The use of sounds in avian systematics and the importance of bird sound archives

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The use of sounds in avian systematics and the importance of bird sound archives

by Per Alström & Richard Ranft

SUMMARY

The steady increase in the global total of bird species is in part due to the discovery of distinct vocalisations which reveal hitherto unrecognised information, either the presence of entirely new species or the level of differentiation in taxa previously treated as conspecific. There are many examples of both types of discovery (and some where taxa previously given species status prove conspecific). The importance of vocal analysis in establishing the relationships between taxa is also demonstrated by numerous examples. Avian sound archives are clearly crucial to the advancement of such studies, but many more recordings are needed, their quality must be high, the circumstances of recordings need to be documented, the identity of vocalising birds needs to be firm, and a fuller system of cooperation between sound archives is required.

Introduction

The number of bird species in the world was estimated to be *c.*8,600 by Mayr (1946), *c.*9,000 by Bock & Farrand (1980), and *c.*9,700 by Sibley & Monroe (1990). This increase widely exceeds the number of newly described species in that time period. Part of this increase can be attributed to the growing knowledge of bird vocalisations in combination with the current trend to recognise allopatric taxa with distinctive songs as species rather than as subspecies (Sibley & Monroe 1990, Parker 1991, Price 1996, Peterson 1998).

Although sounds have mainly been of use in the ranking of closely related allopatric taxa, vocalisations have also been used to infer relationships, both within and between genera, and have been crucial in the discovery of several new species. We here review the use of vocalisations and other acoustic signals in systematics; see also Payne (1986) for a thorough review and Morel & Chappuis (1992) for a review of West African taxa. We also discuss the importance of sound archives and suggest how they may be made more useful to future researchers.

The importance of vocalisations in the discovery of new species

Several new species have been discovered because of their distinct vocalisations. Some of these escaped attention because they are highly secretive and difficult to see, and others because they are sibling species which are morphologically similar to other species. Several examples are given here.

A rallid heard in September 1997 on a steep mountain slope in primary forest in the Talaud archipelago, Indonesia, later proved to be an undescribed species, the Talaud Bush Hen *Amaurornis magnirostris* (Lambert 1998).

The existence of two new species of Andean pygmy-owls, Subtropical Pygmy Owl *Glaucidium parkeri* (Robbins & Howell 1995) and Cloud Forest Pygmy Owl *G. nubicola* (Robbins & Stiles 1999), was first indicated from tape-recordings of their voices.

The Cryptic Warbler *Cryptosylvicola randrianosoloi* was first detected in 1992 in eastern Madagascar by its voice (Goodman *et al*. 1996) and it was subsequently found to be common (Morris & Hawkins 1998). Likewise it was its song that first disclosed the presence of the Jocotoco Antpitta *Grallaria ridgelyi* in the Andes of southern Ecuador (Krabbe *et al*. 1999).

The Ancient Antwren *Herpsilochmus gentryi* was discovered by José Alvarez Alonso and Bret Whitney when Whitney identified it as a new species from among Alvarez's unclassified tape-recordings of unseen canopy birds from Peru (Whitney & Alvarez Alonso 1998). They later managed to find it in the field (and to collect two birds), confirming its distinctness.

Four new species of *Scytalopus* tapaculos from South America, Chocó Tapaculo *S. chocoensis*, Chusquea Tapaculo *S. parkeri* (Krabbe & Schulenberg 1997), Diademed Tapaculo *S. schulenbergi* (Whitney 1994) and Tall-grass Wetland Tapaculo *Scytalopus iraiensis* (Bornschein *et al*. 1998), were discovered because their songs differed from other known species.

The observation that there were 'two markedly different vocal types', and pronounced differences in display, in what was originally believed to be Suiriri Flycatcher *Suiriri suiriri* led to the discovery of the Chapada Flycatcher *Suiriri islerorum* (Zimmer *et al*. 2001).

The song of the Nepal Wren Babbler *Pnoepyga immaculata* (Martens & Eck 1991) was long thought to be a variant of the song of Scaly-breasted Wren Babbler *P. albiventer*. It was later realised that the individuals with this kind of song also differed morphologically from Scaly-breasted Wren Babbler, and the existence of a previously unknown species was thus revealed.

Three previously unknown species of warblers were discovered in China during the 1990s as a result of their vocalisations. Emei Leaf Warbler *Phylloscopus emeiensis*, restricted to a small area in central China, was first noted because its song and call differed markedly from two other sympatric, similar-looking species, Blyth's Leaf Warbler *P. reguloides* and White-tailed Leaf Warbler *P. davisoni* (Alström & Olsson 1995). Vocalisations were also of paramount importance in the discovery of two new species of *Seicercus* warblers, *S. soror* and *S. omeiensis*, and in the elucidation of a group of sibling species (Alström & Olsson 1999, 2000, Martens *et al*. 1999; see below). Other new warblers have been found because of their distinct vocalisations, e.g. Dorst's Cisticola *Cisticola dorsti* (Chappuis & Erard 1991) and River Prinia *Prinia fluviatilis* (Chappuis 1974), both from West to Central Africa.

The Taiwan Bush Warbler *Bradypterus alishanensis* was previously treated as the subspecies *melanorhynchus* of Russet Bush Warbler *B. mandelli* (=*seebohmi*), but was described as a new species (Rasmussen *et al*. 2000a) when it was realised

that its song differed markedly from other populations of Russet Bush-warbler and that no name was available for this population.

No fewer than three indigobirds, Jos Plateau *Vidua maryae*, Goldbreast *V. raricola* and Barka *V. larvaticola*, were discovered mainly because of their songs (Payne 1982, 1998, Payne & Payne 1994). However, the discrimination of the first of these species led to the even more remarkable discovery of the Rock Firefinch *Lagonosticta sanguinodorsalis* (Payne 1998). Indigobirds are species-specific brood parasites that mimic the songs of their host species, mainly firefinches *Lagonosticta* spp. (e.g. Payne 1968, 1973a, 1973b, 1982, Payne & Payne 1994), so when it was realised that the song of the Jos Plateau Indigobird differed from the songs of all other indigobirds, it was predicted that there must be an unknown firefinch song model in the area.

At least two new species of corvid, Sinaloa Crow *Corvus sinaloae* from western Mexico (Davis 1958) and Little Raven *C. mellori* from southern Australia (Rowley 1967a,b), were discovered because of differences in vocalisations from other species, in the second case a sympatric species (Australian Raven *C. coronoides*).

The importance of vocalisations in the assessment of taxonomic rank

There are many cases, in a wide range of genera, where allopatric taxa have been 'upgraded' from the rank of subspecies to species, or even from colour morph to species, because of differences in their acoustic signals. The converse is less common. Some examples are presented here.

The North American Western Grebe *Aechmophorus occidentalis* and Clark's Grebe *A. clarkii* were previously considered to be colour morphs of the same species (Western Grebe *A. occidentalis*). However, Nuechterlein (1981) showed that the 'advertising call' used in mate attraction differs significantly between the two and that, in an area of sympatry, each 'morph' responded almost exclusively to its own call. This confirmed the studies of Storer (1965) and Ratti (1979), which had shown strong assortative mating in these 'morphs'.

In many seabirds, especially those that breed in burrows and only visit their breeding islands at night, females probably identify conspecific males by their vocalisations, at least at long range (James & Robertson 1986, Bretagnolle 1990, 1995, Bretagnolle *et al*. 1990, Bretagnolle & Robinson 1991). Studies of sounds have sometimes revealed differences between populations that were considered conspecific, and have been used in conjunction with other evidence to show that these taxa are better considered separate species. The Antarctic Prion *Pachyptila desolata*, Salvin's Prion *P. salvini*, Broad-billed Prion *P. vittata*, Slender-billed Prion *P. belcheri* and Fairy Prion *P. turtur* have been treated differently by different authors on the basis of morphological data. Bretagnolle *et al*. (1990) studied these taxa on their breeding islands, where two to four occurred in sympatry. They showed that their voices (as well as morphology, phenology of breeding and diet) differed

consistently, especially in sympatric taxa, and they therefore considered all to be separate species.

Bretagnolle (1995) analysed the vocalisations of Soft-plumaged Petrel *Pterodroma mollis* from several different localities. Based on this (in conjunction with morphological characters), he concluded that the Soft-plumaged Petrel should be split into two species, one in the northern hemisphere, *P. feae*, and one in the southern hemisphere, *P. mollis*. (It should be mentioned that others, following the lead of Bourne [1983], believe that the North Atlantic taxa *feae* and *madeira* should be treated as separate species based on morphological differences, although Bretagnolle [1995] remarked that their calls were similar and overlapped.)

The Herald Petrel *Pterodroma heraldica* was formerly believed to have a dark-bellied and a pale-bellied colour morph. However, Brooke & Rowe (1996) noted consistent differences in the vocalisations of pale and dark birds (especially in the rate of delivery of the calls in a series). These differences, in combination with evidence of assortative mating and lack of gene flow, led them to propose that the two morphs are in fact separate species, Herald Petrel *P. heraldica* and Henderson Petrel *P. atrata*.

The 22 currently recognised species of megapode Megapodiidae differ little in plumage, but markedly in bare-part colours and proportions (Roselaar 1994, Jones *et al*. 1995). Although their vocalisations are imperfectly known, there are 'minor differences between the races and sometimes marked ones between species', supporting the proposed classification (R. W. R. J. Dekker in Roselaar 1994).

Even in groups such as bustards Otididae, which are not very vocal, voice has proved useful in taxonomic assessments. It is now widely accepted that the Crested Bustard *Eupodotis ruficrista* involves three allopatric species owing to differences in vocalisations and morphology (Chappuis *et al*. 1979, Morel & Chappuis 1992, Payne *et al*. 1997); and it has been suggested by Gaucher *et al*. (1996) that the Houbara Bustard *Chlamydotis undulata* is better treated as two allospecies, *C. undulata* and *C. macqueenii*, owing to differences in 'display call' and courtship display (supported by morphological and genetic differences).

Acoustic signals have been used comparatively rarely in wader taxonomy, despite the fact that most waders have distinct sound displays. The Amami Woodcock *Scolopax mira* is an exception. It was once treated as a subspecies of the Eurasian Woodcock *S. rusticola*, but Brazil & Ikenaga (1987) pointed out differences in (among other things) vocalisations and the apparent lack of a display flight.

Thönen (1969), Olsson (1987) and Miller (1996) remarked that the 'drumming' made by the tail-feathers during flight display differed between European (nominate) and North American (subspecies *delicata*) populations of Common Snipe *Gallinago gallinago*. Based on this (in combination with morphological differences), they suggested that these should be considered separate species.

American Golden Plover *Pluvialis dominica* and Pacific Golden Plover *P. fulva* were formerly treated as conspecific (under the name American Golden Plover *P. dominica*). Connors *et al*. (1993) studied these taxa in an area of sympatric breeding

in western Alaska and showed that there were consistent differences in vocalisations ('song', alarm calls and other calls) and in habitat choice, and that mating was assortative. Byrkjedal & Thompson (1998) came to the same conclusions. These results supported the proposition by Connors (1983), based on a study of specimens, that these taxa are separate species.

Miller (1996) noted differences in five variables in the display vocalisations of Common Ringed *Charadrius hiaticula* and Semipalmated *C. semipalmatus* Plovers, but only very slight intra-taxon differences over large areas. These findings lent support to the widely accepted notion that these taxa are better treated as separate species.

Song characteristics have been used to re-estimate species limits in several cuckoos: Square-tailed Drongo Cuckoo *Surniculus dicruroides*, Round-tailed Drongo Cuckoo *S. lugubris*, Moluccan Drongo Cuckoo *S. musschenbroeki* and Philippine Drongo Cuckoo *S. velutinus* (Payne 1997, in press); Horsfield's Cuckoo *Cuculus optatus* (=*horsfieldi*) and Oriental Cuckoo *C. saturatus* (Payne 1997, but lumped in Payne [in press] 'because a larger sample of songs shows some overlap, and specimens show overlap also': R. B. Payne *in litt*.); Common Cuckoo *C. canorus* and African Cuckoo *C. gularis* (Payne 1986, Morel & Chappuis 1992); Rufous Hawk Cuckoo *Hierococcyx hyperythrus*, Philippine Hawk Cuckoo *H. pectoralis*, Whistling Hawk Cuckoo *H. nisicolor* and Javan Hawk Cuckoo *H. fugax* (Payne 1997, in press, King 2002); and Asian Lesser Cuckoo *C. poliocephalus* and Madagascar Lesser Cuckoo *C. rochii* (Becking 1988, Payne in press).

In owls, voice has often been of major importance in the assessment of taxonomic rank. The classic study by Marshall (1978) on small Asian owls, in which he classified taxa with dissimilar vocalisations as separate species and, conversely, taxa with similar vocalisations as conspecific, led to a multitude of taxonomic rearrangements. For example, he suggested species status for no fewer than seven scops owls (genus *Otus*) that had previously been treated as subspecies. Other studies on the voices of Asian scops owls have been important in resolving taxonomic matters, and have further increased the number of recognised species (Roberts & King 1986, Marshall & King 1988, Becking 1994, Lambert & Rasmussen 1998).

Another example is that all the taxa previously associated with *Otus rutilus* of Madagascar have been shown to differ in voice (and morphology), and have been suggested to be treated as separate species: *O. moheliensis* (Lafontaine & Moulaert 1998), *O. capnodes* (Safford 1993), *O. pauliani* (Herremans *et al*. 1991), *O. [r.] mayottensis* (Lewis 1998), *O. madagascariensis* and *O. rutilus* (Rasmussen *et al*. 2000b). Chappuis (1974–1985) and Morel & Chappuis (1992) suggested that European Scops Owl *O. scops* and African Scops Owl *O. senegalensis* should be considered separate species based on differences in voice.

The Least Pygmy Owl *Glaucidium minutissimum*, which is widely distributed in South America, was formerly treated as a polytypic species. However, Howell & Robbins (1995) analysed vocalisations and in conjunction with morphology and other evidence suggested that it ought to be treated as four separate species.
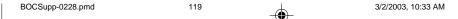
Vocalisations have been used extensively in taxonomic revisions of nightjars. For example, Jerdon's Nightjar *Caprimulgus atripennis*, Sulawesi Nightjar *C. celebensis* and Philippine Nightjar *C. manillensis* were all split from Large-tailed Nightjar *C. macrurus* because of their distinctive vocalisations (Mees 1985, Ripley & Beehler 1987, Rozendaal 1990). Likewise, Tawny-collared Nightjar *C. salvini*, Yucatan Nightjar *C. badius* and Silky-tailed Nightjar *C. sericocaudatus* have been judged to be specifically different on the basis of differences in voice (Hardy & Straneck 1989). Conversely, Dowsett & Dowsett-Lemaire (1993) pointed out that the songs of Fiery-necked Nightjar *C. pectoralis* and Black-shouldered Nightjar *C. nigriscapularis* were similar, and suggested that these should be treated as conspecific. They also showed that the taxa *ruwenzorii* (Ruwenzori Nightjar), *guttifer* (Usambara Nightjar) and *poliocephalus* (Abyssinian Nightjar), which have at one time or another been considered separate species, are best treated as conspecific, under the name Montane Nightjar *C. poliocephalus*, owing to basically similar vocalisations. (It should, however, be noted that Cleere [1995], also using vocal characters, disagreed with this assessment.)

Voice has been important in the assessment of species status of a taxon that is believed to be extinct in the wild: Grayson's Dove *Zenaida graysoni* from Socorro Island south-west of Baja California (Baptista *et al*. 1983). It was established that the voice (and visual display) of this bird differ significantly from the Mourning Dove *Z. macroura*, with which it has often been considered to be conspecific. It was also noted that it only rarely interbreeds with Mourning Dove in captivity.

Vocalisations have been used to assess the taxonomic rank in other doves. The insular endemic Grenada Dove *Leptotila wellsi* was shown to differ vocally (as well as morphologically) from the closely related continental Grey-fronted Dove *L. rufaxilla* (Blockstein & Hardy 1989). Playback tests were also of importance in this re-evaluation. Chappuis (1974–1985) and Morel & Chappuis (1992) showed that the vocalisations of the morphologically closely similar Eurasian Collared Dove *Streptopelia decaocto* and African Collared Dove *S. roseogrisea* differ markedly, and proposed species status for them.

Pittas Pittidae have loud, relatively simple songs which have been used (in conjunction with especially morphology) to show that the mainly allopatric Fairy Pitta *Pitta nympha*, Blue-winged Pitta *P. moluccensis*, Indian Pitta *P. brachyura* and Mangrove Pitta *P. megarhynchus* are best treated as separate species (Lambert 1996, Lambert & Woodcock 1996).

The Neotropical Tyrannidae include many species that are poorly differentiated morphologically, and vocalisations have often been of great importance in the recognition of species. Lanyon (1978) used vocalisations and playback tests extensively in his monumental revision of the genus *Myiarchus*, because he was 'convinced that the use of vocal characters, in conjunction with more conventional morphological characters, would be the key to any successful attempt to determine specific limits and relationships within the genus'. He proposed several taxonomic rearrangements based on this research.

Willow Flycatcher *Empidonax traillii* and Alder Flycatcher *E. alnorum* were formerly considered conspecific, but Stein (1958, 1963) showed that they differed in vocalisations and other aspects, did not respond to playback of each other's songs and were partly sympatric. Similarly, studies of vocalisations together with morphology and allozymes showed that the Western Flycatcher *E. difficilis* of western North America was in fact two separate, partly sympatric, species: Pacific-slope Flycatcher *E. difficilis* and Cordilleran Flycatcher *E. occidentalis* (Johnson 1980, Johnson 1994).

The species in the South American suboscine genus *Scytalopus* (tapaculos) are extremely similar in plumage and structure, and are very secretive and difficult to observe (e.g. Fjeldså & Krabbe 1990, Ridgely & Tudor 1994). Until recently, their classification was based on comparative studies of museum specimens (Zimmer 1939, Peters 1951). A review by Krabbe & Schulenberg (1997) using vocalisations (in combination with morphology and distribution) led to a virtual 'explosion' of species, from 11 recognised by Zimmer and Peters to no fewer than 37. Three of these, Chocó Tapaculo *S. chocoensis*, Ecuadorian Tapaculo *S. robbinsi* and Chusquea Tapaculo *S. parkeri*, were new to science, and an additional two or three were considered to be undescribed. Several of the species were shown to be sympatric. Krabbe & Schulenberg classified allopatric taxa with unique songs as species, an approach that was supported by DNA data presented by Arctander & Fjeldså (1994).

The use of vocalisations has led to the recognition of many South American Thamnophilidae and Formicariidae as species. For example, Isler *et al*. (1997) suggested that the widely distributed polytypic Slaty Antshrike *Thamnophilus punctatus* is better treated as at least six separate allospecies; Isler *et al*. (1999) argued that Streaked Antwren *Myrmotherula surinamensis* should be treated as four species; and Whitney *et al*. (2000) concluded that the Black-capped Antwren *Herpsilochmus pileatus* complex consists of three species, of which one, Caatinga Antwren *H. sellowi*, was previously undescribed because it had been confused with *pileatus* for almost a century.

The Bengal Bushlark *Mirafra assamica* was previously treated as a polytypic species ranging from India to Sri Lanka and Vietnam. However, Alström (1998) showed that there are pronounced differences in songs, calls and song-flights (as well as morphological differences, and in one case in habitat) between four allopatric taxa. Based on this, he proposed that they be treated as four separate species.

Bicknell's Thrush *Catharus bicknelli* has received much interest lately, because it has been shown to differ from Grey-cheeked Thrush *C. minimus* (with which it was formerly considered conspecific) in a number of aspects, including song (and lack of response to playback to two other subspecies of Grey-cheeked Thrush, *minimus* and *aliciae*) (Ouellet 1993).

Old World warblers are renowned for being morphologically poorly differentiated, although the species usually differ more clearly by their songs. This was noted more than 200 years ago, when White (1789) remarked that 'I have now, past dispute, made out three distinct species of the willow-wrens (*motacillæ trochili*) which

constantly and *invariably* use distinct notes.' He was referring to Willow Warbler *Phylloscopus trochilus*, Common Chiffchaff *P. collybita* and Wood Warbler *P. sibilatrix*, of which only the first had at that time been named. In fact, in the genus *Phylloscopus* (leaf warblers) in Eurasia excluding the Philippines, Greater Sundas and Wallacea, the number of recognised species went up by 31% in the last decade, and in all except two species, songs were important in the assessment of their taxonomic rank (Irwin *et al*. 2001). Two examples are given below.

Pallas's Warbler *P. proregulus* used to be considered a wide-ranging polytypic species, breeding in Siberia, northern Mongolia and north-east China (nominate *proregulus*); central China and the Himalayas west to central Nepal (subspecies *chloronotus*); and western Himalayas (subspecies *simlaensis*); a fourth taxon, *kansuensis*, from northern central China, was treated as a synonym of either *proregulus* or *chloronotus*. First, Alström & Olsson (1990) proposed that *proregulus* and *chloronotus/simlaensis* should be treated as two separate species based on pronounced differences in vocalisations and lack of response to playback of each other's songs. Subsequently, Alström *et al* (1997) pointed out that *kansuensis* also differed considerably in vocalisations from the others, and did not respond to playback of their songs, and concluded that it ought to be treated as a separate species. Meanwhile, Alström *et al*. (1992) found a species with unique vocalisations that was sympatric with *chloronotus* in central China (differing also in morphology, habitat choice and nest site). It was described as a new species, Chinese Leaf Warbler *P. sichuanensis*, though it was later realised that this name was pre-dated by *yunnanensis* (Martens & Eck 1995, P. Alström & U. Olsson unpublished).

The taxonomy of the Common Chiffchaff *Phylloscopus collybita* complex has received much attention in recent years. It was formerly considered a single polytypic species, although extensive studies of its vocalisations and other data (e.g. Martens & Hänel 1981, Martens 1982, Salomon 1987, 1989, Martens & Meincke 1989, Helbig *et al*. 1996) have led to the suggestion that at least four species ought to be recognised: Common Chiffchaff *P. collybita*, Iberian Chiffchaff *P. brehmii*, Canary Islands Chiffchaff *P. canariensis* and Mountain Chiffchaff *P. sindianus*, leaving the relationships of the Siberian taxon *tristis* unresolved (Helbig *et al*. 1996). These taxa are allopatric, except for Mountain and Common Chiffchaffs, which occur together in western Asia, and the latter meets Iberian Chiffchaff in a narrow zone in the Pyrenees. Hansson *et al*. (2000) showed that Swedish populations of Common Chiffchaff of the subspecies *collybita* and *abietinus* responded more strongly to song of their own than to the other subspecies and, based on other differences such as habitat choice, they predicted that there would be only limited hybridisation if these taxa met in the future.

The Golden-spectacled Warbler was until recently treated as a single polytypic species, *Seicercus burkii*, with a wide distribution in mountains of southern Asia (mainly the Himalayas and China). Alström & Olsson (1999, 2000) and Martens *et al*. (1999) demonstrated that this is actually a complex of no fewer than six sibling species, with up to four occurring at different altitudes on the same mountain (two,

S. soror and *S. omeiensis*, were previously undescribed: see above). Differences in vocalisations and playback tests were of major importance in the elucidation of this situation.

Song has been used extensively in the classification of African cisticolas *Cisticola*, both to split and to lump taxa (e.g. North 1964, Chappuis 1974, 1980, Erard 1974, Morel & Chappuis 1992). Keith & Gunn (1971), Chappuis (1974–1985), Chappuis (1980) and Morel & Chappuis (1992) used vocalisations to review the taxonomy of some apalis *Apalis* species.

One remarkable case where possible cryptic species were revealed by their vocalisations is the study of North American Common (Red) Crossbill *Loxia curvirostra sensu lato* by Groth (1988, 1993a,b). He (1988, 1993a) studied a large number of individuals from across the continent, and correlated sonograms of calls with measurements of the same individuals. Based on these variables, the birds clustered into eight different groups. Several of these are sympatric, e.g. six in the Pacific Northwest. Strong assortative mating was shown to occur in two different populations in the Appalachians (1993b). He concluded (1993a) that '*L. curvirostra* is a group of sibling species' but, owing to the morphological similarity and overlap in measurements, he was unable to assign names to all of these species. The American Ornithologists' Union (1998) recognised only one species but interpreted Groth's results as indicating the probable existence of at least nine different species in North America. Studies of vocalisations by Robb (2000) have suggested that there may be cryptic species of crossbills also in Europe.

Some of the most amazing discoveries involving vocalisations involve the African indigobirds *Vidua* (e.g. Nicolai 1964, Payne 1968, 1973, 1976, 1982, 1990, 1998, Payne & Payne 1994, 1995, Payne *et al*. 1992, 1993; see above). Although most indigobird species are morphologically poorly differentiated, their songs are often markedly different. This insight has led to the recognition of several 'forms' as distinct species (all 10 indigobird species now recognised were at one time or another considered to be either subspecies or colour morphs of Village Indigobird *V. chalybeata*, or overlooked).

Crows *Corvus* are morphologically relatively poorly differentiated, but their voices are often clearly different. Vocalisations have been of major importance in the classification of the North American species American Crow *C. brachyrhynchos*, North-western Crow *C. caurinus*, Tamaulipas Crow *C. imparatus*, Sinaloa Crow *C. sinaloae* and Fish Crow *C. ossifragus* (Brooks 1942, Davis 1958, Hardy 1990).

Use of vocalisations in inferring relationships

Although vocalisations have mainly been used to answer questions of species status, some authors have used voice to judge relationships among species. In a few cases, features of songs and calls have been used as characters to infer phylogenetic relationships.

Bretagnolle (1995) compared the vocalisations of several different *Pterodroma* species and drew conclusions about their relationships based on the similarities and dissimilarities between them.

The calls of downy Anatidae young were analysed by Kear (1968), who concluded that they had phylogenetic information. The shape and frequency range of the distress call tended to be similar in closely related species and to be more divergent in more distantly related ones. For example, she remarked that the call of White-backed Duck *Thalassornis leuconotus*, whose taxonomic position had been in doubt, was 'very like those of *Dendrocygna* and quite unlike the distress call of *Oxyura*'. A recent phylogenetic analysis (McCracken *et al.* 1999) confirms that *Thalassornis* is not closely related to *Oxyura*, but also suggests that the similarity between *Thalassornis* and *Dendrocygna* is due to retention of ancestral character states in the former.

Andersson (1973, 1999) studied calls and displays of skuas (Stercorariini) and concluded that some of these are synapomorphies (shared derived characters) for Great Skua *Stercorarius skua* and Pomarine Skua *S. pomarinus*—supporting the controversial but now well-supported (see Andersson 1999) view that the latter is more closely related to the large skuas (which are often placed in the genus *Catharacta*) rather than to the smaller Arctic *S. parasiticus* and Long-tailed Skua *S. longicaudus*.
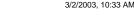
Miller (1996) used characteristics of nuptial vocalisations to infer relationships among *Pluvialis* plovers and some *Calidris* sandpipers. He also concluded that 'acoustic characters seem to have great potential for resolving species relationships at various levels' in *Gallinago* snipes and *Charadrius* plovers.

Acoustic data were used by Winkler & Short (1978) to infer relationships among pied woodpeckers (*Picoides/Dendrocopos*). In many cases, their analysis corroborated previous studies (e.g. the probable monophyly of the New World group). In other cases the vocal data were in conflict with other evidence (e.g. Middle Spotted Woodpecker *Dendrocopos medius* was considered to be more distantly related to White-backed Woodpecker *D. leucotos* than previously thought, and the same applied to Black-backed *Picoides arcticus* and Three-toed *P. tridactylus* Woodpeckers).

Vocalisations were used to determine probable relationships of some antwrens in the genus *Myrmotherula* (Whitney & Pacheco 1997). Based partly on vocalisations, Whitney (1992) suggested that Bicoloured Antvireo *Thamnomanes occidentalis* be placed in the genus *Dysithamnus* instead. Whitney & Pacheco (1994) also used vocalisations in discussing the affinities of the little-known monotypic genera *Gyalophylax* and *Megaxenops*.

Songs, calls and display flight were used in addition to other data to show the close relationship between Berthelot's Pipit *Anthus berthelotii*, endemic to the Canary Islands and Madeira, and Tawny Pipit *A. campestris* (Alström & Mild 1993), a circumstance later corroborated by molecular data (Arctander *et al.* 1996, Voelker 1999).

King (1989) showed that the different species in the genera *Tesia* and *Urosphena* clustered in two groups according to characteristics of their songs. Based on this (in conjunction with other behavioural and morphological differences) he proposed a new classification of these genera.

The relationships of various treecreepers *Certhia* have been discussed based on their vocalisations (Martens 1981, Martens & Geduldig 1988), and the affinities of Brown Creeper *C. americana* to Short-toed Treecreeper *C. brachydactyla* and Eurasian Treecreeper *C. familiaris* have recently been studied using sounds (Baptista & Krebs 2000).

The Black-collared Bulbul *Neolestes torquatus* from the Afrotropics has variously been treated as a bulbul (Pycnonotidae) or a shrike (Malaconotidae, Laniidae or Prionopidae). A recent investigation (Dowsett *et al*. 1999) used vocalisations (together with morphology and DNA) in support of the view that it is not a shrike, but most closely related to bulbuls.

Payne (1986) stated that 'similarities in song quality may express genetic similarities' even in species in which song is learned, and accordingly may be of use in phylogenetic analyses. He used vocal characters to reconstruct the phylogeny of the Black-throated Green Warbler *Dendroica virens* complex. Since his tree was largely congruent with a previous hypothesis of relationships (Mengel 1964), he concluded that 'the distribution of song traits among species indicates that cultural changes may have followed the same branching events as in the genetic differentiation of the species'.
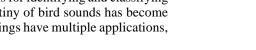
Characteristics of song were also used by Stein (1968) to analyse relationships among North American *Vermivora* warblers.

The role of bird sound archives

Modern studies on bird vocalisations would have been impossible without the collecting of sound recordings, yet, in comparison with the collecting of physical specimens, the means to do so have been available only recently. The first recording of any bird (a captive White-rumped Shama *Copsychus malabaricus*) was made in Germany in 1889, and the first recording of a wild bird was made in England in 1900, on wax cylinders (Boswall 1969). However, it has only been in the past 40 years, long after the invention of electrical amplification and with the development of new recording technologies and the wider availability of portable, battery-operated tape-recorders, directional microphones and parabolic reflectors, that recording in the field has become truly practicable. Further refinements in recording techniques and equipment since then means that birds in any environment around the world can now be recorded relatively easily with high-quality equipment that is modestly priced, portable and reliable.

In the pre-recording era, the value of vocalisations for identifying and classifying birds was well known. But a far more detailed scrutiny of bird sounds has become possible with technological advances. Sound recordings have multiple applications,

not only in taxonomic research: they reveal the structure of sounds, and facilitate their description and comparison between different populations and species, while playback experiments can test reactions of birds to answer questions about song function, or to identify and draw out hidden birds for identification in faunal surveys (Johnston *et al* 1981, Parker 1991) as well as identifying individual birds (e.g. McGregor 1992). Recordings are used by birdwatchers and field researchers for familiarisation of species' diagnostic sounds, a key factor in efficiently determining their ranges in a short time-frame (Parker 1991); to help trap birds for ringing and relocation projects; to help deter pest species from urban areas, agricultural crops and airports; in educational programmes in museum and zoo exhibitions, audio and multimedia publications and websites, and in television and radio broadcasts.

The emerging science of bioacoustics received a boost after Thorpe's (1954) use of the sound spectrograph to analyse and compare Chaffinch *Fringilla coelebs* songs. Originally developed as a speech aid for the deaf (Potter *et al*. 1947), the sound spectrograph allowed more rapid and objective description and comparison of bird vocalisations.

The first archive of bird sounds was formed from a collection originally started in 1932 at Cornell University in the USA (Gulledge 1979). There are now numerous

TABLE 1

Major institutional bird sound archives, based upon Kettle (1989) with updated figures from archive curators (*in litt.*).

	Location	Year established	Number of bird species represented	Total number of bird recordings	Collection strengths
Macaulay Library of Natural Sounds	Cornell University, New York state, USA	1956	6,400	130,000	Worldwide, especially neotropics
British Library National Sound Archive	London, England	1969	7,800	120,000	Worldwide
Tierstimmenarchiv	Humboldt University, Berlin, Germany	1952	1,800	100,000	Central Europe, Mongolia
FitzPatrick Bird Communication Library	Transvaal Museum, Pretoria, South Africa	1979	3,000	30,000	Africa
Australian National Wildlife Collection Sound Library	CSIRO, Lyneham, Australia	1961	400	25,000	Australasia
Borror Laboratory of Bioacoustics	Ohio State University, USA	1945	876	21,000	USA
Florida Museum of Natural History	Florida, USA	1973	2,700	15,000	USA and neotropics
Arquivo Sonoro Neotropical	Campinas University, São Paulo, Brazil	1978	1,000	12,000	Brazil

institutional collections worldwide (Kettle 1989; see also Frommolt 1996, Nelson & Gaunt 1997, Ranft 1997); however, only the eight largest collections (Table 1), which altogether hold around half a million recordings, receive public funding to ensure the long-term preservation of and access to the recordings in their care. These collections have been built up mainly through the donations from many scientists and recordists, and they represent many hundreds of thousands of hours of work in the field. As with traditional museum collections of bird skins, they are invaluable especially for comparative studies between individuals, populations and species where it is often impossible for one person to replicate, even in a lifetime of work, the dedicated efforts of so many collectors of sounds.

The rapid growth in systematic collections of bird sound recordings has been encouraging and the value of this material is now widely appreciated (Parker 1991, Kroosdma *et al* 1996). Some of the challenges these collections are faced with are discussed below.

(1) There is an urgent need to add many more recordings to these collections. Comparative studies of bird sounds usually require a large sample of recordings from different localities. Yet even for well-recorded species there are many gaps in geographical range (see, e.g., Kroodsma *et al.* 1996). As expected, the tropical regions are the most inadequately covered, with many species represented by few recordings often from a single, well-studied site, or by single recordings from widely scattered localities or even simply by a single recording. Many recordings exist in private collections without adequate access or long-term preservation (Kroodsma *et al* 1996, Harrington 1997). To deal with all the extra recordings, however, requires a substantial effort on the part of the recordists, and of course a commitment of resources by the archives, some of which are seriously underfunded. Publishing recordings on cassettes and CDs or on the internet is a useful way to make them widely accessible but this is not a solution to their long-term availabilty: recordists should be urged to commit their recordings to archival facilities.

The vocalisations and behaviour of many species of bird, especially tropical songbirds, are so poorly known that it may be difficult to judge whether variation between individuals or populations is of taxonomic significance or merely indicative of a rich repertoire. Large samples of recordings can help assess such variation. An analysis of the catalogues from the major sound collections, and many other smaller private collections, reveals that there are no recordings at all of around 940 species of bird, or nearly 10% of the total. Over 100 of the missing species are hummingbirds (Trochilidae). For taxa currently treated as subspecies, the situation is much worse. For example, based primarily on morphological differences, Collar & van Balen (2002) suggested that the Blue-tailed Trogon *Apalharpactes reinwardti* is better treated as two species, Javan Trogon *A. reinwardti* and Sumatran Trogon *A. mackloti*; the Javan form apparently lacks the distinctive song of the Sumatran one, but the paucity of recordings from Java meant that vocalisations were not conclusive in supporting the rearrangement. Similarly, Garrido *et al.* (2002) judged the Hispaniolan and Cuban forms of Grey-headed Quail Dove *Geotrygon caniceps* to be sufficiently

different morphologically to be treated as different species, but they lacked examples of the song of the Hispaniola race to support their contention.

(2) Recordings need to be of the highest technical quality to be of full value for analysis. C. Chappuis (*in litt.*) has remarked that the speed of cassette recorders is often wrong, and suggested that a reference sound (e.g. from a tuning fork) should be recorded in the field. A frequent problem when making sonograms of recordings is that the sounds of interest are obscured by background noise, or reverberation from vegetation. Recordings should ideally be made with the microphone as close as possible to the subject, using well-maintained professional audio recording equipment. Nevertheless, a great deal of useful information can often be extracted from a poor recording. For example, computer techniques have improved the quality of a unique recording of the almost extinct Slender-billed Curlew *Numenius tenuirostris* that was otherwise nearly obliterated by a louder and similar song of a Eurasian Curlew *N. arquata* (Chappuis 2000). Further advice on recording can be obtained from the major sound archives.

(3) The paucity of collection data associated with each recording needs to be addressed. A recording must be accompanied with data collected at the time it was made, including locality, time of day, date and other details. The more complete the data, the more applications the recording will have for future researchers. As with skin collections, missing or insufficient locality data in bioacoustic collections can reduce their value. Efforts have been made recently to encourage the standardisation of data collection (see Kettle & Vielliard 1991, Bradbury *et al.* 1999).

(4) Certain identification of the species involved is required. Few sound recordings are associated with skin specimens, so that corroboration of their identity depends either on the skills of the original recordist or matching against known reference recordings, which may of course also be unreliable (see, e.g., Payne 1973a, 1982, 1998 for recordings linked to museum specimens). There are several instances of rare recordings that were for some years archived as authoritative recordings and published as such, only later to be found to have been misidentified. For example, a recording of the Boreal Owl *Aegolius funereus* erroneously attributed to Northern Hawk Owl *Surnia ulula* was published in several American and Swedish identification guides in the period 1960–1980 (Hardy *et al.* 1989). Similarly, Wahlström (1968) revealed that a recording made in 1948 and published several times in Europe until 1968 as the voice of Baillon's Crake *Porzana pusilla* was in fact that of Little Crake *P. parva*.

(5) Sound archives need to be able to share and make more widely available their collections. All the largest archives can provide basic inventories of their holdings. But so far just two archives, the Borror Laboratory and The British Library's National Sound Archive, have their full catalogues on the internet (see http://blb.biosci.ohio-state.edu/BLBCatalog.htm and http://cadensa.bl.uk/). These catalogues contain full details about recordings, but not the actual sounds. Sound recordings can be easily replicated and distributed over digital networks such as the internet, and several audio archives are presently implementing the means to enable

worldwide direct access to at least parts of their collections over the internet. A large-scale roll-out of these collections depends on the resolution of technical and copyright issues, in particular achieving the right balance between safeguarding the unauthorised use of recordings and providing unrestricted access, and allowing access to sounds over a worldwide web that is currently too slow for rapid distribution of high-quality audio files.
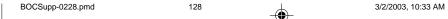
Discussion and conclusions

We have firmly established that acoustic signals have been of great use in a wide range of birds in (1) the discovery of new species, (2) the assessment of taxonomic rank of allopatric taxa under the biological species concept (Mayr 1942) and (3) phylogenetic analyses. The importance of vocalisations in the discovery of new species is now widely acknowledged, and it seems likely that more sibling species will be discovered in the future as a result of thorough vocal analyses, especially in geographical areas that have been poorly surveyed. However, it seems unlikely that such discoveries will substantially increase the total number of bird species.

By contrast, growing knowledge of the vocalisations of different taxa (which is largely due to the increased use of tape-recorders and sound analysis software, and the greater ease of travel in recent years), in combination with the current trend to afford species status to allopatric taxa with distinctive vocalisations, will probably produce a steady increase in the number of recognised species. A large proportion of all bird taxa (estimated at 27,000–28,000 by Mayr & Gerloff 1994) is poorly known with respect to their vocalisations, and the taxonomic status of many of these will undoubtedly be re-evaluated when their voices become better known. It is thus vital that more taxa are tape-recorded, especially those that are currently treated as subspecies, and that recordings are properly documented, curated and made accessible.

All bird species produce sounds (even the New World vultures Cathartidae, which lack a syrinx, make functional sounds). Songs, in particular, are usually fairly loud and hence can be detected and recorded from a distance without disturbance. For birds that are difficult to observe, i.e. nocturnal or cryptic species, or those occurring in dense habitats such as forests and reedbeds, recordings may be the only convenient method of data collection. The usefulness of recordings in systematic research has increased in recent years since (a) recordings are relatively easy and cheap to collect, preserve, replicate and share; (b) there is an existing extensive dataset of bird recordings in sound archives to draw upon; and (c) tools such as computer software for sound analysis are now cheap and widely available.

There is still a need to refine and standardise the methodology for employing sound recordings as a systematist's tool. Such an attempt was made by Isler *et al*. (1998), who analysed vocalisations of eight syntopic, similar-looking and similar-sounding antbird species (Thamnophilidae). Based on this, they proposed that when deciding the rank of allopatric antbird taxa, three diagnosable vocal characters (the minimum number that distinguished the syntopic pairs in the study) should be used

as a point of reference. They recommended that for taxa that are very poorly differentiated in other respects, more than three vocal characters are required to allow classification as species, whereas for taxa that differ strongly in other ways, fewer vocal characters may suffice.

Finally, sounds alone should not be used in making taxonomic decisions. However, they can be a first pointer to the field ornithologist to gather additional evidence such as further morphological, DNA or behavioural data, and these data can then be used in conjunction in taxonomic revisions.

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