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Diagnosable versus Distinct: Evaluating Species Limits in Birds

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I review new species of birds described from 1993 to 2002, comparing the methods used to diagnose (identify) new bird species with those used for other classes of vertebrates. Birds are described and subsequently identified using a far more restrictive set of criteria than other organisms, with field diagnosability being the ultimate criterion of distinctiveness. This has led to a large number of evolutionarily distinct bird taxa that are not recognized as distinct taxonomic units. This disparity has important consequences for ornithology and for other disciplines that use birds as biodiversity measures.

Keywords: diagnosability, taxonomy, vertebrates, biodiversity, philosophy

The field of phylogenetic systematics has burgeoned in the past decade, with highly resolved phylogenetic hypotheses being developed for many groups of organisms. Advances in molecular techniques, cladistic analysis methods, and vicariant biogeography have matched this growing knowledge, and the increasingly prominent role of systematics has prompted reevaluation of how species concepts are defined, applied, and tested (Sites and Marshall 2002). Discussions of species concepts in ornithology have largely kept pace with this general trend, with a number of recent reviews and discussions (Peterson 1998, Pratt and Pratt 2001, Helbig et al. 2002). Most debate has centered on the relative merits of the biological species concept (BSC) and the phylogenetic species concept (PSC). Some ornithologists are concerned that the widespread adoption of the PSC would be problematic, as evidenced by this recent statement: "The PSC trivializes the species taxon and introduces new problems of deciding when a population becomes diagnosable, the possibility that species could appear and disappear in a reticulate fashion, and the likelihood that genetically diagnosable but phenotypically identical, and therefore not field identifiable, populations could be ranked as species" (Pratt and Pratt 2001, p. 680; see also Collar 1996).

While diagnosability is frequently seen as synonymous with the PSC, this is not the case. A species should be diagnosable regardless of the species concept used. The term *diagnosable* is open to interpretation, however, and this is not merely a semantic issue; the usage of this term is crucial to how species limits are assigned. There is a strongly held view among the ornithological community that bird species should be identifiable under field conditions. This position

has not previously been explicitly acknowledged nor critically evaluated.

In this contribution, I evaluate how bird species are currently distinguished, quantify the reliance of ornithologists on traits visible under field conditions (field marks), and compare field diagnosability with independent measures of evolutionary distinctness. To assess the criteria used to determine species limits in birds, I conducted a series of quantitative comparisons between the alpha taxonomic methods (species circumscription and description) used in ornithology and those used in other groups of vertebrates. Unlike previous authors, I do not discuss historic trends in species descriptions (Peterson 1998), evaluate the validity of the taxa being described (Vuilleumier et al. 1992), nor compare the scope of studies on different organismal groups (Bonnet et al. 2002). Rather, I review descriptions of new species and compare the methods used to define species limits in birds with those used in other classes of vertebrates. While ultimately governed by the International Code of Zoological Nomenclature (ICZN 1999), these rules are subject to considerable interpretation, and to date it is unclear whether they are applied differently in different groups of organisms. I propose that the gap between evolutionarily distinct and operationally diagnosable species is wider in birds than in other groups, leading to many distinct bird taxa that are not considered different species. Rather than being driven by differences in the organisms or in the

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prevailing species concept, this disparity is related to how species limits are applied and how these diagnostic methods differ among disciplines. In addition to exploring the underlying reasons for this imbalance, I offer some solutions, recommending that field diagnosability be dropped as the ultimate criterion of avian species limits. Rather than changing the current rules for how species are defined and named, I suggest that researchers need to reevaluate how these rules are applied and ensure that species limits decisions are consistent and indicative of underlying evolutionary patterns.

Diagnosability

As part of describing a new species, the authors of the description prepare a diagnosis: an explicit set of features that together distinguish the organism from all other described species. Similarly, when identifying an unknown individual, its features are compared with those of described species (often using dichotomous keys originally prepared with reference to specimens of those taxa). Hence, the attributes that are chosen—initially to diagnose species and subsequently to identify unknown individuals—provide insight into how species limits are assigned within a group.

To gain an operational understanding of how species limits are applied, I compared new species descriptions of birds with those of three other classes of vertebrates: reptiles, amphibians, and mammals. I restricted my search to new species described from 1993 through 2002 (inclusive), excluding elevations of previously recognized subspecies to minimize historical bias. During this period, 68 papers were published in which new species of birds were described. Of these, 60 were published in readily accessible journals captured by electronic abstracting services (excluding 8 new species descriptions from three journals). To facilitate substantiation, the analyses presented here were calculated using the reduced set of 60 papers, but the results were qualitatively equivalent to analyses based on the entire data set of all 68 species descriptions. The number of new species of reptiles, amphibians, and mammals described in journals captured by electronic abstracting services over the same time period greatly exceeded this number, so I randomly selected 60 new species from each of these three groups to provide a comparable sample. If several new species were described in the same article, one species was randomly chosen to prevent biasing the data toward that lineage or that particular author.

For all 240 descriptions, I scored which sources of information were used in the diagnosis (table 1), recording only those sources of data that varied sufficiently to be useful in distinguishing the new taxon. I compared the frequency of different data sources between groups and calculated the statistical significance of any differences using Fisher's exact test (two-tailed; 5 percent type I error rate).

New species described 1993–2002

Full details of all 240 species are summarized at *www.csu. edu.au/faculty/sciagr/eis/staff/watson.htm.* Of the 60 new species of amphibians evaluated, there were 11 salamanders,

Table 1. Sources of information used to diagnose new species.

Data type	Description, examples
Appearance	External appearance visible in wild individual, typically at close range (e.g., color, overall pattern, presence and location of stripes)
Morphometrics	External measurements, mostly possible on live animal (e.g., mass, cranial measurements, overall dimensions, wing formula)
External morphology	Features observable on live animal in hand (e.g., scalation, dentition, number of toes, details of feather shape or structure)
Internal morphology	Features observable on anatomical specimen (e.g., detailed skeletal characteristics, myology, location of nerves and arteries)
Range	Distributional range of species, often expressed relative to ecologically similar species or congeners
Habitat	Typical habitat of species, particularly if it differs from that of otherwise similar species
Behavior	Behavioral traits (e.g., vocalizations, posture, biotic associates)
Molecular data	Molecular measurements (e.g., sequence divergence of DNA, allozymes)
Karyology	Number and morphology of chromosomes
Reproduction	Information about breeding behavior (e.g., breeding trials, hybridization, litter or clutch size, playback trials)

10 tree frogs, 6 toads, and 3 poison dart frogs. The 60 new reptile species were dominated by snakes and lizards (including 16 colubrid snakes, 10 geckos, and 10 skinks), with 5 blind snakes and 4 turtles. The 60 new mammal species included 28 rodents, 14 bats, 7 marsupials, 1 whale, and 1 monkey. (Note that for all three groups, many more new species were described between 1993 and 2002 than those included in this study; the details here relate only to those 60 species randomly selected for analysis.) Of the 60 new bird species described in the same period, there were 7 owls, 7 tyrant flycatchers, 2 hummingbirds, and 1 parrot (see *www.csu.edu.au/faculty/sciagr/ eis/staff/watson.htm* for full details).

The geographic distribution of these new species did not differ substantially among the four classes. Latin America was the source of approximately half the new species for all groups, followed by Asia and Africa, with 5 to 14 species from the remaining continents in each group. Between one and six data sources were used to distinguish new species, and comparisons of means determined that reptiles were the only group to differ significantly from the others: New reptile species were typically diagnosed using two data sources, compared with three for the other groups (figure 1). Specimen numbers were also comparable, although one bird species was described without a complete type specimen (photographs and a DNA sample were deposited in lieu of a museum specimen). This occurred in spite of widespread condemnation of the previous attempt to describe a new bird species without a type specimen some 11 years earlier (see
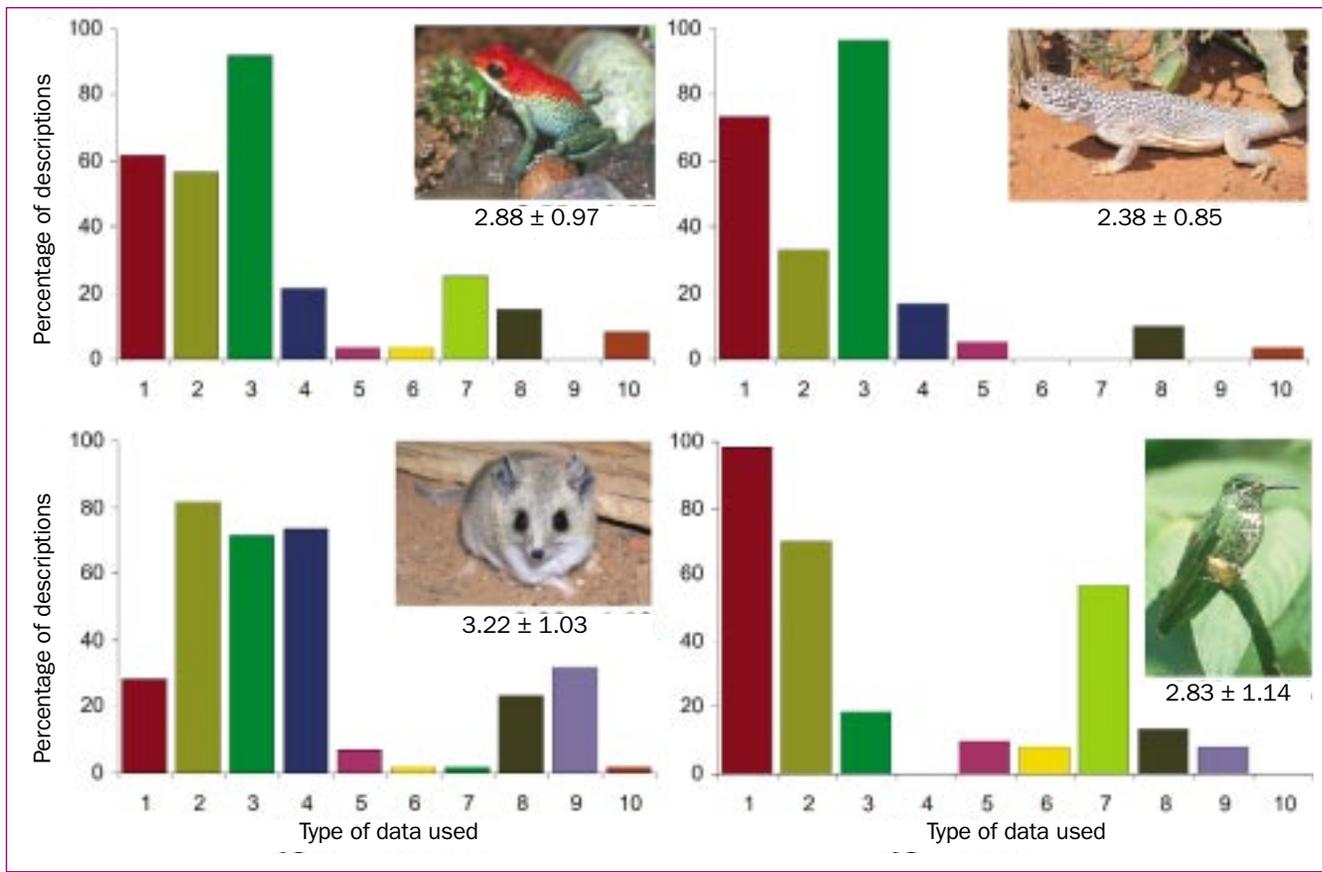
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Figure 1. Comparison of the sources of data used to diagnose new species of amphibians (top left), reptiles (top right), mammals (bottom left), and birds (bottom right), based on a sample of 60 species descriptions for each group published from 1993 through 2002. Mean and standard deviations on each graph refer to the number of data sources used for each group. Data types: 1, appearance; 2, morphometrics; 3, external morphology; 4, internal morphology; 5, range; 6, habitat; 7, behavior; 8, molecular data; 9, karyology; 10, reproduction. Photographs show a granular poison arrow frog (**Dendrobates granuliferus,** *top left*), *central netted dragon (***Ctenophorus nuchalis,** *top right*), *fat-tailed dunnart (***Sminthopsis crassicaudata,** *bottom left*), *and green-crowned brilliant (***Heliodaxa jacula,** *bottom right*). *Photographs: David M. Watson.*

Peterson and Lanyon 1992). This case notwithstanding, there appear to be few underlying differences between the classes in terms of where recently described species originate and the number of specimens used as the basis for diagnosis.

Are species limits applied differently to birds?
The sources of data used to diagnose new species varied dramatically among classes (figure 1). New species of amphibian were typically diagnosed using three data sources—external appearance, morphometrics, and external morphology—while reptiles were typically diagnosed using two (appearance and external morphology). Mammals were generally described using morphometrics, external morphology, and internal morphology, whereas new bird species diagnoses relied on external appearance, morphometrics, and behavior (figure 1). Birds were the only group described primarily using external appearance (98 percent; only one species description did not use plumage characteristics), compared with an overall frequency of 54 percent for the other three groups combined ($P \ll 0.001$). In contrast to the other

three classes—for which 95 percent of new species descriptions used internal morphology, external morphology, or both—only 18 percent of new bird descriptions used external morphology ($P \ll 0.001$), and none used internal morphology for species-level diagnosis (although some internal morphological traits were used to assign new bird species to genus). Ecological data (distributional range, habitat, and behavior) were used for 62 percent of new bird descriptions, significantly more than the 14 percent for the other three classes combined ($P \ll 0.001$). The use of molecular data was consistent across all four classes; by contrast, behavioral traits (typically vocalizations) were used for amphibians and birds but not for reptiles or mammals (figure 1).

Some of these differences highlight actual differences among the organisms themselves. Thus, given the prominence of vocalizations in frogs and birds, it is not surprising that behavior was used more frequently than in other classes. Likewise, since reptiles typically have indeterminate growth, it follows that morphometric data are used less frequently. Other differences, however, reflect fundamental differences in

Box 1. Representative excerpts from species diagnoses, highlighting the importance of field marks in diagnosing new bird species.

Birds

Lipaugus weberi: "Easily distinguished from all congeners by the combination of chestnut-brown crown feathers, overall darker grey plumage, conspicuous yellow orbital ring; and bright yellow gape, tongue and commissure.... [D]istinguished from *L. fuscocinereus* by its bare-part and crown colouration differences and much smaller size. Males of *L. weberi* have only two primaries with stiffened outer remiges, compared to three in *L. fuscocinereus....* Vocalizations of *L. weberi* are distinctive...." (Cuervo et al. 2001, pp. 354–355).

Garrulax ngoclinhensis: "Differs from the eight *G. erythrocephalus* taxa which occur west of the Salween River (except *G. e. woodi*) by the absence of dark brown scaling on the mantle and breast, the presence of a black alula (absent in *G. e. connectens*), and the absence of buff, brown or olive tones in its plumage" (Eames et al. 1999, p. 6).

Atlapetes melanops: "Characterized by a rather pale ochraceous-tawny cap, black forehead, whitish 'supraloral horns,' short and rather indistinct malar stripe, entirely black orbital areas (much larger than in *A. rufigenis forbesi*) and faint yellow flammulations on the under-side" (Valqui and Fjeldså 1999, p. 195).

Aethopyga linaraborae: "Has metallic plumage colors in the upper tail coverts, ear, lesser and greater wing coverts, and edges to the scapulars and secondaries that are lacking in *A. boltoni.* The metallic forehead is well developed and extends onto the crown in *A. linaraborae* but is nearly absent or more restricted to the forecrown in *A. boltoni.* The metallic color of the forehead is Emerald Green in *A. linaraborae,* pale Paris Green 63 in *A. b. boltoni,* and Ultramarine in *A. b. malindangensis.* Tail color also differs...." (Kennedy et al. 1997, p. 4).

Vireo masteri: "Most closely resembles Yellow-winged Vireo *Vireo carmioli* but is much smaller (wing chord *c.* 50–55 mm v 65 mm or more), slightly duller in general colouration and with a different and highly distinctive facial pattern: a dark orbital line and pale superciliary stripe, both of which extend posteriorly to above the posterior portion of the auriculars.... The combination of conspicuous wing bars and well developed pale superciliary readily distinguishes *V. masteri* from all other species of the genus *Vireo*" (Salaman and Stiles 1996, p. 612).

Xenoperdix udzungwensis: "Diagnostic features are olive-brown upperparts with rufous bars margined with black. Inner vanes of the humerals are chestnut with broad black bars. A black forehead interrupts the anterior supercilium. Underparts below the throat are grey with large round black spots centrally on most feathers" (Dinesen et al. 1994, p. 3).

Amphibians

Eleutherodactylus tonyi: "Larger body size...; a more robust body shape (flattened in *E. p. planirostris*); relatively longer legs; head length less than width...; wide (extending beyond external margin of choana) and strongly arched vomerine odontophores (shorter and more nearly straight in *E. planirostris*); ventrolateral skin texture moderately rugose (smooth in *E. p. planirostris*), a call with a lower dominant frequency...." (Estrada and Hedges 1997, p. 228).

Osteocephalus exophthalmus: "Can be distinguished from *O. subtilis*...by its Buff iris with a black cross (vs. black), smaller overall size...relatively larger toe pads...and less well developed hand and foot webbing.... [I]t differs in possessing large and bulgy eyes, more vomerine teeth (21 vs. 12, total), ulnar tubercles, and lacking spiculate tubercles on dorsum, a bifid subarticulat tubercle on Finger IV, a bifid and smaller palmar tubercle" (Smith and Noonan 2001, pp. 348–349).

Reptiles

Lycodon cardamomensis: "Dorsal scales feebly keeled, in 17 rows at midbody; anal undivided; 12 well defined, broad white bands, evenly spaced along the entire length of the black body, and six white bands across tail; presence of both a single preocular and a loreal, causing absence of prefrontal-eye contact; loreal contacts neither eye nor internasals; three postoculars, two anterior temporals" (Daltry and Wüster 2002, p. 499).

Diplodactylus klugei: "Rostral and supralabial both entering nostril; posterior supraliabials not much larger than general head scales; mental in long contact with first infralabial; digits with single pair of enlarged apical plates, claws project well forward of plates; other subdigital scales small, rounded arranged in transverse rows; dorsal pattern usually a series of 4–5 large, dark-rimmed pale blotches on red-brown ground colour...." (Aplin and Adams 1998, p. 204).

Mammals

Myotis annamiticus: "Margin of plagiopatagium attached to the middle of the metatarsus. Frontal part of skull distinctly elevated from low rostrum.... Both small upper premolars in tooth row and similar in shape unlike in most of other species of *Myotis* (Leuconoe); pseudodiastem enlarged, P^3 sometimes not in contact with posterior large premolar (P^4)" (Kruskop and Tsytsulina 2001, p. 65).

Oryzomys seuanezi: "Tail slightly smaller or equal to combined length of head and body; dorsal body pelage grey-brown, ventral coloration greyish white; skull with supraobital region beaded, a large incisive foramina with long and wide maxillary septum, postglenoid foramen small, stapedial foramen present, sphenofrontal foramen and squamosal channel absent; diploid number equal 48 and fundamental number equal 60" (Weksler et al. 1997, p. 456).

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how taxa in the four classes are diagnosed and, hence, differences in how species limits are applied.

Bird species were diagnosed primarily on the basis of appearance, overall dimensions, and vocal characteristics. All of these are externally expressed phenotypic characteristics, observable in wild animals under natural conditions. While these character traits are all useful and appropriate, they pertain solely to field diagnosability and, as such, are more restrictive criteria for diagnosing (and subsequently identifying) new species than those used for other classes of vertebrates. This bias is demonstrated in box 1, which summarizes key diagnostic traits from diagnoses of six bird species described from 1993 through 2002, with similar information for two species from each of the three other classes.

Are all evolutionarily distinct species field diagnosable?

The reliance of ornithologists on field marks for diagnosing and identifying species has not been described or scrutinized. It has been assumed, because birds seem to rely primarily on plumage and vocalizations for conspecific recognition and mate selection, that these are therefore the most appropriate sources of data to use when determining species limits. The validity of this bias toward field marks hinges on two assumptions, neither of which has been explicitly acknowledged nor critically evaluated. First, do field marks accurately reflect overall variation—are field marks representative? Second, is avian internal morphology as conservative at the species level as has often been assumed, and therefore not a useful source of diagnostic character traits?

Are field marks representative of overall variation?

Current methods and sources of information used to diagnose and distinguish bird species may be adequate, provided they reflect the actual underlying patterns of differentiation (i.e., field marks are representative of all other character traits). In order to evaluate this, an independent source of data is needed that estimates the overall variation within a population or among populations. Recent phylogeographic studies and fine-scale phylogenetic reconstructions use molecular data (primarily mitochondrial DNA [mtDNA] and nuclear DNA) to provide estimates of divergence among taxa, allowing phenotypic evolution to be compared with direct estimates of genotypic change. An instructive example comes from a recent study of logrunners (Orthonychidae: *Orthonyx temminckii*) in New Guinea (Joseph et al. 2001) that revealed a deep genotypic division between New Guinean and Australian birds. Estimated at approximately 20 percent sequence divergence (mtDNA haplotype), this difference exceeds the differences between many genera (Johns and Avise 1998), yet the plumage of birds from these two populations is so similar that they had formerly been considered conspecific. Moreover, molecular divergence between two populations of New Guinean birds was found to exceed 5 percent, but individuals could not be consistently distinguished using measurements or plumage attributes (Joseph et al. 2001) and could not be

reliably identified in the hand (Frith and Frith 1987). While many other studies have found a mismatch between molecular divergence and external appearance (Crochet at al. 2000, Pavlova et al. 2003, Hoglund and Shorey 2004), this example is startling—two entire clades were obscured by the retention of ancestral plumage characteristics. Hence, basing species limits decisions purely on plumage or other phenotypically expressed traits can be misleading and, as such, can generate unreliable and unstable taxonomies. As more researchers incorporate molecular methods to explore phylogeographic and phylogenetic patterns, many more cryptic taxa will emerge, and the need for a consistent and realistic procedure for recognizing them will become increasingly pressing.

Genetic divergence need not indicate separate species status (Omland et al. 2000, Muira and Edwards 2001), but it does indicate that the populations being studied have undergone sufficient isolation (over space, time, or both) for repeated nucleotide substitutions to occur. Similarly, lack of genetic divergence need not preclude separate species status; there are several notable examples of ecological segregation overwhelming genotypic uniformity (Piertney et al. 2001, Helbig et al. 2002). Rather than the definitive arbiter of species status, molecular data provide an additional source of information that can guide decisions on species limits, often revealing patterns that are not evident from phenotypic variation and stimulating further corroborative work.

Is internal morphology an underutilized source of characters?

In comparing the diagnoses of recently described bird species with those of other vertebrates, one of the most dramatic contrasts was the complete absence of internal morphological data in birds. Most avian families and orders (and many genera) are diagnosed solely on the basis of skeletal morphology, myology, and anatomy (Sibley and Ahlquist 1990). This disparity reflects the widespread view that birds exhibit little variation in internal morphology at the species level, due, in part, to the constraints placed on avian physiology and anatomy by powered flight (Rayner 1987, Gill 1995). Whether flight really is such a powerful constraint has not been tested and must await a thorough comparative analysis. A question of more direct relevance to avian species limits is whether the internal morphologies of birds exhibit sufficient variability at the species level to yield useful diagnostic features.

One aspect of internal morphology that has received considerable attention (albeit not recently) is the detailed structure of the syrinx, the vocal apparatus of birds. Although syringeal attributes have been used to diagnose higher-level taxonomic groups (families and orders in particular; Sibley and Ahlquist 1990), few researchers have investigated their potential value at the species level. A notable exception is the work of Wesley E. Lanyon, Richard O. Prum, and their colleagues (e.g., Lanyon 1985, Prum 1992) with the neotropical group Tyrannoidea (Tyrannidae, Cotingidae, Pipridae, and allies). Indeed, syringes of manakins (Pipridae) are so distinctive that species can be diagnosed on the basis of syringeal morphol-

ogy alone (Prum 1992; Richard O. Prum, Yale University, New Haven, Connecticut, personal communication, 31 October 2003). Whether they are similarly variable in other lineages is unclear; few preparators keep syringes of bird specimens. This is demonstrated by the fact that, of the 60 papers discussed here that describe new bird species, only one mentioned that syringes were preserved.

Another potentially useful source of diagnostic traits is the skeleton, which is widely used in diagnosing reptile and mammal species. As with syringes, skeletal morphology has yielded important traits for the higher-level classification of birds, but has rarely been used at the species level. Recent phylogenetic treatments of many groups have used skeletal morphology, with skeletal data routinely used to identify birds to the species level from fossil and subfossil material (Olson and James 1982). Yet, of the 60 new bird species discussed here, skeletal specimens were only prepared for 6. While new species of mammals are described and diagnosed solely on the basis of osteological characteristics, this is not the case in ornithology.

Mechanisms and potential solutions

Having established that avian species limits are defined primarily by field marks, the next step is to establish why birds are treated differently from other taxa. The great majority of bird species were described in the 18th and 19th centuries by early taxonomists such as Linnaeus and his contemporaries—scientists who worked on a broad range of organismal groups. This raises further questions: Why did these early workers treat birds differently? Why has this inconsistency persisted, and how can it be corrected?

Part of the answer relates to specimens, which provide the raw material used as the basis of new species descriptions and the assigning of species limits. The standard specimen in ornithology is the round skin, from which a range of external measurements can be made and plumage readily categorized. Although generally considered to have begun in the 17th century, the preparation of mounted birds has been documented as early as the 1200s (Schulze-Hagen et al. 2003), indicating that taxidermy was already widely practiced and well established before it was used for the scientific description of bird species. Anatomical specimens (i.e., spirit specimens and skeletons) are rarely prepared, accounting for a tiny fraction of the total number of specimens. In a global analysis of avian anatomical specimens, Jenkinson and Wood (1985) noted more than 2700 species for which there was not a single skeletal specimen available, and more than 2900 species without a spirit specimen (from a total of 9005 species surveyed). Even more telling is that, of those species with anatomical specimens, 70 percent and 78 percent were represented by fewer than 10 skeletal or spirit specimens, respectively—the minimum number needed for many research questions. Since this review, more ornithologists became aware of the need for anatomical specimens, but round skins are still the standard preparation. This is demonstrated with the 60 new species discussed here, of which 49 were repre-

sented exclusively by skins. For those 11 species with anatomical specimens, only three were represented by both a skeleton and a spirit specimen. This compares with 37 of the 60 species descriptions that included sonograms or deposited recordings of the new species' vocalizations in sound libraries. Hence, the reason that morphology is seldom used to assign avian species limits may simply be that the absence of anatomical specimens precludes study of their morphology. Note that the addition of anatomical specimens to a type series need not entail the sacrifice of any more individuals; the trunk removed during the preparation of a study skin can be saved as either a partial skeleton or a spirit specimen (Winker 2000). This is exemplified by the recent description of the chestnut-capped piha (*L. weberi*), based on a type series of three individuals: an adult male (photographs and sonograms, round skin, stomach contents, external parasites, and tissue sample preserved); an adult female (photographs, round skin, fluid-preserved trunk, stomach contents, and parasites); and a juvenile male (round skin).

Regarding the continued bias toward field marks, birdwatching may be a contributing factor. In most taxon-specific disciplines in biology, there is a small group of specialists who are able to identify individuals accurately to species, typically with reference to extensive collections. When species-level identification is required, specimens are sent to these specialists or identified with reference to diagnostic keys prepared by them. Since birds are diagnosed primarily using field marks, species identification is not restricted to specialists. Indeed, it has become an extremely popular pursuit, evidenced by the proliferation of field guides published in recent years. Rather than directly influencing professional ornithologists, these amateur enthusiasts (or parataxonomists, as Daniel Janzen has called birdwatchers) represent the largest group of end users of bird species classifications. Species that cannot be reliably identified in the field are often treated with suspicion—a subtle but pervasive influence that may help maintain the status quo in ornithology worldwide.

Unlike other disciplines, in which species described according to the rules of the International Code of Zoological Nomenclature (ICZN 1999) remain valid until determined invalid by further research, ornithology has additional levels of scrutiny. Various committees and other groups at national and international levels review putative new species and, in so doing, act as de facto arbiters of taxonomic decisions (Vuilleumier et al. 1992, AOU 1998). It is noteworthy that these decisions have no legal standing (i.e., according to the Code) in the broader community—they are merely opinions. Nonetheless, as these committees oversee the revision of the regional checklists and official species lists that are then used as taxonomic standards within the field of ornithology (communicated primarily in journals published by their societies), these opinions are highly influential in the ornithological community and may prevent widespread acceptance of valid species. These committees generally consist of senior ornithologists with extensive experience. While this arrangement ensures high standards and consistency, this "quality con-

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trol" is often at the expense of adopting new data sources, new ways of analyzing existing data, or new taxonomic concepts (see, for example, the continued domination of the BSC in bird taxonomy). Ensuring that these committees are representative of current ornithology and that they are composed of researchers that are active practitioners of modern ornithology and evolutionary biology may improve the situation and diminish the importance of field marks in the determination of species limits.

Case study: Scrub jays of the Americas

Prior to 1990, the genus *Aphelocoma* was considered to comprise three species: the scrub jay (*A. coerulescens*), gray-breasted jay (*A. ultramarina*) and unicolored jay (*A. unicolor*), occurring from western North America to northern Mesoamerica with a disjunct (but disproportionately well-studied) population in Florida. As indicated by their common and scientific names, these three species differ primarily in their plumage patterns but also dramatically in size, ecology, and habits. Series of specimens collected at 35 sites throughout the range of this genus provided the basis for a detailed molecular analysis using allozymes (Peterson 1992). These initial data suggested that both scrub jays and unicolored jays were derived independently from populations of gray-breasted jays, rendering *A. ultramarina* paraphyletic. Evidence was also clear for broad variation in rates of molecular evolution, with three isolated populations (scrub jays of Florida and Santa Cruz Island, and unicolored jays of the mountains of Guerrero, Mexico) displaying two to three times faster protein divergence than other populations. Perhaps most important, the protein studies suggested that the traditional scrub jay included five parapatric or allopatric units that are genetically distinct from one another; gray-breasted jays had three such units, and unicolored jays at least two. The essence of these results was corroborated with subsequent phylogenetic analysis of mitochondrial genes (Rice et al. 2003). While several taxa are difficult to identify using plumage alone, experienced (or well-read) observers can readily distinguish all 10 taxa by combining field marks with range and behavioral traits. Rather than being geographically restricted ecological analogs, these taxa fulfill quite different roles in their respective ranges. Specifically, some scrub jay populations have a short hooked bill and feed primarily on acorns, while others have longer, more pointed bills associated with extracting seeds from pine cones (Peterson 1993).

The most recent edition of the American Ornithologists' Union's *Check-list of North American Birds* (AOU 1998) recognizes five species in the genus. While the gray-breasted and unicolored jays have been retained unchanged, the scrub jay has been split into three species, elevating the highly divergent Santa Cruz and Florida populations to full species (*Aphelocoma insularis* and *A. coerulescens* respectively) and treating the remaining populations as the western scrub jay (*Aphelocoma californica*). This arrangement not only creates a paraphyletic species containing both acorn and piñon specialists (*A. californica*) but also misrepresents levels of differentiation among taxa. The Guerrero population of the unicolored jay, for example, is more divergent from eastern unicolored jays than the Florida scrub jay is from western populations and just as disjunct, and yet the population is subsumed with *A. unicolor*. Furthermore, a genetic break in parapatry between northern and southern gray-breasted jays presents even more clear evidence of species-level differentiation (Peterson 1992 and references therein). Thus, the current taxonomy bears little resemblance to our current understanding of actual diversity, combining ecologically and evolutionarily distinct taxa, obfuscating the underlying diversity, and presenting serious confusions for researchers contemplating further work on the group.

Where to from here?

The possibility that there are many species of birds that can only be identified in the hand (or laboratory) may seem alarming to field researchers, but this realization need not cause sweeping changes to current practices in field ornithology. Rather, it will merely bring ornithology closer to the other vertebrate disciplines regarding how species are identified. In the vast majority of cases, these taxa will be allopatric or parapatric, so, using locality, these cryptic species can still be identified (at least provisionally), as exemplified by the scrub jay case study. In localities where several species are thought to exist, or to confirm species identity, birds may need to be caught and additional measurements and/or samples taken. Given that birds are routinely caught for banding, this need not be impractical, and the required expertise and licensing arrangements are already in place worldwide.

Rather than alienating the bird-watching community, this process may actually foster a greater level of amateur involvement in ornithology. While a species may initially be diagnosed on the basis of detailed morphology or molecular divergence, extensive field experience with the taxon may reveal subtle behavioral or life-history traits, allowing reliable identification under field conditions. A pertinent example comes from research on crossbills (*Loxia* spp.) in North America (Groth 1993, Benkman 2003), traditionally regarded as a single widely distributed species. Detailed spectrogram analysis revealed clear and consistent patterns of call differentiation, much of it imperceptible to human ears. These data served as the basis for the description of seven species, clearly identifiable using flight calls. Subsequent molecular research confirmed the groupings, with additional morphological work finding subtle but distinctive differences in bill morphology. Finally, field observations revealed that these different taxa fed on different species of conifer, their bills ideally suited to the cones of their preferred tree species. Hence, using a range of methods and involving the public through innovative programs (crossbills can be identified using an Internet-based flight call library), the actual diversity of these morphologically conservative birds was revealed. Unfortunately, this example is as rare as it is apposite—few other taxa have received such attention, and it is therefore

unclear how exceptional or commonplace such hidden diversity really is.

One of the arguments against the widespread adoption of the PSC is the prohibitively large number of species that would necessarily eventuate (Collar 1996), and a similar argument could easily be leveled at the central tenet I have developed here. However, in addition to being fundamentally incorrect, this perception is irrelevant. Surely, the aim of alpha taxonomy and the goal of species-limit decisions is to discern the total number of evolutionarily distinct units as accurately as possible (Moritz 1994); the actual number of these units is immaterial to this goal.

Rather than advising against the use of some sources of information or placing undue emphasis on others, I would encourage ornithologists to consider taking a more holistic approach to the diagnosis and subsequent identification of bird species, allowing the actual breadth of avian diversity to be recognized. This will necessarily yield more valid bird species (under any species concept) than are presently recognized. The fact that species may be more difficult to identify in the field does not mean that they are in any way less important or less distinct. This is not a "splitting versus lumping" issue, nor is it a question of semantics or choice of species concepts. Rather, I recommend that researchers use all the tools available to recognise the actual units of avian diversity, not only to ensure the ongoing currency of ornithology but to help in the effective conservation and management of birds worldwide (Hazevoet 1996, Sangster 2000).

The relevance of consistent and appropriate species limits was succinctly summarized 10 years ago by Prum (1994): "This lack of appropriate documentation of avian diversity in the Neotropics has resulted in part from reliance by professional ornithologists on inadequate, current species taxa. Current species names are insufficient to characterize many of the units of diversity in the Neotropical avifauna, and they constitute a significant burden to the documentation and analysis of avian biogeographic patterns that are critical to establishing diversity estimates and conservation priorities" (p. 700). Ornithologists clearly have recognized this shortcoming for some time, and now, having established the underlying mechanisms, we can collectively start to address it.

Acknowledgments

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