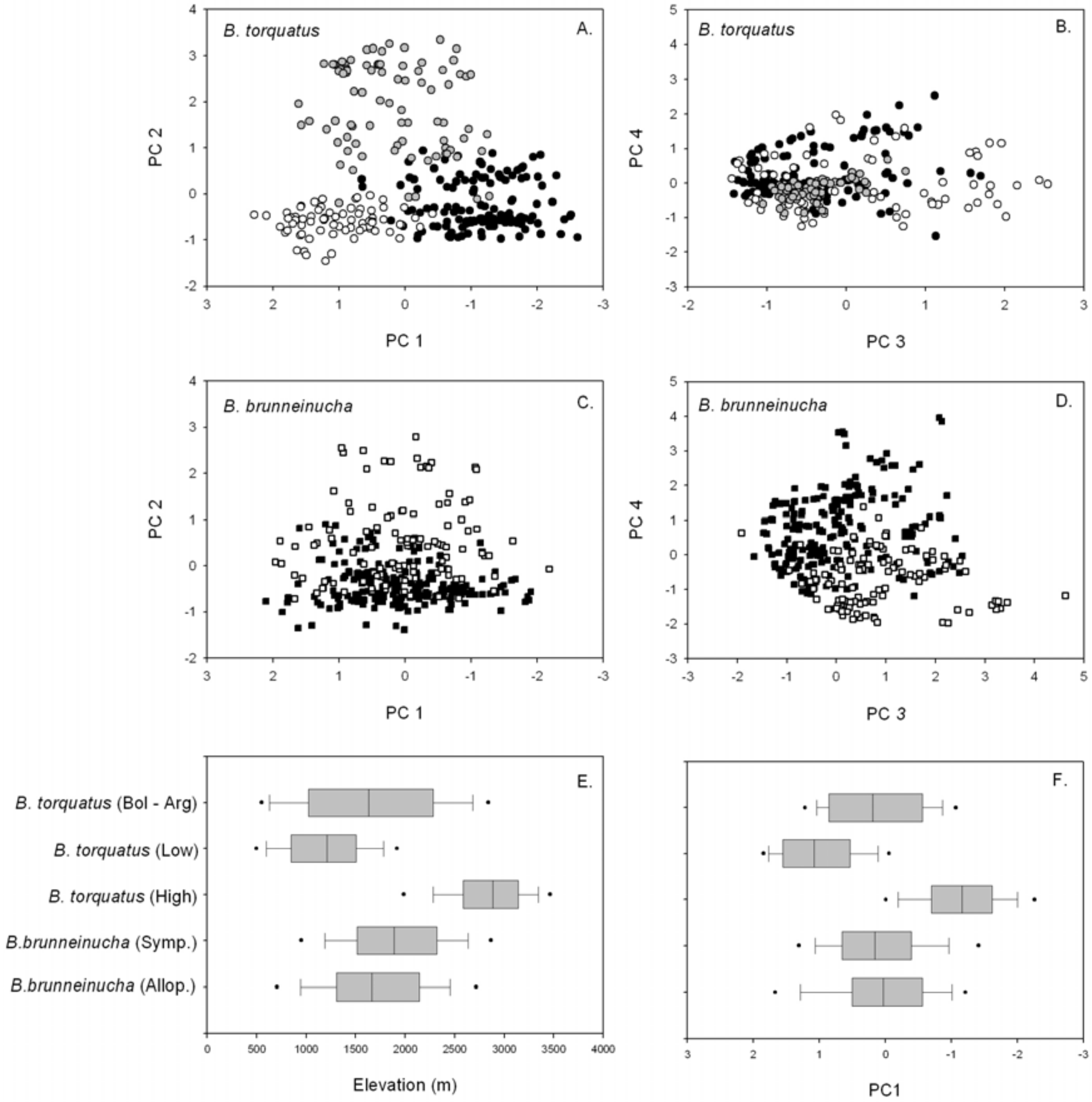

3
2
1
0
-1
-2
-3
PC1
0
500
1000
1500
2000
2500
3000
3500
4000
Elevation (m)
4
3
2
1
0
-1
-2
PC2
-30
-20
-10
0
10
20
30
Latitude

FIGURE 6


B. torquatus
A.
PC 2
PC 1
B. torquatus
B.
PC 4
PC 3
B. brunneinucha
C.
PC 2
PC 1
B. brunneinucha
D.
PC 4
PC 3
E.
B. torquatus (Bol - Arg)
B. torquatus (Low)
B. torquatus (High)
B.brunneinucha (Symp.)
B.brunneinucha (Allop.)
Elevation (m)
0
500
1000
1500
2000
2500
3000
3500
4000
F.
PC1

CHAPTER 4

How Many Species is "*Buarremon torquatus*" (Aves, Emberizinae)? Insights from Molecules, Ecological Niche Modeling, Songs, and Morphology

INTRODUCTION

Two central questions in biology are what species are, and what criteria should systematists use to recognize them. Much of the heated debate surrounding the so-called "species problem" has resulted from failing to distinguish these two questions (de Queiroz 1998, 1999, 2005a, 2005b). A solution to the problem is to accept that the only necessary property of species is that they are segments of lineages at the population level of organization, and that the multiple species definitions that have been proposed are only different criteria that can be used to distinguish lineages on the basis of secondary properties that arise at different stages of evolutionary differentiation. An acceptance of this unified concept of species (de Queiroz 2005b) implies that systematists can focus on identifying lineages and on testing hypotheses about where those lineages stand in the process of differentiation by examining whether they have attained properties such as phenotypic diagnosability, reciprocal monophyly, or mechanisms of reproductive isolation. That these properties are not by themselves necessary conditions of the definition of species does not undermine their central importance in evolutionary biology (e.g. reproductive isolation, see Coyne and Orr 2004).

The best approximation to the delimitation of lineages and to testing the emergence of secondary properties is achieved by integrating information from multiple sources (Wiens and Penkrot 2002; Sites and Marshall 2003, 2004; Yoder et al. 2005). Wiens and Graham (2005) recently proposed that ecological niche models constructed on the basis of environmental variables thought to shape species' geographic ranges can be used as a novel tool to inform species delimitation. Embracing the concept that species are segments of population lineages, they presented a hypothetical example involving two allopatric populations of uncertain status to describe the implications for species limits of different scenarios regarding the relationship between the climatically defined niche of each population and the projection of that niche onto geographic space. First, they proposed that populations could be considered distinct species if their climatic niches are equivalent and are separated geographically by areas outside their climatic niche envelopes that would limit gene flow. Second, they reasoned that if the two populations share similar climatic niche envelopes and their ranges are connected by areas of suitable environmental conditions, the likelihood of dispersal and gene flow would be high, which would not add support to the hypothesis that they represent different species. Finally, they proposed that if the populations have dissimilar niche envelopes, niche conservatism would maintain their geographic separation, supporting the hypothesis that they are distinct species.

We agree with Wiens and Graham (2005) in that ecological niche modeling (ENM) can illuminate species delimitation, but the scenarios they described are amenable to alternative interpretations, particularly when ENM is employed in conjunction with other sources of information. Specifically, the scenario in which two populations with similar niches are connected by areas of continuous suitable environments not only does not imply that these populations represent a single lineage, but indeed provides an ideal scenario to test the hypothesis that the populations are evolutionarily isolated from each other. If allopatric or parapatric populations do not show evidence of intergradation (phenotypic intermediacy or extensive gene flow) despite the opportunity for interbreeding offered by habitat continuity, this scenario may in fact suggest they are distinct lineages evolving in isolation. On the other hand, the occurrence of populations under distinct climatic conditions in allopatry can hardly be considered evidence that they have different environmental tolerances, and thus correspond to different species (i.e., Figure 1d in Wiens and Graham 2005). To make such a claim, one would need to demonstrate that the realized environment (i.e., the combination of environmental conditions that actually exists in a given landscape; Jackson and Overpeck 2000) is comparable in the areas where each population occurs. Otherwise, such a pattern may simply reflect that the fundamental niche of a single lineage is constrained differentially by varying environmental conditions in different parts of its geographic range (see Kearney and Porter 2004).

We propose that the real value of ENM for studies on species delimitation is that it can highlight the continuity of habitable areas in space, which in turn allows drawing on various kinds of data to test hypotheses related to the status of lineages in the process of evolutionary differentiation. Thus, we argue that a scenario in which two populations occur in areas where they could be connected by dispersal, but where individuals of each of them consistently occur under distinct climatic conditions, represents a much more compelling case illustrating how niche conservatism may maintain lineages as independent units than the example where populations are widely spaced. Here, we illustrate these ideas with a multidimensional analysis of species limits in the *Buarremon torquatus* complex (Aves, Emberizinae), a widespread group of Neotropical passerine birds exhibiting unparalleled patterns of geographic variation and within which species delimitation has been contentious. Combining ENM with data on phylogenetic relationships, genetic differentiation, morphometrics, plumage, vocalizations, and distribution ranges, we provide a new hypothesis of species limits in the group, highlighting cases of clear-cut evolutionary distinctiveness, previously unnoticed patterns of differentiation, and several outstanding challenges, both practical and conceptual, for future studies.

We assume species are segments of population lineages, but focus on assessing the status of differentiation of lineages in terms of secondary properties (sensu de Queiroz 2005b), particularly on reproductive isolation. From a theoretical standpoint, reproductive isolation is the cornerstone of research in speciation, which deals with understanding the origin of isolating barriers that prevent gene flow in sympatry (Coyne and Orr 2004). From a more pragmatic perspective, although consensus may be emerging regarding the ontological status of species (de Queiroz 1998, 2005b), in practice taxonomy still relies on particular contingent properties, among which reproductive isolation is one of the most prominent because it is central to the pervasive biological species criterion (BSC; Mayr 1942, 1963). In particular, the BSC prevails in ornithology, being adopted by authoritative classification committees (e.g. A.O. U. 1998, Helbig et al. 2002, Remsen et al. 2006). Species lists produced by such authorities serve as baselines for most research in avian biology and conservation, so their reliance on the BSC influences ornithological science profoundly. Although taxonomy may be best served by embracing a new view of species (de Queiroz 2005b), this is unlikely to occur in the near future, and many researchers will continue to base their species diagnoses on the criterion of reproductive isolation. Therefore, the development of new approaches that allow applying the BSC more objectively remains an important priority in systematics (Remsen 2005). As we shall show below, models of species distributions based on niche theory, when combined with other data, can be brought to bear on situations in which the application of the BSC has been most contentious, namely those in which reproductive isolation cannot be assessed directly because members of populations of uncertain status are not known to occur in strict sympatry.

STUDY SYSTEM

The *B. torquatus* complex is a clade comprising 14 taxa currently treated as subspecies (A.O.U. 1998, Remsen et al. 2006) that occur in montane areas of the Neotropics, ranging from central Costa Rica south to northern Argentina (Chapman 1923, Paynter 1978; Figure 1). Although presently considered a single species, several authors have suggested that *B. torquatus* may comprise two and possibly more species, but the ideas of how these are to be circumscribed are conflicting (see Paynter 1978 and Remsen and Graves 1995b for reviews). Much of the controversy relates to the status of the *atricapillus* group, which occurs in mid-montane areas of the three cordilleras of the Colombian

Andes (*atricapillus*), eastern and central Panama (*tacarcunae*), and, according to some, Costa Rica and western Panama (*costaricensis*). Some authors have treated the *atricapillus* group as a distinct species, whereas others consider its members as subspecies of *B. torquatus*; even among those that separate *atricapillus* as a species there is disagreement, as some include and others exclude *costaricensis*. Part of the confusion has arisen from conflicting perspectives on patterns of geographic variation in the group. The populations of eastern Panama including *tacarcunae* have been said to "form a nearly perfectly graded series between *costaricensis* of western Panama and Costa Rica, and *atricapillus* of South America" (Wetmore et al. 1984). At the same time, however, at least some specimens of *costaricensis* are remarkably similar in plumage to South American members of the *torquatus* group (i.e., *assimilis*), and quite distinct from *atricapillus*, which has led to statements such as the following. "I cannot appreciate how *tacarcunae* can be considered to be intermediate between *costaricensis* and *atricapillus.* On the contrary, I find *tacarcunae* difficult to distinguish from *atricapillus* and to be well-differentiated from *costaricensis*" (Paynter 1978). Clearly, making sense of geographic variation in plumage patterns to understand species limits in the *B. torquatus* complex has proved challenging.

Cadena et al. (Chapter 1) described phylogenetic relationships and patterns of geographic variation in mitochondrial DNA (mtDNA) sequences in *B. torquatus* based on a total of 78 individuals representing 13 of the 14 named taxa. Their analyses indicated that *costaricensis* is the sister group of a well-supported clade formed by all other members of the complex, including *atricapillus* and *tacarcunae*, which are each other's closest relatives (Figure 1). Relationships among major groups within this large clade were not strongly supported, but several distinct clades were recovered, with the interesting outcome that some populations occurring in distant geographic locations are more closely allied than they are to populations occurring in close geographic proximity. For the most part, named taxa within the complex formed reciprocally monophyletic mtDNA clades, and genetic distances among many of these clades were substantial (see below). The patterns of mtDNA variation indicating long-term isolation of several populations and the phenotypic distinctiveness of several of them (Paynter 1978), suggest that *B. torquatus* comprises more than one species. How such species are circumscribed, however, would vary according to the operational criteria used to delimit them.

The levels of genetic divergence observed among clades of *B. torquatus* may suggest more than one "biological" species is involved because they exceed those observed between many pairs of reproductively isolated passerines, both in the temperate zone and in the Neotropics (reviewed by Lovette 2005 and Weir 2006), but using only genetic distance and reciprocal monophyly of mtDNA to assess reproductive isolation is fraught with problems due to the weak nature of the association between time of divergence and the attainment of reproductive isolation (Price and Bouvier 2002, see also Edwards et al. 2005). However, mtDNA genealogies reflect evolutionary differentiation and provide hypotheses for species limits that can be evaluated with additional data (Templeton 2001, Yoder et al. 2005). Here, we use the mtDNA framework presented in Chapter 1 to guide our discussion of species limits based on other sources of information.

We begin by focusing on two pairs of populations (i.e., subspecies in current taxonomy) in the *B. torquatus* complex that represent distinct lineages (sensu De Queiroz 2005b) that may have differentiated sufficiently to attain reproductive isolation. One of these pairs consists of *assimilis* and *atricapillus*, both of which occur widely across the Andes of Colombia, but have never been collected or observed at the same geographic location and generally occur at different elevations (Remsen and Graves 1995; Figure 1). The second pair consists of *poliophrys* and nominate *torquatus;* these have linear and presumably non-overlapping ranges along the Andes of Peru and Bolivia, although it is possible that they may be parapatric and meet in a contact zone in southern Peru (Figure 1). These pairs of taxa are not each other's closest relatives and appear to form monophyletic mtDNA clades with respect to other taxa in the complex (Figure 1). However, it is unclear whether this is a result of lack of opportunities for gene flow due to spatial disjunction of their ranges or to their status as distinct, potentially overlapping, and reproductively isolated species. Based on patterns observed in these pairs of taxa, we discuss variation in *B. torquatus* as a whole.

BACKGROUND ON ECOLOGICAL NICHE MODELING

The term ecological niche modeling was first used explicitly by Peterson (2001) to refer to the use of environmental (mostly climatic) data recorded at sites where species are known to occur to generate models that characterize their ecological niches in environmental space and to predict potential distribution ranges by projecting these models spatially (reviewed by Guisan and Zimmermann 2000, Elith et al. 2006). There has been some confusion in the literature over whether these models approximate species' fundamental niches (sensu Hutchinson 1957), or if they only describe realized niches considering that the known occurrence sites used to construct them have already been influenced by factors that constrain the fundamental niche such as interactions, dispersal limitation, or extinction (reviewed by Soberón and Peterson 2005). We favor the idea that ecological niche models can only be interpreted as characterizations of realized niches in environmental dimensions. Accordingly, cases in which models indicate two populations occur in distinct environments do not imply that each of them is unable to occur under the conditions that characterize localities occupied by the other. Alternatively, in cases in which models indicate two populations occur under the same environmental conditions, it can be concluded that their geographic ranges could potentially overlap, assuming other niche requirements are met. This inference requires assuming that locality data do not include wandering individuals occurring in sink habitats, which strictly speaking are not part of realized niches (Pulliam 2000). Although we cannot reject this possibility, its effect at the coarse scale of our analyses is likely to be minor.

MATERIALS AND METHODS

CHARACTERIZATION AND GEOGRAPHIC PROJECTION OF CLIMATIC NICHE ENVELOPES

We georeferenced primary occurrence data for *B. torquatus* obtained from museum specimens, published reports, and reliable field records. For details on data sources and protocols followed to verify the accuracy of georeferences, see Chapter 3.

We characterized ecological niches climatically using a set of 19 climate surfaces on a 30 arc-second resolution grid (i.e., 0.00833 decimal degrees or c. 1 km on the side) obtained from WorldClim version 1.2 (Hijmans et al. 2005). These surfaces reflect annual trends (e.g. mean annual temperature), seasonality (e.g. annual range in rainfall), and extreme conditions (e.g. temperature of the coldest month) in variables that are thought to be important in limiting geographic ranges (Hijmans et al. 2005). Prior to constructing models, we reduced the 19 environmental variables to sets of uncorrelated axes of climatic variation using principal components analyses (PCA). For each pair of populations being modeled, we defined a focal region for analysis (i.e., Colombia for *assimilis* and *atricapillus* and Peru and Bolivia for *poliophrys* and *torquatus*) and sampled environmental variation across the region by recording the values of each bioclimatic variable at 3000-6000 points placed randomly within an elevation range that encompassed all occurrence records of the taxa being modeled plus or minus 200 m. Although the range of *assimilis* extends through Ecuador and into Peru, and that of *atricapillus* into Panama, we focus in Colombia because this is where these taxa may come into contact. After standardizing climatic variables using Z-scores, we subjected the matrices to PCA (PROC FACTOR, SAS version 9.1, SAS Institute, Cary, NC), and selected axes describing non-trivial variation by comparing their eigenvalues to a broken-stick model. Based on the PCA eigenvector coefficients, we generated GIS layers for each of the selected axes using the raster calculator in ArcMap version 9.0 (ESRI). These layers, consisting of grids of equal size to those of the original climate surfaces (i.e., 0.00833 x 0.00833 decimal degrees), were then used for ENM.

To generate niche models and project them onto geographic space we used the DOMAIN algorithm (Carpenter et al. 1993) implemented in DIVA-GIS version 5.2 (http://www.diva-gis.org). DOMAIN produces an output that is readily interpretable in the context of ecological niche theory (Hill and Binford 2002). The algorithm identifies sites that are potentially suitable for occurrence based on multivariate similarity to sites where the target taxa occur. Here, we consider sites to be suitable if DOMAIN models indicated their similarity to sites of known occurrence was equal or greater than 95%, but our conclusions would not change if the threshold were reduced to 90%.

MORPHOMETRIC AND PLUMAGE VARIATION

Phenotypic traits such as bill dimensions may readily change in different environments as a result of selection, implying they are often of limited value as characters to assess the status of populations that occur in geographic isolation. However, patterns of variation in areas of regional sympatry or contact zones can provide insights about interbreeding that can complement inferences made from genetic variation. Accordingly, we examined differentiation in morphometrics between *atricapillus* and *assimilis* and *poliophrys* and *torquatus* based on measurements taken on museum specimens. For the former pair, whose ranges are intermingled in the Colombian Andes, we assessed diagnosability in external morphology using scatter plots to portray variation in bill length, height, and width. If the two taxa intergrade, these measurements should overlap. For the latter pair, a simple assessment of variation of this sort would be insufficient to assess the possibility of intergradation owing to their non-overlapping ranges. Our approach to assess intermediacy was to conduct discriminant function analyses (PROC DISCRIM and PROC CANDISC in SAS) independently for male and female specimens using six morphological measurements (the three bill measurements mentioned above plus tarsus, tail, and wing length), and to plot discriminant function scores as a function of latitude. If *poliophrys* and *torquatus* intergrade where their ranges abut, scores obtained for specimens of each taxon should resemble each other more closely in areas closer to the contact zone (i.e., localities at similar latitudes).

We did not conduct quantitative analyses of plumage coloration. However, we noted whether specimens conformed to patterns of plumage variation described for each subspecies (Chapman 1923, Paynter 1978), paying special attention to possible hybrids in areas of geographic contact.

VOCAL VARIATION

Vocal characters are seldom used in taxonomy of oscine passerines because songs in these birds are learned, and therefore, substantial variation often exists within species as a result of processes such as cultural transmission of local dialects (Baptista 1996, Podos et al. 2004). However, we concur with Remsen (2005) in that the predisposition for learning the song of the parental population rather than other species' songs in oscines (Baptista 1996) implies that vocalizations are at least under partial genetic control, and are thus useful for delimiting species. Indeed, it has been shown that once elements that are consistent across individuals and geography within species are identified, oscine song can reflect phylogenetic relationships closely (Price and Lanyon 2002). Clearly, however, studies of song variation in oscines should sample broadly, allowing the extent of individual and geographic variation within species to be addressed.

To assess the extent of differentiation in vocalizations between *atricapillus* and *assimilis* and *poliophrys* and *torquatus,* we compiled a total of 41 sound recordings, each comprising vocalizations of a different individual. We examined overall sound quality in Adobe Audition 1.5 (Adobe Systems Inc. 2004) and generated spectrograms using Syrinx-PC (www.syrinxpc.com—developed by John Burt, University of Washington, Seattle). We analyzed only the 24 recordings that conformed to unsolicited songs with undistorted notes that could be unambiguously distinguished from other sounds (Appendix). This implied that relatively few recordings were available for any given taxon, particularly for *atricapillus,* for which only three recordings were considered adequate. This limited sample size could be problematic in light of the potential for ample within-species variation in songs in oscines mentioned above. However, recordings of *atricapillus* were made in three different slopes of two different cordilleras where this species co-occurs with elevational segregation with *assimilis.* Because recordings of *assimilis* from these areas are available, we assume that if these taxa differ vocally in a consistent fashion across slopes, it would be unlikely that differences are artifacts of small sample sizes and poor geographic coverage. Small sample sizes and sparse geographic coverage are more of an issue for the comparison between *poliophrys* and *torquatus*, so we interpret our results for these taxa conservatively.

An individual *B. torquatus* may sing uninterruptedly for a few minutes, repeating series of four to nine notes (i.e., note complexes; see Podos et al. 2004) that vary in pace. Because the arrangement of note complexes may vary through singing, and to minimize the effects of environmental distortion (e.g. reverberation, which may make notes appear longer than they are), we quantitatively examined

3-5 consecutive note complexes per individual recording. For each note complex, we recorded the following 14 acoustic variables: maximum frequency, minimum frequency, bandwidth (frequency range), maximum note bandwidth, minimum note bandwidth, peak frequency (frequency with the highest amplitude), duration, number of notes, note pace (number of notes divided by duration), summed note duration, note proportion (summed note duration divided by duration), maximum note duration, minimum note duration, and mean note duration. We obtained these measurements directly from spectrograms in Syrinx-PC, except for peak frequency, which we measured by generating amplitude spectra using the frequency analysis function of Adobe Audition. Although we took measurements on only 3-5 note complexes per song, we examined many more qualitatively to verify the consistency of patterns of variation.

To assess differences in vocalizations between pairs of taxa (i.e., *assimilis-atricapillus* and *poliophrys-torquatus*), we used univariate and multivariate analyses. First, we compared the mean of each individual song variable between taxa using t-tests. Second, we determined whether taxa in each pair were vocally diagnosable using discriminant function analyses based on 13 log-transformed acoustic variables (we did not include number of notes because it is the only one variable not related to frequency or time).

To examine the extent of vocal differentiation between the taxa that are the focus of this study in the broader context of variation across the whole *B. torquatus* complex, we compiled recordings of natural songs from as many localities as possible. Unfortunately, the availability of recordings for many populations occurring in distinct geographical areas and for some of the clades revealed by mtDNA is rather limited, which implies that quantitative analyses of the available material would be premature. Thus, here we chose to only describe the extent of vocal variation we observed across the complex by presenting representative spectrograms for different populations. Detailed quantitative analyses of vocal variation throughout the range of *B. torquatus* will be presented in forthcoming studies.

GENETIC VARIATION

Phylogenetic relationships and general patterns of geographic variation in mtDNA were presented in Chapter 1 and are summarized schematically in Figure 1. Here, we employ data from that study to calculate levels of sequence divergence observed between different populations, and discuss the implications of phylogenetic relationships and of the extent of genetic differentiation for species limits in relation to variation in other aspects.

RESULTS AND DISCUSSION

DIFFERENTIATION BETWEEN *ASSIMILIS* AND *ATRICAPILLUS*

1. *Ecological differentiation*

Niche models indicate that *assimilis* and *atricapillus* occur in distinct environments. Areas of suitable habitat for *assimilis* occur extensively along the Cordillera Oriental and Cordillera Central of the Colombian Andes, whereas suitable areas are smaller and more sparsely distributed in the Cordillera Occidental, where sites at high elevations are more limited (Figure 2). The potential distribution of *atricapillus* appears somewhat more patchy, but also extends broadly along the three cordilleras (Figure 2). However, none of the point localities of *atricapillus* was located in areas where the model predicted presence of *assimilis* or vice versa. In fact, the DOMAIN algorithm did not classify a single grid cell in Colombia as potentially suitable for both taxa based on the climate data.

2. *Morphometric and plumage variation*

External morphology indicates that *assimilis* and *atricapillus* are 100% diagnosable taxa that exhibit no evidence of intermediacy. Independently of sex and of geographic location, specimens of *atricapillus* have substantially larger bills than specimens of *assimilis:* measurements of bill width, height, and length of each taxon are entirely nonoverlapping (Figure 3). Furthermore, we examined more than two hundred specimens of these taxa combined and did not encounter a single one that could not be assigned to one or the other taxon unambiguously based on the pattern of plumage pigmentation of the head: *atricapillus* has a mostly solid black head with only a few grey feathers in some specimens, whereas *assimilis* exhibits wide grey markings through much of the head.

3. *Vocal variation*

Vocal variation further confirms the distinctiveness of *assimilis* and *atricapillus* (Figure 4). The songs of *atricapillus* are higher pitched and are composed of notes emitted at a faster pace than those of *assimilis*, but encompass a much narrower frequency range and are less structurally complex, exhibiting lower overall note richness and lacking notes that cover wide frequency ranges over short periods of time, which are typical of the song of *assimilis* (Table 1). Despite limited sample sizes, nine out of the 14 song variables we compared were significantly different between *assimilis* and *atricapillus* (Table 1). The discriminant function analysis indicated that vocalizations of these taxa are diagnosable: all songs were correctly classified to their corresponding taxon.

4. Genetic variation

As indicated above (Figure 1), *assimilis* and *atricapillus* are not each other's closest relatives: *assimilis* forms a strongly supported clade with subspecies *nigrifrons* and *poliophrys* from Ecuador and Peru, and *larensis* from northeast Colombia and Venezuela; the affinities of the *atricapillus*-*tacarcunae* clade are unresolved. Genetic distances between *assimilis* and *atricapillus* are substantial: the minimum observed sequence divergence was 6.3%. In contrast, the highest sequence divergence observed between individuals throughout the whole range of *assimilis* and the closely allied *nigrifrons* was only 2.0%. The maximum distance observed within the clade formed by *atricapillus* and the closely allied *tacarcunae* was 2.4%.

ARE *ASSIMILIS* AND *ATRICAPILLUS* REPRODUCTIVELY ISOLATED?

Our data show that *assimilis* and *atricapillus* are diagnosable taxa that show no evidence of intermediacy in external phenotype, have distinct voices, and have been evolving in isolation for a substantial time. Although it had not been previously shown quantitatively, our finding that *assimilis* and *atricapillus* are phenotypically distinct is not novel: this is the argument invoked by authors that have advocated treating *atricapillus* as a different species (e.g. Ridgely and Tudor 1989, but see Paynter (1970), who expressed doubt about the possibility of phenotypic intergradation in western Colombia, which can be ruled out based on our analyses). However, the relevance of the lack of intergradation between *atricapillus* and *assimilis* for addressing their taxonomic status was brought into question by Remsen and Graves (1995), who argued these taxa have no opportunity to intergrade because they are separated in altitudinal distribution, with *atricapillus* occurring at lower elevations.

ENM shows that *assimilis* and *atricapillus* indeed occur under rather different environmental conditions, a reflection of their different elevational distributions. This scenario matches one of those described by Wiens and Graham (2005), in which populations occur under distinct climatic regimes (their Figure 1d). These authors argued that such situations indicate that niche conservatism is likely to maintain the populations in geographic isolation and thus, that they could be considered different species in a broad sense. We do not disagree with this interpretation (see below), but the way in which environments that appear to be suitable for the occurrence of these taxa are distributed spatially can and should inform the inference of whether populations are in the position to intergrade or not. Although not a single cell was classified as sufficiently similar in climate to sites of known occurrence of both *assimilis* and *atricapillus*, many sites suitable for each of them are in very close geographic proximity (within 1-2 km of each other). In addition, our models are based on climate data from only the past 50 plus years (Hijmans et al 2005), a minute period of time relative to the time frame over which these taxa have been isolated, which probably exceeds 2-3 million years (Chapter 1). Thus, in light of the history of climate change in the Colombian Andes over the Quaternary (Hooghiemstra and van der Hammen 2004), sites matching climatic conditions suitable for the occurrence of both taxa may have existed in the past, implying that historical opportunities for gene flow have likely been higher than what a static view of present-day climatic conditions would suggest. In sum, we argue that although conditions suitable for the occurrence of both *atricapillus* and *assimilis* may not presently occur in any 1 km^2 cell, and that these taxa have not been collected in syntopy, the way in which suitable environments are arrayed implies that for the practical purpose of assessing their taxonomic status, these taxa can be considered sympatric. This view is supported by patterns of mtDNA variation (i.e., rather limited population genetic structure within *assimilis* and *atricapillus* across their ranges, Chapter 1), which imply that dispersal over historical time frames has not been limited to small spatial scales. We also do not discard the possibility that these two taxa actually occur in syntopy. The range of *atricapillus* remains little known, and its retiring habits, local distribution, and apparently low abundance can make it difficult to detect, implying that continued fieldwork may result in finding it in sites below c. 2000 m where *assimilis* is known to occur.

In addition, the gap in elevation separating the ranges of *assimilis* and *atricapillus* described by Remsen and Graves (1995) has been bridged by recent records indicating that *assimilis* ranges down to 1800 m, whereas *atricapillus* extends to 2000 m in the same cordillera (T. Donegan and O. Laverde, unpublished data). Therefore, we suggest that that the observation that these forms generally remain segregated by elevation indicates that habitat selection driven by niche conservatism likely plays a role in maintaining them as distinct entities where they occur in the same geographical area. The significance of patterns of habitat use stands out considering they are consistent over a wide geographical setting: both *atricapillus* and *assimilis* have been recorded in all but one of the six slopes of the Colombian cordilleras (*atricapillus* is not known from the east slope of the Cordillera Occidental, which may reflect lack of historical exploration; see Cuervo et al. 2003). Remsen and

Graves (1995) rightly pointed out that the occurrence of *atricapillus* at lower elevations is not unique in the *B. torquatus* complex, and argued that this cannot be considered a sufficient criterion to support its status as a distinct species. Certainly, the elevational range of *atricapillus* does not indicate that it is ecologically distinct from allopatric low elevation taxa, but it does serve as an important ecological mechanism isolating it from *assimilis*, the only taxon with which it is known to coexist at the landscape scale (see also Olson et al. 2004). This ecological isolating mechanism likely acts in concert with the marked differentiation in songs we observed; we hypothesize that vocalizations are likely to serve as an important mate recognition mechanism that would impede these taxa from hybridizing where their ranges may come into contact.

In sum, our analyses show unequivocally that *assimilis* and *atricapillus* are two distinct lineages evolving in isolation that have attained multiple secondary properties of species that include diagnosability in plumage, morphometrics, and vocalizations, reciprocal monophyly in mtDNA, and reproductive isolation likely mediated by habitat selection and differentiation in songs. Therefore, we suggest these taxa should be treated as different species in classifications that apply essentially any species criterion, including the BSC.

DIFFERENTIATION BETWEEN *POLIOPHRYS* AND *TORQUATUS*

1. Ecological differentiation

Projecting ecological niche models onto geography shows that although *poliophrys* and *torquatus* do not have broadly overlapping ranges, their distributions do not appear to be constrained by discontinuities in climatic niche space. Models classified fairly extensive areas of the range of *poliophrys* as climatically suitable for *torquatus* and vice versa (Figure 5). Of the 34 point localities of *poliophrys*, 16 occurred at sites classified as suitable for *torquatus*, whereas the reverse was true for 5 of 26 localities. Moreover, much of the intervening area between the southernmost record of *poliophrys* and the northernmost of *torquatus* we employed for modeling was predicted to be suitable for both taxa (compare Figure 1 and Figure 5). Interestingly, however, models identified a large area within the extent of the range of *poliophrys* in southern Peru where the environments are dissimilar to those under which either taxon is known to occur. This apparent gap in potential distributions corresponds to a remarkably humid area (Killeen et al. 2006).

2. *Morphometric and plumage variation*

Discriminant function analyses based on morphological measurements correctly classified 90% of male specimens and 94% of female specimens to their respective taxa. Plotting the discriminant function scores with respect to latitude does not reveal trends that would suggest clinal variation leading to more similar morphology near the area where the ranges of *poliophrys* and *torquatus* may abut (Figure 6), which suggests intergradation is limited. However, because we did not have access to many specimens from near the potential area of parapatry, the morphological distinctiveness of the two taxa may not be as clear if they intergrade in a narrow contact zone (see below).

Although *torquatus* and *poliophrys* are superficially similar in plumage patterns, the two taxa are diagnosable: *torquatus* has a distinct white superciliary that is grey in *poliophrys*. Unfortunately, there are few available specimens from southern Puno Department (Peru), so material that would allow assessing intermediacy in plumage patterns in areas of possible contact is limited. Several specimens from near the Peru-Bolivia border (Abra Maruncunca) housed at LSUMZ (see acknowledgements for museum acronyms) are typical *torquatus* plumage types, and at least one of them has *torquatus* mtDNA (Chapter 1). Also, an individual captured and photographed by F. Schmitt near Masiapo (Puno) is referable to *torquatus.* In turn, specimens from easternmost Cusco Department (e.g., YPM 81959) appear to be typical *poliophrys.* Collections from the intervening area very sparse, but a specimen from Limbani, Carabaya, Puno (AMNH 520399) is intermediate in plumage between *poliophrys* and *torquatus*, showing a mixture of grey and white feathers in the superciliary. It is possible that this bird is a hybrid, but it is not morphometrically intermediate as would be expected if this were the case, since the discriminant analysis clearly classified it as *poliophrys* (Figure 6). Thus, the possibility that this specimen represents an aberrant *poliophrys* cannot be ruled out, but we do not discard the hypothesis that *poliophrys* and *torquatus* may hybridize in a narrow contact zone. Should hybridization occur, its extent and the width of the hybrid zone are unknown. The only other specimen from this area we are aware of (MVZ 126435 from Agualani, near Limbani) is a subadult individual that seems to be a “pure” *poliophrys*.

It is also worth noting that at least part of the superficial similarity of *poliophrys* and *torquatus* is either plesiomorphic or the result of convergence or parallel evolution of plumage patterns. Analyses to be reported in detail elsewhere (C. D. Cadena unpubl. data) indicate that plumage traits are highly homoplasious in *B. torquatus,* and that characters such as the black pectoral band have been lost or gained repeatedly throughout the history of the group. In this particular case, it is readily apparent that *poliophrys* and *torquatus,* both of which exhibit collars, are closely allied to taxa that lack this trait (e.g. *assimilis* and *borelli,* respectively).

3. *Vocal variation*

Vocal variation in *poliophrys* and *torquatus* is consistent with taxon designations. The vocalizations of *poliophrys* have significantly longer and lower-pitched notes than those of *torquatus* (Table 1, Figure 4). Although many acoustic variables showed some overlap, the variability in vocal traits appeared to be higher in *poliophrys*, and maximum frequency and bandwidth tended to differ between taxa. The discriminant function analysis indicates that *poliophrys* and *torquatus* can be diagnosed based on vocalizations: 100% of the songs analyzed were correctly classified to their corresponding taxon. Plotting discriminant function scores with respect to latitude does not indicate that songs are more similar in areas where the ranges of both taxa are closer to each other (Figure 7), which suggests there is no evidence for clinal variation in vocalizations over broad scales. However, our sampling is not sufficiently detailed to entirely rule out this possibility at finer scales.

4. *Genetic variation*

Phylogenetic analyses show that *poliophrys* and *torquatus* belong to different major clades within *B. torquatus* (Chapter 1). Whereas *poliophrys* is sister to a clade formed by *assimilis* and *nigrifrons,* and these three taxa are sister to *larensis, torquatus* belongs to a clade of unresolved affinities, within which it is sister to a clade formed by *borelli* and *fimbriatus.* Both *poliophrys* and *torquatus* appear to be reciprocally monophyletic with respect to other taxa, but sampling for the latter taxon is insufficient to confirm this pattern (Chapter 1). The minimum level of sequence divergence observed between *poliophrys* and *torquatus* is 6.6% (uncorrected *p* distance). The individuals of each taxon assayed for mtDNA variation occurring in closest geographic proximity are separated by c. 300 km, and are at least 7.5% different in mtDNA sequences. This contrasts with variation within each taxon, which reaches only 2.8% within *poliophrys* and 0.5% within *torquatus* over distances of c. 900 and c. 475 km, respectively.

ARE *POLIOPHRYS* AND *TORQUATUS* REPRODUCTIVELY ISOLATED?

Ecological niche models indicate environments climatically suitable for the occurrence of *poliophrys* and *torquatus* are largely continuous in the area where their ranges abut, a scenario that corresponds to the one portrayed in Figure 1c by Wiens and Graham (2005). We suggest that the continuity of climatic niche envelopes in space implies that it is unlikely that niche conservatism impedes these taxa from being sympatric, which in turn leads to the prediction that if they are not reproductively isolated, there should be evidence of gene flow and intergradation near their range boundaries. The ability of these taxa to disperse historically over areas exceeding the potential gap in their distributions is clear based on patterns of genetic variation indicating limited to no genetic structure across all of their ranges.

Inferences of whether *poliophrys* and *torquatus* may exchange genes to the extent that it is no longer justifiable to maintain they correspond to a single species under the BSC are somewhat tentative because relevant data are not available at the very fine spatial resolution that one would like. The best approximation we have are data on morphometric and plumage variation, which suggest these taxa exhibit little to no intergradation, and that the phenotypic transition from one form to the other occurs over a maximum distance of 50 km of mostly continuous habitat. Hybrid zones of some avian taxa considered “good” species under the BSC are wider than this (e.g. Rising 1983, Brumfield et al. 2001), an observation that could be used to support the argument that *poliophrys* and *torquatus* demonstrate “essential” reproductive isolation (sensu Johnson et al. 1999).

The hypothesis that *poliophrys* and *torquatus* are different species under the BSC is not free of caveats, the most significant of which are the 300 km gap in sampling of mtDNA variation that exists in southern Peru and the lack of recordings of songs from areas of possible contact. In the absence of sequence data at the same spatial resolution as morphological data, we cannot reject the hypothesis that variation may be decoupled, and that the transition from one to another mtDNA phylogroup actually occurs within the range of the *poliophrys* phenotype. Studies on hybrid zones have shown that plumage traits may introgress asymmetrically from one lineage into another, resulting in discordance in the geographical position of molecular and phenotypic contact zones (Brumfield et al. 2001). These patterns need not occur at small spatial scales; a contact zone between highly divergent mtDNA clades in *Phaeothlypis* warblers is more than 1000 km away from the area where different plumage forms are known to hybridize (Lovette 2004). Because the distribution of available song recordings is also sparse, the exact correspondence between plumage, vocal, and mtDNA variation in the area of potential contact cannot be established with complete certainty at this time. We believe that the possibility of molecular, phenotypic, and vocal decoupling is unlikely because differences in all of these traits are rather striking, and suspect that detailed analyses in the area will confirm that *poliophrys* and *torquatus* are reproductively isolated taxa. In addition, even if traits do not vary exactly in parallel, it is not clear to us what would be the implications for species delimitation, considering how such cases are treated in other avian taxa. For example, plumage clines in the manakin hybrid zone located in Panama are known be displaced several kilometers with respect to molecular and morphometric clines (Parsons et al. 1993, Brumfield et al. 2001), but no one seems to question the status of *Manacus vitellinus* and *M. candei* as different species. However, some researchers might believe it is best to err on the side of caution, and maintain the taxonomic status of *poliophrys* and *torquatus* unchanged until the abovementioned hypothesis and also the possibility that there is clinal variation in song and mtDNA in southern Peru are ruled out (see Brumfield 2005, Isler et al. 2005).

HOW MANY REPRODUCTIVELY ISOLATED SPECIES COMPRISE THE *BUARREMON TORQUATUS* COMPLEX?

We have demonstrated that *atricapillus* and *assimilis* on one hand, and likely *poliophrys* and *torquatus* on the other, are reproductively isolated species. The remaining challenge is to decide to which of these “biological” species, if any, should all other members of the *B. torquatus* complex be assigned. In an effort to develop an objective framework for the application of the BSC in ornithology, Remsen (2005) suggested that allopatric populations should be treated as species if their degree of divergence is at or beyond that of taxa known to have reached reproductive isolation (see also Isler and Isler 1998, Helbig et al. 2002). Following this logic, one could use the degree of differentiation attained by *assimilis* and *atricapillus* (and perhaps by *poliophrys* and *torquatus*) as an approximate yard stick to assess whether other populations may represent reproductively isolated species. We attempt to do so in the following paragraphs, but we note at the outset there is an important caveat to this approach, namely the problem of distinguishing causes and consequences of reproductive isolation. Although two populations reproductively isolated from each other may differ in a suite of characteristics, the significance of any of these by itself as a mechanism preventing interbreeding is unclear; it may well be that one or a few of them confer reproductive isolation, and that others diverge as a consequence of lack of gene flow. This issue is important because when comparing allopatric populations with reference to known pairs of reproductively isolated species, one may find that they are more divergent in some aspects and less divergent in others. Indeed, this is the case in *B. torquatus.*

Genetic divergence between several populations of *B. torquatus* is comparable to, and actually greater than, the divergence observed between *assimilis* and *atricapillus*, reaching values of uncorrected sequence divergence of c. 9% (e.g. *costaricensis* vs. *poliophrys)*. Levels of sequence divergence within the genus *Arremon*, the sister group of *B. torquatus*, reach 11% in the same mtDNA region, but several of the seven reproductively isolated species of *Arremon* recognized by current taxonomy are in the range of c. 7 to 9% divergence (J. Klicka, C. D. Cadena and J. L. Pérez-Emán, unpublished data). We present these comparisons to indicate that based on what has been observed for good species within the complex and in a closely allied group, many populations of *B. torquatus* have been isolated from each other for periods of time over which mechanisms of reproductive isolation may well have evolved. Although genetic distances are rather poor surrogates of species status under the BSC because the correlation between time of divergence and reproductive isolation is weak, such a correlation does exist (reviewed by Coyne and Orr 2004).

Ecology has long been thought to play a crucial role in speciation, and the divergence of populations in allopatry to the point where they can no longer interbreed is often believed to be a byproduct of adaptive evolution resulting from varying selective pressures in different environments (Mayr 1942). Accordingly, much of the residual variation of the regression between genetic distance (i.e., time) and measures of reproductive isolation can be accounted for by ecological differentiation (Funk et al. 2006). Our data demonstrate that reproductive isolation may correlate with differences in ecology in *B. torquatus* based on the patterns observed in *assimilis* and *atricapillus.* Several sets of populations arguably are just as ecologically distinct as these two, the most obvious being those occurring at high-elevations (e.g. *assimilis, poliophrys*) and those occurring in mid-montane areas (e.g. *atricapillus, costaricensis, larensis, phygas*). Other patterns of ecological differentiation may not be as obvious at first glance, but become clear using ENM. For example, Cadena and Loiselle (Chapter 3) showed that the sites where *basilicus* occurs in the Sierra Nevada de Santa Marta of northern Colombia are environmentally distinct from those occupied by populations occurring in the Andes of northeast Colombia and in northwest Venezuela (i.e., *perijanus, larensis*). Similarly, the environments occupied by populations occurring at relatively high latitudes in Bolivia and Argentina (*fimbriatus, borelli*) are markedly distinct from those occupied by other members of the complex (Chapter 3).

On the other hand, ecological similarity in the environments connecting populations not known to occur in sympatry but that do not show evidence of intermediacy suggests that intrinsic barriers to gene flow may prevent them from merging into a single species. We have discussed the case of *poliophrys* and *torquatus* in some detail, but there are others. One of them is that of *assimilis* and *poliophrys,* whose ranges closely approach each other along the Peruvian Andes. These two taxa are readily diagnosable based on plumage and form distinct mtDNA clades that differ by a minimum

3.8% sequence divergence (Chapter 1). The southernmost locality of *assimilis* and the northernmost of *poliophrys* are separated by c. 70 km over which climatically suitable environments for both taxa are entirely continuous (see Figure 5 for *poliophrys*, data for *assimilis* not shown). Another case of distinct populations that occupy similar environments in close proximity is that of *atricapillus* and the population occurring in Depto. Norte de Santander, Colombia (these birds have been historically referred to taxon *perijanus,* but mtDNA data indicate they are much more closely allied to *larensis* from the Venezuelan Andes; Chapter 1). Both taxa occur on the west slope of the Cordillera Oriental of Colombia over a similar elevational range, and have been collected within 120 km of one another on this slope. They are arguably more distinct phenotypically from each other than *assimilis* and *atricapillus,* and they are divergent to roughly the same level in mtDNA and in vocalizations (see below).

The available material is too limited to allow quantitative analyses of vocal differentiation among all populations of *B. torquatus*, but the extent of vocal variation in the complex is substantial (Figure 8). In spite of the variation, there are somewhat distinct groups of taxa with generally similar vocalizations. First, the songs of *assimilis*, *nigrifrons, poliophrys*, *larensis, phaeopleurus,* and *phygas* are rich in note variety, encompass a wide frequency range, and consist of notes that are evenly interspaced. The songs of these taxa are not characterized by distinct phrases, but rather by individual, highly variable notes emitted at regular intervals. Among these taxa, the songs of *phaeopleurus* and *phygas* stand out for having buzzing notes that we have not observed in any other member of the complex. Second, the songs of *borelli, fimbriatus*, *torquatus, costaricensis, atricapillus*, and *tacarcunae* are overall simpler, higher pitched, and are composed of one to three alternated, distinct phrases interspersed with silent periods. Despite the substantial variation in songs we observed, this general description of patterns of vocal variation is consistent in some ways with phylogenetic relationships. Most of the taxa in the group exhibiting more complex songs form a well-supported clade (i.e., *assimilis*, *nigrifrons, poliophrys*, *larensis*), whereas the phylogenetic position of the other two taxa with complex songs is uncertain (analyses are inconclusive for *phygas* and sequence data are not available for *phaeopleurus*), and they differ in having the unique buzzing notes. On the other hand, taxa with simpler songs occurring in Bolivia and Argentina (*torquatus*, *fimbriatus,* and *borelli*) and in Colombia and Panama (*atricapillus* and *tacarcunae*) also form distinct clades.

It is noteworthy that vocalizations of populations from distant geographical areas (e.g. *tacarcunae* from Panama and *fimbriatus* from Bolivia) are more similar to each other than any of them are to those of intervening populations (e.g. *assimilis* from Colombia, Ecuador, and Peru). This “leapfrog” pattern of geographic variation is pervasive in plumage patterns among Andean birds (Remsen 1984), but to our knowledge it has not been reported previously for patterns of vocal variation, except perhaps for ring species (Irwin et al. 2001). Two plumage traits (the presence or absence of a black pectoral band and the color of the superciliary – white vs. grey–) also vary in leapfrog fashion in *B. torquatus,* but the two traits do not vary in parallel, leading to a complicated mosaic of geographic variation in plumage (Chapman 1923, Paynter 1978). Leapfrog variation in vocal characters is not congruent with variation in either of the two leapfrogging plumage traits (compare Figure 8 with Figure 20 in Paynter 1978).

Comparisons across broad geographic areas are likely to reveal morphometric variation, but whether this indicates anything about the ability of populations to interbreed is at best dubious, so we did not perform comparisons involving allopatric populations. Plumage variation is also best used in sympatry and parapatry to identify intermediate phenotypes that may have resulted from hybridization, but plumage patterns may be important for mate choice and thus be useful indicators of reproductive isolation. Some pairs of populations of *B. torquatus* are arguably more divergent in plumage than *atricapillus* is from *assimilis.* The main difference between these taxa is that *atricapillus* has a solid black head, whereas the head of *assimilis* has conspicuous grey stripes. An example of taxa that could be considered more divergent are *costaricensis* and *torquatus:* the former has a black head with broad grey stripes and an entirely white chest, whereas the latter has a white superciliary and a conspicuous black collar band. However, arguing that these differences could confer reproductive isolation would be premature without knowing the role of plumage signaling in mate selection. At any rate, considering that these populations occur thousands of kilometers apart, this is probably of little relevance.

In sum, our attempt to use the degree of divergence between reproductively isolated species occurring in geographic contact as a guide to making decisions about the status of allopatric populations has not taken us very far. In some aspects (e.g. divergence times, plumage), some populations are more divergent from each other than *assimilis* and *atricapillus*, but in other aspects (e.g. songs, ecology) they may be more similar. Therefore, making any recommendations regarding species status for many pairs of allopatric populations would still involve a substantial degree of subjectivity because it would require giving more importance to some traits over others without knowing which of them are the cause, and which a consequence of reproductive isolation between *assimilis* and *atricapillus*. Indeed, *poliophrys* and *torquatus* appear very likely candidates to be considered different species under the BSC, but these taxa are arguably less different from each other in several aspects than *assimilis* and *atricapillus*, indicating that differentiation in all the aspects these taxa differ is probably not required for populations to reach reproductive isolation.

PREVIOUSLY PUBLISHED ALTERNATIVES

Because we are unable to provide a novel and satisfactory BSC-based classification, we consider treatments that have been proposed in the literature. The two views of how *B. torquatus* may be split into more than one species are to recognize (1) *atricapillus* and *tacarcunae*, or (2) *atricapillus, tacarcunae,* and *costaricensis*, as members of a different species from the rest of the complex. Adopting any of these options would result in recognizing non-monophyletic species. Although polyphyletic and paraphyletic species are not inconsistent with the philosophy of the BSC, which emphasizes interbreeding and not common ancestry (Donoghue 1985, de Queiroz & Donoghue 1988, Olmstead 1995), the appropriateness of recognizing nonmonophyletic species is far from generally accepted. One of the most compelling arguments against this practice is that it implies a misrepresentation of the evolutionary units involved in the process of speciation (Cracraft 1989, Zink and McKitrick 1995). For the case of *B. torquatus*, even if we ignore this criticism, we see no compelling genetic, phenotypic, ecological, or vocal evidence that would support the recognition of the nonmonophyletic species circumscribed by earlier authors. For example, we find it impossible to contend that taxa as different in all aspects such as *costaricensis* and *poliophrys* belong to a cohesive, collectively evolving group (see Rieseberg and Burke 2000) to the exclusion of *atricapillus* and *tacarcunae.*

RESOLVING THE CONUNDRUM?

There is still much more to learn about patterns of variation in *B. torquatus*, particularly in potential contact zones of parapatrically distributed taxa. Also, increased availability of recordings should improve our ability to distinguish clusters of vocally distinct populations through more detailed analyses. However, achieving a complete picture of patterns of variation may take years of work and may still be inconclusive because some of the difficulties related to using the divergence between the only two sympatric and reproductively isolated taxa available as a yard stick to establish species status for allopatric taxa will remain. Also, it is already clear from our analyses that there will not be strict correspondence between patterns of geographic variation in plumage, morphometrics, song, and ecology; genetic distances; and phylogeny.

Clearly, the *B. torquatus* complex is no exception to the idea that species have fuzzy boundaries (Baum 1998). However, there is no doubt, under any species criterion, that the hypothesis that *B. torquatus* is one species is untenable, which implies that a revised classification is required. Under established taxonomic practices, advocating taxonomic changes based on our analyses may appear to create turmoil because it would disturb the *status quo*, but would fail to provide an entirely resolved picture of how many reproductively isolated species comprise the *B. torquatus* complex and how are they delimited. Although we appreciate the need for taxonomic stability, we contend that a classification that highlights that we already know some populations are reproductively isolated from each other conveys much more useful information about our understanding of evolution than a classification in which all taxa are lumped because we do not know enough about the potential for interbreeding across all members of the clade. In other words, we would argue that if taxonomy is to really provide a meaningful foundation for studying the biology of these birds, a classification that explicitly states what we do know and what we do not is preferable to a stable one that for all practical purposes amounts to assuming we do not know anything.

In theory, a solution that allows incorporating what we know and what we do not into classifications is having taxonomy be consistent with the emerging view of what species are, rather than with recognizing lineages on the basis of secondary properties that arise at different stages of differentiation (de Queiroz 2005b). *Buarremon torquatus* clearly comprises several species, that is segments of lineages at the population level of organization. Some of these are phenetically distinguishable, some statistically diagnosable based on morphology, songs, or ecology, some reciprocally monophyletic, and some reproductively isolated. In practice, however, existing taxonomic conventions do not readily lend themselves to incorporating all this information into baseline lists used by non systematists, which consist only of binomials and trinomials.

To bridge the gap between a classification that emphasizes only reproductive isolation that may turn out to be objectively unworkable even in the long run, and a novel classification scheme that would be consistent with the ontology of species (sensu de Queiroz 1998) but in practice difficult to implement and communicate, we suggest that the best available alternative is to consider treating the different major clades of *B. torquatus* identified by mtDNA data as different species. We realize there are many reasons why gene trees and organismal trees may be incongruent and that mtDNA may be a poor surrogate for differentiation in other traits. However, aside from the resolution of phylogenetic relationships, the mtDNA data indicate clearly there are several discrete lineages of comparable age that are in independent evolutionary trajectories. Also, these lineages occur in different biogeographic regions, and examining other traits when there is information (e.g. song) reveals that their members have characteristics in common that may be important in maintaining them as cohesive units. Therefore, delineating lineages on the basis of mtDNA data and biogeographic and vocal considerations is consistent with methods of species delimitation proposed by authors that favor an evolutionary species criterion (e.g. Wiens and Penkrot 2002) and has the advantage that the recognition of nonmonophyletic species is avoided. Also, although we are aware of the fact that some lineages may comprise more than one species (they certainly include diagnosable and ecologically distinct populations and group nonintergrading taxa whose ranges may be nearly parapatric), we believe it is very unlikely that members of different major lineages will be shown to be conspecific. We also note that although some lineages may seem heterogeneous in plumage patterns and members of different lineages can be difficult to distinguish, similarity in plumage is a very poor surrogate of evolutionary relationships in this group (C. D. Cadena in prep.).

Therefore, we propose a provisional classification that recognizes seven species-level taxa as follows: (1) *B. costaricensis* from Costa Rica and western Panama; (2) *B. atricapillus* from central and eastern Panama and the Colombian Andes (includes *atricapillus* and *tacarcunae*); (3) *B. basilicus* from the Sierra Nevada de Santa Marta, northern Colombia; (4) *B. perijanus* from the Serranía del Perijá, northeast Colombia and northwest Venezuela; (5) *B. assimilis* from the Andes of Venezuela, Colombia, Ecuador, and most of Peru (includes *larensis, assimilis, nigrifrons,* and *poliophrys*); (6) *B. torquatus* from the Andes of extreme southern Peru, Bolivia, and Argentina (includes *torquatus, fimbriatus,* and *borelli*); and (7) *B. phygas* from the Cordillera de la Costa Oriental, northeast Venezuela. The position of taxon *phaeopleurus* is uncertain because it is the only taxon for which sequence data are lacking. Its vocalizations resemble those of members of *B. assimilis* closely, so this appears to be the best place to allocate it for now, although it may represent yet another distinct lineage, or it could be conspecific with *B. phygas*, which it resembles closely in plumage and with which it shares some vocal traits (i.e. buzzing notes). The lack of vocal data for *B. basilicus* and *B. perijanus* is unfortunate, but these taxa are just as genetically distinct as others (Chapter 1).

CONCLUSION

Despite the central importance of species in biology, delimiting them objectively remains one of the most challenging problems faced by systematists. In this study we have begun to tackle the thorny issue of species delimitation in a complicated group of Neotropical birds in which sets of characters vary substantially across space, but do not obviously vary in a concerted fashion. To earlier discussions of species limits in the group, we have added a historical perspective offered by a molecular phylogeny, have presented quantitative analyses of morphological and vocal variation, and have incorporated the new tool of ENM to highlight cases of ecological distinctiveness and cases where populations seem to be in independent evolutionary trajectories despite being connected by environments unlikely to represent barriers to gene flow. Although our provisional classification is likely to change as more detailed work is conducted particularly within some groups (e.g. *B. assimilis*), it helps to better describe the diversity of this clade, which is obscured when all taxa are subsumed into a single species name. Because species are the units most commonly used by biologists working in various fields, there are important implications of this increased understanding of diversity beyond systematics. For example, arguably part of the explanation for the patterns of elevational distribution of *B. torquatus* (sensu lato) that have long puzzled ecologists and biogeographers (Remsen and Graves 1995, Chapter 2, Chapter 3) is that some populations with disparate distributions are referable to different species. An improved understanding of the diversity of this group may also be of importance from a conservation standpoint because some of the newly recognized lineages are endemic to rather small areas, and may become endangered if processes of habitat degradation continue at the present pace (e.g. *B. perijanus,* see Fjeldså et al. 2005).

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Table 1. Mean values and standard deviations for 14 acoustic variables measured on spectrograms of songs of *assimilis, atricapillus, poliophrys*, and *torquatus.* Numbers in parentheses are the number of individual recordings on which measurements were taken. For each pair of taxa, results of t-tests comparing means are shown, with significance levels indicated by asterisks.

Song variables	***assimilis*** **(12)**	***atricapillus*** **(3)**	**T-test**	***poliophrys*** **(5)**	***torquatus*** **(4)**	**T-test**
Maximum frequency	9.941±0.54	10.200±0.59	-0.73	9.857±0.35	10.364±1.02	-1.06
Min. frequency	3.164±0.64	6.043±0.39	-7.30***	3.602±0.98	5.089±0.46	-2.77*
Bandwidth	6.777±0.66	4.157±0.88	5.81***	6.255±0.84	5.276±1.23	1.43
Max. note bandwidth	5.269±0.94	3.306±0.91	1.29**	3.786±0.74	3.821±1.51	-0.05
Min. note bandwidth	0.751±0.44	0.574±0.30	3.24	0.740±0.26	0.398±0.25	2.01
Peak frequency	6.675±1.91	8.150±0.52	0.65**	6.120±1.24	7.920±1.45	-2.02
Song duration	4.679±1.55	1.738±1.13	3.05**	4.945±1.73	4.924±2.05	0.02
Number of notes	8.500±1.75	4.667±2.08	3.30**	7.300±1.48	8.500±1.73	-1.12
Note pace	1.975±0.56	2.937±0.78	-2.49*	1.577±0.49	1.842±0.37	-0.89
Summed note duration	1.984±0.53	1.130±0.35	-3.38	1.838±0.20	1.720±0.54	0.46
Note proportion	0.448±0.12	0.741±0.21	2.63**	0.399±0.11	0.361±0.03	0.65
Max. note duration	0.376±0.07	0.377±0.05	-0.77*	0.389±0.06	0.332±0.04	1.68
Min. note duration	0.109±0.06	0.147±0.09	-0.03	0.135±0.07	0.092±0.04	1.09
Mean note duration	0.231±0.05	0.256±0.07	-0.96	0.257±0.04	0.199±0.02	2.49*

***$P < 0.001$, ** $P < 0.01$, * $\mathrm{P} < 0.05$

FIGURE LEGENDS

Figure 1. Geographic distribution of members of the *B. torquatus* complex in Central and South America. Areas above 1500 m elevation are shown in grey. Each dot indicates a site where members of the complex have been collected, tape-recorded, or reliably observed. Brackets indicate the ranges of each taxon. Unbracketed points within Colombia correspond to localities of *assimilis* and *atricapillus*, which are shown separately in the inset for clarity. Question marks indicate areas where the identity of populations is uncertain owing to lack of specimens or to the existence of possible intergrades. In southern Ecuador and northern Peru, records on the West slope of the Andes correspond to taxon *nigrifrons* and those on the east slope to *assimilis.* The inset on the right shows a simplified diagram of phylogenetic relationships among members of the complex as determined from mtDNA sequence data by Cadena et al. (Chapter 1). Nodes that did not receive significant bootstrap or posterior probability support are collapsed into polytomies; all relationships shown as resolved are strongly supported. Stars indicate nodes connecting pairs of taxa that are not reciprocally monophyletic with respect to each other; the number of individuals per taxon assayed for mtDNA variation is shown in parentheses.

Figure 2. Geographic projections on maps of Colombia of ecological niche models constructed using the DOMAIN algorithm for *assimilis* and *atricapillus.* Black areas are those with DOMAIN scores ≥ 95%. Models were constructed on the basis of three independent climatic axes obtained from principal components analysis of 19 climatic variables. Although climatically suitable areas for both taxa are widespread in some of the same mountain ranges, they do not overlap with each other, indicating their very different ecologies.

Figure 3. Scatter plot showing variation in three bill dimensions measured on Colombian specimens of *assimilis* and *atricapillus.* Taxa are indicated by the shape of the symbols and sex by fill patterns. Samples of specimens of both taxa included material from all three Cordilleras of the Colombian Andes. None of the bill measurements overlap, a strong indication that these taxa are diagnosably distinct and do not intergrade.

Figure 4. Spectrograms showing representative examples of the songs of taxa *assimilis* (Colombia, Risaralda, Parque Regional Ucumarí*;* recording by C. D. Cadena, BSA 6780), *atricapillus* (Colombia, Santander, Lebrija, Portugal; recording by J. E. Avendaño, not yet archived), *poliophrys* (Peru, La Libertad, E Tayabamba on Trail to Ongón; recording by T. A. Parker III, LNS 17282), and *torquatus* (Bolivia, La Paz, Franz Tamayo, Madidi National Park; recording by B. A. Hennessey, LNS 120885).

Figure 5. Geographic projections on maps of Peru and Bolivia of ecological niche models constructed using the DOMAIN algorithm for *poliophrys* and *torquatus*, and intersection of climatically suitable areas for both taxa. Black areas are those with DOMAIN scores ≥ 95%. Models were constructed on the basis of three independent climatic axes obtained from principal components analysis of 19 climatic variables. Climatically suitable areas for both taxa occur widely, including part of the area separating the southernmost records of *poliophrys* and the northernmost of *torquatus* (for reference, see Figure 1).

Figure 6. Scores obtained from discriminant function analyses based on six morphological measurements taken on female and male specimens of *poliophrys* (black dots) and *torquatus* (white dots) plotted as a function of latitude. The star indicates an individual that was presumed to be a hybrid based on plumage patterns, but appears closest to *poliophrys* morphometrically. Plots indicate most specimens can be readily assigned to their corresponding subspecies and that there are no trends that would indicate specimens are more difficult to distinguish near areas of potential contact (c. 14°

S). One male *poliophrys* that is clearly an outlier is from an isolated population (Cordillera Vilcabamba). There are no additional specimens from this locality so we cannot determine whether this represents errors in measurements or that birds in the area are in fact more similar to *torquatus.*

Figure 7. Scores obtained from discriminant function analysis based on thirteen acoustic measurements on song spectrograms of *poliophrys* (black dots) and *torquatus* (white dots) plotted as a function of latitude. More than one song is shown for several individuals (total individuals = 4 *poliophrys* and 5 *torquatus*), but the pattern and statistical results of the analysis are identical when mean values for songs of each individual are used. Plots indicate all recordings can be readily assigned to their corresponding subspecies, and although sampling is geographically sparse, they do not suggest there are trends that would indicate songs are more difficult to distinguish in areas that approach the potential contact zone more closely.

Figure 8. Geographic variation in vocalizations in the *B. torquatus* complex. A single spectrogram is shown for each taxon for which recordings are available, with arrows indicating the locality where the recording was made. Sample sizes are insufficient to determine the extent of vocal variation within taxa, but the spectrograms shown seem representative in general terms of vocalizations over the ranges of each taxon (see Figure 1 for distributions). Note the superficial similarity of songs from the southern extreme of the range (*torquatus, fimbriatus,* and *borelli*) to those of northern taxa (*costaricensis, atricapillus, tacarcunae*). Songs of other populations are much more complex, yet similar in overall structure to one another.

Spectograms show songs from the following localities: *costaricensis* (Costa Rica, Puntarenas, Las Cruces Biological Station; J. R. Zook, unarchived), *tacarcunae* (Panama, Cerro Jefe; T. A. Parker III, LNS 25634), *phygas* (Venezuela, Monagas, Cerro Negro; P. Boesman, unarchived) *atricapillus* (Colombia, Santander, Lebrija, Portugal; J. E. Avendaño, unarchived), *phaeopleurus* (Venezuela, Miranda, Oripoto; P. Schwartz, LNS 67488), *assimilis* (Colombia, Risaralda, Parque Regional Ucumarí*;* C. D. Cadena, BSA 6780), *larensis* (Venezuela, Mérida, Chorotal, Carretera La Azulita-Mérida; D. Ascanio, unarchived), *nigrifrons* (Ecuador, Azuay, upper Yunguilla Valley, J. V. Moore, Krabbe et al. 20001), *poliophrys* (Peru, La Libertad, E Tayabamba on Trail to Ongón; T. A. Parker III, LNS 17282), *torquatus* (Bolivia, La Paz, Franz Tamayo, Madidi National Park; B. A. Hennessey, LNS 120885), *fimbriatus* (Bolivia, Santa Cruz, Siberia; T. A. Parker III, LNS 33643), *borelli* (Argentina, Jujuy, Parque Nacional Calilegua; J. Mazar Barnett, Mayer 2000). See appendix for references.

FIGURE 1

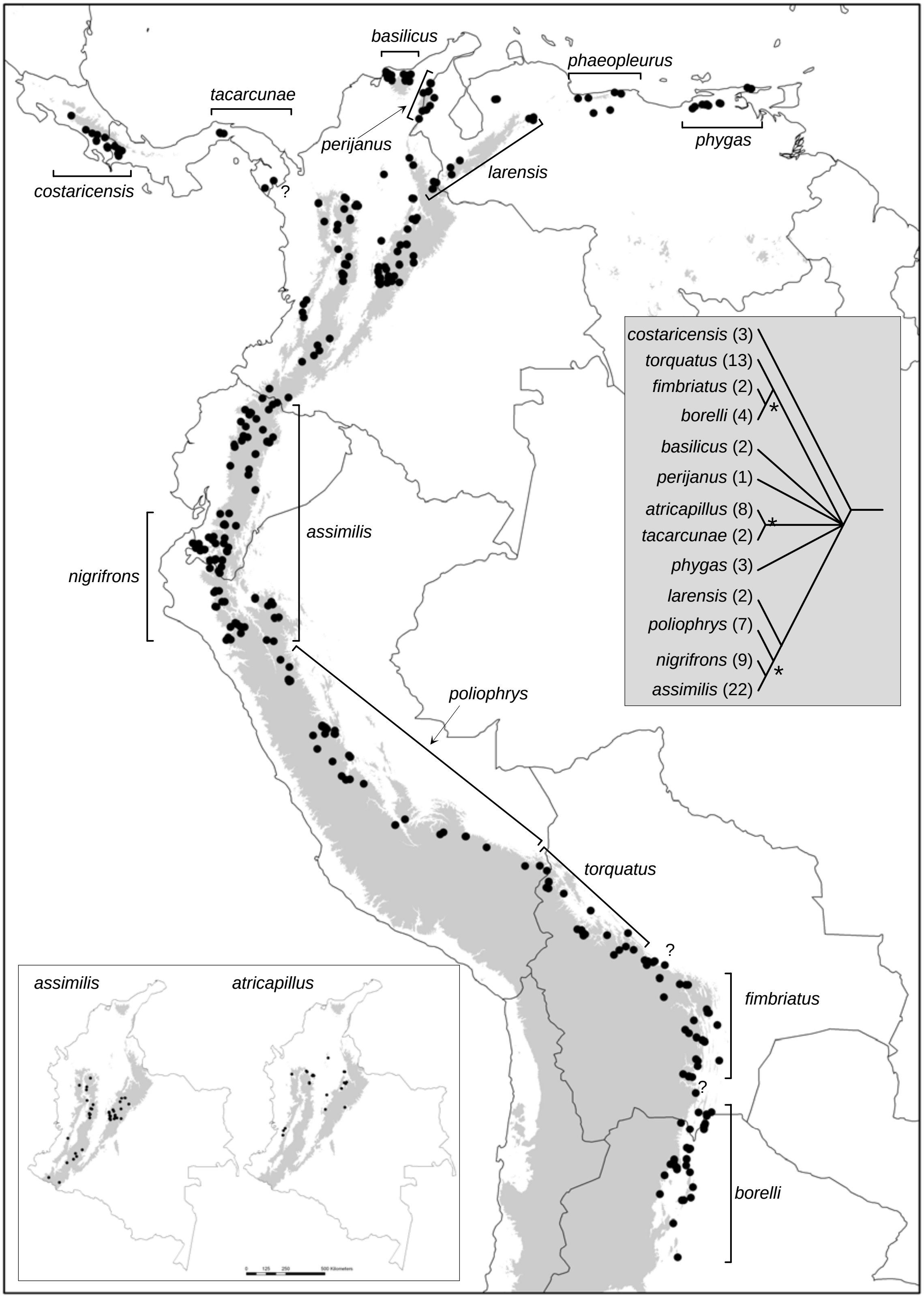

basilicus
tacarcunae
phaeopleurus
perijanus
phygas
costaricensis
?
larensis
costaricensis (3)
torquatus (13)
fimbriatus (2)
borelli (4)
*
basilicus (2)
perijanus (1)
atricapillus (8)
*
tacarcunae (2)
phygas (3)
larensis (2)
poliophrys (7)
nigrifrons (9)
*
assimilis (22)
assimilis
nigrifrons
poliophrys
torquatus
?
fimbriatus
?
borelli
assimilis
atricapillus
0 125 250 500 Kilometers

FIGURE 2

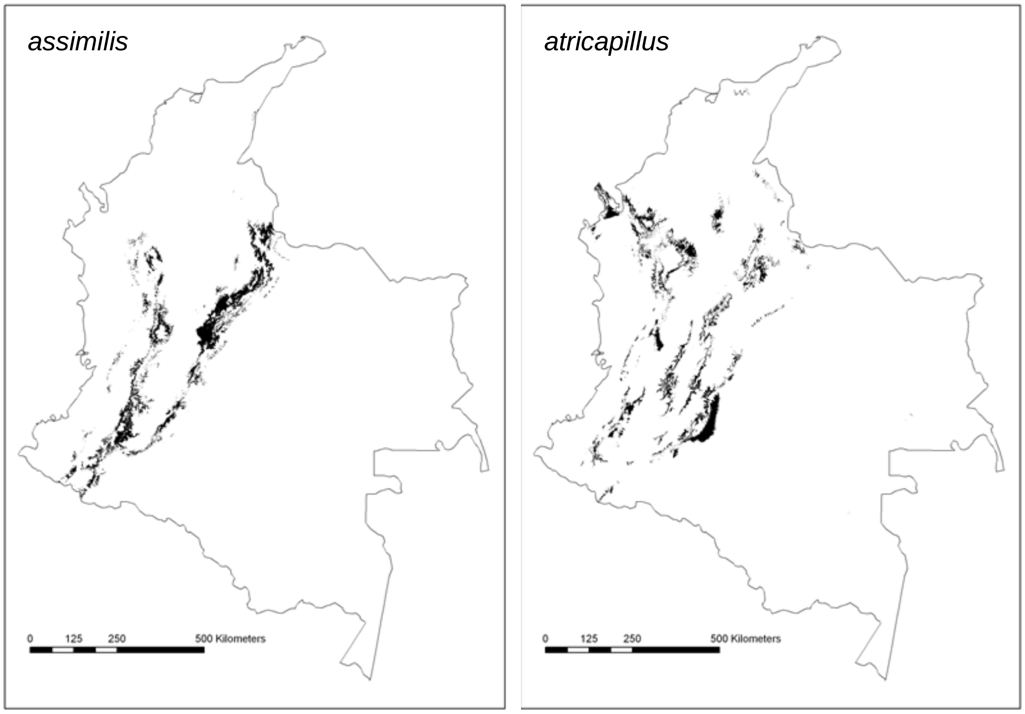
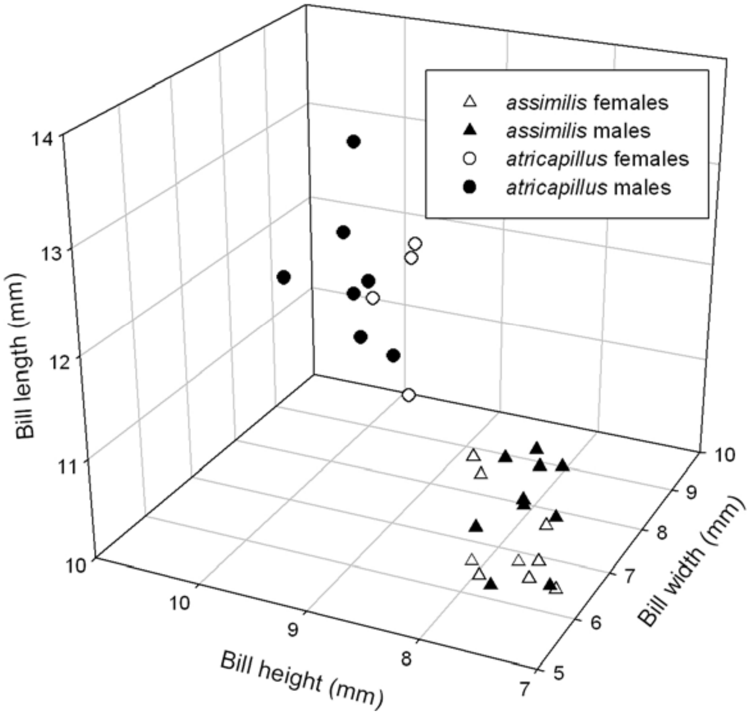

assimilis
0 125 250 500 Kilometers
atricapillus
0 125 250 500 Kilometers

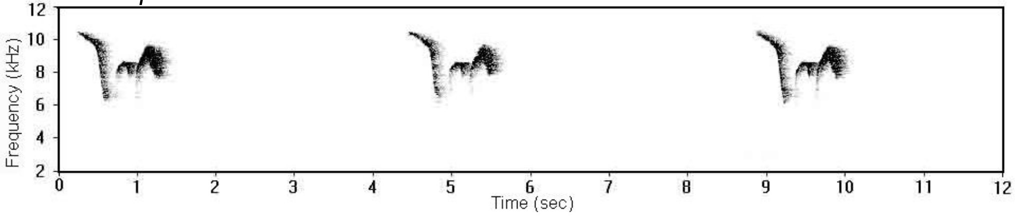
FIGURE 3



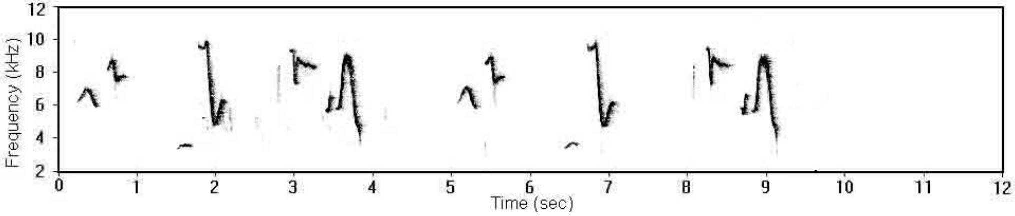
△ *assimilis* females
▲ *assimilis* males
○ *atricapillus* females
● *atricapillus* males
Bill length (mm)
14
13
12
11
10
Bill height (mm)
10
9
8
7
Bill width (mm)
10
9
8
7
6
5

FIGURE 4

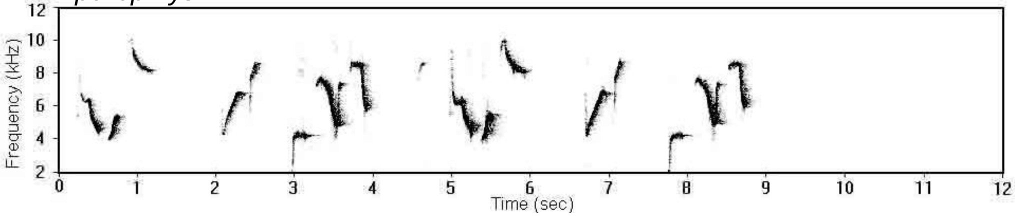
atricapillus



assimilis



poliophrys



torquatus

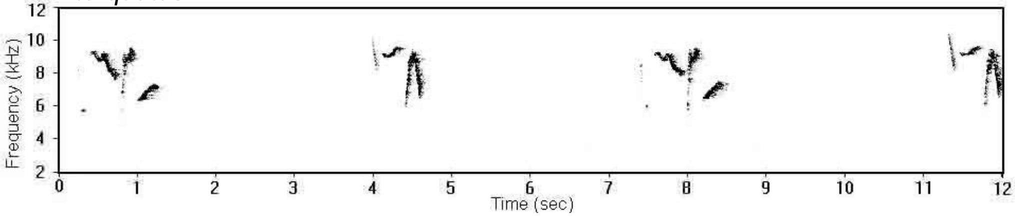


FIGURE 5

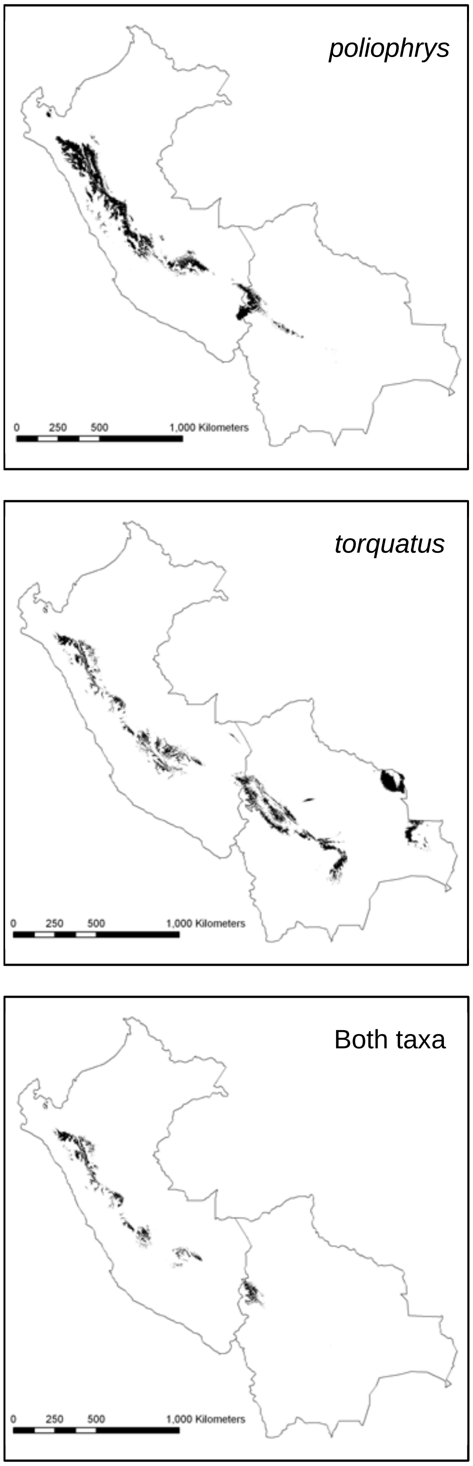

poliophrys
0 250 500 1,000 Kilometers
torquatus
0 250 500 1,000 Kilometers
Both taxa
0 250 500 1,000 Kilometers

FIGURE 6

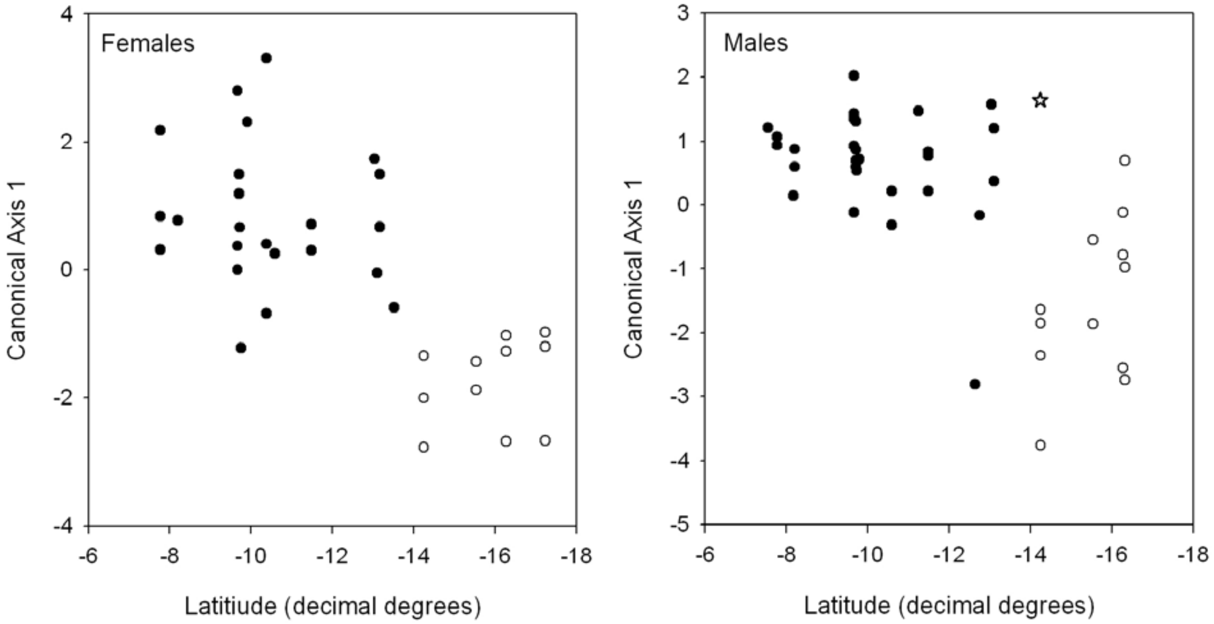

Females
Canonical Axis 1
4
2
0
-2
-4
-6
-8
-10
-12
-14
-16
-18
Latitiude (decimal degrees)
Males
Canonical Axis 1
3
2
1
0
-1
-2
-3
-4
-5
-6
-8
-10
-12
-14
-16
-18
Latitude (decimal degrees)

FIGURE 7

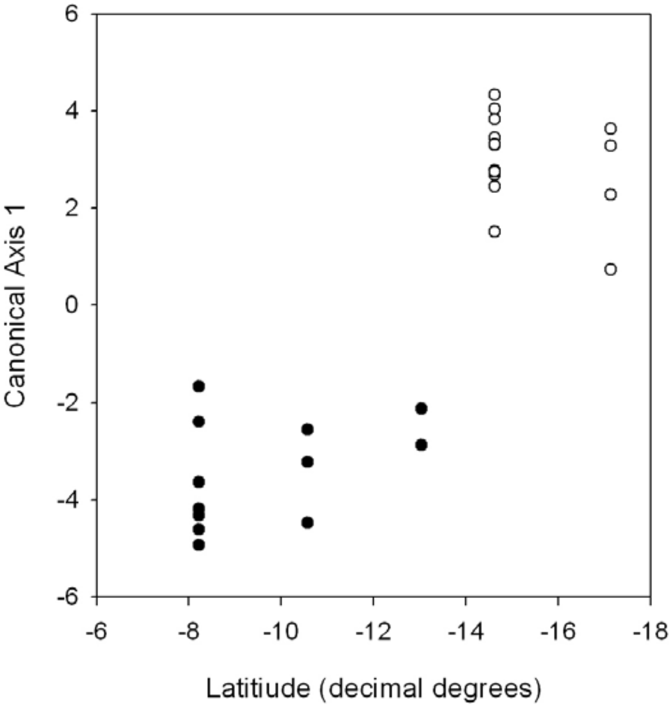
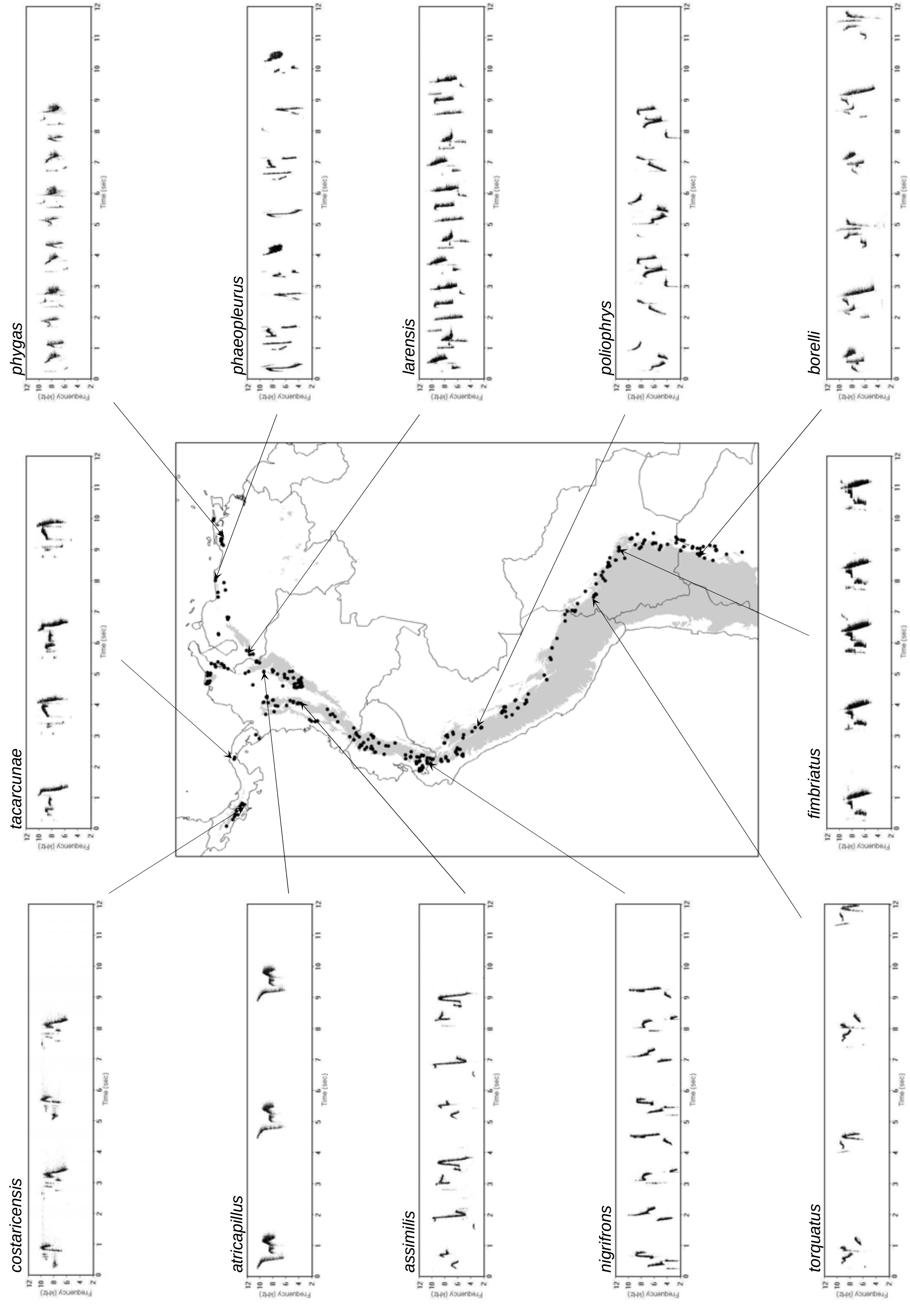

6
4
2
0
-2
-4
-6
Canonical Axis 1
-6
-8
-10
-12
-14
-16
-18
Latitiude (decimal degrees)

FIGURE 8


phygas
phaeopleurus
larensis
poliophrys
borelli
tacarcunae
fimbriatus
costaricensis
atricapillus
assimilis
nigrifrons
torquatus
Frequency (kHz)
Time (sec)

Appendix. Recordings of songs of *assimilis*, *atricapillus*, *poliophrys*, and *torquatus* used in quantitative analyses. Acronyms for sound archives: BSA = Banco de Sonidos Animales, Instituto Alexander von Humboldt, Villa de Leyva, Colombia; LNS = Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, USA.

Taxon	**Source**	**Recordist**	**Locality**	**Latitude**	**Longitude**
assimilis	BSA 6324	C. D. Cadena	Colombia, Cundinamarca, Parque Natural Chicaque	4.6087	-74.3066
assimilis	BSA 6338	C. D. Cadena	Colombia, Cundinamarca, Bojacá, Finca Macanal	4.6625	-74.3458
assimilis	BSA 6773	C. D. Cadena	Colombia, Risaralda, Parque Regional Ucumarí	4.7214	-75.4685
assimilis	BSA 6778	C. D. Cadena	Colombia, Risaralda, Parque Regional Ucumarí	4.7214	-75.4685
assimilis	BSA 6780	C. D. Cadena	Colombia, Risaralda, Parque Regional Ucumarí	4.7345	-75.4621
assimilis	BSA 6804	C. D. Cadena	Colombia, Risaralda, Parque Regional Ucumarí	4.7088	-75.4901
assimilis	BSA 7697	S. Córdoba – M. Alvarez	Colombia, Caldas, Aranzazu, Vereda El Laurel	5.2225	-75.4883
assimilis	Krabbe et al. (2001) CD 4, # 5	N. Krabbe	Ecuador, Chimborazo, Orregán	-1.6500	-78.5000
assimilis	Krabbe and Nilsson (2003), #14	J. Nilsson	Ecuador, Napo, Pass of Cordillera Guacamayos	-0.6125	-77.8292
assimilis	Krabbe and Nilsson (2003), # 17	N. Krabbe	Ecuador, Imbabura, Apuela Road	0.3458	-78.4375
assimilis	Krabbe and Nilsson (2003), # 18	N. Krabbe	Ecuador, Napo, 3-5 km below Oyacachi	-0.2125	-78.0375
assimilis	Krabbe et al. 2001 CD 4, # 1	J. V. Moore	Ecuador, Pichincha	-0.1000	-78.2833
atricapillus	Not archived or published	J. Avendaño	Colombia, Santander, Lebrija, Portugal	7.1625	-73.2792
atricapillus	BSA 6815	C. D. Cadena	Colombia, Antioquia, Don Matías, Estación Pradera	6.5292	-75.2625
atricapillus	Not archived or published	O. Laverde	Colombia, Santander, San José de Suaita	6.1875	-73.4292
poliophrys	LNS 17258	T. A. Parker III	Peru, La Libertad, E Tayabamba, on trail to Ongón	-8.22083	-77.1958
poliophrys	LNS 17282	T. A. Parker III	Peru, La Libertad, E Tayabamba, on trail to Ongón	-8.22083	-77.1958
poliophrys	LNS 35950	T. S. Schulenberg	Peru, Pasco, Oxapampa, Cumbre de Ollón	-10.5792	-75.2958
poliophrys	LNS 36006	T. S. Schulenberg	Peru, Pasco, Oxapampa, Cumbre de Ollón	-10.5792	-75.2958
poliophrys	LNS 24051	T. A. Parker III	Peru, Cusco, Canchaillo, below (N) Abra Málaga	-13.1167	-72.3667
torquatus	Mayer 2000, # 2	S. Herzog	Bolivia, Cochabamba – Villa Tunari Rd, Carrasco NP	-17.1375	-65.5792
torquatus	LNS 120885	A. B. Hennessey	Bolivia, La Paz, Torcillo-Sarayoj; Madidi NP	-14.5958	-68.9458
torquatus	LNS 120922	A. B. Hennessey	Bolivia, La Paz, Torcillo-Sarayoj; Madidi NP	-14.5958	-68.9458
torquatus	LNS 121717	A. B. Hennessey	Bolivia, La Paz, Tokoaque; Madidi NP	-14.5958	-68.9458

References: Krabbe, N., J. V. Moore, P. Coopmans, M. Lysinger, and R. E. Ridgely. 2001 Birds of the Ecuadorian Highlands: The Upper Montane and Paramo Zones of Ecuador. John V. Moore Nature recordings, San Jose, CA. Mayer, S. Birds of Bolivia, CD-ROM. Bird Songs International. Enschede, Netherlands. Krabbe, N. and J. Nilsson. 2003. Birds of Ecuador: Sounds and Photographs, DVD-ROM. Bird Songs International. Enschede, Netherlands