

# The application of species criteria in avian taxonomy and its implications for the debate over species concepts

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## ABSTRACT

The debate over species concepts has produced a huge body of literature on how species can, may or should be delimited. By contrast, very few studies have documented how species taxa are delimited in practice. The aims of the present study were to (i) quantify the use of species criteria in taxonomy, (ii) discuss its implications for the debate over species concepts and (iii) assess recent claims about the impact of different species concepts on taxonomic stability and the ‘nature’ of species. The application of six species criteria was examined in taxonomic studies of birds published between 1950 and 2009. Three types of taxonomic studies were included: descriptions of new species ( $N = 329$ ), proposals to change the taxonomic rank of species and subspecies ( $N = 808$ ) and the taxonomic recommendations of the American Ornithologists’ Union Committee on Classification and Nomenclature ( $N = 176$ ). In all three datasets, diagnosability was the most frequently applied criterion, followed by reproductive isolation and degree of difference. This result is inconsistent with the popular notion that the Biological Species Concept is the dominant species concept in avian taxonomy. Since the 1950s, avian species-level taxonomy has become increasingly pluralistic and eclectic. This suggests that taxonomists consider different criteria as complementary rather than as rival approaches to species delimitation. Application of diagnosability more frequently led to the elevation of subspecies to species rank than application of reproductive isolation, although the difference was small. Hypotheses based on diagnosability and reproductive isolation were equally likely to be accepted in a mainstream checklist. These findings contradict recent claims that application of the Phylogenetic Species Concept causes instability and that broader application of the Biological Species Concept can stabilise taxonomy. The criteria diagnosability and monophyly, which are commonly associated with Phylogenetic Species Concepts, were used throughout the study period. Finally, no support was found for the idea that Phylogenetic Species Concepts have caused a change in the ‘nature’ of species taxa. This study demonstrates that there is a discrepancy between widely held perceptions of how species are delimited and the way species are actually delimited by taxonomists. Theoretically oriented debates over species concepts thus may benefit from empirical data on taxonomic practice.

*Key words:* biological species concept, birds, integrative taxonomy, Phylogenetic species concept, species limits, taxonomic stability.

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## I. INTRODUCTION

The species problem is a persistent controversial issue that continues to engage taxonomists, evolutionary biologists and philosophers (e.g. Ereshefsky, 1992; Claridge, Dawah & Wilson, 1997; Wilson, 1999; Wheeler & Meier, 2000; Hey, 2001; Stamos, 2003). In taxonomy and in the fields of biogeography, biodiversity assessment and conservation biology, the species problem is primarily an operational problem: how can, may or should species be delimited? Even about this subset of the species problem a large body of literature has accumulated over the last three decades (reviewed by Mayden, 1997; Sites & Marshall, 2003, 2004). By contrast, very few studies have documented how species taxa are delimited in practice (Luckow, 1995; McDade, 1995; Watson, 2005; Sangster, 2009). The paucity of empirical data on species delimitation in taxonomy is unfortunate because studies of taxonomic practice may usefully inform and perhaps direct more theoretically oriented work (McDade, 1995).

The Biological Species Concept is believed to be the most widely used species concept in biology, and ornithology in particular (Gill, 1990; Arnold, 1997; Haffer, 1997; Templeton, 1998; Johnson, Remsen & Cicero, 1999; Schodde & Mason, 1999; Cowlshaw & Dunbar, 2000; Mayr, 2000; White & Kiff, 2000; Cohan, 2002; Newton, 2003; Groves, 2004; Podulka, Rohrbaugh & Bonney, 2004; Winker *et al.*, 2007). The alleged dominance of the Biological Species Concept in taxonomy is an important element in the debate over species concepts. For instance, many biologists have presented the Biological Species Concept as the 'current' species concept in taxonomy and the Phylogenetic Species Concept as a 'contender' (e.g. Mayr, 1992; Avise, 1994; Snow, 1997; Schodde & Mason, 1999; Newton, 2003; Winker *et al.*, 2007). Some authors have used the dominance

of the Biological Species Concept as an argument against the introduction and broad application of the Phylogenetic Species Concept (Short, 1993; Haffer, 1997; Mayr, 2000; Winker *et al.*, 2007). The idea that avian taxonomy is dominated by the Biological Species Concept also has affected taxonomic practice. For instance, Atwood (1988) refrained from naming two diagnosable bird populations as species because he believed that this would represent a breach with current taxonomic practice. Short (1993) went even further and proposed to denote taxa recognised by the Phylogenetic Species Concept by a term other than species. Haffer (1997), Eck (2001) and Agapow (2005) subsequently used the term 'phylopecies' for such entities.

Recently, it was suggested that application of alternative species concepts such as the Phylogenetic Species Concept would change the 'nature' of species (Mace, Gittleman & Purvis, 2003) and would produce a 'flood' of new species (Agapow, 2005) which in turn would lead to 'taxonomic inflation' (Isaac, Mallet & Mace, 2004) and 'chaos' (Short, 1993; Schodde & Mason, 1999). Conversely, it has been suggested that continued application of the Biological Species Concept would enhance stability (Agapow *et al.*, 2004; Mace, 2004; Winker *et al.*, 2007). These are empirical claims that must be addressed by analyzing how species are, and have been, delimited by taxonomists.

Despite its broad acceptance and prominent place in the debate over species concepts, the dominance of the Biological Species Concept in taxonomy has not been critically examined. In fact, only three studies have attempted to quantify the use of species concepts in taxonomy. McDade (1995) sampled 104 botanical monographs published in 3 journals between 1984 and 1993 to determine whether botanists are involved in the debate over species concepts and to identify the problems encountered by botanists in delimiting species. McDade (1995) limited her assessment

to the species concept or species criteria identified by the authors of the monographs but did not attempt to deduce this information herself when the authors did not explicitly state their methods. She found that most monographers did not discuss their concepts and criteria and that of those who did, most used a 'taxonomic' or 'morphological' species concept. McDade (1995) could not verify the relative importance of the Biological Species Concept.

Luckow (1995) examined how species concepts were being applied in practice. She surveyed a sample of 114 botanical studies published in *Systematic Botany* and 16 studies in *Systematic Zoology/Biology* during a 5-year period (1989–1993). Luckow (1995) assigned each taxonomic paper to a species concept and scored which data were studied. 'Phylogenetic', 'Quantitative' and 'Phenetic' species concepts dominated the botanical literature whereas 'Biological' and 'Monophyletic' species concepts were most common in the papers in *Systematic Zoology/Biology*. These journals focus on methodological issues and are probably not representative of the taxonomic literature. This problem and the small sample of zoological studies cast doubt on the generality of Luckow's (1995) results.

Finally, in a study aimed at testing key predictions of the 'taxonomic inflation' hypothesis (Isaac *et al.*, 2004), Sangster (2009) quantified the use of species criteria in birds from 1950 to 2007 and showed that increasing numbers of bird species are not primarily caused by epistemological changes but are driven by new empirical data. This study rejected the claims made by Isaac *et al.* (2004) but did not address any other controversial claims about the dominance or impact of species concepts.

To assess how species taxa are delimited in practice, it is necessary to recognise the difference between species concepts and species criteria (de Queiroz, 1999). Until recently, there has been a tendency to confuse species concepts (ideas on what species are) and species criteria (ideas on how species should be delimited in practice). The species concept defines species according to some biological universal, whereas species criteria provide the rules by which to judge if (groups of) populations are distinct species (Paul, 2002).

At least 21 'concepts' of species have been proposed and supported by biologists and philosophers (Mayden, 1997) but all these 'concepts' agree that species are lineages or, more precisely, segments of population lineages (Mayden, 1997; de Queiroz, 1999). Both Mayden (1997) and de Queiroz (1999) concluded that there is therefore a single 'primary' or 'general' concept of species, which they called the 'Evolutionary Species Concept' (Mayden, 1997) or the 'General Lineage Concept' (de Queiroz, 1999). They argued that the various species concepts that have been proposed by different authors merely highlight different properties of species rather than fundamentally different natural taxa. de Queiroz (1999) further argued that, apart from forming lineages, no single property should be regarded as defining for the recognition of species taxa. This view of species-as-lineages was built on previous insights (Simpson, 1951; Hennig, 1966; Wiley, 1978; Wilson, 1995) and has several important implications. For instance, it emphasizes the unity of various

'rival' approaches to species delimitation by underscoring the fact that they all identify population lineages. At the same time, it recognises that taxonomy is necessarily pluralistic because species have different properties, and all properties are potentially informative for various research questions.

The aims of the present study were to (i) quantify the use of various species criteria in a broad range of taxonomic studies, (ii) discuss its implications for the debate over species concepts and (iii) assess recent claims about the impact of different species concepts on taxonomic stability (Agapow *et al.*, 2004) and the 'nature' of species (Mace *et al.*, 2003). To this end, the following predictions and hypotheses are tested.

First, if the Biological Species Concept is the most widely used species concept in avian taxonomy one would expect that reproductive isolation is, and has long been, the most widely used criterion for the ranking of species and subspecies.

Second, if Mayden's (1997) and de Queiroz's (1999) interpretation of the species problem is correct then one would expect that (i) various criteria are used to identify species in practice (i.e. species-level taxonomy is pluralistic); (ii) criteria are used in various combinations (i.e. species-level taxonomy is eclectic); (iii) taxonomists consider different criteria as complementary rather than as 'rival' approaches to species delimitation; and (iv) none of the taxonomic criteria is considered as defining (necessary and sufficient) by all taxonomists.

Third, if there has been a change in the 'nature' of species due to the introduction of the Phylogenetic Species Concept in the 1980s (Mace *et al.*, 2003), one would expect that application of diagnosability was rare before its introduction and has increased after its introduction.

Finally, to test whether the Biological Species Concept is better at promoting stability than the Phylogenetic Species Concept (as claimed by Collar, 1997; Agapow *et al.*, 2004; Isaac *et al.*, 2004; Winker *et al.*, 2007), I examine whether application of reproductive isolation results less often in the recognition of additional species than does diagnosability. I also examine whether species proposed on the basis of reproductive isolation are more likely to be maintained in a subsequent mainstream taxonomic reference work than species proposed on the basis of diagnosability.

The present study uses the taxonomy of extant birds to address these issues. Birds are particularly suitable subjects for this study for two reasons. First, the taxonomy of no other group of animals is believed to be as mature as that of birds (Mayr, 1982; Price, 1996). Second, it is believed that application of the Biological Species Concept has been particularly common in birds, more so than in any other major group of animals (Mayr, 1980; Endler, 1989; Schodde & Mason, 1999). I use extant birds because key elements of reproductive isolation, such as assortative mating and hybrid fitness, are difficult to study in extinct species. These aspects imply that the use of extant birds is conservative with regard to the principal hypothesis (i.e. that the Biological Species Concept is the most widely used species concept in ornithology).

The use of species criteria is assessed in three types of taxonomic publications: (i) new species descriptions, which

provide information on how species are discovered and how these enter the taxonomic literature; (ii) taxonomic proposals in leading ornithological journals, which provide information on how a change in taxonomic rank is proposed and argued; and (iii) taxonomic recommendations of the American Ornithologists' Union (AOU), which indicate how a taxonomic proposal becomes widely adopted. The AOU has stated that it uses the Biological Species Concept to rank species (AOU, 1983). The taxonomic reports of the AOU have been used in previous studies of taxonomic and nomenclatural changes (Rising & Schueler, 1972; Olson, 1987).

## II. MATERIALS AND METHODS

### (1) Data sources

#### (a) Newly described bird species

This dataset consists of extant bird taxa that were originally described as species taxa in the period 1950–2009. Type descriptions published between 1950 and 1990 were identified using inventories of Mayr (1957, 1971), Mayr & Vuilleumier (1983), Vuilleumier & Mayr (1987), Vuilleumier, LeCroy & Mayr (1992) and Bahr (1995). Type descriptions published from 1991 up to and including 2009 were located in the zoological literature and using *Zoological Record* (BIOSIS), *Web of Science* (Thomson Scientific) and *Recent Ornithological Literature*. Descriptions of species likely or known to be extinct at the time of publication and introductions of new names for previously described species were excluded.

#### (b) Taxonomic proposals

This dataset is an expanded version of that of Sangster (2009) and consists of taxonomic papers published in the period 1950–2009 which contain (i) a proposal to change the taxonomic rank of at least one taxon from subspecies to species, (ii) a change of rank from species to subspecies, or (iii) a proposal to remove a subspecies taxon from one species and re-allocate it to another species. Taxonomic proposals were located in seven major ornithological journals: *The Auk* (published USA; coverage worldwide but with focus on New World), *Bulletin of the British Ornithologists' Club* (published Great Britain; coverage worldwide), *The Condor* (published USA; coverage worldwide but with focus on New World), *Emu* (published Australia; coverage Southern Hemisphere), *Ibis* (published Great Britain; coverage worldwide, but with focus on Old World), *Ostrich* (published South Africa; coverage Afrotropics) and *The Wilson Bulletin* (renamed *The Wilson Journal of Ornithology* in 2006) (published USA; coverage worldwide but with focus on New World). These journals were selected because each regularly publishes taxonomic papers, has a wide geographic coverage, serves a broad community of ornithologists and has a complete run in the study period.

#### (c) Recommendations of the American Ornithologists' Union Committee on Classification and Nomenclature

This dataset consists of taxonomic recommendations about species-level taxa published by the AOU Committee on Classification and Nomenclature in *The Auk* in the period 1950–2009. Recommendations were of three types: (i) a change of rank from subspecies to species, (ii) a change of rank from species to subspecies, and (iii) the removal of a subspecies taxon from one species and its transfer to another species. These taxonomic reports were published yearly in the period 1950–1956, in 1973, 1976, 1982, biannually from 1985 to 1997, in 1998, 2000, and again annually from 2002 to 2009, making a total of 27 reports during the study period. Until 1983, reports only covered North American taxa. Since 1983, coverage also included Central America and the Caribbean region. Taxonomic recommendations involving newly described species taxa were excluded.

### (2) Data recorded

For each taxonomic hypothesis, the following data were recorded:

#### (a) The type of proposal or recommendation

It was recorded whether the taxonomic proposal or AOU recommendation referred to (i) a change from subspecies to species (a 'split'), (ii) a change from species to subspecies (a 'lump'), or (iii) a re-allocation of a subspecies taxon from one species to another (a 'transfer').

#### (b) The presentation of a rationale

It was examined whether a rationale was presented for the taxonomic rank of the focal taxon proposed or adopted by the author(s) (i.e. why the focal taxon is treated as a species, rather than as a subspecies). A description of differences between the focal taxon and other taxa was not considered a 'rationale' unless the author(s) stated that it was used to support the rank of the focal taxon. Because AOU recommendations typically involve reviews of previous studies, the rationale in the papers that were cited by the AOU were treated as that of the AOU.

#### (c) Taxonomic criteria

If a rationale for the taxonomic rank of the focal taxon was given by the authors, the rationale was categorized as one or more of six categories of ranking criteria: diagnosability, degree of difference, monophyly, exclusive coalescence, adaptive zone and reproductive isolation (Table 1). These six ranking criteria were selected because these criteria feature prominently in discussions over species concepts (e.g. Mayden, 1997; de Queiroz, 1998) and each represents the primary criterion of one or more species concepts (Table 2).

The ranking criterion was determined based on the criteria that were actually used by the authors even if they stated that their case is based on a different criterion or species concept.

Table 1. Criteria for species recognition (adapted from de Queiroz, 1998)

Ranking criterion	Supporting case for treatment as species
Distinguishability	
1. Diagnosability	The taxon possesses a unique, fixed character state or a unique (combination of) character state(s)
2. Degree of difference	The taxa differ too much to be treated as subspecies
Phylogeny	
3. Monophyly	The taxa should be separated to prevent recognition of a paraphyletic species taxon
4. Exclusive coalescence of gene trees	Gene trees of the taxa are reciprocally monophyletic (phylogroups)
Cohesion	
5. Adaptive zone	The taxa occupy different niches
6. Reproductive isolation	
6a. Actual interbreeding/fusing	The taxa are not in contact during the breeding season (extrinsic isolation)
	The taxa are in contact during the breeding season but do not interbreed/fuse (intrinsic isolation)
Recognition (prezygotic isolation)	The taxa do not form mixed pairs (or produce fertilized eggs)
Viability or fertility (postzygotic isolation)	Hybrids are less viable or fertile than individuals of the parental taxa
6b. Potential interbreeding/fusing	The taxa are not believed to interbreed/fuse if they come into contact
Recognition (prezygotic isolation)	The taxa are not believed to form mixed pairs if they come into contact
Viability or fertility (postzygotic isolation)	The taxa are believed to form hybrids that are less viable or fertile than individuals of the parental taxa if they come into contact

Table 2. Selected species concepts and criteria

Species concept (synonyms)	Author/proponent	Criterion
Biological species concept (isolation concept)	Mayr (1942, 1963, 1969) and Coyne & Orr (2004)	Reproductive isolation
Recognition species concept	Paterson (1985) and Masters & Spencer (1989)	Difference in mate recognition systems
Phylogenetic species concept (diagnosable species concept)	Cracraft (1983, 1987), Nixon & Wheeler (1990), Davis & Nixon (1992) and Doyle (1995)	Diagnosability
Phylogenetic species concept (monophyletic species concept)	Donoghue (1985) and de Queiroz & Donoghue (1988)	Monophyly
Genealogical species concept	Baum & Donoghue (1995) and Baum & Shaw (1995)	Exclusive coalescence (of gene trees)
Ecological species concept	Van Valen (1976)	Adaptive zone
Genetic species concept	Bradley & Baker (2001)	Genetic similarity (degree of difference)
Genetic cluster species concept	Mallet (1995)	Phenetic or genetic similarity

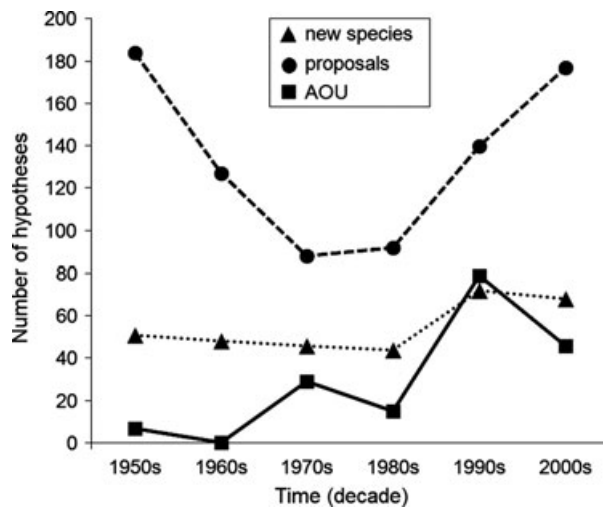
For instance, if an author stated that he used the Biological Species Concept but his case was based on diagnostic differences only (without a case for reproductive isolation), the taxonomic criterion was scored as ‘diagnosability’. Examples of rationales are given in Table 1.

A full description of the six criteria is given in Sangster (2009). Hypotheses based on ‘intergradation’ were sometimes difficult to classify because taxonomists use this term for two phenomena: (i) the gradual (clinal) change of a character from one taxon to another; (ii) the interbreeding of two distinct taxa resulting in individuals with mixed characters. Therefore, taxonomic hypotheses that are based on ‘intergradation’ (or lack thereof) may refer to different taxonomic criteria (diagnosability and reproductive isolation, respectively). In cases where the relevant taxa were allopatric, and no actual interbreeding could be observed, the taxonomic criterion was scored as ‘diagnosability’. In cases where

‘intergradation’ was used to support a case involving sympatric or parapatric taxa, the taxonomic criterion was scored as ‘reproductive isolation’, unless there were clear indications that ‘diagnosability’ was actually intended.

#### (d) *The comparison species/subspecies*

It was recorded to which species (or subspecies) the focal species (or subspecies) was compared. In descriptions of new species, the species to which the focal species was compared by the original authors was regarded as the comparison species. If the comparison species was not explicitly mentioned, the most closely related species was selected as the comparison species. In proposals and AOU recommendations, the comparison species is the taxon with which the focal species (subspecies) was or becomes lumped in the new arrangement.



**Fig. 1.** Changes in taxonomic activity of three types of taxonomic hypotheses during the study period (1950–2009).

(e) *The geographic position of the taxa in question*

To assess whether geographic contact influences the use of ranking criteria it was recorded for each taxonomic hypothesis whether the breeding distribution of the relevant taxa is allopatric, parapatric or sympatric. The geographic position of the taxa was determined primarily from information provided in the pertinent publications. If such information was lacking, the geographic position was determined from various sources, including handbooks, monographs and breeding atlases.

Definitions of parapatry vary (Haffer, 1989, 1992; Amadon & Short, 1992). In the present study, the term is applied to situations where the breeding ranges of two taxa do not overlap widely but are marginally in contact so that interbreeding between members of the two taxa is possible. The term is applied irrespective of whether interbreeding actually occurs and thus refers to situations ranging from marginal overlap without interbreeding to a hybrid zone.

(f) *The current status of the focal taxon*

For each newly described species and taxonomic proposal published between 1950 up to and including 1999, the current taxonomic status was determined using Dickinson (2003). The current status of new species and taxonomic

proposals was classified in one of four categories: (i) the taxon is invalid (i.e. not recognised at any rank), (ii) the taxon is recognised as a subspecies, (iii) the taxon is recognised as a species, (iv) the taxon is re-allocated and treated as a subspecies of another species. If a newly described taxon represented a valid *overlooked* species but the new name represented a synonym of a previously published name, it was treated as a valid species.

### (3) Statistical analysis

To test statistically whether there was any relation between two or more categorical variables (with two levels), I used  $\chi^2$  tests with Yates' correction and type I error rate set at 5%. When expected cell frequency in at least one the cells was less than 5, Fisher's exact test was used.

The three datasets were combined for analyses of temporal variation in the application of species criteria, and for comparisons among geographic settings. In cases where a study included in the taxonomic proposals dataset was critical to an AOU recommendation (i.e. the study provided information on species properties that was not provided by any other study cited by the AOU), the proposal was omitted from the proposals dataset. In total, 54 taxonomic proposals were omitted from the combined dataset.

## III. RESULTS

In total, 1313 taxonomic hypotheses were included in the analysis: 329 newly described species (25.1%), 808 proposals to change the taxonomic rank of species and subspecies (61.5%), and 176 recommendations of the AOU (13.4%). Four taxonomic hypotheses were excluded from some analyses because pertinent publications were either unavailable or inaccessible. These refer to two descriptions of new species in Russian and Vietnamese and two AOU recommendations that were partly based on publications in Russian.

The dynamics in taxonomic activity differed among the three datasets, with the lowest activity of the AOU in the 1960s, of proposals in the 1970s, and of new species descriptions in the 1980s (Fig. 1). All datasets, however, showed a marked increase in activity in the 1990s.

Of all newly described species in the study period, only 50.8% included a rationale (Table 3). This proportion

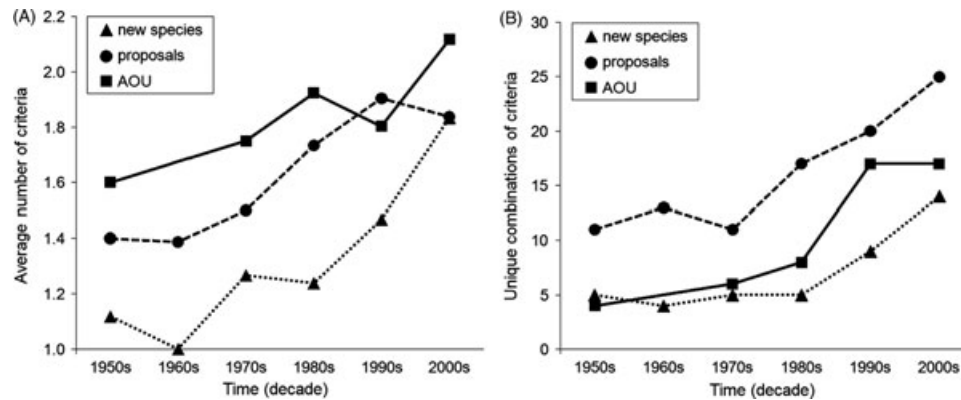
**Table 3.** Proportion of taxonomic hypotheses with an explicit rationale for ranking taxa as subspecies or species

Period	New species ( <i>N</i> = 327)	Proposals ( <i>N</i> = 808)	AOU recommendations ( <i>N</i> = 174)	Total ( <i>N</i> = 1309)
1950s (%)	33.3	62.5	71.4	56.6
1960s	50.0%	83.5%	—	74.3%
1970s (%)	34.1	95.5	55.2	71.4
1980s (%)	47.7	97.8	100.0	83.2
1990s (%)	65.3	96.4	96.2	88.7
2000s (%)	61.8	95.5	93.5	87.3
1950–2000s (%)	50.8	86.5	87.9	77.8

Table 4. The number of criteria used in support of taxonomic hypotheses (1950–2009)

Dataset	<i>N</i>	Number of criteria per hypothesis					
		1	2	3	4	5	6
New species	166	117	35	11	2	0	1
Proposals	697	369	221	87	18	2	0
AOU recommendations	153	58	62	26	6	1	0
Total	1016	544	318	124	26	3	1
Proportion (%)	100	53.5	31.3	12.2	2.6	0.3	0.1

Taxonomic hypotheses without a rationale are excluded.

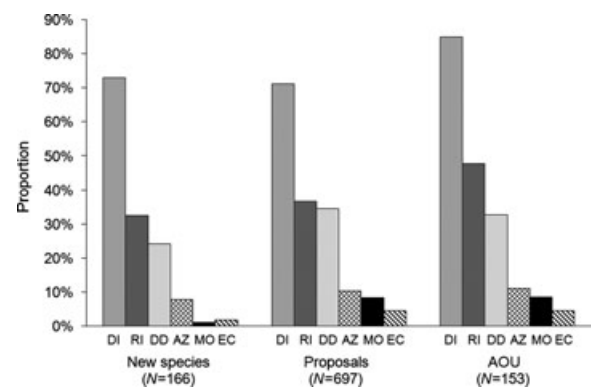


**Fig. 2.** Proliferation of species criteria in avian taxonomy in 1950–2009. (A) Changes in the average number of criteria per taxonomic hypothesis, illustrating the increasingly pluralistic nature of species delimitation; (B) changes in the number of unique combinations of six criteria, illustrating the increasingly eclectic nature of species delimitation.

was significantly higher for proposals (86.5%;  $\chi^2 = 162.1$ , d.f. = 1,  $P < 0.001$ ) and AOU recommendations (87.9%;  $\chi^2 = 66.2$ , d.f. = 1,  $P < 0.001$ ). In all datasets, the proportion of studies with a taxonomic rationale increased during the study period, although there was a slight decrease for all three in the 1990s–2000s. Nevertheless, more than one-third of the newly described bird species in the 1990s and 2000s lacked an explicit taxonomic rationale (Table 3).

Hypotheses that included a rationale were often based a single criterion, although 46.5% of all hypotheses used two or more criteria (Table 4). The average number of species criteria that were used to support newly described species, proposals and AOU recommendations increased during the study period (Fig. 2A), although it dropped slightly for AOU recommendations in the 1990s and for proposals in the 2000s. Proposals and AOU recommendations were supported by more criteria than new species descriptions. The number of unique combinations of criteria increased in all three datasets during the study period (Fig. 2B). Overall, 36 different combinations of criteria were used.

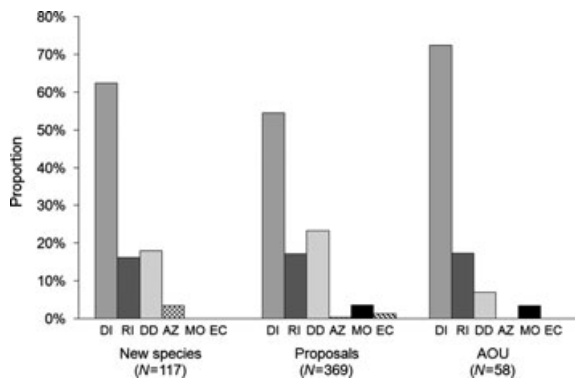
In all three datasets, diagnosability was the most frequently used criterion, followed by reproductive isolation and degree of difference (Fig. 3). In studies employing a single species criterion, diagnosability also was the most frequently used criterion (Fig. 4). In all datasets, the criteria adaptive zone, monophyly and exclusive coalescence played a minor role, and were used in less than 15% of taxonomic



**Fig. 3.** Application of species criteria in taxonomic studies published between 1950 and 2009, expressed as the proportion of studies that used the criteria. DI, diagnosability; RI, reproductive isolation; DD, degree of difference; AZ, adaptive zone; MO, monophyly; EC, exclusive coalescence.

hypotheses (Figs 3 and 4). Overall, 40.2% of hypotheses that included a rationale ( $N = 1016$ ) were based on either diagnosability or reproductive isolation.

In all three datasets, hypotheses supported by the criterion of reproductive isolation more often used actual than potential reproductive isolation, and invoked pre-mating isolating barriers more often than post-mating isolating barriers (Table 5).



**Fig. 4.** Application of species criteria in taxonomic hypotheses between 1950 and 2009 in studies based on a single criterion, expressed as the proportion of studies that used the criteria. DI, diagnosability; RI, reproductive isolation; DD, degree of difference; AZ, adaptive zone; MO, monophyly; EC, exclusive coalescence.

Temporal variation in the use of species criteria is shown in (Fig. 5). During the entire study period, diagnosability was used more often than reproductive isolation. Since the 1950s, the proportion of hypotheses based on diagnosability has fluctuated between 57 and 85%, and showed a strong increase from the 1960s to the 1990s. Use of the criterion of reproductive isolation peaked in the 1970s and subsequently declined. Use of degree of difference decreased from the 1950s to the 1970s but this trend reversed in the 1980s. The mirror-image pattern of reproductive isolation and degree of difference was also found in separate plots of the three datasets (data not shown). By contrast, use of adaptive zone peaked in the 1980s and showed a strong decline thereafter. The criteria monophyly and exclusive coalescence both showed a strong increase since the 1970s and 1980s, respectively.

The application of species criteria differed among geographic settings (Fig. 6). Diagnosability was more often used in allopatric than in parapatric species ( $\chi^2 = 5.5$ , d.f. = 1,  $P < 0.05$ ) but its use did not differ significantly between allopatric and sympatric, or between parapatric and sympatric species. By contrast, reproductive isolation was used much less often in allopatric species than in parapatric species ( $\chi^2 = 156.1$ , d.f. = 1,  $P < 0.001$ ) or sympatry ( $\chi^2 = 109.3$ , d.f. = 1,  $P < 0.001$ ).

In the taxonomic proposals dataset, diagnosability led more often to the separation of species (77%) than reproductive isolation (68%;  $\chi^2 = 8.1$ , d.f. = 1,  $P < 0.005$ ). In the proposals dataset, degree of difference was the criterion that led least often to the separation of species (56%; Table 6). Taxonomic proposals using degree of difference led less often to the separation of species than proposals using reproductive isolation ( $\chi^2 = 7.0$ , d.f. = 1,  $P < 0.01$ ) and diagnosability ( $\chi^2 = 36.0$ , d.f. = 1,  $P < 0.001$ ). AOU recommendations using diagnosability led to the separation of species in 91% of cases, whereas reproductive isolation led to the separation of species in 79%. This difference was significant ( $\chi^2 = 5.0$ , d.f. = 1,  $P < 0.05$ ).

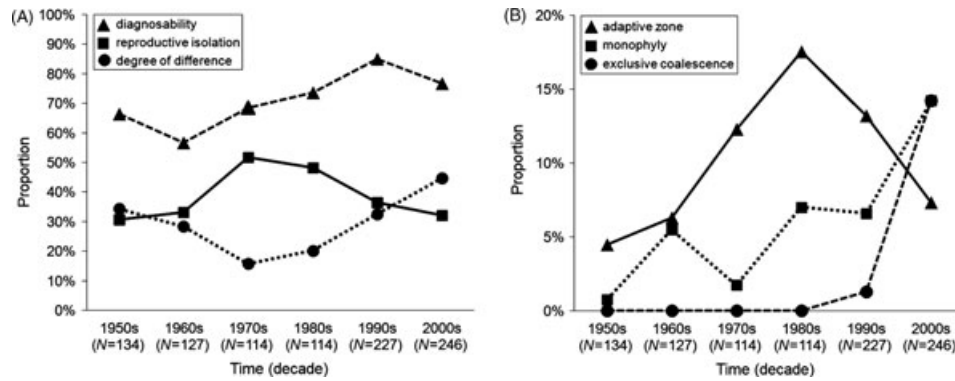
The current status of newly described species and proposals for lumps and splits during the study period is given in Table 7. Test statistics and significance levels are given in Table 8. Of 261 species described in 1950–1999, 192 (74%) were still regarded as valid species by Dickinson (2003). Newly described species of which the rank was supported by a rationale were more often maintained as species than new species that were described without a rationale (83% versus 65%;  $P < 0.005$ ). No difference was found in the continued recognition of new species that were supported by the criteria of reproductive isolation and diagnosability (89% versus 87%). New descriptions where species rank was supported by degree of difference were maintained less often (74%) but this did not differ significantly from descriptions based on reproductive isolation or diagnosability. The sample size for the remaining criteria (adaptive zone, monophyly and exclusive coalescence) was too small for meaningful comparisons.

Splits proposed in 1950–1999 were more often adopted by Dickinson (2003) than proposals for lumps (84% versus 42%;  $P < 0.001$ ;  $N = 614$ ). This was also true for partitions of the dataset into proposals supported by a rationale (splits maintained in 84% of cases, lumps in 51% of cases;  $P < 0.001$ ) and proposals without a rationale (64% versus 19%;  $P < 0.005$ ). Proposals for splits based on reproductive isolation were equally often maintained as those based on diagnosability and degree of difference (85, 85 and 84%, respectively). Proposals for lumps supported by reproductive isolation were equally often maintained as proposals supported by diagnosability (i.e. 57% versus 54%). Proposals for lumps using the degree of difference as a

**Table 5.** Use of actual and potential reproductive isolation, and pre-mating and post-mating isolating barriers, as criteria for ranking bird species in 1950–2009

Criterion	Isolating barriers	New species ( $N = 54$ )	Proposals ( $N = 256$ )	AOU recommendations ( $N = 73$ )
Actual reproductive isolation	Pre-mating	32	162	51
	Post-mating	0	5	0
	Both pre- and post-mating	1	13	5
Potential reproductive isolation	Pre-mating	21	75	16
	Post-mating	0	0	1
	Both pre- and post-mating	0	1	0

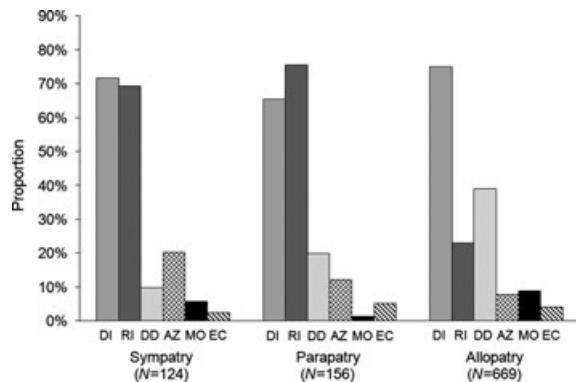




**Fig. 5.** Changes in the use of species criteria in 1950–2009: (A) diagnosability, reproductive isolation, and degree of difference, (B) adaptive zone, monophyly, and exclusive coalescence.

Table 6. Involvement of different species criteria in splits, lumps and transfers (1950–2009)

Criterion	Proposals				AOU recommendations			
	N	Split	Lump	Transfer	N	Split	Lump	Transfer
Reproductive isolation	256	175 (68%)	79 (31%)	2 (1%)	73	58 (79%)	15 (21%)	0 (0%)
Diagnosability	496	381 (77%)	103 (21%)	12 (2%)	130	118 (91%)	11 (8%)	1 (1%)
Degree of difference	240	135 (56%)	102 (43%)	3 (1%)	50	46 (92%)	3 (6%)	1 (2%)
Adaptive zone	72	61 (85%)	11 (15%)	0 (0%)	17	16 (94%)	1 (6%)	0 (0%)
Monophyly	58	49 (84%)	5 (9%)	4 (7%)	13	13 (100%)	0 (0%)	0 (0%)
Exclusive coalescence	32	30 (94%)	2 (6%)	0 (0%)	7	6 (86%)	1 (14%)	0 (0%)



**Fig. 6.** Application of species criteria in different geographic settings. DI, diagnosability; RI, reproductive isolation; DD, degree of difference; AZ, adaptive zone; MO, monophyly; EC, exclusive coalescence.

criterion were significantly less often maintained (35%) than proposals for lumps based on diagnosability ( $P < 0.05$ ) and reproductive isolation ( $P < 0.05$ ).

#### IV. DISCUSSION

##### (1) Is avian taxonomy dominated by the biological species concept?

The results of this study demonstrate that reproductive isolation was not the dominant criterion for species recognition

in avian taxonomy in the 1950s–2000s (Figs 3 and 4). Consequently, this study does not support the view that the Biological Species Concept is the dominant species concept in avian taxonomy. This outcome is robust given that it is based on a large body of data (> 1300 hypotheses), representing a broad spectrum of taxonomic studies (from first description to mainstream acceptance). Thus, there is a discrepancy between widely held perceptions of how species are delimited and the way species are actually delimited by taxonomists.

Several factors may have contributed to the assumption that the Biological Species Concept is the dominant species concept in taxonomy. First, until the Phylogenetic Species Concept was formulated (Cracraft, 1983), no alternative species concepts had been proposed that included operational criteria. Simpson’s (1961) Evolutionary Species Concept and Van Valen’s (1976) Ecological Species Concept essentially lacked operational criteria and had little influence on taxonomic practice. The Phenetic Species Concept (Sokal & Crovello, 1970) was not a new operational concept but provided a name for the procedure already adopted by taxonomists. The lack of new operational ‘concepts’ of species until the 1980s may have led to the perception that the Biological Species Concept has been the dominant operational species concept in taxonomy.

Second, the Biological Species Concept is discussed and promoted in Mayr’s influential evolutionary and taxonomic textbooks (Mayr, 1942, 1963, 1969, 1970). Moreover, the Biological Species Concept is often the preferred concept of species in contemporary textbooks of ornithology (Gill, 1990; Newton, 2003; Podulka *et al.*, 2004), taxonomy (Minelli,

Table 7. The current status (*sensu* Dickinson, 2003) of newly described species and taxonomic proposals between 1950 and 1999

Dataset (hypothesis)	Current status (Dickinson, 2003)	Overall	Without taxonomic rationale	With taxonomic rationale	Reproductive isolation	Diagnosability	Degree of difference	Adaptive zone	Monophyly	Exclusive coalescence
New species	<i>N</i>	261	135	124	37	83	27	8	0	1
	Invalid taxon	44 (17%)	35 (26%)	9 (7%)	1 (3%)	5 (6%)	3 (11%)	0 (0%)	0 (0%)	0 (0%)
	Valid subspecies	25 (10%)	12 (9%)	12 (10%)	3 (8%)	6 (7%)	4 (14%)	1 (12%)	0 (0%)	0 (0%)
Proposal: lump	<b>Valid species</b>	<b>192 (74%)</b>	<b>88 (65%)</b>	<b>103 (83%)</b>	<b>33 (89%)</b>	<b>72 (87%)</b>	<b>20 (74%)</b>	<b>7 (88%)</b>	<b>0 (0%)</b>	<b>1 (100%)</b>
	<i>N</i>	272	83	189	70	96	82	11	5	0 (0%)
	Invalid taxon	5 (2%)	2 (2%)	3 (2%)	1 (1%)	1 (1%)	3 (4%)	1 (9%)	0 (0%)	0 (0%)
Proposal: split	<b>Valid subspecies</b>	<b>113 (42%)</b>	<b>16 (19%)</b>	<b>97 (51%)</b>	<b>40 (57%)</b>	<b>52 (54%)</b>	<b>29 (35%)</b>	<b>7 (64%)</b>	<b>4 (80%)</b>	<b>0 (0%)</b>
	Valid species	150 (55%)	63 (76%)	87 (46%)	28 (40%)	42 (44%)	50 (61%)	3 (27%)	1 (20%)	0 (0%)
	Transferred	4 (1%)	2 (2%)	2 (1%)	1 (1%)	1 (1%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
<i>N</i>	342	14	328	136	273	73	56	24	3	
Proposal: split	Invalid taxon	4 (1%)	0 (0%)	4 (1%)	3 (2%)	3 (1%)	0 (0%)	0 (0%)	1 (4%)	0 (0%)
	Valid subspecies	45 (13%)	3 (21%)	42 (13%)	15 (11%)	33 (12%)	12 (16%)	12 (21%)	2 (8%)	0 (0%)
	<b>Valid species</b>	<b>286 (84%)</b>	<b>9 (64%)</b>	<b>277 (84%)</b>	<b>116 (85%)</b>	<b>233 (85%)</b>	<b>61 (84%)</b>	<b>43 (77%)</b>	<b>21 (88%)</b>	<b>3 (100%)</b>
Transferred	7 (2%)	2 (14%)	5 (2%)	2 (1%)	4 (1%)	0 (0%)	1 (2%)	0 (0%)	0 (0%)	

Values in bold indicate original hypotheses that were accepted by Dickinson (2003).

1993), molecular biology (Avice, 1994, 2000), evolutionary biology (Coyne & Orr, 2004) and general biology (Sadava *et al.*, 2006). Groves (2004) remarked that rather than the most popular species concept, the Biological Species Concept is probably the most *familiar* species concept, especially among non-taxonomists.

Third, the Biological Species Concept was the starting point for many discussions about species, species concepts and speciation (e.g. Hull, 1978; Bremer & Wanntorp, 1979; Key, 1981; Barton & Hewitt, 1985; McKittrick & Zink, 1988; Frost & Hillis, 1990; Frost, Kluge & Hillis, 1992; Tattersall, 1992; Beurton, 1995; Corbet, 1997; Cracraft, 1997; Peterson, 1998; Johnson *et al.*, 1999; Kullander, 1999; Wu, 2001; Coyne & Orr, 2004; Groves, 2004). Proposals for alternative species concepts were usually motivated by critical analyses of the Biological Species Concept (e.g. Sokal & Crovello, 1970; Cracraft, 1983; Donoghue, 1985; Paterson, 1985; Templeton, 1989). It is likely that this has contributed to the perception that the Biological Species Concept is the 'current' and 'most important' concept of species.

Finally, the term 'biological species concept' has changed its meaning between the 1940s and the 1980s (de Queiroz, 1999, 2005). Mayr (1942) distinguished between a general 'biological species concept' and his more explicit 'biological species definition'. Mayr's (1942) 'biological species concept' referred to the fact that it could only apply to biological entities, contrary to the typological concepts of species in the 18th and 19th centuries which also applied to non-biological entities. Mayr's (1942) 'biological species concept' was based on the view that species are populations rather than types. This concept of species has indeed become dominant in the thinking of species, at least among workers on sexually reproducing organisms (O'Hara, 1997). In this general sense, all species concepts, including the phylogenetic species concept, are 'biological' (e.g. Cracraft, 1997). Mayr's 'biological species definition' referred to the operational (taxonomic) criteria of potential interbreeding and reproductive isolation (Mayr, 1942, 1963). This definition and the associated taxonomic criteria were controversial and did not become broadly accepted (e.g. Sokal & Crovello, 1970; Whittmore, 1993) or broadly applied (this study). However, in recent debates over species concepts the term 'biological species concept' no longer refers to Mayr's general view of species as biological populations but has become more narrowly associated with the criterion of reproductive isolation (de Queiroz, 1999). Recent statements about the dominance of the 'biological species concept' confuse the wide acceptance of the species-as-populations notion with the idea that species are defined by reproductive isolation.

## (2) Temporal and geographic patterns in the use of species criteria

The two most frequently applied taxonomic criteria showed different trends over time. The proportion of taxonomic hypotheses using diagnosability showed a slight overall increase since the 1950s, whereas the proportion of

Table 8. Statistical tests of differences in the acceptance (Dickinson, 2003) of taxonomic hypotheses proposed during 1950–1999

Comparison	Dataset	Statistical significance ( $\chi^2$ )
Comparisons of splits and lumps		
Splits <i>versus</i> lumps	All proposals	$P < 0.001$ (116.1)
Splits <i>versus</i> lumps	Proposals with rationale	$P < 0.001$ (64.1)
Splits <i>versus</i> lumps	Proposals without a rationale	$P < 0.005^a$
Comparisons of hypotheses with and without a rationale		
Hypotheses with <i>versus</i> without a rationale	New species	$P < 0.005$ (9.8)
Hypotheses with <i>versus</i> without a rationale	Lumps	$P < 0.001$ (23.1)
Hypotheses with <i>versus</i> without a rationale	Splits	n.s. <sup>a</sup>
Comparisons of hypotheses based on different taxonomic criteria		
Reproductive isolation <i>versus</i> diagnosability	New species	n.s. <sup>a</sup>
Reproductive isolation <i>versus</i> diagnosability	Lumps	n.s. (0.1)
Reproductive isolation <i>versus</i> diagnosability	Splits	n.s. (0.0)
Degree of difference <i>versus</i> diagnosability	New species	n.s. <sup>a</sup>
Degree of difference <i>versus</i> diagnosability	Lumps	$P < 0.05$ (5.6)
Degree of difference <i>versus</i> diagnosability	Splits	n.s. (0.0)
Degree of difference <i>versus</i> reproductive isolation	New species	n.s. <sup>a</sup>
Degree of difference <i>versus</i> reproductive isolation	Lumps	$P < 0.05$ (6.4)
Degree of difference <i>versus</i> reproductive isolation	Splits	n.s. (0.0)

<sup>a</sup>Fisher's exact test

hypotheses using reproductive isolation showed a continuous decline since the 1970s (Fig. 5). The cause of these trends is unclear. The increased use of diagnosability pre-dates the formal introduction of the Phylogenetic Species Concept (Cracraft, 1983) by several decades. Therefore, these trends cannot be explained by a shift away from the Biological Species Concept towards the Phylogenetic Species Concept. The decrease in the use of reproductive isolation and the increase in the use of diagnosability may reflect a preference for taxonomic criteria that can be applied directly and objectively.

A plot of the changes in the use of degree of difference represents an almost mirror image of that of reproductive isolation (Fig. 5), a pattern that was also found in separate plots of the three datasets. However, it is not clear if there is a relationship between the two trends. The strong increase of monophyly and exclusive coalescence as ranking criteria reflect the increasing use of molecular and phylogenetic methods in species-level taxonomy. The decline of adaptive zone as a taxonomic criterion in recent decades is more difficult to explain, but may be related to the lack of well-defined operational criteria (but see Peterson, Soberón & Sánchez-Cordero, 1999).

Reproductive isolation was much less frequently used in studies of allopatric taxa than in studies focusing on taxa that are distributed sympatrically or parapatrically (Fig. 6). By contrast, diagnosability was used equally or more often in allopatry than in other geographic settings. This suggests that avian taxonomists are reluctant to speculate on whether allopatric taxa are reproductively isolated. Because most taxonomic problems involve allopatric taxa (Fig. 6) one would expect that potential interbreeding exceeds the use of actual interbreeding. However, the reverse is true; taxonomic hypotheses focused less often on potential interbreeding than on actual interbreeding (Table 5). The

criterion of reproductive isolation is directly applicable only in situations where taxa are in contact (i.e. in sympatry or parapatry), and cannot be directly applied to populations with allopatric breeding ranges (Mayr, 1969; Cracraft, 1983). Diagnosability, on the other hand, can be applied irrespective of the geographic setting of taxa. The differential use of reproductive isolation in different geographical settings thus supports the view that taxonomists prefer to use criteria that can be applied directly.

### (3) Implications for the debate over species concepts

#### (a) *The special position of the biological species concept is not justified*

The results of this study challenge the special position that is often awarded to the Biological Species Concept. The criterion of diagnosability was applied almost twice as often in species-level taxonomy as the criterion of reproductive isolation (Figs 3 and 4); and proposals using either criterion were equally often adopted and maintained in an influential standard work (Dickinson, 2003) (Table 7). These results indicate that the special position of the Biological Species Concept as the 'titleholder' in the debate over species concept is not justified.

The Phylogenetic Species Concept was formalised in the early 1980s (Cracraft, 1983) but its criterion of diagnosability was used long before that time and, as the present study documents, was used more frequently than reproductive isolation even during the height of the popularity of 'Evolutionary systematics' (1950–1980s). This does not necessarily mean that authors who used diagnosability to delimit species had adopted the Phylogenetic Species Concept. Rather, these results demonstrate that the criterion

for species recognition under the Phylogenetic Species Concept (i.e. diagnosability) has been used much longer than is generally assumed in debates over species concepts. From a methodological point of view, the recognition of species during the era of 'Evolutionary systematics' did not differ fundamentally from that under the Phylogenetic Species Concept. The fact that both reproductive isolation and diagnosability were commonly applied during the second half of the 20th century indicates that it is misleading to ask whether one species concept should replace or supersede the other (e.g. Avise, 1994; Snow, 1997).

(b) *The artificiality of the BSC-PSC conflict in taxonomy*

Taxonomists have spent a great deal of time and energy debating species concepts. This debate has highlighted disagreements on numerous issues, including the role of phylogeny, hybridization and gene flow in species delimitation, the importance of the processes involved in the cohesion and divergence of species, and the relevance of subspecies (e.g. Cracraft, 1983, 1987, 1997; McKittrick & Zink, 1988; Avise & Ball, 1990; Doyle, 1992, 1995, 1997; Mayr, 1992, 2000; Zink & McKittrick, 1995; Mishler & Theriot, 2000; Wheeler & Platnick, 2000). Although there appears to be a dichotomy in the systematic and evolutionary philosophies of the proponents of Biological and Phylogenetic Species Concepts, this dichotomy is not reflected in taxonomic practice. In this study, less than half (40.2%) of all hypotheses that included a rationale were based on either reproductive isolation or diagnosability. Consequently, most taxonomic hypotheses (59.8%) were either based on other criteria, or used reproductive isolation and diagnosability in combination with other criteria.

The lack of a clear dichotomy of species concepts in taxonomy is underscored by the fact that proponents of Biological and Phylogenetic Species Concepts often use the same criteria, including the criteria of the other concept. Thus, outspoken proponents of the Biological Species Concept have used not only reproductive isolation as the defining criterion for their taxonomic studies, but also monophyly (Helbig & Seibold, 1999), exclusive coalescence (Rising & Avise, 1993) and diagnosability (Collar & Long, 1996; Maley & Winker, 2007). Similarly, supporters of the Phylogenetic Species Concept have identified species using not only diagnosability but also exclusive coalescence (Zink *et al.*, 2002; Pavlova *et al.*, 2005) or both (e.g. Beresford & Cracraft, 1999). Hybrid-zone dynamics indicating reproductive isolation have also been used in support of a proposal based on diagnosability (Sangster *et al.*, 1999).

The sharing of taxonomic criteria by the proponents of seemingly rival taxonomic philosophies may be termed 'methodological introgression' (Goldstein & Brower, 2002). Methodological introgression among species concepts may be explained by several factors. First, taxonomists may need multiple lines of evidence to convince their peers and workers in other fields. Second, the two concepts are not methodologically independent because diagnosability is

often necessary to demonstrate that taxa are reproductively isolated. Third, intrinsic or extrinsic reproductive isolation is a prerequisite for the *fixation* of diagnosable differences. In sympatry, intrinsic isolation of two species is necessary for the *maintenance* of diagnostic differences (Mayr, 1963; Avise & Wollenberg, 1997). Therefore, there are good reasons for methodological introgression among seemingly rival species 'concepts'.

Given the (increasingly) diverse ways in which taxonomists delimit species (Fig. 2), and the adoption of each other's criteria by proponents of different species concepts, it is no longer useful to view Biological and Phylogenetic species 'concepts' as major alternative approaches to taxonomy. This conflict has become artificial and overlooks how species are delimited in practice.

(c) *Taxonomic practice supports a general concept of species*

The results of this study confirm four predictions of the Evolutionary Species Concept or General Lineage Concept. First, avian species-level taxonomy is pluralistic. At least six criteria were used to identify species in practice. Second, these criteria are used in multiple combinations. The eclectic nature of species-level taxonomy is underscored by the use of at least 36 different combinations of species criteria. Third, taxonomists consider different criteria as complementary rather than as 'rival' approaches to species delimitation. This is supported by the high proportion of taxonomic hypotheses (46.5%) that were based on multiple criteria (Table 4), and numerous genera in which new species were recognised based on different criteria, often in different combinations, but which are widely accepted by mainstream ornithological works (e.g. Dickinson, 2003; Clements, 2007). Finally, none of the six taxonomic criteria was considered as defining (necessary and sufficient) for species rank by all taxonomists. This was demonstrated by the use of multiple criteria in all datasets, throughout the study period and in all geographic settings (Figs 3–6), and by the adoption by a mainstream taxonomic reference work of species taxa that have been proposed using different criteria (Table 7).

Thus, although reproductive isolation, diagnosability and other criteria (monophyly, exclusive coalescence, degree of difference) are often associated with different species 'concepts', in practice these are used to delimit species taxa under a more general, unified view of species. Due to the use of several criteria in various combinations, it is meaningless to classify any of these taxa as either 'biological' or 'phylogenetic' species, or to characterize the research programs of the relevant authors as based on either the Biological or Phylogenetic Species Concept. Avian species-level taxonomy is pluralistic and eclectic, and there is evidence that taxonomy becomes more so (Fig. 2). No taxonomic criterion can be viewed as 'defining' (i.e. necessary and sufficient) for species status. Thus, avian taxonomy is broadly consistent with the Evolutionary/General Lineage Concept of species.

Several authors have argued that if species are lineages, taxonomists should strive to incorporate multiple lines of

evidence whenever possible, and integrate these to provide a full perspective of lineage divergence (e.g. Dayrat, 2005; Will, Mishler & Wheeler, 2005). This approach, integrative taxonomy, is gaining popularity, especially now that various practical aspects have recently been clarified (Padiál & de la Riva, 2010; Padiál *et al.*, 2010). My results reflect this trend by showing that species-level taxonomy is becoming increasingly diverse, with a clear trend towards using multiple taxonomic criteria (Fig. 2).

#### (4) The ‘nature’ of species

Many participants in the debate over species concepts have argued that a change in species ‘concept’, such as a shift towards the Phylogenetic Species Concept, would change the ‘nature’ of species (Short, 1993; Schodde & Mason, 1999; Mace *et al.*, 2003; Newton, 2003; Bock, 2004). My study indicates that this concern is unfounded because (i) criteria typically associated with the Phylogenetic Species Concept have been used throughout the study period, and (ii) diagnosability always has been the most frequently used criterion (Fig. 5). Although the terms monophyly, paraphyly and polyphyly were rarely applied in species-level taxonomy before the 1980s, taxa that were believed to be not closely related were separated as species on these grounds as early as the 1950s and 1960s (e.g. Snow, 1956; Goodwin, 1960, 1964; Brooke, 1969; Fry, 1969). The criterion of exclusive coalescence (reciprocal monophyly) is new and has been used only after the introduction of phylogeographic methods (Avise *et al.*, 1987). However, given its uncommon use in avian taxonomy (< 15%, Fig. 5), application of this criterion has hardly changed the ‘identity’ of species. Similarly, there is no convincing evidence that reproductive barriers characterized the nature of species until the Phylogenetic Species Concept was introduced. During the 1950s–1970s, many taxonomic hypotheses lacked a rationale (Table 3) and those that included a rationale often did not indicate the presence of reproductive barriers (Fig. 5A). Therefore, the idea that there has been a shift from the Biological Species Concept towards the Phylogenetic Species Concept, and that this is changing the ‘nature’ of species, is not supported by the present study.

A more fundamental problem with the claim that application of a supposedly new species concept changes the ‘nature’ of species is that it assumes that the nature of species taxa is defined by the criteria that are used to recognise them. According to this logic, a diagnosable species (i.e. a species delimited by the Phylogenetic Species Concept) is a fundamentally different ‘kind’ of species than a species based on the criterion of reproductive isolation (i.e. according to the Biological Species Concept). However, as was pointed out above, species-level taxonomy is pluralistic and eclectic, and has been so for many years (Fig. 5). Several criteria are used to recognise bird species and often in different combinations. If the ‘nature’ of species depends on the criteria that are used to recognise them, there must be as many ‘natures’ of species as there are combinations of taxonomic criteria. Different species criteria do not identify different kinds of species but

emphasize different *properties* of species. De Queiroz (1999) has argued that there is a fundamental difference between the *species concept*, which tells us what species are (i.e. their ‘nature’), and *species criteria*, which determine how species should be recognised in practice (i.e. the properties that are deemed sufficient for accepting species rank). The Biological and Phylogenetic Species Concepts use different criteria but both identify segments of population lineages as species (de Queiroz, 1998, 1999). Although the use of phylogenetic criteria to delimit species taxa is sometimes viewed as a problem for the identity of species (Mace *et al.*, 2003), these criteria merely highlight additional properties of species taxa. Therefore, rather than changing the identity of species, these criteria help to characterise and understand that identity.

#### (5) Taxonomic stability

The proportion of splits (‘split ratio’) in proposals using diagnosability was higher than in proposals using reproductive isolation. AOU recommendations using diagnosability also led to a higher proportion of splits than those using reproductive isolation. However, in both datasets, the split ratios of diagnosability (77–91%) and reproductive isolation (68–79%) were both rather high and the differences in split ratio between these criteria were rather small (Table 6). Hypotheses based on diagnosability and reproductive isolation were equally likely to be accepted by Dickinson (2003) (Tables 7 and 8). This pattern was observed for descriptions of new species taxa, for proposals for splits and for proposals for lumps. These findings indicate that application of the Biological Species Concept does not necessarily result in a much smaller number of new species than the Phylogenetic Species Concept and that it does not produce taxonomies that are more stable than those of the Phylogenetic Species Concept.

The idea that the Biological Species Concept results in more stable taxonomies appears to be based on a combination of two factors: default lumping and lack of information on reproductive barriers. Even today, many distinctive taxa remain part of polytypic species based on the principle of geographic representation. According to this principle, closely related taxa should be included in a single species unless their ranges overlap geographically. This principle has been applied widely since the early 1900s and has resulted in a major reduction of the number of recognised bird species (Mayr, 1982; Haffer, 1992). The default lumping of distinctive taxa in polytypic species is often misconstrued as a result of the application of the Biological Species Concept. The Biological Species Concept requires an assessment of the degree of reproductive compatibility to determine the taxonomic rank of the taxa under study. In practice, however, ornithologists in the first half of the 20th century continued to lump geographically non-overlapping taxa into polytypic species, and performed few proper studies into the reproductive compatibilities of the relevant taxa. Thus, although taxonomists may have considered species to be populations that are reproductively isolated from other such populations, taxonomic decisions were often made without

sufficient documentation or discussion of the actual degree of reproductive isolation. This is underscored by the low proportion of taxonomic studies that applied the criterion of reproductive isolation during the study period (overall less than 50%, Figs 3 and 5).

A second factor that contributed to the perceived stability of avian taxonomies under the Biological Species Concept was a lack of information on the reproductive compatibility of allopatric taxa. A problem of the Biological Species Concept is that it is difficult, if not impossible, to apply directly to taxa that do not overlap geographically (Mayr, 1969). Both factors—default lumping and lack of information—had a major effect on the number of bird species. Application of the principle of default lumping has downgraded many distinct allopatric taxa to subspecies rank, whereas the difficulty of demonstrating reproductive barriers between allopatric taxa made it hard to falsify their subspecies status. Thus, the perceived stability of avian taxonomy in the second half of the 20th century was not caused by the successful application of the Biological Species Concept but rather by the difficulties of applying it.

## V. CONCLUSIONS

(1) Contrary to widely held beliefs, avian taxonomy has not been dominated by the Biological Species Concept. The special position of the Biological Species Concept in debates over species concepts in taxonomy is therefore not warranted.

(2) Diagnosability was the most frequently applied taxonomic criterion, followed by reproductive isolation and degree of difference.

(3) In ornithology, species are recognised on the basis of several criteria that are used in at least 36 different combinations. It is argued that the Biological/Phylogenetic Species Concept distinction is a false dichotomy, which obscures how species are actually delimited.

(4) Several predictions of the Evolutionary or General Lineage Concept of Species are supported by this study: species-level taxonomy is pluralistic and eclectic; taxonomists apply different criteria as complementary rather than as rival approaches to species delimitation; and none of the taxonomic criteria are considered as defining (necessary and sufficient) for recognition as species. Taxonomic practice is more unified than is implied by the controversy over species concepts. Thus, there are good reasons to ‘get over’ ideological divisions between seemingly alternative concepts of species.

(5) There have been no large or sudden shifts in the use of diagnosability in the second half of the 20th century. The results of this study, therefore, do not support claims that the introduction and application of the Phylogenetic Species Concept has changed the ‘nature’ of species.

(6) Diagnosability was more often involved in proposals for additional species than reproductive isolation but the difference was small. Proposals based on diagnosability and reproductive isolation were equally often adopted in

a mainstream taxonomic reference work. There do not seem to be major differences between these concepts in the degree by which they enhance (or threaten) taxonomic stability.

(7) Theoretically oriented debates over species concepts may benefit from empirical data on taxonomic practice.

## VI. ACKNOWLEDGEMENTS

I thank René Dekker, Janet Griffin-Bell, Cornelis Hazevoet, Janet Hinshaw and Arthur Smith for providing literature. I am grateful to the staff of the library of the Netherlands Centre for Biodiversity, Leiden, for access to their library and for helping me locate numerous publications. Kees Roselaar helped with enquiries about Russian publications. E. Gittenberger and Menno Schilthuizen read a previous version of the manuscript. The referees, Frank B. Gill and José M. Padiá, provided insightful comments and suggestions which improved the quality of the manuscript. Alison Cooper made helpful editorial suggestions. I am grateful to Henk de Boer and Jolanda Luksenburg for their encouragement during various stages of this project.

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(Received 22 July 2012; revised 10 June 2013; accepted 19 June 2013; published online 19 July 2013)