

By studying and defining this variation, ornithologists are able to add to the knowledge of the earth's history. Obviously, not all variation among closely related bird populations has progressed to the point at which those populations merit species status. To recognize these populations by naming them as subspecies is to acknowledge their existence and to demonstrate how the earth's history has affected them. This idea is nowhere better illustrated than in the Andes, where geographic variation is obvious and populations are often isolated from each other. I think that the subspecies concept is a valid one but that it should be connected to an evolutionary unit. If subspecies are evolutionary units, then the usefulness of the concept is greatly enhanced. If there is no break in gene flow (i.e. a smooth cline), then all populations in that "aggregate of populations" should be considered to belong to one form. When there is a break in the gene flow by any type of separation (geographic, ecological, etc.) then recognition of a second unit or subspecies would be warranted. Variation within a cline can be discussed and described, but only a single name need be applied. Two subspecies that seem to be morphologically alike but are separated by a form that is different would be separate evolutionary units and thus would not be referable to the same subspecies.

Graves (1980) re-examined the Colombian population of *Diglossa (carbonaria) brunneiventris* and found that the population was separable from the Peruvian birds. I feel that his action was correct in that the Colombian and Peruvian brown-bellied birds, which are separated by all-black populations, are separate evolutionary units and should not be placed together under one name.

To make the subspecies concept embrace an evolutionary unit would not affect its convenience, would make it more useful, and would get rid of the need to differentiate between the "evolutionary" and the "taxonomic" implications that seem to be so often misused. I have obviously oversimplified many of the problems and have left out a great amount of information that warrants discussion, but this is necessary because of space constraints. I do, however, find the concept to be very valuable and very useful in the 1980's.

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SUBSPECIES AND SPECIES: FUNDAMENTALS, NEEDS, AND OBSTACLES

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Populations are nature's building blocks. When they do not differ consistently from other (usually more or less adjacent) populations, the whole series forms a single subspecies—or species if essentially isolated reproductively. Character complexes commonly varying, at these levels, are measurements, details of colors, or more rarely facial patterns or colors of soft parts. In most widespread species (especially if not strongly migratory or nomadic),

one or more of these complexes does vary geographically, forming more-or-less well-defined subspecies. There may also be areas where the variations are inconstant; such variable populations should not be arbitrarily squeezed into one or another of the truly distinct subspecies. Common patterns of racial or subspecific variation are clinal or convergent, open-ring, broken-ring or divergent, parallel, and nonclinal or random (which should normally not be named) (Phillips 1959).

Treatment of species and subspecies has varied widely. Most Europeans before Hartert rejected the subspecies concept, calling every

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recognizable form a species. Hellmayr, at the other extreme, considered nearly every allopatric form a subspecies, paving the way for Mayr and Amadon (1951) to reduce the world's Recent avifauna to 8,519 species. Mayr's followers have most recently (Bock and Farrand 1980) conceded that at least 9,021 species exist, a figure surely well short of reality. [I still consider my guess (Phillips 1959) of about 10,000 species a reasonable one.] But instead of these guesses, we urgently need *field* studies and explorations. Mayr, Bock, and Farrand are quite wrong in stating that "the biological species concept . . . becomes less and less applicable to populations replacing one another over increasing geographical distances." Biology is not dependent on distance, and only slightly on ecology. Mayr and his followers would do well to familiarize themselves with avian *biology*: nests, eggs, flesh colors, behavior (including vocalizations), and skeletal structures. Their belief that all forms of *Morus*, *Anhinga*, *Haematopus*, etc. are allopatric does not prove that these forms are subspecies (cf. Brodtkorb 1963, *Morus*; Phillips et al. 1973, Phillips MS, *Polioptila*; Baker 1974, *Haematopus*). Simple vicariance of surviving taxa does not determine their taxonomic levels. As Coues long ago wrote, species are better determined in the field than in the closet! An excellent example of the sort of field approach that is needed is provided by Lanyon's (1978) vocalization playback studies of *Myiarchus* flycatchers. Such investigations are urgently needed of many more genera, especially in the tropics.

Subspecies are morphologically or geographically significant populations whose members differ morphologically, at some stage, from those of other populations (of the species) to a conventional degree; commonly, we insist that at least 75% of the birds must be distinguishable from 99% of those of other populations. This convention has been misinterpreted to mean they must differ in some one character to that extent. Often, however, more than one character is involved, and at least 75% of the birds must be separable from other populations in one or another character. Single-character races are, in fact, unusual and often rather weak. If a bird is darker, this will usually affect various parts of the plumage; if an insular bird's bill is larger, it will usually be both longer and deeper (or perhaps wider),

though this may be hard to measure. We must not be blind slaves to statistics.

Note that the *members* of the populations must differ; entire populations are not compared. White and dark geese are color phases or "morphs"; while each occupies certain parts of the breeding range exclusively, in other parts they mix, and no one recognizes Snow and Blue geese as subspecies. Selander's proposal (1959) to recognize races based on occurrence of "morphs" is unacceptable; what happens when unexpected individuals turn up in other populations, and how do we identify single specimens? True subspecies are more substantial.

Subspecies are no new discovery; they have been known longer than sibling species, though at first termed species or varieties. Thus, 3 subspecies of *Motacilla flava* (Yellow Wagtail) from northern Eurasia had been named by 1789 and 6 palearctic races of *M. alba* (White or Pied Wagtail) were described by 1838, whereas before 1811 only 1 species (2 subspecies) of the various Eurasian *Phylloscopus* warblers had been described, and only 1 of the 5 species of eastern North American *Empidonax* flycatchers. Only the most distinctive of the other, western United States *Empidonax* was recognizably described before 1856; indeed the status and nomenclature of these species in North America was not finally settled until 1973! Other sibling species, like subspecies, continue to turn up.

In the past 30 yr, several writers have sought to convince the unknowing that subspecies are a fictional concept, unstable in time, and that their recognition is at best dubious. Uniformly, they studiously ignore the many truly dramatically different subspecies, such as the above *Motacillae*, Canada Geese, flickers, various juncos, and other sparrows, etc. Johnston and Selander's "House Sparrows: rapid evolution of races in North America" (1964) may be instructive. They claimed that recent fall series from 20 points in North America (plus Hawaii and Bermuda) showed that each population "has differentiated to greater or lesser degree from any other and from the Old World stock," and that this was genetically controlled (including a "conspicuous yellow wash" at Oaxaca, Oax., México, where in fact *Passer* arrived not long before 1962). They correlated color variation with temperature and humidity

but ignored soot, smog, or other discoloration in urban populations, plus the basic fact that the birds were not washed before skinning. They concluded: (a) "levels of differentiation . . . are fully equivalent to those shown by many polytypic native species . . . application of subspecific trinomials to certain New World populations . . . would be fully warranted . . ."; and (b) much of the "differentiation" must have occurred in the present century; this they found concordant with changes within historic time in other groups, citing among other authors Wilson and Brown (1953). In cold fact, the differentiation in color had probably occurred since the preceding August, having nothing to do with genetics. Interestingly, when someone misled by this *did* map a few of these supposed subspecies, Johnston and Selander replied (1966): "We did not . . . describe 'subspecies' of house sparrows . . . Designating and mapping the ranges of five 'subspecies' of house sparrows in North America . . . clearly demonstrates several objectionable features of the subspecies concept and strengthens the argument for abandoning it altogether."

What Johnston and Selander did in fact demonstrate was selection for larger size in areas with cold winters. But only specimens demonstrating the full range of variation of the original stocks, introduced from various points, could show that variation has increased. Because evolution implies *change* from ancestral stocks, not mere reshuffling of averages, Johnston and Selander's title is patently untrue. Yet it has had an unfortunate effect on the beliefs of others.

Many subspecies have, to be sure, been misunderstood. To err is human, especially with poor material. Probably no one's record on subspecies is perfect, and my own could be much better. But *species* have also been abused and misunderstood (cf. "*Psaltriparus melanotis*," "*Pipilo ocai*," *Junco* "*caniceps*," etc.); so have genera [cf. Oberholser (1974), particularly on "*Phasmornis*" and "*Oreothlypis virginiae*"]. Should we then abandon these "concepts" altogether? If we cease recognizing subspecies, we must re-elevate all notable ones, at least, to species rank, thus destroying the biological species and plunging our classification back toward the early 19th century. This would surely be a great step backward. Rather, we must refine subspecies with far better material,

leaving less room for doubts and disagreements.

The utility of subspecies would undoubtedly be enhanced if all competent taxonomists agreed on all details. This utopian ideal is unattainable, if for no other reason than differences in ocular acuity, combined with the difficulty of verbally expressing differences visible to the eye. Nevertheless, much could be done to improve the present unsatisfactory situation.

For one thing, I am constantly impressed by the minute taxonomic value of the average museum's skins. Most are badly worn, and often dirty, and would have been better preserved for anatomical studies than as skins. Add to this that, in most parts of the world, the vast majority of bird populations has never even been sampled, but only those of easy access or promising habitats. Yet we are constantly told that the day of the collector has passed! Not only are the points from which we have specimens widely scattered on even a small-scale map, and the specimens in poor condition and poorly dissected and annotated, but collections are usually badly skewed toward adult males at the expense of females and young of different ages. Yet, in dimorphic species, it is often the adult male that is least useful taxonomically. For example, in *Carduelis psaltria* (Lesser Goldfinch), studies over several years have shown me that currently recognized taxonomy, based on the available adult male plumage, is quite inadequate; yet besides being scarce, material of females and young must be divided into five age/sex classes before reliable comparisons can be made. Yet goldfinches are easily collected. Those who complain about the instability of subspecific concepts or nomenclature should get busy in the field. It is inexcusable that useful material of even common birds remains unavailable from vast extents of accessible territory. (Nor will single specimens assure correct results; we should have series.)

A case in point in the eastern United States is the Brown Creeper (*Certhia* "*familiaris*" = *americana*). A supposed Appalachian race, *nigrescens*, was named years ago from breeding birds of little if any taxonomic value. As yet, so far as I know, all major collections together have exactly one useful specimen among them to judge the characters, validity, and winter range of the race. Every year the period from

mid-August (when birds are coming into fresh basic plumage) to mid-September (when fully molted migrants start arriving from the north) passes with no one collecting Appalachian creepers, Winter Wrens, etc. What right, then, have the idle to criticize? When adequate material becomes available, taxonomists will be only too happy to study it. Meanwhile, of course, all reports of *nigrescens* migrating or wintering here or there necessarily represent more-or-less educated guesses, based, one suspects, on foxing (post-mortem changes in museum skins) and soot-discoloration. There is reason for dissatisfaction.

Finally, scientific specimens should be the property of science, available for study by specialists at any time. But this is not the case with some small colleges, and even the important Moore Laboratory of Zoology refuses to loan specimens for months at a time, a corollary of the situation about which Olson so rightly complains (1981).

Subspecies, despite all misleading attacks, remain basic units in ornithology. As Marshall states (1964), they constitute whole populations marked by certain peculiarities, enabling us to trace them on migration and in winter. They are thus the basis of much of our knowledge of migrations.

The difference between species and subspecies is biological, requiring field studies of a vast number of kinds of birds in rapidly vanishing habitats. We shall never know how many full species of birds inhabited the planet when we began its destruction, or even when we recently accelerated this destruction. It is past time to get afield and away from minutiae and speculations, back to solid facts of bird distribution, variation, and migration. Successful conservation will require intelligence, realism, and *knowledge*, based on better collecting of what there *is* to conserve. It cannot be based on lying politics, fanaticism, or some inapplicable ethic. It should include, in emergencies, captive breeding, with due respect for the integrity of stocks—again implying subspecies. It can hardly be achieved while “conservationists” and misled officials impede the collecting, preservation, and study of our fast-vanishing wealth. This is concentrated in the tropics, the very areas most under assault for blind, short-term “development” and most in

need of surveys. Meanwhile, our scientific “establishment” unanimously ignores most subspecies and concentrates on supporting industry (profitably) by emphasizing computers and expensive equipment designed to give fantastic Ultimate Answers (based on proteins and molecules) that, to date, have been largely wrong. Truly, we are in a new Decline and Fall, with our scientific establishment fiddling while Rome burns, instead of conserving biological diversity.

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