

Guidelines for assigning species rank[†]

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Developments in several fields of study (including bio-acoustics and the analysis of DNA) together with reappraisals of the nature of species have impacted significantly on avian taxonomy. The BOU's Taxonomic Subcommittee has developed guidelines for the application of species limits to sympatric, parapatric, allopatric and hybridizing taxa. These are published here to assist researchers understand the rationale behind the committee's taxonomic recommendations relating to the British List.

Evolution and speciation are continuous biological processes. The naming of species is an attempt to recognize these processes and apportion their outcomes into discrete parcels that have biological meaning. The various species concepts that have been proposed (see Mayden 1997, Johnson *et al.* 1999, for overviews) are all based on the same phenomenon: observable discontinuities between groups of organisms. They differ primarily in the particular aspects of the phenomenon they stress in an attempt to translate the products of evolutionary divergence between population lineages into taxonomic practice.

No species concept so far proposed is completely objective or can be used without the application of judgement in borderline cases. This is an inevitable consequence of the artificial partitioning of the continuous processes of evolution and speciation into discrete steps. It would be a mistake to believe that the adoption of any particular species concept will eliminate subjectivity in reaching decisions. Adopting a different species concept merely moves the boundaries, and changes the individual taxonomic decisions that are controversial.

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The present authors are members of the BOU Taxonomic Sub-committee, and have drawn up these 'guidelines' to assist them in the assessment of species rank for the British List (see Sangster *et al.* 2002, for an application of these guidelines to some European birds). This report is not intended to be a review of species concepts or of the species debate. The guidelines are outlined here and briefly discussed to help interested parties to understand the rationale behind our recommendations published elsewhere. Unjustified or unsubstantiated changes in taxonomy frequently lead to confusion. We propose to maintain the stability of the British Checklist (British Ornithologists' Union 1992, and subsequent modifications as published in the Reports of the BOU Records Committee in *Ibis*) except where there is clear, published evidence in support of a change. Wherever possible, we will only use material published in peer-reviewed journals, supported by statistical analysis where this is appropriate. It should be recognized that taxonomic recommendations are hypotheses of the diagnosability and evolutionary relationships of taxa, made using an interpretation of the evidence available at the time. As such, they are subject to revision and reinterpretation, particularly as new information becomes available.

THEORETICAL BACKGROUND: SPECIES CONCEPTS

According to the Evolutionary Species Concept (ESC: Mayden 1997) and the very similar General

Lineage Concept (GLC: de Queiroz 1998, 1999), species are evolutionary lineages that maintain their integrity (with respect to other such lineages) through time and space. de Queiroz (1999) points out that, as lineages evolve and diverge, they become distinguishable to us in genotype and phenotype. At some point all members of two lineages can be unequivocally assigned to one or other lineage. The distinguishing features may be ecological, behavioural, morphological or physiological, and they are what we need to be able to recognize when we attempt to define the status of a taxon. The Biological Species Concept (BSC) defines species as reproductively isolated groups of populations. Reproductive isolation, of course, is the crucial prerequisite for evolutionary lineages to maintain their integrity through time and space (i.e. not merge back into each other), but it can only be directly observed if populations coexist in space and time. Thus, the BSC stresses a practical aspect of how to recognize species, but from its theoretical background it is entirely compatible with the ESC. The Recognition Species Concept (RSC) sees the species as a group of individuals with a common fertilization system and/or a Specific Mate Recognition System (SMRS), i.e. it stresses the fact that species are populations of interbreeding individuals (Paterson 1985). This approach can be especially useful in avian taxonomy, because of the great reliance of many birds upon visual displays and vocalizations for sexual display and territorial defence. Under the Phylogenetic Species Concept (PSC) species are population lineages ('clusters of individuals with a pattern of ancestry and descent' Cracraft 1983) that are diagnosably different. Diagnosability is a logical requirement of all species concepts, although what exactly is meant by this term has rarely been stated explicitly (see below).

It can be seen from this brief overview that differences between concepts are largely a matter of emphasis. The essence of what most biologists, for purely practical reasons, want to call a species is perhaps best encompassed in the GLC. If we define species as population lineages maintaining their integrity with respect to other such lineages through time and space, this means that species are diagnosably different (otherwise we could not recognize them), reproductively isolated (otherwise they would not maintain their integrity upon contact) and members of each (sexual) species share a common mate recognition and fertilization system (otherwise they would be unable to reproduce). All concepts require species to have had their own independent, evolutionary

histories (otherwise they would not be diagnosable). However, the PSC and a less stringent version of the ESC (Wiley 1978) do not require species to maintain their integrity in the future, because, it is argued, one cannot predict with certainty whether currently allopatric taxa will merge if they come into contact.

It is this point – implicit predictions about the future – where species concepts differ, and we have to make a decision: do we want to call any recognizable population a 'species' no matter how likely it is that it may fuse with other populations once they come into contact? Or do we want to call 'species' only those taxa for which we feel reasonably certain that they will retain their integrity, no matter what other taxa they might encounter in the future? For the purpose of recommending a practical taxonomy of West Palearctic birds, we have opted for the latter. We believe that taxa should only be assigned species rank if they have diverged to the extent that merging of their gene pools in the future is unlikely.

Species can be delimited only in relation to other species. To do this (for two given taxa), two questions must be answered:

- 1 Are the taxa diagnosable?
- 2 Are they likely to retain their genetic and phenotypic integrity in the future?

We outline first what we mean by diagnosability, after which we examine the distributional relationships of taxa. We then define a set of requirements for the assignment of species rank. The latter are meant to apply to birds, not necessarily to all organisms. This simplifies the problem, because:

- avian speciation is normally allopatric (we are aware of no case of strictly sympatric speciation),
- hybridogenic speciation is unknown in birds, although it may be possible,
- there are no asexual or unisexual lineages of birds.

We see little point in defining criteria for situations that we will not encounter. However, we note that our criteria relate to problems in avian taxonomy, and that researchers working with other groups will be faced with problems not addressed here.

DIAGNOSABILITY

Diagnosability is a logical requirement to distinguish any category of organism. Taxon diagnosis is based on characters or character states (i.e. different manifestations of the same character such as a white vs. a yellow wing-bar). Since taxon diagnosis is a purely practical undertaking of the human observer (e.g. a systematist, a birder), it does not matter whether or

not characters used in diagnosis are relevant to the birds themselves, for instance in mate recognition. The mere fact that they differ between taxa indicates that there has been a period during which genetic differences have accumulated. However, characters used in diagnosis must be the result of evolution: they must be genetically based and not purely caused by environmental factors such as nutrition. We recognize that many characters have a genetic (heritable) basis, but are modified by the environment (e.g. some parameters of body size in Canada Geese *Branta canadensis*, Leafloor *et al.* 1998). Only characters with a low environmental component of variation are suitable for taxon diagnosis.

It must be stressed that we are concerned here with diagnosability *at the taxon level*, not diagnosability of individuals or arbitrarily delimited populations. For instance, two local populations at the endpoints of a gradual cline may be fully diagnosable but, if they are named as separate taxa (as has been done for many avian subspecies), there will not be complete diagnosability because they are connected by a cline, i.e. a gradual change of the supposedly diagnostic character states. For the same reason, hybridizing taxa are, by definition, not 100% diagnosable, even if populations away from the hybrid zone are, because there will be intermediate individuals that do not meet the diagnostic criteria of either parental taxon.

We regard a taxon as fully diagnosable if either:

1 Individuals of at least one age/sex class can be distinguished from individuals of the same age/sex class of all other taxa by at least one qualitative difference. This means that the individuals will possess one or more discrete characters that members of other taxa lack. Qualitative differences refer to presence/absence of a feature (as opposed to a discontinuity in a continuously varying character). In many species pairs, examples would be the presence/absence of a wing-bar, an extra pair of tail feathers or a distinct plumage colour. We recognize that qualitative phenotypic differences (e.g. in the number of vertebrae or tail feathers) are often the result of quantitatively varying genetic traits.

2 At least one age/sex class is separated by a complete discontinuity in at least one continuously varying character (e.g. wing-length) from the same age/sex class of otherwise similar taxa. By complete discontinuity we mean that there is no overlap with regard to the character in question between two taxa given large sample sizes. An example is the yellow on the bill of Whistling Swan *Cygnus (columbianus) columbianus* and Bewick's Swan *Cygnus (c.) bewickii*;

there seems to be little or no overlap in the area of yellow in these two taxa (Evans & Sladen 1980, Scott 1981).

Overlap in a quantitatively varying character might be found if sufficient individuals were to be investigated. Consequently, application of this criterion requires sound judgement. Preferably, a character should vary little within each taxon and, if at all practical, a large number of individuals of each taxon should be compared.

When there is overlap in the range of variation of several characters between taxa, 'statistical diagnosis' may be possible by combining the characters using a multivariate technique such as Discriminant Function Analysis. This refers to both discrete (presence/absence) characters, which may occur at different frequencies between taxa, and continuously varying characters. If there is no single diagnostic character, we regard a taxon as statistically diagnosable, if

3 individuals of at least one age/sex class can be clearly distinguished from individuals of the same age/sex class of all other taxa by a combination of *two or three functionally independent* characters. For example, Mediterranean Yellow-legged Gull *Larus michahellis* and Armenian Gull *L. armenicus* can be distinguished by a combination of wing-tip pattern, darkness of mantle and mtDNA haplotypes, although none of these characters is diagnostic on its own (Liebers & Helbig 1999). Actually or potentially covarying characters, such as leg and bill lengths of individuals within a population of waders, or wing and tail lengths in a passerine population, will not be regarded as independent.

By increasing the number of characters, each of which differs only slightly between two taxa, even very marginally differentiated populations may be statistically diagnosable, i.e. each individual may be assigned with a high probability to one or other population. In species-level taxonomy therefore it is not advisable to use more than two or three such characters in diagnosis. If more are needed, it is most likely that the populations differ so slightly that their evolutionary distinctness and future integrity is doubtful. We recognize a logical weakness here. Two populations may differ consistently by, for example, a single base substitution in a DNA sequence, or a single barb on a single feather. They are diagnosably distinct and must have spent a sufficiently long period of isolation for the unique character states to have become fixed in each of the two populations (this will happen more quickly in small than in large populations). However, we think that it would be

unwise to base a taxonomic rank upon such slight differences, and do not propose to do so.

THE DISTRIBUTIONAL RELATIONSHIPS OF TAXA

Sympatry. Taxa that are syntopic at pair-formation (i.e. coexist in sympatry and at the same altitude) remain distinct because there is little or no gene flow between them: they are reproductively isolated. If there were no reproductive barriers, gene flow would long since have blurred the differences between them and they would no longer be recognizably distinct. For sympatric taxa, we can predict with a high degree of confidence that they will retain their integrity in the future. We do not know of a single documented case of breakdown of reproductive isolation (i.e. a reversal to full reproductive compatibility between species that were incompatible before) in any class of organism. Physiological reproductive isolation therefore is a point of no return in the differentiation process. This point may be reached long before hybridization stops entirely (Grant & Grant 1996), which is why hybridization does not necessarily preclude treating the taxa involved as separate species. On the other hand, once there is no more hybridization between two sympatric taxa, the point of no return has definitely been traversed.

Parapatry. Strictly parapatric taxa have abutting breeding ranges (i.e. do not overlap) and do not interbreed. Such situations are rare at temperate latitudes, but more common in the tropics. Most often, parapatric taxa are separated altitudinally, sometimes very sharply, or by an ecotone (abrupt break in habitat), but occasionally they occur in similar habitat and are only separated by a seemingly 'trivial' ecological barrier (e.g. toucans in Amazonia separated by a river; Haffer 1998). Parapatry reflects a situation where two taxa are ecologically identical or so similar that they cannot coexist in the same habitat. The fact that they do not hybridize, despite occurring in very close proximity, indicates that some intrinsic reproductive isolation is very likely to be operating.

Allopatry. If the taxa in question are allopatric (geographically separated), reproductive isolation cannot be observed. Playback of vocalizations may be used to judge whether mate recognition systems are compatible, but such tests do not provide conclusive proof one way or the other. Neither can experimental

cross-breeding in captivity, because hybridization *per se* does not tell us anything about potential levels of gene flow in nature. At the least, one would have to breed several generations to see whether F1 and later generation hybrids are fully fertile. This is not only impractical for most birds, it also does not tell us whether it would ever happen under natural circumstances when there was a free choice of mates. The likelihood that allopatric taxa will remain distinct can only be judged by the degree of their divergence, preferably in comparison with taxa that are closely related to the group under investigation and that are known to coexist in sympatry. Assignment of species rank in such cases will necessarily be based on a hypothesis, rather than on proven facts.

Hybrid zones. The same holds for taxa connected by a hybrid zone. Hybrid zones probably always indicate an intrinsic barrier to gene flow. They often coincide with ecotones (Barton & Gale 1993), and in such situations the gene flow barrier may be reinforced by different habitat preferences of the taxa on either side. The breadth of a hybrid zone relative to the dispersal distance of the taxa involved is a good indicator of the degree to which gene flow is restricted: the more hybridization and back-crossing there is, the broader will be the zone. Populations in a hybrid zone contain one or both pure phenotypes of the hybridizing taxa plus first-generation and back-cross hybrids; an example is the zone of contact between crows *Corvus cornix* and *C. corone* in Northern Italy (Rolando 1993). This distinguishes it from a clinal transition zone, in which local populations are intermediate between populations on either side of the zone, but are phenotypically uniform (for example, the progressive change in plumage from olive to grey in Chiffchaff subspecies *Phylloscopus c. collybita*, *abietinus*, *falvescens* from western to easternmost Europe: Vaurie 1959). It is unpredictable whether a particular hybrid zone will slowly break down and develop into a broad transition zone, or whether it will be reinforced by increasingly selective mate choice to become a complete reproductive barrier.

ASSIGNING SPECIES RANK

Since reproductive incompatibility is the fundamental requirement that keeps gene pools from merging, it is useful, in practical terms, to devise guidelines for assignment of species rank with respect to the four distributional situations discussed above:

- sympatry, where gene flow is prevented by intrinsic isolating mechanisms (rather than geographical isolation),
- parapatry and hybrid zones, where gene flow may be restricted to various extents by intrinsic isolating mechanisms and/or an ecotone, but not by geographical isolation,
- allopatry, where the lack of gene flow may be due solely to geographical isolation.

In allopatry, parapatry and hybrid zones, the implication (inherent in our species definition) that the taxa are unlikely to merge is hypothetical. When this cannot be judged with reasonable confidence, the taxa may be treated as members of a superspecies (as proposed by Amadon 1966, and Short 1969). A superspecies is a monophyletic group of allospecies (geographically separated) and/or semispecies (connected by a hybrid zone). Allo- and semispecies are terms that can be used to label qualitatively different categories of species whose evolutionary independence cannot be determined empirically.

1. Sympatry. Diagnosable taxa will be ranked as species if they are broadly sympatric, i.e. over areas beyond the average natal dispersal distance of the species involved, and

1.1 do not hybridize (as is true for the vast majority of co-occurring species), or

1.2 hybridize only rarely, so that gene flow between them either does not occur (because hybrids are sterile or do not backcross for other reasons) or occurs at such a low frequency (often difficult to detect) that it is unlikely their gene pools will ever merge (e.g. Black Redstart *Phoenicurus ochruros* and Common Redstart *P. phoenicurus*).

In these situations, we can infer a complete (1.1) or very strong (1.2) barrier to gene flow between the taxa merely from the observation that they are presently diagnosably different in sympatry. This intrinsic barrier may be prezygotic (e.g. different recognition systems) or postzygotic (developmental incompatibility), or – perhaps most often – it may involve both kinds of factors. Which isolating mechanisms are involved is not important for the taxonomic conclusions. Since a breakdown of such isolation has never been observed, we can safely assume that such taxa will remain distinct in the future (i.e. until they speciate again or go extinct).

2. Parapatry. Diagnosable taxa that are strictly parapatric (i.e. exclude each other geographically) and do not hybridize (this must be established empirically)

will be ranked as species, because it appears unlikely that such a situation can be maintained without intrinsic reproductive isolation.

Natural selection would favour interbreeding between two populations that are in contact at an ecotone or 'trivial' ecological barrier (e.g. a river), if hybrids have no fitness disadvantage. The fact that such interbreeding does not occur although the taxa, by definition, are not separated by any absolute extrinsic barrier, indicates that mixing is prevented by intrinsic isolating mechanisms. Parapatric taxa are probably always in secondary contact (i.e. they diverged in allopatry), but have not evolved sufficient ecological differences to be able to co-occur sympatrically.

3. Hybrid zones. Otherwise diagnosable taxa that hybridize as a result of secondary contact will be ranked as species if:

3.1 they have only recently come into contact either naturally (through range expansion) or artificially (through human habitat alteration or introduction) and the level of their overall divergence suggests that they will remain distinct (e.g. the introduced Ruddy Duck *Oxyura jamaicensis* and the endemic White-headed Duck *O. leucocephala* in the Iberian peninsula). Upon first contact, isolating mechanisms are often incomplete resulting in some hybridization. If hybrids have a fitness disadvantage, incomplete reproductive isolating mechanisms will be reinforced by selection, and hybridization will become progressively less common (Butlin 1989). A well-documented example is the first contact in the 1930s and 1940s of Herring Gull *Larus argentatus* and Lesser Black-backed Gull *Larus fuscus* along the southern North Sea coast (Haffer 1982).

Otherwise diagnosable taxa will be termed semi-species if:

3.2 a stable, distinct hybrid zone joins them. We regard a hybrid zone as distinct if historically it has changed little in breadth (although it may have moved in position) and if local populations contain one or both pure phenotypes (phenotypically indistinguishable from birds in the respective allopatric areas) plus first-generation and back-cross hybrids. Such cases always indicate a substantial restriction of gene flow, e.g. Carrion Crow *Corvus corone* and Hooded Crow *C. cornix* (reviewed by Parkin *et al.* in prep.).

Note that a hybrid zone may show a mosaic pattern with isolated populations of one species far within the range of the other, as in the case of Pied Flycatcher *Ficedula hypoleuca* and Collared Flycatcher *F. albicollis* (Saetre *et al.* 1999). Such a

pattern cannot be interpreted as true sympatry and, as long as substantial hybridization occurs (as in the flycatchers), the taxa may be regarded as semispecies.

Populations at opposite ends of a cline, even if they are fully diagnosable, should not be ranked as separate species, as gene flow is limited only through isolation by distance, not as a result of an intrinsic barrier. Diagnosable populations joined by a cline may be treated as subspecies (see guidelines proposed by Patten & Unitt 2002).

4. Allopatry. As far as we are aware, species occurring sympatrically almost invariably differ in multiple characters, often involving structure, plumage and/or vocalizations. This is because sympatric occurrence is only possible when two requirements are fulfilled:

- a certain degree of ecological segregation, which in turn correlates with phenotypic differences (e.g. bill structure), and
- reproductive isolation, without which such differentiation could not be maintained (gene flow would eliminate any differences).

In sympatry therefore it is usually fairly easy to establish the diagnosability of taxa, and diagnosability in sympatry always indicates significant reproductive isolation. From this, we can infer that allopatric taxa differing consistently in several independent characters would most likely remain distinct if they ever came in contact. This is particularly so where the differences refer to separate functional contexts (such as structure, plumage colour, vocalizations), and where characters reflect differing ecologies or are associated with mate-recognition.

In Europe, the most similar sympatric species pairs include examples such as Crested Lark *Galerida cristata* and Thekla Lark *G. theklae*, Marsh Tit *Parus palustris* and Willow Tit *P. montanus*, Eurasian Treecreeper *Certhia familiaris* and Short-toed Treecreeper *C. brachydactyla*, all of which differ in multiple, independent characters. Taxa meeting in a hybrid zone, on the other hand, are often phenotypically less well differentiated and sometimes differ in only a single character, even if there is a considerable barrier to gene flow between them (e.g. partially grey vs. all black plumage in Carrion and Hooded Crows, which form distinct and stable hybrid zones in several areas). The very reason why their ranges do not overlap may be because of limited ecological differentiation, which is reflected in poor character divergence. Reproductive incompatibility may arise before sufficient ecological and phenotypic differen-

tiation has evolved to allow coexistence in sympatry. Predictions about possible reproductive isolation between allopatric taxa that differ only slightly (e.g. in size or darkness of plumage) are very uncertain. Such taxa are best treated as subspecies.

With these considerations in mind, allopatric taxa will be assigned species rank if:

4.1 they are fully diagnosable in each of *several* discrete or continuously varying characters related to different functional contexts, e.g. structural features (often related to foraging strategy), plumage colours, vocalizations (both often related to mate recognition) or DNA sequences, and the sum of the character differences corresponds to or exceeds the level of divergence seen in related species that coexist in sympatry.

To assess these criteria, a comparative analysis of related species is necessary and evidence pertaining to potential incompatibilities of mate recognition systems (e.g. lack of response to song playback) may be particularly relevant. Characters known to evolve quickly in response to latitude, climate or migration behaviour must be regarded as less informative, e.g. differences in body size or proportions (such as wing length and shape), timing and number of broods per season, clutch size and moult patterns. Such characters frequently differ among populations and are thus less relevant taxonomically.

Allopatric taxa will be termed allospecies if they do not fulfil criterion 4.1, but:

4.2 at least one character is fully diagnostic and the level of divergence is equivalent to that of the most closely related sympatric species, or

4.3 they are statistically diagnosable by a combination of two or three characters. The characters may be either discrete (e.g. presence or absence of a wing bar) or vary continuously, but they must be functionally independent. Covarying measures related to overall body size would not count as independent characters, but size and colour characters would.

Characters may also be molecular sequences (e.g. of mtDNA), but a single fixed nucleotide difference would not be sufficient to justify allospecies rank: the degree of divergence must be taken into consideration through a comparative analysis.

These taxa have been referred to as allospecies (e.g. Amadon 1966, Short 1969) to indicate that, although they are unambiguously phenotypically divergent, their level of divergence is towards the lower end of the spectrum of differences generally seen between sympatric (reproductively isolated) species. It therefore appears likely that some degree of reproductive incompatibility has already evolved,

but it cannot be predicted with confidence that the taxa represent truly independent evolutionary lineages.

DISCUSSION

These guidelines satisfy all species concepts for sympatric taxa. In the case of parapatric taxa forming a hybrid zone, every species concept faces difficulties. For allopatric taxa, our criteria are more stringent than those applied by proponents of the PSC (e.g. Sangster *et al.* 1999), because we require levels of divergence (whether in single or multiple character differences) comparable with those between sympatric species. Thus, diagnosability is necessary, but not sufficient on its own, for the assignment of species rank. Our criteria are less stringent than those traditionally applied by most proponents of the BSC, because we place more weight on reproductive incompatibility than on full reproductive isolation.

A similar attempt to establish criteria for the determination of species limits has been undertaken by Isler *et al.* (1999). Their study is largely based upon morphology and vocalizations, and is directed towards antbirds of the *Myrmotherula surinamensis* complex – a group of suboscine passerines. Like us, they recognize that situations of sympatry, parapatry and allopatry require different criteria: reproductive isolation for sympatric taxa, diagnosability with no clinal connectivity for parapatric taxa, multicharacter diagnosability for allopatric taxa. These are akin to our criteria 1.1, 3.2 and 4.1, respectively. We have proposed additional criteria since we are dealing with a greater variety of species and circumstances. We have proposed criteria that are applicable to the problems of introductions, and we take account of molecular and biochemical data in our characters for diagnosability. Isler *et al.* (1999) include behavioural data in the list of characters of 'potential taxonomic value', but are more wary about using ecology and habitat preferences because of their limited documentation. Nevertheless, there is an encouraging degree of overlap between their 'criteria' and our 'guidelines'. The main area in which we differ is that Isler *et al.* (1999) treat taxa meeting at a narrow, stable cline as conspecific. We regard such taxa as semispecies, since the stability and steepness of a zone like this would indicate a restriction of gene flow.

The role of molecular data in delimiting and ranking taxa deserves some discussion. Molecular characters (e.g. nucleotide sequences) can be used for taxon diagnosis. Note, however, that taxa need not be represented by mutually monophyletic

lineages in a gene tree to be either diagnosable or to be ranked as species (Doyle 1995). A species may well be represented by a paraphyletic group of alleles or haplotypes in a gene tree. This merely indicates incomplete lineage sorting, but does not make it a 'paraphyletic species'. If, on the other hand, two taxa in geographical contact are represented by mutually monophyletic lineages in a gene tree (e.g. tree of mitochondrial haplotypes), this is a strong indication that they are reproductively isolated and should therefore be ranked as species (Helbig 2000). Molecular divergence is not a character (a particular sequence is), but sequence divergence estimates can be used as an objective measure of overall divergence in comparative analyses. Molecular divergence, although not linearly correlated with phenotypic divergence, is proportional to the time that has elapsed since two taxa diverged from a common ancestor and thus gives a rough indication of how likely it is that reproductive incompatibilities have evolved between two taxa.

The distinction between species and allo-/semi-species reflects two stages of evolutionary divergence that are relatively easy to recognize in cases of sympatry and hybrid zones, respectively. Some researchers designate these by using binomials for species, and trinomials for semispecies and allospecies. Following Amadon (1966) and Short (1969), allo- and semi-species are members of a superspecies, and the superspecies [middle] name is given in square brackets. For example, the Common Chiffchaff *Phylloscopus [collybita] collybita* (in short *Phylloscopus [c.] collybita*) is a member of the superspecies *Phylloscopus [collybita]*, which includes (among others) the Iberian Chiffchaff *P. [c.] brehmii* (semispecies with respect to *collybita*) and the Canary Island Chiffchaff *P. [c.] canariensis* (allospecies with respect to the other two).

The taxonomic category of superspecies has been used by Sibley and Monroe (1990) and others, and is conceptually helpful. A superspecies is the smallest monophyletic group of allo- and semi-species that can safely be assumed not ever to merge with any other such group. It thus satisfies the requirement (explicitly formulated in the ESC) that taxa which are on truly independent evolutionary trajectories (species and superspecies) should be distinguished from those for which this cannot be assumed with a high degree of confidence (allospecies or semispecies). The monophyly of a superspecies is, of course, a phylogenetic hypothesis, which should be based on phylogenetic analysis (as should be the allocation to any higher taxon such as genus or family).

RECOMMENDATION

Authors preparing taxonomic lists, and committees responsible for producing checklists or bird reports, should decide for themselves whether they wish to use a trinomial system (with square brackets) to indicate superspecies. We consider it legitimate to list bird species using either a binomial or a trinomial system, depending on how much phylogenetic information the authors wish to encode. As well as including superspecies, information content would be further increased by indicating families or other higher-level groups. Where trinomials are not deemed necessary, taxa may be designated unambiguously using binomial nomenclature. On behalf of the British Ornithologists' Union Taxonomic Sub-committee, we recommend listing all species binomially in the British List.

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REFERENCES

- Amadon, D.** 1966. The superspecies concept. *Syst. Zool.* **15**: 245–249.
- Barton, N.H. & Gale, K.S.** 1993. Genetic analysis of hybrid zones. In Harrison, R.G. (ed.) *Hybrid Zones and the Evolutionary Process*: 13–45. New York: Oxford University Press.
- British Ornithologists' Union (BOU).** 1992. *Checklist of Birds of Britain and Ireland*, 6th edn. Tring: British Ornithologists' Union.
- Butlin, R.K.** 1989. Reinforcement of pre-mating isolation. In Otte, D. & Endler, J.A. (eds) *Speciation and its Consequences*: 158–179. Sunderland, MA: Sinauer.
- Cracraft, J.** 1983. Species concepts and speciation analysis. *Current Ornithol.* **1**: 159–187.
- Doyle, J.J.** 1995. The irrelevance of allele tree topologies for species delimitation, and a non-topological alternative. *Syst. Bot.* **20**: 574–588.
- Evans, M.E. & Sladen, W.J.L.** 1980. A comparative study of the bill markings of Whistling and Bewick's Swans and out-of-range occurrences of the two taxa. *Auk* **97**: 697–703.
- Grant, P.R. & Grant, B.R.** 1996. Speciation and hybridization in island birds. *Phil. Trans. Royal Soc. London B* **351**: 765–772.
- Haffer, J.** 1982. Systematik und Taxonomie der *Larus argentatus* – Artengruppe. In Glutz Von Blotzheim, U.N. & Bauer, K.M. (eds) *Handbuch der Vögel Mitteleuropas, Bd 8*: 502–515. Wiesbaden: Akad.-Verlagsges.
- Haffer, J.** 1998. Species concepts and species limits in ornithology. In Del Hoyo, J., Elliott, A. & Sargatal, J. (eds) *Handbook of the Birds of the World*, **4**: 11–24. Barcelona: Lynx Edicions.
- Helbig, A.J.** 2000. What is a bird 'species'? A contribution to the debate about species concepts in ornithology. *Limicola* **14**: 243–246.
- Isler, M.L., Isler, P.R. & Whitney, B.M.** 1999. Species limits in antbirds (Passeriformes: Thamnophilidae): the *Myrmotherula surinamensis* complex. *Auk* **116**: 83–96.
- Johnson, N.K., Remsen, J.V. & Cicero, C.** 1999. Resolution of the debate over species concepts in ornithology: a new comprehensive biologic species concept. In Adams, N.J. & Slotow, R.H. (eds) *Proceedings of the International Ornithol. Congr., Durban*: 1470–1482. Johannesburg: Birdlife South Africa.
- Leafloor, J.O., Ankney, C.D. & Rusch, D.H.** 1998. Environmental effects on body size of Canada Geese. *Auk* **115**: 26–33.
- Liebers, D. & Helbig, A.J.** 1999. Phänotypische Charakterisierung und systematische Stellung der Armenienmöwe *Larus armenicus*. *Limicola* **13**: 281–321.
- Mayden, R.L.** 1997. A hierarchy of species concepts: the denouement in the saga of the species problem. In Claridge, M.F., Dawah, H.A. & Wilson, M.R. (eds) *Species: the Units of Biodiversity*: 381–424. London: Chapman & Hall.
- Paterson, H.E.H.** 1985. The recognition concept of species. In Vrba, E.S. (ed.) *Species and Speciation. Transvaal Museum Monograph no. 4*: 21–29. Pretoria: Transvaal Museum.
- Patten, M.A. & Unitt, P.** 2002. Diagnosability versus mean differences of Sage Sparrow subspecies. *Auk* **119**: 26–35.
- de Queiroz, K.** 1998. The general lineage concept of species, species criteria, and the process of speciation. A conceptual unification and terminological recommendations. In Howard, D.J. & Berlocher, S.H. (eds) *Endless Forms: Species and Speciation*: 57–75. Oxford: Oxford University Press.
- de Queiroz, K.** 1999. The general lineage concept of species and the defining properties of the species category. In Wilson, R.A. (ed.) *Species, New Interdisciplinary Essays*: 49–89. Cambridge, MA: MIT Press.
- Rolando, A.** 1993. A study on the hybridisation between Carrion and Hooded Crow in northwest Italy. *Ornis Scand.* **24**: 80–83.
- Saetre, G.-P., Kral, M., Bures, S. & Ims, R.A.** 1999. Dynamics of a clinal hybrid zone and a comparison with island hybrid zones of flycatchers (*Ficedula hypoleuca* and *F. albicollis*). *J. Zool., Lond.* **247**: 53–64.
- Sangster, G., Hazevoet, C.J., Berg, A.V.D., Roselaar, C.S. & Sluys, R.** 1999. Dutch Avifaunal List: species concepts, taxonomic instability, and taxonomic changes in 1977–1998. *Ardea* **87**: 139–165.
- Sangster, G., Knox, A.G., Helbig, A.J. & Parkin, D.T.** 2002. Taxonomic recommendations for European birds. *Ibis* **144**: 153–159.
- Scott, D.K.** 1981. Geographical variation in the bill patterns of Bewick's Swans. *Wildfowl* **32**: 123–128.
- Short, L.L.** 1969. Taxonomic aspects of avian hybridization. *Auk* **86**: 84–105.
- Sibley, C.G. & Monroe, B.L.** 1990. *Distribution and Taxonomy of Birds of the World*. New Haven & London: Yale University Press.
- Vaurie, C.** 1959. *The Birds of the Palearctic Fauna*. London: Witherby.
- Wiley, E.O.** 1978. The evolutionary species concept reconsidered. *Syst. Zool.* **27**: 17–26.