



Fifteen New Species of Amazonian Birds

Bret M. Whitney¹ and Mario Cohn-Haft²

Amazonia, in a vast and awesomely complex paleohistorical and biological dynamic, has fostered the evolution of far more species of birds than any other biome and probably also harbors the most species-diverse avifauna per unit area. It is no surprise, therefore, that Amazonia has been the source of, in the past few decades, more species of birds unknown to science – and more highly distinctive new species – than has any other place on our planet. In affirmation of these realities and to herald that the era of discovery not only continues but is poised for a leap forward, in this chapter we introduce fifteen new species of birds from the Amazon basin. As it turns out, all are described from Brazil, just as were the approximately forty named by August von Pelzeln when he took up the extensive collections of Johann Natterer in 1871, which was the last time so many species were introduced under one cover. Included is a wide range of birds – non-passerines, suboscine passerines, and oscine passerines – described in independent, peer-reviewed publications authored by, in most cases, their discoverers, together with colleagues spearheading phenotypic and, for most of the species, DNA-based phylogenetic analyses.

The result is a collaborative, international call to arms. Now more than ever we must address head-on the inadequacy of geographic coverage and of taxon or population-level representation among museum specimen collections. This is the single greatest impediment to the definition and conservation of Amazonian bird species and, at the root of it all, to our understanding of speciation patterns and processes. We cannot properly consider or objectively justify proposals to safeguard some sectors of Amazonia as opposed to others without a clear vision of what we could choose to prioritize. We argue from extensive experience in Amazonia, and as scientists working with the best-known group of vertebrates, that we certainly do not have the data required to make the wisest decisions for studying and safeguarding the richest biodiversity treasure-trove our planet yet holds.

To the point, contemporary thinking on bird conservation has relied heavily on identifying areas of endemism (regions where distributions of multiple, often rangerestricted species coincide), and this is surely one productive weight to place on the scale. But focusing too tightly on endemism fails to address a more basic and crucial question: "How did the unparalleled diversity of species in Amazonia arise and how is it maintained?" and then, "Given these species' population dynamics in the modern world (*i.e.*, with global weather patterns changing, human population needs increasing, landscape alteration accelerating in many places), what predictable evolutionary fate might we identify for some of them?" Clearly, we cannot protect everything everywhere, which makes it critically important to identify key areas for intensive ornithological study – which must include not only centers of endemism (themselves much too large to fully protect, and holding many species inhabiting only part of the area) but also numerous heretofore unidentified zones where species diversity is undergoing remarkable change today – to best inform conservation action.

In inviting our colleagues to help describe a large number of new species in this final, *Special Volume* of *The Handbook*, we wish to point out, for the contemplation of all, some of the wide range of ornithological thought and methodology that comes to bear on "what a species of bird is" in the early 21st century, and also express our concerns for the future of Amazonian species and the processes that create and maintain them. For background, we provide an overview of the "ages of discovery" in Amazonian ornithology but we will not enter into the age-old debate on species concepts, and do not wish to advance any novel concept. To the contrary, we employ a case-by-case assessment of independent datasets non-formulaic by nature, and of necessity. Results are, therefore, educated judgments of the most appropriate placement of naturally defined populations within the Linnaean taxonomic framework; proposed rankings represent "best-fit" estimates by the authors of each description as an independent publication.

<

The Campina Jay (Cyanocorax hafferi, described in this volume by Cohn-Haft, Santos Junior, Fernandes, and Ribas) is a startling addition to the world's avifauna. The first new iav described in over 75 years occurs in the heart of the Amazon basin, in remote natural savannas (campinas) not far from some of the region's largest cities. Like jay species everywhere, its pretty colors and noisy and gregarious habits make it conspicuous when it wants to be. This species was missed by centuries of scientific exploration in the Amazon, surely because its habitat had never before been visited by ornithologists. Yet now it is born into the roll of known birds as an already endangered species. Its small geographic range, very specific and limited breeding habitat, and the pressure from ambitious development projects and human population expansion conspire to offer a very real challenge to the new parks and reserves created in part to protect it. This small group of jays depicted in their natural habitat was painted by Larry McQueen who brought the new species to life in this attractive frontispiece, capturing from his studio in the northwestern United States the spirit, actions, colors, attitudes, and habitat of the bird, without ever having seen it alive.

¹ Louisiana State University, Department of Biological Sciences, Museum of Natural Science, 119 Foster Hall, Baton Rouge, Louisiana 70803, USA. (ictinia@earthlink.net)

² Departamento de Biodiversidade (CBio) e Coleções Zoológicas - Aves, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas. Brasil CEP 69080-971. (mario@buriti.com.br)

First and foremost, we propose that Amazonia and surely most other regions of the tropics worldwide harbor a significantly higher number of avian taxa that most scientists would accept as *species* than are currently "on the books" or perhaps even estimated. As a clear sign of the times, we recognize that most taxonomically oriented ornithologists have largely shifted away from worries about whether phenotypically differentiated, allopatric sister-populations merit species status or not. When we say "phenotypically differentiated," we mean those taxa or populations displaying presumably genetically determined, diagnostic combinations of morphological and vocal traits (more on this below). These cases, most of which have involved multiple subspecies, generated considerable concept-based angst just a few years ago but an overwhelming majority has now been accepted at the species rank and we see every reason to continue with reevaluations of taxonomic rankings of Amazonian birds through application of concerted data sets. Which brings us to our second point.



Figure 1.

The authors of the fifteen new species descriptions that follow this essay have based their hypotheses on assessments of differentiation in morphology (plumage and morphometrics), vocalizations, and genetic divergence between closely related populations. They propose that congruence in at least two of these three independent data sets – without a threshold in any one set of characters – is a coherent approach to recognizing both existing and as-yet undescribed species. This specimen is the holotype of the new species Hypocnemis rondoni (Manicore Warbling-Antbird) Whitney, Isler, Bravo, Aristazábal, Schunck, Silveira, Piacentini, Cohn-Haft, and Régo described in this volume. Descriptions of "earthen-colored" plumages are nowadays often based on comparison to the standardized color swatches in the Munsell® Soil Color Charts. Image by Bret Whitney.

We will discuss the basic criteria that the new-species authors involved in this endeavor have employed across the board: All species described herein are significantly diagnosable from their closest, known relative(s) by a minimum of two among three fundamental character sets: morphology, vocalizations, and genetics (Fig. 1). Where only one of these data sets differed (sometimes because one or more sets were unavailable for analysis), we left the bird out of this work to await further study. There were many potential, even probable, new species that fell into this category, which necessitated the use of a collective and conservative "good sense" to arrive at consensus without excluding any descriptions based solely on perceived degree of subtlety of diagnostic characters. Of course, one set of ornithologists' "good sense" may not ring true with that of some colleagues; we present a few of the more complicated examples below. In all cases, we have tried to maintain focus on identifying and evaluating differentiation, wherever it may have evolved, because it is always correlated with species recognition, both among individuals looking for mates and ornithologists looking to maintain a taxonomy. Finally, we offer some observations on and predictions for the future, mostly relative to how our definition of species may continue to evolve through the present, exciting era of discovery and touch on how additional new species may be discovered.

The new species descriptions in this volume are presented in current taxonomic order. Most (12 of 15) continue the tradition of honoring people whom the authors have chosen for reasons provided in the etymology section of each description. Individuals from various walks are represented, ranging from conservationist-activists (1 species), conservation-oriented ornithologists (3), collections-oriented ornithologists and technicians (2), and Neotropical avian biogeographers (3, including, as a pleasant surprise, one of us!), to appointed or elected government officials (2) and a widely respected personality of nature-television fame (1). We speak for all of our colleagues when we acknowledge that we are greatly privileged to be alive and active in Amazonia *right now*, while populations of most birds are reasonably intact and technological, medical, and infrastructural resources are fast advancing.



Amazona kawalli (Kawall's Parrot) was described to science only in 1989, based on a pet bird in São Paulo, Brazil. Several years went by before it was identified in the wild. That a widespread species so large, colorful, and noisy – being quite distinctive both morphologically and vocally – could have escaped description for centuries is perhaps the ultimate indicator that there remains a lot to learn about diversity of Amazonian birds. Among the things Bret Whitney has learned is "Never caress the toes of a Kawall's Parrot"! This (A) seemingly friendly individual was (B) unsupervised by a shopkeeper in the Amazonian frontier town of Jacareacanga, Pará, where the species is perhaps the most common Amazona parrot in surrounding forests. Images by Paulo César Balduíno.

HISTORICAL PERSPECTIVE

Most of the approximately 1300 currently recognized species of Amazonian birds were described in the 18th and 19th centuries, when thousands of specimens were shipped to museums in Europe, mostly from the ports of Cayenne (French Guiana), Pará (now the city of Belém), Baía (now the city of Salvador), and Rio de Janeiro. The 20th century brought a significant hiatus in new species descriptions, but this must be viewed in large part as an artifact of the guiding ideology of avian taxonomists during this period, when the vogue was recognition of unnamed, allopatric forms as "geographic replacements" best designated as subspecies. Thus, scores of new Amazonian birds were described at the subspecies level by museum-based taxonomists such as the venerable Charles Hellmayr at the Field Museum, John Todd Zimmer of the American Museum of Natural History, W. E. Clyde Todd at the Carnegie Museum of Natural History, Emilia Snethlage and Fernando Novaes of the Museu Paraense Emílio Goeldi, and Oliverio Pinto of the Museu de Zoologia da Universidade de São Paulo. Most of them spent little or no time in the Neotropics, but rather described these taxa in the course of studying specimens, many of which had recently been obtained by prolific collectors like the Olalla family, Samuel Klages, Ernst Garbe, and Emílio Dente.

In general, only taxa known to be in sympatry with a presumed close relative without clear evidence of interbreeding were given species rank, and this remains, for all ornithologists, the single strongest line of evidence for recognizing two closely related taxa as separate species today. The description of Micrastur buckleyi (Buckley's Forest-Falcon, Swann, 1919), Todd's Snethlagea minima, 1925 (now Hemitriccus minimus, Zimmer's Tody-Tyrant), Zimmer's brilliant revelation of Dendroplex necopinus, 1934 (now D. kienerii, Zimmer's Woodcreeper), and Wetmore's stunning illumination of Cathartes melambrotus, 1964 (Greater Yellow-headed Vulture) as a widespread species are prime examples among the few from Amazonia that were originally described as species during the 20th century "subspecies era", all of these found in sympatry with the sister-species or very similar relatives from which they were distinguished. So strong was the call to acknowledge "subspecies replacement" that, for one example, the highly distinctive Capito brunneipectus (Brown-breasted Barbet; Chapman, 1921) was soon relegated by Peters (1948) to subspecies rank in the widespread Capito niger (Black-spotted Barbet) complex without comment. In fact, hundreds of taxa originally described as species, sometimes much earlier, were similarly summarily "demoted" to subspecies during this period. Gradually, these taxa are being reclassified as species using new methods (more on this below).

The slowdown in descriptions of full species through the middle 20th century led some to suggest that the age of discovery of birds unknown to science had passed. But a new wave was just offshore, and it came as a real shock as some of the most remarkable and unexpected new species to come from Amazonia in a hundred years were introduced in the final third of the 20th century and the start of the 21st. Outstanding among these were Conioptilon mcilhennyi (Black-faced Cotinga; Lowery and O'Neill, 1966); Grallaria eludens (Elusive Antpitta; Lowery and O'Neill, 1969); Clytoctantes atrogularis (Rondonia Bushbird; Lanyon, Stotz, and Willard, 1990); Nannopsittaca dachilleae (Amazonian Parrotlet; O'Neill, Munn, and Franke, 1991); Pyrilia aurantiocephala (Bald Parrot; [Gaban-Lima, Raposo, and Höfling, 2002]); Thamnophilus divisorius (Acre Antshrike; Whitney, Oren, and Brumfield, 2004); and Cnipodectes superrufus (Rufous Twistwing; Lane, Servat, Valqui, and Lambert, 2007). Amazona kawalli (Kawall's Parrot; Grantsau and Camargo, 1989; Fig. 2), a large, colorful, noisy, widespread bird, is surely the single most ornithologically humbling Amazonian species described in the past quarter century; this one truly "rocked our worlds"!

It is likely, we believe, that there remain at least a few more stunning new birds to be found in unexplored regions of Amazonia; the new *Cyanocorax* jay described in the following pages is an example! In keeping with the global trend, however, it appears that the wave of discovery of new species has made the inevitable shift toward the more obscure and smaller birds that have escaped detection or description because they conform to one or more of the following three characteristics, being: 1) difficult to recognize or identify; 2) concentrated in under-sampled habitats including forest canopies; or 3) of highly restricted global distributions, most of which should be more easily accessible today than they were just a few decades ago. Classic examples are the ecologically diverse suite of new species recently described from the neglected, patchily distributed white-sand forests at the outskirts of Iquitos, Peru, one of the oldest and largest human population centers in Amazonia: *Herpsilochmus gentryi* (Ancient Antwrer; Whitney and Álvarez, 1998), *Percnostola arenarum* (Allpahuayo Antbird; Isler, Álvarez, Isler, and Whitney, 2001), *Zimmerius villarejoi* (Mishana Tyr-

annulet; Álvarez and Whitney, 2001), and *Polioptila clementsi* (Iquitos Gnatcatcher; Whitney and Álvarez, 2005).

To be sure, many *widespread* populations of Amazonian birds were not described as subspecies or species for various reasons (but usually because earlier workers did not possess sufficient samples of them or of other, related populations to reveal subtle levels of morphological differentiation). These forms are likely to receive names in today's new age of avian taxonomy, when multiple data sets including vocalizations and molecular phylogenetics are routinely evaluated in concert. The underlying question oscillating through the ages is where to draw the taxonomic limits.

DOCUMENTING AVIAN SPECIES DIVERSITY

Species arise through random genetic drift and natural selection within closed gene pools, the size of which heavily influences the rates at which mutations become fixed; evidence for independently evolving lineages is often identified by the presence of reciprocally monophyletic groups in a phylogenetic tree (Coyne and Orr 2004). Sexual selection acting within any size population will speed up the process of differentiation (Panhuis et al. 2001). In recognition of these basic processes, one could argue that ornithologists' notion of what a species is has not changed dramatically through the "ages of discovery"; the reality is that we are now, for better or worse, embarking on a new period of demarcation that is itself evolving as technology roars forward. In a kind of mad race against the advance of habitat destruction, also increasingly enabled through advancing technologies, scientists from all disciplines are spurred on to uncover and describe the underestimated biodiversity that most now acknowledge. In this regard, we should have no preconception of the number of species of birds that might exist. For each of the fifteen species described below we expect that there are a great many others still not recognized as species, whether named as subspecies or yet to be described or discovered.

We believe that assessment of congruence among independent data sets - without a threshold in any one set of characters - is a coherent approach to recognizing both existing and as-yet undescribed species. When practiced in the context of comparing relative levels of differentiation among, at the first tier, sister members of species complexes and then, at a second tier, especially in the cases of monotypic species, also among phylogenetically confirmed congeners, taxonomic judgment may be viewed as holistic as well as conservative. A useful, existing framework for communication among taxonomists resides in the recognition of superspecies and allospecies groups or complexes (referred to as "aggregates" in the International Code of Zoological Nomenclature [1999]). For example, the widespread Amazonian genus Hypocnemis comprises two well-defined clades in extensive sympatry over vast areas: H. hypoxantha (Yellow-browed Antbird), currently classified as one species with two subspecies, and H. cantator (Warbling Antbird), until recently considered to constitute a single species with twelve subspecies and now judged to comprise six species with six additional subspecies (sensu Isler et al. 2007). This aggregate will be joined by a new allospecies in the H. cantator complex described in this volume, and anticipated further taxonomic revision will recommend recognition of multiple allospecies within relatively poorly known H. hypoxantha, some of which are presently undescribed. An objective and especially informative resulting arrangement would be recognition of two clearly related and highly differentiated, widely sympatric superspecies within *Hypocnemis*, each comprising multiple, phenotypically differentiated allospecies that demonstrate little or no genetic exchange; within these allospecies, some populations that appear to be minimally differentiated and also incompletely genetically isolated could be recognized at the subspecies level.

With this perspective, based on a structure of congruence among mutually reinforcing datasets, the new species – nearly all of which might be more precisely defined as allospecies – described in the following pages are consistently and significantly diagnosable from their closest, known relative(s) by at least two among three fundamental character sets: morphology (including both morphometrics and plumage), vocalizations, and molecular genetics. In the relatively few cases to date where all of these data have been investigated in concert, subtle morphological distinctions have been accompanied by more conspicuous differentiation in vocalizations, and the resulting variable levels of phenotypic expression have been underscored, to some positive extent, by molecular divergence (*e.g.*, Cohn-Haft 2000; Cuervo *et al.* 2005; Carneiro *et al.* 2012). We do not weight any one of the three sets preferentially, and we further recognize that other mechanisms, such as pre-copulatory (*e.g.*, mating behaviors) or prezygotic (*e.g.*, incompatible sperm morphology) reproductive barriers may be operative in maintaining some species' integrities.



Over approximately the past twenty years, differentiation in avian vocalizations has figured prominently in the diagnoses of new species of birds because vocalizations are phenotypic traits known to be highly relevant to mate choice and thus, speciation. It is relatively much easier to collect recordings of birds than it is skins, skeletons, or tissues, which effectively "auto-weights" the influence of vocalizations in many diagnoses and analyses of species-limits. Furthermore, because the geographic spread of recordings is often more robust than that for specimen collections, mapping of diagnostic vocalizations often provides the most accurate picture of taxon distributions. Aside from the profound biological significance of vocalizations, unique practical advantages are that digital or digitized recordings of them can be duplicated perfectly and distributed instantaneously without cost, even should the "original" be lost. Many of the recordings used in diagnoses and vocal analyses of the new species described in this volume may be listened to on the Internet Bird Collection (IBC) website, where readers can make inter-taxon comparisons while looking at the audiospectrograms in the species descriptions. Image by Fabio Schunck.

It is almost invariably the case, however, that phylogeographic and taxonomic studies of birds (especially widespread Amazonian birds) depend on rather unbalanced availability of the different data types. For example, study skins and audio recordings are almost inevitably much more abundant and geographically representative than tissue samples (Fig. 3). This naturally places greater weight on interpreting the phenotypic data. This is not all bad, or even old-fashioned, really, when we consider that birds' mate choice is likely based on these phenotypic traits of voice and appearance, not on the variation of the presumably neutral genes most often used in studies of population genetics (more on this in the next section). In other words, phenotype may tell us more about *mechanisms* of speciation, whereas the genetics reveal more about its *consequences* in terms of gene flow and reproductive isolation over time, and relatedness among populations.

Recent genetic isolation, especially of small populations, can lead to abrupt change in phenotype, especially under sexual selection and local adaptation to the environment, that is tightly associated with mate choice and, so, speciation. Thus, strikingly different looking or sounding species may show only shallow genetic differentiation simply because they are young. On the other hand, long-isolated populations, particularly large ones, may accumulate measurable "neutral" genetic differences (including those genes currently used in most molecular analyses) without changing much or at all in phenotype or reproductive compatibility and so effectively not have speciated. In practice, then, when at least two, and especially when more than two independent data sets demonstrate or at least imply the same result, regardless of degree of difference between populations compared, our confidence in that result is strengthened. And regardless of the different strengths of each type of data, when taken together they should tell a coherent story, with no dataset *conflicting* the others. To that end, some of the new species presented in this volume have lingered for more than a decade as data pertinent to their descriptions have accumulated. They will now become available for scrutiny by the scientific community, taking their turn in the queues before such taxonomic committees as the South American Classification Committee (SACC) of the American Ornithologists' Union, and the Comitê Brasileiro de Registros Ornitólogicos (CBRO), where colleagues will evaluate proposed taxonomic rankings. Regardless of outcomes, the fact is that each of the new species presented in this volume has undergone far more rigorous examination than the overwhelming majority of new species of birds described before the turn of the century, greatly facilitating their objective evaluations.

FITTING GENES IN TAXONOMY

Molecular sequence data are used easily nowadays to produce phylogenetic trees, showing the evolutionary relationships among individuals and populations. These trees form an important part of many of the species descriptions presented here in that they demonstrate (as far as the sampling allows inferring) that the new species are coherent and natural - meaning monophyletic - groups, distinct from but related to other species in their genera. This in itself is a powerful and valuable contribution of molecular analyses, especially because the genes sequenced (see below) are believed to be "neutral" with respect to natural selection. This means that they are not expected to be linked directly with morphological or vocal characters, which themselves definitely are subject to selection. In other words, detected divergence in these genes probably has nothing to do with the direct acquisition of reproductive isolation (*i.e.*, evolution of the population into a species) but it does allow us to infer relatedness among taxa or populations without being confused by phenotypic similarities (in voice or plumage, for example) that might be due to natural selection acting to maintain similar phenotypic characteristics (especially expected in the case of cryptic "camouflaging" plumage, for example), convergence, or merely flawed human perception.

"Genetic differentiation" between postulated populations is currently expressed most often as a percentage of sequence divergence in mitochondrial DNA (mtDNA), using genes such as NADH dehydrogenase subunit 2 (ND2) and cytochrome *b* (cyt *b*). "Genetic distance" is the number of base pairs in the sequences that differ between individuals, or the average difference among individuals between populations. The reason there is genetic differentiation is that sufficient time in isolation has gone by to fix mutations. Mitochondrial genes are used in part because they evolve rapidly and provide robust indicators of patterns of population history, and also because they are presumed to be neutral. As such, estimated divergences in mtDNA may mostly reflect the effects over time of relative population sizes, mutation rates, dispersal capability, and, of course, the geographic spread of points sampled for analysis. Another important consideration is that, even in the absence of any phenotypic differentiation, some genetic divergence is expected between two geographically isolated populations, whether separated by rivers, habitat discontinuities, or just large areas of potentially suitable but unoccupied habitat. This is especially true for small populations, which accumulate genetic differences more rapidly than closely related but much larger populations. What is *not* expected under the above geographic circumstances, or when only a few individuals of purported populations are included in molecular phylogenetic analyses, is a finding of no mtDNA-based genetic differentiation.



Figure 4.

Gustavo Bravo at work in the molecular lab at the Louisiana State University Museum of Natural Science. Molecular genetic analysis of birds is critically important for understanding taxon or population-level relationships. The recent and increasing application of these analyses in taxonomy of birds is less readily embraced, in part because we still do not know the genes that control phenotypic attributes pertinent to mate-choice and reproductive isolation and in part because the mitochondrial (mtDNA) genes currently most often being employed are expected to indicate only whether parapatric populations, for example, are genetically isolated from each other. Despite some shortcomings, an increasing number of studies showing generally high congruence of mtDNA divergence with phenotypic differentiation assures us that we are on the right track in analyzing phenotypic and these genetic datasets in concert. The most serious impediment to population-denetic analysis in birds is not methodological, it is lack of sufficient samples from enough localities to permit reasonably robust assessment of gene flow and introgression between populations, past and present. Image by Bret Whitney.

A general (unsurprising) trend is that the larger the percentage of genetic divergence the greater the chance that it will be accompanied by some phenotypic differentiation, even for large populations. There are, however, special concerns here as well, because it is rarely the case that geographic sampling has been sufficiently robust to reasonably document the absence of points of pervasive gene flow between neighboring populations. If, for example, multiple tissue samples are not collected from various points throughout the distribution of postulated populations, and specifically from regions where genetic introgression might reasonably be expected to occur, the resulting analysis will likely mask, and we suspect often overestimate, true populational divergence levels.

As if these considerations were not enough to raise warnings about interpretation of genetic sequence data from mtDNA, some recent studies have documented deep (3.5%+) divergences *within species* as diverse as *Manacus manacus* (Whitebearded Manakin; Kerr *et al.* 2009), *Corvus corvax* (Common Raven; Webb *et al.* 2011), and *Phoenicurus phoenicurus* (Common Redstart; Hogner *et al.* 2012). Such a result could, of course, point to the presence of cryptic species – and in understudied Amazonia, this possibility must always be investigated! – but this hypothesis was refuted in all of the above analyses, thus providing a serious caveat on the use of mtDNA sequence divergence *alone* in defining species of birds. On balance, however, numerous studies revealing high congruence of mtDNA divergence estimates with phenotypic differentiation certainly reinforce our confidence in considering the three above-mentioned data sets in concert (Fig. 4).

The bottom line for species-level taxonomy is simple: Evidence of *spatial isolation* indicated by genetic data must be assessed in concert with various independent datasets that offer a complementary perspective on *reproductive isolation* between populations. In the absence of data confirming diagnosable differences in those phenotypic traits directly involved in mating and reproduction between closely related parapatric or allopatric populations, we have no evidence that the populations would not interbreed pervasively in contact. In other words, there is no hint, let alone clear indication, that the speciation process has advanced beyond some potential or incipient stage enabled through a (usually unknown) degree of isolation. Which lands us squarely on the subject of subspecies.

WHAT ISN'T A SPECIES?

Some recent taxonomic studies (e.g., Isler et al. 2002, 2007; Krabbe and Ridgely 2010) have described or recommended retention of one or more subspecies that show minimal phenotypic characterization either throughout or in parts of the ascribed geographic range. This could be due to the fact that a subspecies, by definition, is not a reproductively isolated population or because not enough time in isolation has transpired to fix significant differences, whether or not it is known or suspected to be in physical contact with a sister population. Also of great relevance to the judgment of diagnosability is, of course, size and spread of the available sample and also the *time*frame in the diversification process at which researchers examine the system. This last point is rarely acknowledged by phylogeographers but is critically important in recognition of the fact that all species that arise through vicariance (physical fragmentation of a cohesive population impeding or interrupting gene flow between fragments) must pass through a unique pathway toward differentiation (no two populations will ever share exact experiences) beginning with some degree of isolation that, in concert with various levels of selective pressures and deterministic abiotic events, may or may not lead to true closure of the gene pool, in a word, speciation.

Stages in the process before cessation of gene flow, wherein some phenotypic differentiation can be identified across a reasonable sample, define the subspecies scene. The subspecies timeframe must be expected to persist for hundreds of thousands, potentially even millions of years! But it can be argued that the subspecies stage(s) in the speciation process is identifiable (or soon will be clearly identifiable as new technologies are applied to adequate samples) as precisely that – a *stage*, because it is not a phenotypically clearly diagnosable population shaped by cessation of significant gene flow. Following closely on this is another baseline reality: There is no assurance that any of perhaps several isolated populations in question will achieve species status or persist at all, nor any guarantee that some that have developed what appear to be reproductive isolating mechanisms and considerable mtDNA divergence (for example) have an irreversible destiny in the face of secondary contact (more on this later). Thus, there exist compelling, indeed irrefutable (try as one might), reasons to continue to recognize some of this phenotypic diversity – especially clinal differentiation, whether demonstrated or suspected – at the subspecies rank.

The lament that subspecies are lesser beings than species, voiced most frequently by conservationists who feel their hands are tied to protect biodiversity below the species level because legislation in most countries is based on the species as the terminal taxon, is, in one regard, well-founded. Subspecies, as we have characterized them above, are incompletely differentiated from other closely related taxa; they lack the "pedigree" of species. Far more significant, however, is the fact that subspecies represent variably long-lived, often early stages in a fundamental, functioning dynamic that is, above all exactly because it underpins the evolution of all life forms, *critically* important to protect and forever strive to understand. If retention of subspecies as terminal taxa causes frustration in conservation circles, we suggest adjusting the legislative system in the countries involved (as has been done via the Endangered Species Act in the United States) to focus less on species and more on habitats and processes with a long overdue emphasis on the study of "subspeciation". To address a perceived taxonomic/conservation-legislation mismatch in Brazil, the latest Livro Vermelho (Red Data Book) treating birds threatened with extinction expanded the traditional scope of considering the plight of only full species to include 45 selected subspecies that the authors judged worthy of immediate official protection because waiting for taxonomic revisions, presumed to result in their upgrading to species rank, would be counter-productive to their preservation (Silveira and Straube 2008).

HAIR-SPLITTING OR HAIR-PULLING?

During the preparation of the numerous new species descriptions for this volume, a number of cases exemplified challenges of the sorts that taxonomists are increasingly coming to confront. Back in the mid-1990s, BMW (working in the Kayapó Indigenous Reserve in Pará) and Luís Silveira of the Museu de Zoologia da Universidade de São Paulo (collecting near Vila Rica, Mato Grosso), at sites 250 km apart with no intervening rivers or other obvious barriers to dispersal of understory birds, independently discovered and collected small series of a *Synallaxis* spinetail obviously pertaining to the *Synallaxis ruficapilla* (Rufous-capped Spinetail) complex (*sensu* Pacheco and Gonzaga 1995). They naturally assumed they had found the same animal. A recent phylogenetic analysis of an enlarged *S. ruficapilla* complex (Batalha-Filho *et al.* 2013) recovered a polytomy including a moderately well-supported and "deep" (3.3%)

mtDNA divergence) sister-relationship of the Vila Rica series to a well-supported clade comprising *S. ruficapilla+S. whitneyi* (Bahia Spinetail; Fig. 5); the Kayapó series was not analyzed.

There is no morphological diagnosis separating the Vila Rica and Kayapó series, but a vocal analysis of nine individuals from the two sites revealed that there is virtually no overlap in two independent characters. Furthermore, the Vila Rica means and ranges of these characters were completely embedded within a sample of *S. rufica-pilla* from near the type locality of that taxon whereas Kayapó birds, together with vocalizations of two individuals from the Alta Floresta region of Mato Grosso, more closely approached a sample of *S. whitneyi*. This especially perplexing situation becomes even more difficult to untangle when one realizes that there exist vocally quite similar satellite populations probably geographically isolated from the birds discussed above. We agree with Batalha-Filho *et al.* (2013) that diversification of populations in eastern Brazil, at least, has been recent and requires much more focused collecting before relationships and taxonomy can be reasonably resolved. We deferred description of any new taxa in the complex until that work can be done, and we are presently accumulating appropriate samples.

Another situation we view as data-deficient, this one despite extensive examination of morphology and vocalizations and some genetic sequence data, is resolution of taxonomy for the *Myrmeciza hemimelaena* (Chestnut-tailed Antbird) group. A recently discovered population inhabiting the Aripuanã-Machado interfluvium has a distinctive song easily distinguished from that of neighboring *M. h. pallens* across the Machado thence south and east, east of the Rio Madeira, and also from that of the nominate form, which inhabits most of the Amazon basin west of the Madeira (Isler *et al.* 2002). These Aripuanã-Machado birds appear to be phenotypically diagnosable only by voice (BMW *pers. obs.*), and analysis of a large sample of specimens and vocalizations of *M. h. pallens* and *M. h. hemimelaena* showed that those two were not diagnosable from each other morphologically or vocally (Isler *et al.* 2002). Two independent genetic analyses of mtDNA using most but not all of the same sequences revealed a polytomy in which the three populations were about 3% divergent from each other, hence it was not possible to determine which two are most closely related (Fernandes *et al.* 2012, Gustavo A. Bravo *pers. obs.*; Fig. 6).

The restricted Aripuanã-Machado population has apparently fixed phenotypic (and probably also genetic) differentiation faster than has happened in the relatively much larger gene pools of the other two taxa. Despite the fact that the vocally and genetically distinct Aripuanã-Machado population impresses us as a good species-level unit, we opted for no treatment in favor of obtaining a more robust sample of tissues from the probable contact zones between populations. Seddon and Tobias (2007) documented "minor but significant geographic variation in the structure of male loudsongs" of a geographically isolated population of M. h. pallens in eastern Bolivia and presented it as evidence of incipient peripatric speciation that was "far from completion".

A somewhat different case is the description (in this volume) of the Roosevelt Stipple-throated Antwren, in which genetic analysis revealed a polytomy among four of the five lineages in the "stipple-throated antwren" complex separated by about 3-6% ND2 sequence divergence (Fig. 7). Three taxonomic treatment options are apparent: consider them as one species with five subspecies; call them four species with *dentei* as a subspecies of *E. amazonica*; or call them five separate species (these are the only options because otherwise one would be erecting paraphyletic species). The fact that all were accompanied by subtle to considerable differentiation in loudsongs and some plumage traits convinced us that the course better illustrating their diversification would be to rank them all as separate species (as we have them named in Figure 7).

The complex contains an additional taxon currently recognized as a species: *E. fjeldsaai* (Brown-backed or Yasuni Antwren), which occupies a fairly extensive area of Amazonian Ecuador and far northern Peru. It is immediately diagnosable from the other, Amazonian taxa by its brown instead of distinctly reddish back, and was described as a species based on the perceived (without any molecular genetic analysis) lack of introgression across sharp geographic breaks with neighboring populations of close relatives (Krabbe *et al.* 1999). We do not have a sufficient sample of loudsongs of *E. fjeldsaai* to permit a thorough vocal analysis, but the few available recordings do not suggest that a larger sample would reveal much distinctiveness. It is extensively parapatric with *E. h. haematonota*, and there are one or two apparent hybrids among the handful of specimens that have been collected in the range of *fjeldsaai*. The two populations share many mitochondrial haplotypes, with *fjeldsaai* embedded in *haematonota* despite the fact that the samples of *haematonota* came from localities fairly distant from the range of *fjeldsaai*. The authors of the description of the Roosevelt Stipple-throated Antwren recommend reclassifying *E. fjeldsaai* as a

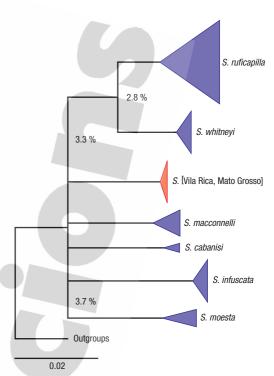


Figure 5.

Maximum-likelihood tree topology of the Synallaxis ruficapilla complex showing S. ruficapilla+S. whitneyi sister to S. [Vila Rica, Mato Grosso] (moderate node support of about 89%) in a polytomy comprising all other analyzed members (modified from Batalha-Filho et al. [2013]). Height of triangles indicates relative sizes of samples for each taxon; horizontal depth reflects relative amounts of within-sample genetic variation. Lack of congruence in morphology or vocalizations with apparent genetic divergence at one Amazonian locality, together with several considerations enumerated in the text, convince us that more data are needed before a reasonably objective taxonomy for the eastern Brazilian components of this group can be proposed. All resolved nodes have bootstrap support values based on 1000 replicates >70 and posterior probability values >0.5.

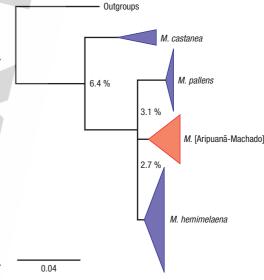


Figure 6.

Maximum-likelihood tree topology of the Myrmeciza hemimelaena complex showing M. castanea (Zimmer's Antbird) sister to a polytomy comprising the three other members. Despite having a smaller sample than the other two, the vocally distinctive "Aripuanã-Machado" population had greater genetic variation within i. Deeper sampling and analysis of morphology, vocalizations, and genetics is indicated to shed light on the best taxonomic arrangement for these birds. All resolved nodes have bootstrap support values based on 1000 replicates >70 and posterior probability values >0.5.

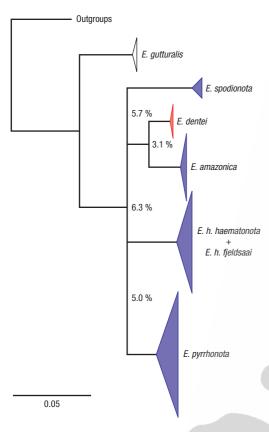


Figure 7.

Maximum-likelihood tree topology of the Epinecrophylla haematonota (Stipple-throated Antwren) complex showing Guianan E. gutturalis (Brown-bellied Antwren) sister to a geographically extensive Amazonian and Andean foothill radiation in a polytomy comprising five distinct lineages. A clear match between geographic distributions and mtDNA haplotype distributions corresponding, albeit in variable extent, to plumage and vocal differentiation of the five taxa represented by triangles within the polytomy convinces us that the best taxonomic treatment currently indicated is recognition of five separate species with E. fjeldsaai (Brown-backed or Yasuni Antwren) as a subspecies of E. haematonota. All resolved nodes have bootstrap support values based on 1000 replicates >70 and posterior probability values >0.5. subspecies within *E. haematonota* (for a more detailed discussion, see Whitney *et al.* 2013, this volume). The case would seem to be an ideal one for intensive behavioral and population genetics study because these birds are common and easily mistnetted, facilitating the analysis of a sample large enough and widespread enough to inspire confidence in its results.

As far as we can determine from available data, the E. fjeldsaai scenario represents secondary contact (rather than incomplete lineage sorting, especially because of the sharp turn-over of phenotypes along the middle Rio Pucacuro) of two populations the smaller of which is being subsumed on their biological battleground in eastern Ecuador and northern Peru. The case begs the question of "evolutionary direction," which is rarely addressed in phylogeographic analyses and would usually be impossible to even infer because of undersampling and inadequate geographic spread of the sample. The overwhelming tendency, even bias, has been to postulate that barriers, usually rivers in Amazonia, are acting to foster genetic diversification through the blockage of gene flow, and they clearly are doing so (Haffer 1985; Capparella 1991; Aleixo 2004; Bates et al. 2004; Ribas et al. 2011; Fernandes et al. 2012), at least in their lower, wider sections. However, the flip-side of the scenario has not been acknowledged, namely that these barriers may, particularly in the cases of small populations, ultimately act as "population traps" or "vicariance cages" by both limiting the geographic expansion of the isolated population(s) and stagnating the "flow rate" of their genetic pools. We suggest that such "trapped" populations become susceptible to genetic obliteration through inexorably persistent gene flow from much larger, relatively inexhaustible sister-populations constantly leaking through the headwaters (for example) of the river systems involved. Thus, the basic question of "which way" populations are evolving slips through the cracks: Are they truly on independent evolutionary trajectories (i.e., insufficient genetic exchange with other populations to obscure identity), or is one in the path of eventual genetic swamping by another?

Returning to the case of Myrmeciza hemimelaena and adding to it the Manicore Warbling-Antbird, described in this volume, because it shares the restricted Aripuanã-Machado distribution and is flanked by its sister-species, Hypocnemis ochrogyna (Rondonia Warbling-Antbird) across the Machado, we will not be surprised if our ongoing collections in the narrow headwaters of the interfluvium reveal active genetic introgression by the relatively much larger, closely related populations of M. h. pallens and H. ochrogyna. These small, trapped populations that have for a significant amount of time evolved in isolation, in the face of overbearing secondary contact (exacerbated by an increasingly disturbed landscape that destabilizes assortative mating), could experience natural erosion of their estimated 3 or 4% mtDNA divergence despite some marked vocal differences. That this process might be operative is not to suggest that these birds not be recognized as species today. To the contrary, we recommend that they should, we just suggest that they would represent species on the way out, over the course of millennia, rather than ones continuing along on independent evolutionary trajectories. Should we find, on the other hand, that one or both of these species' contact zones show minimal or no introgression, and there is perhaps even evidence of geographic overlap with sister species, hypotheses that vocalizations are paramount in maintaining reproductive isolation (as postulated for some other members of Hypocnemis by Isler et al. 2007) will have gained even stronger support and it will be important to also look for additional factors that may be operative in maintaining their species-identities. For example, hybridization that leads to lowered reproductive success of individuals in the contact zone, potentially resulting in a geographic hiatus in distributions, would be another process acting to preserve species-identities.

It will certainly be fascinating to one day examine genetic introgression maps to allow comparisons among populations that share potentially "trapped" gene pool distributions in the Aripuanã-Machado "speciation block" or "mini-interfluve" (Cohn-Haft *et al.* 2007) and have neighboring sisters with those that do not have sisters across either of these rivers. On the grand scale, the dynamics of gene flow need focused study along both banks and especially around the headwaters and narrower upper sections of at least *all of the longest and widest rivers*, including numerous rivers not presently hypothesized to represent barriers to population expansion or gene flow. It is only just now that technological advances are permitting genetic analyses of sufficient quantities of data to reveal levels of genetic introgression among parapatric populations, which will likely appear to range from near zero to near 100% depending, once again, on the geographic spread of the samples analyzed. Only widespread sampling, perhaps in concert with statistical inference (Davison 2006), will permit assessment of real or at least realistic, population-wide introgression levels.

How much of the undescribed diversity of species in Amazonia represents forward speciation, and how much of the flow might be pushing backward? We will soon have



the methodologies developed for divining this mega-question, but it will be impossible to accumulate answers without adequate samples of common, often widespread birds from across their distributions. *Now is the time* to start documenting baseline data on introgression levels across the numerous secondary contact zones in Amazonia (and around the world) that still have never been investigated (Fig. 8). Imagine how much more we will understand about speciation patterns and processes and "what a species of bird is" after many more studies like the ones performed by Brumfield (2005) and Isler *et al.* (2005) on Bolivian *Thannophilus caerulescens* (Variable Antshrike), and in-depth studies of avian "suture zones" such as that recently presented by Naka *et al.* (2012) become available.

A NEW AND URGENT ERA

Amazonian river courses and landscapes are currently suffering their most serious period of disturbance since Andean orogeny started defining them 25 million years ago. International roadways and massive hydroelectric dams (more than 20 planned in Brazil alone) are causing obviously catastrophic changes and triggering invisible "domino effects" truly beyond our imaginations. One ominous but currently hidden consequence looks to us to be inevitable: The anthropogenic force driving landscape alteration will play an increasing role in avian differentiation, reshaping speciation patterns and coordinates with an uneven hand. To date, for lack of both time for expression and focused study by population geneticists, anthropogenic habitat alteration has not been implicated in diversification scenarios for Amazonian birds. The study of population genetics must expand in that direction, however, because "anthro-vicariance" that isolates irregular chunks of integral genetic pools - such as a highway and feeder roads traversing the interfluvium of two rivers – may bear no less evolutionary potency than vicariance driven by natural phenomena. Bates (2002), studying genetic structure in the mtDNA of five species of Amazonian forest-understory birds, showed that natural forest fragmentation on a local scale (enclaves of humid forest isolated in cerrado) affected genetic differentiation.

Ironically, the unnatural fragmentation or outright destruction of large areas of Amazonia that is contributing to the extinction of organisms, potentially even birds, will certainly isolate some blocks of habitats, leading to closed gene pools of many of the organisms within them and to an artificial surge in speciation dynamics. Genetic differentiation of some of them, including some birds, may be measurable in our lifetimes, especially for those in smaller blocks and as technology for resolving genetic diversification rates continues to improve. Documentation and continuous monitoring of genetic change of as many organisms in as many of these blocks as possible will provide important baseline data relevant to how incipient diversification advances, or disappears (Fig. 9). In the face of these negative realities, we must do everything possible to ensure the natural, uninterrupted destinies of Amazonian habitats. It is inspiring to see the results of scientific research, particularly ornithological discovery and data analysis,

Figure 8.

Mario Cohn-Haft preparing a specimen of Cyanocorax hafferi (Campina Jay) which Cohn-Haft, Santos Junior, Fernandes, and Ribas describe in this volume (and see chapter frontispiece). Modern, data-rich specimens are the foundation for both scientific study and conservation of Amazonian birds because it will not be possible to defensibly, objectively, define either "species" to protect or areas to be preserved without them. Highly focused specimen collecting should be not only allowed, but encouraged by responsible government environmental ministries and society at large. These precious, preserved specimens become the most important individuals of their kinds, for it is they who mark for mankind that their species exists and deserves to persist. Image by Catherine L. Bechtoldt.



playing a key role in establishment of new legally protected areas, such as the Allpahuayo-Mishana and Pucacuro National Reserves, and the Upper Nanay-Pintuyacu-Chambira Regional Protection Area in Loreto, Peru (Alvarez and Whitney 2001, Alvarez et al. 2013), and in Brazil, the Apuí mosaic between the Tapajós and Madeira rivers and the "ALAP" mosaic of reserves between the Madeira and Purus rivers (Mesquita et al. 2007). This represents a healthy change, because government/political thinking, when it comes time to establish one or more new protection areas, typically outlines polygons on maps modeled only on socio-economic vectors and political paths of least resistance, or even military priorities, rather than biogeographic data and implications for biodiversity conservation. This is, however, only a first step. Implementation and long-term maintenance of these reserves is a much greater challenge. Unfortunately, with the political ping-pong typical of modern democracies such as the one that has been in place in Brazil for less than thirty years, the initiative to create reserves under one government can just as quickly be turned around under the next to "uncreate" or weaken them, as we are witnessing now with national parks and reserves in Amazonian Brazil where hydroelectric dams have been planned (see Bragança 2012).

With the description of these fifteen new species of birds in this *Special Volume* of *The Handbook*, we highlight the "tip of the iceberg" of the emerging documentation of Amazonian biodiversity. What we find exhilarating about the iceberg, however, is not only our enhanced ability to recognize subtle levels of divergence but also the beginning of the construction of genetic introgression maps that will reveal in unprecedented fashion the dynamics of speciation. This directive will eventually provide us with much insight relative to disentangling the complex network of paleohistorical and contemporary speciation mosaics in Amazonia and will surely help us define specific areas of the basin that should be preserved and studied ahead of others. There will be large-scale patterns, especially in processes and geography, but each introgression

Figure 9.

The city of Manaus, Amazonas, Brazil, shown in this satellite image from mid-2011, nearly doubled from something over one million inhabitants in 1990 to more than two million today. The 100 km² block of forest at the periphery of the city is the Ducke Forest Reserve (Reserva Florestal Adolfo Ducke), perhaps the most thoroughly studied forest area in all of Amazonia. The reserve has had some level of protection since the early 1960s but, as the city has grown around it, isolation from continuous forest has increased to the point that natural dispersal of almost all organisms within it must be heavily to slightly interrupted. There is no functioning plan to provide for any corredor, which would represent a bottleneck, albeit a critically important one, between it and, for example, extensive undisturbed forest to the northeast. Thus, it certainly appears that the destiny of Ducke is to become a square, increasingly blurry-edged island for the vast majority of life forms it holds. One might quite reasonably expect the steady erosion of its biodiversity over the coming centuries, but we might also predict that the artificial genetic isolation of essentially everything present will spawn "anthro-populations" of myriad organisms, including some birds, eventually and inevitably (without renewed forest corredors) leading to a new block of "biodiversity" with who-knows-how-many "endemics". Organisms able to persist in the 600-hectare forest property of the Federal University of Amazonas, south of Ducke, where already completely surrounded by the city, are experiencing accelerated rates of genetic and phenotypic differentiation simply because they are on a yet much smaller island. As technology for studying population genetics roars forward, we view monitoring of anthro-populations generated by these kinds of reserves and forest fragments as especially pertinent to the study of both natural and artificially influenced evolutionary processes. Note the dramatic "meeting of the waters" of the dark Rio Negro with the silt-laden Rio Solimões which together form the Rio Amazonas. The new bridge crossing the Negro, visible as a thin, whitish line, was inaugurated in October, 2011.

scenario will have individual characteristics. We suspect that the accumulation and overlay of these scenarios will have much to do with how we delimit species in the middle of the 21st century.

It is our duty as scientists and conservationists who have dearly loved birds and natural habitats for our entire lives to emphasize that it will be impossible to elucidate, understand, and, importantly, monitor speciation processes and bird population trends and dynamics without the clear cooperation of research institutions and society at large to not only allow (see Winker *et al.* 2010) but *encourage* carefully focused, legally authorized collection and permanent, publicly accessible archival of modern, data-rich specimens. As stewards of the planet Earth, this is one responsible action to take. With the new knowledge that comes from every expedition and collection, we can present to society as a whole an ever clearer view of the marvelous wild realm that is the Amazon and help make sure that decisions made to modify it are the result of carefully evaluated plans with a firm scientific foundation.

FINDING NEW SPECIES... BY SATELLITE!

Harking back a few years and leaping into the future, it is fair to say that the discovery and description of the earlier-mentioned set of stunning birds from Amazonia served to catalyze exploration of the basin by an ever more attentive, technologically enabled, and communicative cadre of field ornithologists, certainly including ourselves. With the advent of satellite imagery, especially infrared reflectance technology, it is possible to easily and remotely assess landscape characteristics that, when groundtruthed, verify shifts in biotopes (subtly different habitats within a mosaic) and thus avifaunas (Whitney and Álvarez 1998; Pomara et al. 2012; Fig. 10). Depending on the resolution available and the experience of the image interpreters, some highly localized or scattered biotopes and microhabitats, even some only vaguely perceptible to the untrained eye, may become consistently identifiable (e.g., Tuomisto et al. 1994; Higgins et al. 2011). Both the Campina Jay and Chico's Tyrannulet, described in this volume, were efficiently discovered by first locating a point of access to a distinctive, campina-type habitat (characterized by shrubby/bushy vegetation on special-reflectance, sandy/rocky terrain) in NASA-enabled satellite imagery and using (wonderful, helpful!) Google Earth, then ground-truthing the site with special attention to vocalizations of birds present there.

A refined layer of the puzzle that stems from a well-developed knowledge of biogeography and diversification of Amazonian birds and subregional avifaunas applies "apparent absence" or vacancy of taxa from areas where they might reasonably be expected to occur to invoke "predicted presence" of undiscovered or undescribed relatives or ecological correlates. The descriptions of Predicted Antwren and Inambari Gnatcatcher that appear in this volume provide clear examples of this. That we still have a great deal to learn in such "educated modeling" exercises, however, became apparent during the documentation of the distribution of Chico's Tyrannulet, which was absent from extensive patches of apparently suitable habitat within only 30-80 km of confirmed sites of occurrence. Our "greatest-likelihood" explanation for this is that landscape history plus dispersal capability/tendency of the bird plus competition from ecologically similar species (see the description of the tyrannulet in this volume) has dictated where it can or does occur more than has availability of habitat; the same factors probably apply to many other Amazonian bird distributions.

These cases also underscore that establishing *absence* of species or species-groups from apparently suitable habitats is powerful information, we would argue every bit as important as documenting presence, in piecing together the origins of biogeographic patterns and interpreting the variable effects of such deterministic landscape characteristics as soil types and edaphic properties, and of biotic factors such as niche overlap.

In closing, given what we know about avian distributions and biogeography of Amazonia today, can we predict any "specific treasures" perhaps awaiting discovery? Our vote for the greatest party-starter would be finding the missing link between *Metopothrix aurantiacus* (Orange-fronted Plushcrown) of western Amazonia and *Acrobatornis fonsecai* (Pink-legged Graveteiro) of what we call "Bahian-Amazonian" forests, widely disjunct in eastern Brazil. Such a relic would most likely persist, we suspect, in the canopy of a pocket(s) of *terra firme* forest in the lower Madeira-Tapajós interfluvium or, less likely, in the rapidly disappearing forests east of the Rio Xingu. It would be a regular if not inveterate member of mixed-species foraging flocks and emit a thin, staccato trill near its subcanopy stick nest. If that archetypal little bird has not gone extinct (probably naturally, thus so be it)... it would truly be a wonder to behold!

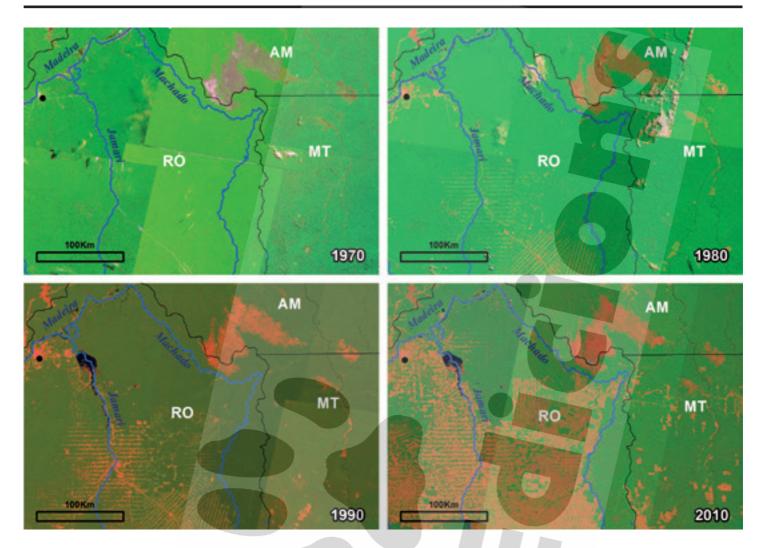


Figure 10. Acknowledgments

Deforestation in the states of Rondônia and northern Mato Grosso has been uncontrolled and accelerating, resulting in the destruction of a vast amount of forest millions of vears old in only forty years; weighing socio-economic needs and interests against this loss is beyond the scope of this essay. Landsat satellite image mosaics ("quiltworks" of images which may have been collected on different days) such as these are composed of three color channels: red, green, and blue. Each color represents the strength of reflectance of a discrete range of wavelengths (i.e., a band) within the electromagnetic spectrum; individual bands may be in the visible-light or nonvisible parts of the spectrum. Different combinations produce different color patterns highlighting distinctive landscape features, such as natural and man-made openings in forest cover. The resulting image can be enhanced with additional map elements such as political boundaries. The three named rivers were colored blue for better visibility: the black dot on the right bank of the Rio Madeira marks the city of Porto Velho, Rondônia. In this set of images and in many of the maps presented in the new species descriptions in this volume, we chose band combinations and color assignments that resulted in shades of green for forest and pinkish/orangish for open areas, with anthropogenic clearings generally appearing brighter/paler than natural campinas and savannas. Irregular patches of cloud cover appear whitish. The croissant-shaped area in the top-center of the images is the BX-044 polygon, a natural. open-vegetation enclave in the Aripuanã-Machado interfluvium of central Amazonia. The 1990 and 2010 images perhaps most clearly show that this little-known enclave comprises a heterogeneous landscape, with notably variable reflectance between western and eastern portions (we suspect the relatively brighter appearance of the western arm of the polygon in the 1970 image represents ground-fog). Images are all from the month of August. These images and many of the maps in the fifteen new species descriptions in this volume may be viewed at high resolution in the Supporting Information (SI) on the Internet Bird Collection website (http://ibc.lynxeds.com) of Lynx Edicions.

Many thanks to Gustavo Bravo for help with preparation of tree topology figures, and again to Gustavo and to J. V. Remsen for especially insightful comments on an earlier draft of the manuscript. The essay benefitted from the comments of Dick Banks, Andrés Cuervo, Dan Lane, Vítor Piacentini, Luís Silveira, and Brian Smith, several of whom provided thought-provoking criticism of late drafts that resulted in a much better piece, and Mike Harvey also offered a couple of influential perspectives. John Rowlett gave it a professional editorial scrutiny late in the process. Fernando Pacheco ably provided the count of approximately 40 species of birds described by Pelzeln (1871). We are on our knees with gratitude to John Hanke and co-scientists who developed Google Earth and have maintained it openly available since its public launch in 2005; without you, we would be several steps behind our present state of Earth-awareness. Marco Antonio Rêgo did a great job preparing the satellite images showing deforestation around Manaus and in the upper Madeira-Tapajós interfluvium, and Lars Pomara helped clarify our explanation of technical attributes relative to their production. We are grateful to INPE for free and open access to the Landsat satellite imagery used to produce the images in figures 9 and 10. MCH wrote the caption for the frontispiece; all figure legends were written by BMW. MCH cannot disentangle his own thinking about Amazonian birds from the learning fostered at the Louisiana State University Museum of Natural Science during his (many) graduate school years, by his advisor Van Remsen, by the inspiration and friendship of the late Ted Parker, by lively exchanges with faculty, staff, and fellow students, and by generous funding from numerous sources. He also thanks Field Guides Incorporated for having initiated and nurtured a long-enduring ornithological partnership with BMW and for having made possible many field trips to remote destinations. BMW sends enormes abraços to Vítor de Q. Piacentini and Luciano Moreira Lima, proprietors of Ornitohouse in Ipiranga, São Paulo, where much of this piece was written. In the papers following this essay, Hilary Burn performed the miracle of producing vibrant and accurate depictions of fifteen previously unknown bird species (and a few others that didn't quite make it into this volume!), providing the world with the definitive illustrations of all these birds whose names will forever be associated with her paintings. Finally, a heartfelt thanks to Josep del Hoyo, Andy Elliott, Amy Chernasky, and Xavier Ruiz of Lynx Edicions for their kind patience and remarkable professionalism as this essay and the fifteen new species descriptions that follow took shape over the past several months.

Literature Cited

- Aleixo, A. (2004). Historical diversification of a terra-firme forest bird superspecies: a phylogeographic perspective on the role of different hypotheses of Amazonian diversification. *Evolution* **58**: 1303–1317.
- Álvarez Alonso, J., M. R. Metz, and P. V. A. Fine (2013). Habitat specialization by birds in western Amazonian white-sand forests. *Biotropica*: doi: 10.1111/btp.12020.
- Álvarez Alonso, J. and B. M. Whitney (2001). A new Zimmerius tyrannulet (Aves: Tyrannidae) from whitesand forests of northern Amazonian Peru. Wilson Bulletin 113: 1–9.
- Batalha-Filho, H., M. Irested, J. Fjeldså, P. G. P. Ericson, L. F. Silveira, and C. Y. Miyaki (2013). Molecular systematics and evolution of the *Synallaxis ruficapilla* complex (Aves: Furnariidae) in the Atlantic Forest. *Molecular Phylogenetics and Evolution* doi: http://dx.doi.org/10.1016/j.ympev.2013.01.007.
- Bates, J. M. (2002). The genetic effects of forest fragmentation on five species of Amazonian birds. *Journal* of Avian Biology **33**: 276–294.
- Bates, J. M., J. Haffer, and E. Grismer (2004). Avian mitochondrial DNA sequence divergence across a headwater stream of the Rio Tapajos, a major Amazonian river. *Journal of Ornithology* 145: 199–205.
- Bragança, D. (2012). *MP que altera tamanhos de UC's na Amazônia vai à sanção*. O Eco, 30 May 2012 < http://www.oeco.com.br/salada-verde/26060-mp-que-altera-tamanhos-de-ucs-na-amazonia-vai-a-sancao > (accessed 24 March 2013).
- Brumfield, R. T. (2005). Mitochondrial variation in Bolivian populations of the Variable Antshrike (*Thamnophilus caerulescens*). Auk 122: 414–432.
- Capparella, A. P. (1991). Neotropical avian diversity and riverine barriers. Acta Congressus Internationalis Ornitologici 20: 307–316.
- Carneiro, L. S., L. P. Gonzaga, P. S. Rêgo, I. Sampaio, H. Schneider, and A. Aleixo (2012). Systematic revision of the Spotted Antpitta (Grallaridae: *Hylopezus macularius*), with description of a cryptic new species from Brazilian Amazonia. *Auk* 129: 338–351.
- Cohn-Haft, M. (2000). A case study in Amazonian biogeography: vocal and DNA-sequence variation in *Hemitriccus* flycatchers. *PhD. Dissertation* Louisiana State University.
- Cohn-Haft, M., A. M. F. Pacheco, C. L. Bechtoldt, M. F. N. M. Torres, A. M. Fernandes, C. H. Sardelli, and I. T. Macêdo (2007). Capítulo 10. Inventário ornitológico. Pp. 145–178 in: Rapp Py-Daniel, L., C. P. Deus, A. L. Henriques, D. M. Pimpão, and O. M. Ribeiro, (orgs.) (2007). *Biodiversidade do Médio Madeira: Bases científicas para propostas de conservação*. INPA: Manaus, 244 pp.
- Coyne, J. A. and A. H. Orr (2004). Speciation. Sinauer Associates, Inc., Sunderland.
- Cuervo, A. M., C. D. Cadena, N. Krabbe, and L. M. Renjifo (2005). Scytalopus stilesi, a new species of tapaculo (Rhinocryptidae) from the cordillera central of Colombia. Auk 122: 445–463.
- Davison, D. (2006). Inferences about the evolutionary history of geographically structured populations: The intersection of population genetics, biogeography and systematics. *PhD. Dissertation* University of Chicago.
- Fernandes, A. M., M. Wink, and A. Aleixo (2012). Phylogeography of the chestnut-tailed antbird (*Myrmeciza hemimelaena*) clarifies the role of rivers in Amazonian biogeography. *Journal of Biogeography* 39: 1524–1535.
- Haffer, J. (1985). Avian zoogeography of the Neotropical lowlands. Ornithological Monographs 36: 113-146.
- Higgins, M. A., K. Ruokolainen, H. Tuomisto, N. Llerena, G. Cardenas, O. Phillips, R. Vasquez, and M. Räsänen (2011). Geological control of floristic composition in Amazonian forests. *Journal of Bioge*ography 38: 2136–2149.
- Hogner, S., T. Laskemoen, J. T. Lifjeld, J. Porkert, O. Kleven, T. Albayrak, B. Kabasakal, and A. Johnsen (2012). Deep sympatric mitochondrial divergence without reproductive isolation in the common redstart *Phoenicurus phoenicurus. Ecology and Evolution* 2(12): 2974–2988.
- ICZN (1999). International Code of Zoological Nomenclature. 4th Edition. International Trust of Zoological Nomenclature, London.
- Isler, M. L., J. Álvarez A., P. R. Isler, T. Valqui, A. Begazo, and B. M. Whitney (2002). Rediscovery of a cryptic species and description of a new subspecies in the *Myrmeciza hemimelaena* complex (Thamnophildae) of the neotropics. *Auk* 119: 362–378.
- Isler, M. L., P. R. Isler, and R. T. Brumfield (2005). Clinal variation in vocalizations of an antbird (Thamnophilidae) and implications for defining species limits. *Auk* **122**: 433–444.
- Isler, M. L., P. R. Isler, and B. M. Whitney (2007). Species limits in antbirds: The Warbling Antbird (*Hypocnemis cantator*) complex. Auk 124: 11–28.
- Kerr, K. C. R., D. A. Lijtmaer, A. S. Barreira, P. D. N. Hebert, and P. L. Tubaro (2009). Probing evolutionary patterns in Neotropical birds through DNA barcodes. *PLoS ONE* 4:e4379.
- Krabbe, N., M. L. Isler, P. R. Isler, B. M. Whitney, J. Álvarez A., and P. J. Greenfield. (1999). A new species in the *Myrmotherula haematonota* superspecies (Aves: Thamnophilidae) from the western Amazonian lowlands of Ecuador and Peru. *Wilson Bulletin* 111: 157–165.
- Krabbe, N. and R. S. Ridgely (2010). A new subspecies of Amazilia hummingbird Amazilia amazilia from southern Ecuador. Bulletin of the British Ornithologists' Club 130: 3–7.
- Mesquita, R., C. E. Marinelli, and P. S. Pinheiro (2007). Quando a ciência ajuda a formulação de políticas de conservação na Amazônia. Pp. 239–244 in: Rapp Py-Daniel, L., C. P. Deus, A. L. Henriques, D. M. Pimpão, and O. M. Ribeiro, (orgs.) (2007). Biodiversidade do Médio Madeira: Bases científicas para propostas de conservação. INPA: Manaus, 244 pp.

- Naka, L. L., C. L. Bechtoldt, L. M. P. Henriques, and R. T. Brumfield (2012). The role of physical barriers in the location of avian suture zones in the Guiana Shield, northern Amazonia. *American Naturalist* 179: E115–E132.
- Pacheco, J. F. and L. P. Gonzaga (1995). A new species of *Synallaxis* of the *ruficapilla/infuscata* complex from eastern Brazil (Aves: Furnariidae). *Ararajuba* 3: 3–13.
- Panhuis, T. M., R. Butlin, R. M. Zuk, and T. Tregenza (2001). Sexual selection and speciation. *Trends in Ecology and Evolution* 16: 364–371.
- Pelzeln, A. von (1871). Zur Ornithologie Brasiliens. Resultate von Johann Natterers Reisen 1817 bis 1835. Vienna: Pichlers.
- Peters, J. L. (1948). Check-list of birds of the world. Vol. VI. Cambridge: Harvard University Press.
- Pomara, L., K. Ruokolainen, H. Tuomisto, and K. Young (2012). Avian composition co-varies with floristic composition and soil-nutrient concentration in Amazonian upland forests. *Biotropica* 0: 1–9.
- Ribas, C. C., A. Aleixo, A. C. R. Nogueira, C. Y. Miyaki, and J. Cracraft (2011). A paleobiogeographic model for biotic diversification within Amazonia over the past three million years. *Proceedings of the Royal Society* 279: 681–689.
- Seddon, N. and J. A. Tobias (2007). Song divergence at the edge of Amazonia: an empirical test of the peripatric speciation model. *Biological Journal of the Linnaean Society* **90**: 173–188.
- Silveira, L.F. and F. C. Straube (orgs.) (2008). Aves ameaçadas de extinção no Brasil. Pp. 379–383 in: Machado, A. B. M., G. M. Drummond and A. P. Paglia (eds.). Livro vermelho da fauna brasileira ameaçada de extinção (Volume 2: 378–679). Brasília, Ministério do Meio Ambiente; Belo Horizonte, Fundação Biodiversitas. Série Biodiversidade n° 19, 2 volumes, 907 + 511 pp.
- Tuomisto, H., A. Linna, and R. Kalliola (1994). Use of digitally processed satellite images in studies of tropical rainforest vegetation. *International Journal of Remote Sensing* 15: 1595–1610.
- Webb, W. C., J. M. Marzluff, and K. E. Omland (2011). Random interbreeding among cryptic lineages of the Common Raven: evidence for speciation in reverse. *Molecular Ecology* 20: 2390–2402.
- Whitney, B. M. and J. Álvarez A. (1998). A new *Herpsilochmus* antwren (Aves: Thamnophilidae) from northern Amazonian Peru and adjacent Ecuador: The role of edaphic heterogeneity of *terra firme* forest. *Auk* 115: 559–576.
- Whitney, B. M., M. L. Isler, G. A. Bravo, N. Aristizábal, F. Schunck, L. F. Silveira, and V. de Q. Piacentini (2013). A new species of *Epinecrophylla* antwren from the Aripuanã-Machado interfluvium in central Amazonian Brazil with revision of the "stipple-throated antwren" complex. Pp. 263–267 in: del Hoyo, J., A. Elliott, J. Sargatal, and D. A. Christie (eds.) (2013). *Handbook of the Birds of the World*. Special Volume: New Species and Global Index. Lynx Edicions, Barcelona.
- Winker, K., T. M. Reed, P. Escalante, R. A. Askins, C. Cicero, G. E. Hough, and J. Bates (2010). The importance, effects, and ethics of bird collecting. Auk 127: 690–695.