Lumping & Splitting

THE COMPLEXITIES OF BIRD TAXONOMY

Are you confused by the appearance of 'new' species and bemused by the disappearance of old friends with every new edition of your favourite field guide? Or are you simply happy to accumulate 'armchair ticks'?

The Percy FitzPatrick Institute's Peter Ryan explains why bird taxonomy – the field that names species – is undergoing rapid revisions after almost half a century of relative stability.

WARWICK TARBOTON

The species is the basic unit by which we classify animals and plants. It is a concept central to birding – the first thing you do when faced by a group of individual birds is to identify them to species. But what *is* a species? This is the question at the heart of the current revolution in bird taxonomy. Two classes of species concepts are battling for supremacy, the outcome of which will have profound consequences for birders.

IAN SINCLAIR

*The isolated race of Groundscraper Thrush (simensis) (**above**) occurring in Ethiopia and southern Eritrea is sufficiently different in call and behaviour from the southern African bird (**top**) that it possibly warrants full species status.*

In the beginning there was the Biological Species Concept (BSC), the formal name for the species concept with which most people are familiar. It states that species are groups of individuals that more or less freely interbreed, and that are reproductively isolated from other such groups. The key feature is that individuals share genes: species comprise populations that interbreed and thus have a common evolutionary history. Of all the taxonomic categories devised to classify birds and other organisms – species, genera, families, orders, etc. (see box on page 65) – only the species has an objective biological 'reality'. Biological species are self-defining, whereas other categories are human constructs. This is neatly encapsulated in the adage: 'Subspecies are a matter of opinion, genera a matter of convenience, but species are a matter of fact'.

The BSC has its origins in the 'modern synthesis' of biology, which married Darwin's theory of evolution through natural selection with Mendel's theory of heredity. The major proponents of the BSC were ornithologists. Two deserve specific mention: David Lack, for his brilliant explanation of variation and speciation among Darwin's Finches, and Ernst Mayr, the chief architect of the BSC.

The Biological Species Concept has been successful because it is in accord with the most plausible mechanism for speciation. Using bird examples, Lack and Mayr showed that speciation occurs when populations are isolated and no longer share genes. Adaptation to local conditions or simply random drift (coupled with the random sampling that occurs when isolated populations form) results in heritable, genetic differences between populations. These differences accumulate over several generations, and when the populations meet again they no longer interbreed and hence have become separate evolutionary entities, or species.

Although the details may vary, this model of speciation still holds, at least for animals that reproduce sexually (asexual organisms and many plants bend the rules, but that needn't worry birders!). Why then is the BSC under siege?

The problems: disjunct populations and hybridization

The greatest practical problem with the BSC is that it fails to provide an objective measure for allopatric taxa (that is, those which do not occur at the same place at the same time). How can we define species on the basis of interbreeding if they never come into contact?

Africa has numerous examples of disjunct populations associated with the south-west and north-east arid zones. In the past these areas were linked, allowing arid-country birds to disperse throughout the eastern part of Africa. Subsequent invasion by moist woodlands throughout central East Africa has isolated the arid zones, dividing the ranges of many birds.

Some of these disjunct populations have changed very little and are still regarded as the same species (for example, Pygmy Falcon *Polihierax semitorquatus*), while others have evolved regional differences and are recognized by at least some authorities as separate species (for example, Northern *Eurocephalus rueppelli* and Southern white-crowned shrikes *E. anguitimens*). However, there is no consensus as to how much the disjunct populations must differ to be recognized as separate species. We enter a grey area of subjective assessment where the BSC provides no assistance.

The other main problem with the BSC relates to hybridization. When isolated populations once again come into contact, we can apply the BSC to test whether speciation has occurred. However, unless the populations have diverged to the point where they no longer perceive each other as potential mates, first contact is a messy process. Often some degree of interbreeding or hybridization takes place. If hybrids are disadvantaged (because of divergence between the genetic composition of the parent species), birds that select the 'right' partner will be favoured, and species boundaries reinforced. Alternatively, if hybrids are not disadvantaged, the two populations will coalesce and form a single species. This process takes many generations to play out, and during this time the taxonomic status of the populations is hard to resolve.

Strict adherents of the BSC lump all taxa that hybridize. However, many well-defined bird species interbreed at least occasionally – a recent review found that about 10 per

WHAT'S IN A NAME?

Taxonomy is the field of study dealing with biological classification. Humans classify objects for many reasons, using a variety of criteria. For example, we could classify birds using criteria such as ease of capture, palatability of their flesh, etc. Such a classification would be useful if you relied on hunting birds as a source of protein. However, it is an 'artificial' classification, because it is unlikely that it would represent the evolutionary history of birds, and the criteria used are subjective, so that different people would arrive at different classifications.

Taxonomists strive for 'natural' classifications which represent the evolutionary history of organisms, using objective criteria. We use the Linnaean system of classification, both for naming organisms and representing their evolutionary relationships. It is hierarchical in structure, placing similar taxa together in a nested series of categories which imply relationships, and thus conveys much more than a simple list of species. Birders are at least peripherally aware of this classification system. Scientific names, unique to each species, are a combination of two categories in the Linnaean system, genus and species names. Thus the Sooty Albatross has the name *Phoebetria fusca*, which is the terminal portion of its full classification:

- **Kingdom**: Animalia (all animals)
- **Phylum**: Chordata (animals with some form of 'backbone')
- **Subphylum**: Vertebrata (the vertebrates)
- **Class**: Aves (all birds)
- **Order**: Procellariiformes (tube-nosed seabirds)
- **Family**: Diomedeidae (albatrosses)
- **Genus**: *Phoebetria* (sooty albatrosses)
- **Species**: *fusca* (the dark sooty albatross)

This system is sufficient to represent the evolutionary history of relatively undiverse taxa such as the albatrosses. However, it struggles to accommodate more diverse groups. Evolutionary relationships within large orders such as the passerines can only be represented by the addition of many more hierarchical levels (parvorder, superfamily, subfamily, tribe, and so on).

The Linnaean system started out as an artificial, phenetically-based classification system – after all, it was developed before Darwin and Wallace described the basic principles of evolution. Today it represents our best understanding of evolutionary relationships. Because ongoing research reveals new and sometimes unexpected relationships between taxa, the system of classification is being modified constantly. The most important development in recent years for birds has been the monumental DNA-DNA hybridization study by Charles Sibley and Jon Ahlquist. The results of this work still have not been accepted fully by the ornithological establishment, in part due to a reluctance to countenance major changes. However, it seems that it will only be a matter of time before bird books are produced in the 'new sequence' which places woodpeckers and parrots ahead of penguins and raptors!

HOW MANY BIRD SPECIES?

The number of described bird species increased steadily from around 3 000 species in 1800, to more than 6 000 species by 1850 and peaked at almost 19 000 species in the early 1900s. However, with the advent of the Biological Species Concept, many of the Linnaean 'morphospecies' were re-interpreted as subspecies, and considerable lumping took place. By 1950 the number of recognized species stabilized at around 8 600, although further field collecting had increased the total number of taxa (including subspecies) to 28 500. Recent trends to recognize allopatric forms as distinct species has reversed some of the earlier lumping, and the latest list produced by Charles Sibley stands at 9 946 species. Clearly there is no definitive bird list, which is why birding is much more dynamic than stamp collecting!

GLOSSARY OF JARGON

Scientists delight in coining new terms for the concepts they devise. The main benefit of creating this jargon is that it forms a convenient shorthand for discussing ideas, but all too often it becomes a shield to exclude the uninitiated. The following brief glossary should help you negotiate the minefield of terms that litter the taxonomic literature.

Allopatric (**allopatry**): taxa whose ranges do not overlap (cf. sympatric and parapatric).

Allospecies: allopatric species that together form a superspecies, assumed to have evolved from a single, geographically variable species.

Analogous character: a character shared between taxa as a result of convergence, not as a result of being present in a common ancestor (cf. homologous character).

Biological species concept: a species is a group of freely interbreeding organisms.

Clade: a group of taxa descended from a common ancestor (also termed a monophyletic group).

Cline (clinal variation): a geographic gradient in average character state (e.g. wing length or plumage colour).

Convergence: the evolution of common characters in unrelated organisms, often as a result of adaptation to similar environmental pressures (for example, wings in birds and bats).

Disjunct distribution: geographically isolated; normally applied to a species with two or more isolated populations.

Ecological species concept: a species is a group of organisms adapted to a specific set of resources (a niche) in the environment.

Genotype: the sum of the genetically-stored information within an individual (cf. phenotype). Because birds have two copies of all genes (one set derived from each parent), not all the components of the genotype are necessarily expressed.

Homologous character: a character trait that is shared between taxa as a result of common ancestry (cf. analogous character).

Lineage: a sequence of populations through time, from ancestors to descendants.

Parapatric (**parapatry**): taxa whose ranges have a common boundary but do not overlap (cf. allopatric and sympatric).

Phenetic species concept: a species is a group of organisms with similar appearance.

Phenotype: an individual's physical appearance and characteristics, which results from the interaction between its genotype and the environment in which it lives.

Phylogenetic species concept: a species is a lineage between speciation events. Operationally, a phylogenetic species is characterized by a common derived character. This is also known as the cladistic species concept.

Phylogeny: the evolutionary history of a group of taxa, often represented as a branching tree (termed a phylogenetic tree).

Recognition species concept: a species is a group of organisms that recognize each other as potential mates as a result of a shared mate recognition system.

Sibling species: species which are so similar phenotypically that they are hard to distinguish.

Speciation: the process by which new species form.

Sympatric (**sympatry**): taxa whose ranges overlap, at least in part (cf. allopatric and parapatric).

Taxon (pl. **taxa**): any named taxonomic group, from subspecies to kingdom.

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cent of birds had been recorded to hybridize with other species. Sometimes these pairings don't involve closest relatives, and it would be ludicrous to lump the species involved. Once again we get into a subjective argument as to how much hybridization is too much.

An allied problem is that many widespread species evolve regional differences. These are typically recognized as subspecies if there are regions where the local variants 'intergrade' or blend into each other. However, some well-defined geographic forms have very distinct characters (often associated with specific habitat types), and contact zones between them are narrow, with limited interbreeding. Lumping these forms conceals important biological diversity. Another classic example of the problem of geographic variation is posed by 'ring species'. Herring *Larus argentatus* and Lesser Black-backed gulls *L. fuscus* are good biological species in Europe, where they co-occur without interbreeding. However, they are linked by a ring of interbreeding populations around the rim of the Arctic Ocean which show that the two forms are merely the extremes of a continuum.

An alternative approach

Where do we go from here? One possibility is to adopt a new species concept, and the main contender is the Phylogenetic Species Concept (PSC). Unlike the BSC, which defines species at a specific moment in time, the PSC views species as parent-ancestor lineages between speciation events. It has its origins among systematists who are interested in the relationships between groups of organisms and attempt to reconstruct evolutionary histories. They see species as the terminal branches of the evolutionary 'tree'.

What does this mean in terms of identifying species at any given time? Phylogenetic species are defined as groups of organisms characterized by at least one common derived character (that is, they differ consistently from related species in at least one feature). This objective criterion avoids the problem of disjunct populations – if the isolated populations differ consistently, they are separate species. It is also more forgiving with regard to hybridization. As long as the core of a population differs consistently from adjacent populations, it doesn't matter if some hybridization occurs, because reproductive compatibility is no longer the ▷

PETER STEYN

***Above** More than 20 subspecies of Spike-heeled Lark have been described, with 11 taxa currently recognized. How many of these subspecies represent phylogenetic species requires further research, although many appear to be merely clinal colour variants. However, recent observations of the isolated population in northern Tanzania suggest it may be a distinct biological and phylogenetic species.*

RICHARD DU TOIT

***Left** The Kori Bustard is another bird of semi-arid savanna with disjunct populations in north-eastern and south-western Africa. The two populations are recognized as different subspecies on the basis of subtle differences in plumage pattern. They may represent different phylogenetic species, but it is debatable whether each 'species' is as important from a conservation perspective as is a well-defined biological species such as Ludwig's Bustard.*

defining criterion. This sounds great, but the PSC is not without its problems. One implication is that every time speciation occurs, two new species form and the old species disappears. This is disconcerting if speciation occurs as a result of colonization of an offshore island, and there is no detectable change in the mainland population.

A more crucial problem is that species lose their special status as self-defining entities. Moreover, the criterion of a common derived character can be taken to absurd lengths – for example, defining species on the basis of a single genetic substitution that doesn't even result in a change in protein structure. Applying this standard would vastly inflate the numbers of species and the frequency of extinctions, as many small species would be created and expire as a result of chance alone. Although strictly correct in terms of the PSC definition, this approach would result in 'species' being very different from our current perception (not to mention making life all but impossible for birders!)

So what's the solution?

The scientific world remains divided on the issue of species concepts. Systematists have forged ahead applying the PSC, while more traditional taxonomists still support the BSC. As in many debates, it seems likely that some form of middle ground will be found. Moderate adherents of the PSC already argue that there must be concordant variation in a number of characters to recognize a species. Many species have regional variation in a variety of characters, but unless the boundaries coincide they should not be treated as species. This application of the PSC results in taxa roughly equivalent to those identified by the BSC, but has the advantage of handling situations where the BSC cannot be applied. It is the use of this type of argument that has resulted in the recent recognition of geographically discrete 'subspecies' as full species.

Another solution may be to adopt a trinomial system to recognize both biological and phylogenetic species. For example, the Purple Heron *Ardea purpurea* is a biological species comprising two phylogenetic species, the widespread Purple Heron *A.* [*p.*] *purpurea* of Africa and the Palearctic, and the Cape Verde Purple Heron *A.* [*p.*] *bournei*, restricted to a single island in the Cape Verdes. Such a system necessitates the scrapping of subspecies for clinal variants.

Ultimately we can't expect to pigeonhole all populations into neatly-defined species boundaries – evolution is an ongoing, dynamic process, with populations splitting and coalescing over geological time. We need a classification system that is both biologically accurate and useful. Species remain the primary currency for setting conservation priorities, and it is important that we do not devalue the species category to the point that people are no longer concerned by the threat of species extinctions. At the same time, we must guard against allowing distinctive allopatric populations from going extinct because they are currently perceived to be 'merely subspecies'. □

FURTHER READING

For a more complete review of this subject, see the June 1997 edition of the *Bulletin of the British Ornithologists' Club* (vol. 117, no. 2). Jeremy Greenwood (pp. 85-96) provides an introduction to taxonomic principles, followed by well-reasoned arguments for and against the Phylogenetic Species Concept by Bob Zink (pp. 97-109) and David Snow (pp. 110-121), respectively. Finally, Nigel Collar considers the implications for conservation of wholeheartedly embracing the PSC (pp. 122-136).