

THE NATURE OF AVIAN SPECIES

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"We may have to acknowledge, in some cases, that species are better determined in the field than in the closet." — Coues, "Birds of the Northwest," 1874:248

There are two main things to bear in mind about avian species. First, birds are the best known of all the relatively large groups of animals (about nine or ten thousand species of Recent birds). Bright, noisy, active, and diurnal, birds have long interested man by the comings and goings of migratory species. They have determinate growth and mature early, reaching almost adult size within a few weeks of hatching, so that they lack the long series of developmental stages that have caused such confusion in other groups, as was mentioned by Dr. Maslin. Their only subsequent changes will be a series of molts into plumages which may or may not be strikingly different in color; the measurements seldom change greatly except in a few large-billed species. Thus, birds have long been studied and provide an enormous amount of data on speciation.

Yet the speciation of birds is not a closed chapter. In many ways it hasn't been opened. This is particularly true in regard to possible reproductive isolation of subspecies, and to morphological differences due to age, sex, and seasonal plumage changes. We hear much talk about comparing populations; but this is hardly ever done. Instead, authors compare museum series, mostly shot in May, June, or July. But most birds of the northern hemisphere molt in August to October. Thus, museum series consist of faded and soiled birds of unknown age, often erroneously labeled as to sex, and in plumages devoid of fine color values (except in species with extensive spring molts). The number and vigor of collectors has decreased alarmingly; most of the birds were collected 40 to 80 years ago. In a number of groups, the specimens are now useless due to "foxing" (post-mortem color changes). So the finer points regarding the subspecies of birds remain unknown. Furthermore, ornithology has opposition that is faced by no other science. Other scientists conduct their researches nearly as they see best; ornithologists cannot take a specimen without the permission of (1) landowners; (2) federal governments; and often (3) local fish and game politicians, who are frequently completely and willfully ignorant of all ecological factors, such as the importance of undisturbed nest-sites, annual population cycles, competition, territory sizes, mobility, and in fact every aspect of the science. No

other biologist is normally so compelled to seek favors of anti-scientific politicians. Thus, due to laziness and barriers, we lack adequate modern series of most species, in good plumage; but this fact has no bearing on their actual geographic variations.

In line with the poor quality of present museum series, we too often read, in a full or partial revision of some species, an introductory second or ninth paragraph admitting that, ideally, we should base a revision on fresh-plumaged material, recently taken on the breeding grounds. But lacking this, authors use such characters as *are* shown by their useless specimens. Thus, the significant geographic variation is thrown out, and we read umpty-ump pages of often meaningless statistics. Though dates of collection are of extreme importance, from the standpoints of both migration and "foxing," they are not mentioned. Useful keys are virtually unknown since the days of Coues, Ridgway, and the Catalogue of Birds in the British Museum. Age differences, even if pronounced, are apt to be dismissed (*cf.* Behle, 1950, on male *Geothlypis*).

To be sure, some birds present almost insuperable obstacles; we cannot collect fresh plumages on the breeding grounds because they migrate *before* molting. We might, however, collect the grown young birds and the freshest-plumaged arrivals in the spring, carefully noting their behavior (singing, territoriality, etc.), gonad size, amount of fat, presence of mate, and other significant data. The typical museum label gives none of this information today; its poor quality is discussed by Van Tyne (1952).

Yet despite serious shortcomings, birds are still the best known major group of animals; a second important point to bear in mind is that birds *migrate*. The student of any group must consider the extent and nature of its movements. Very few species of extra-Tropical birds are strictly sedentary all year. The longer and less regular their migrations, the less probability of well-marked subspecies. Ducks (*Anatinae*) are an extreme example. Their migrations are often lengthy and influenced by ice formation and other meteorological factors; they pair in the winter quarters. The result? Hardly any of the few good subspecies of ducks range over less than a continent. In fact, large water birds seldom show much geographic variation.

THE SPECIES AND SUBSPECIES OF BIRDS

In birds, too, the species is ordinarily an obvious reality which anyone can see. And in birds, too, we find occasional perplexing cases where the usual definition of a species seems to break down. How numerous these may be we can only guess, at present, in view of the very limited amount of experimenta-

¹Space limitations prevent detailing data in some cases where concepts herein are at variance with current literature; but data do exist for these cases.

tion and of information on reproductive barriers. Nevertheless, it seems likely that, like everything else, reproductive isolation cannot be used alone as an automatic 100% criterion of the species. It is easy to see where morphological divergence has outstripped reproductive isolation, as in the various artificial "species" of Flicker (*Colaptes auratus*) and Darkeyed Junco (*Junco hyemalis*), which certainly do not fit any modern species-definition; but it is obviously far more difficult to perceive the reverse, *i.e.* reproductive isolation unaccompanied by distinctive morphological divergence, and we have barely begun to suspect some of these cases.

Thus it seems that we may slightly modify Mayr's well-known definition: a species, at any given level of time, is composed of all those organisms originating in an (actual or potential) common pool of genes; plus those originating in adjacent but more or less isolated pools whose phenotypic expressions include types that essentially duplicate, in morphology, behavior (including the production of sounds and scents), and life history, the phenotypes of a part or all of the original pool. (Normally there will be no gene exchange with any other species-pool in Nature; but neither the ability to produce fertile hybrids nor purely ecological,² or physiological, similarity constitutes proof of conspecificity).

Agreement on what constitutes a satisfactory subspecies is more difficult to obtain. Despite all recent discussion pro and con subspecies, no competent ornithologist denies their existence. Rather, ornithologists' discussions center on the *number* of subspecies that should be recognized, *i.e.* the lower level necessary for formal recognition of a subspecies. My own conception, agreeing with others, is that a usefully recognizable *subspecies* is a (normally geographic) group of populations within a species, occupying a significant portion of the range of the species, at least 75% of each of whose included populations is morphologically separable, at some stage, from 99% of all other such groups; *or* a population occupying a smaller area but either possessing trenchant characters of its own or linking two populations that are unusually remote, either in characters or in geography. (A corollary of such a definition is that there may be areas in which populations are not adequately differentiated; these should be regarded as intermediate and not mapped or catalogued under any one racial name. Thus the species may be more than the sum of its named subspecies.)³

A stepped cline might produce as many subspecies as it has steps, provided that the area occupied by each is significant; but strictly intermediate forms in a single mountain range, such as the "*Aphelocoma*," *Parus inornatus*, and *Psaltriparus* of the Little San Bernardino Mountains⁴ or the *Passerella* of the Mono area of California, or any other minor variant between two major populations, do not seem worth

recognizing in formal nomenclature. Nor need we name supposed physiological races like the "British" Starling (*Sturnus vulgaris "britannicus"*) or "Puget Sound" White-crowned Sparrow (*Zonotrichia leucophrys "pugetensis"*), whose geographic distinction is disproved or purely conjectural. It is particularly objectionable to name the intermediates and then assign them to a "Sonoran Avifauna" which does not include either of the valid (parent) subspecies, as done by Miller (1951).

Surely nothing is to be gained by removing the subspecies from the orderly Linnaean system of nomenclature to the unprincipled chaos of symbols. Still less should we be satisfied with a mention of geography, as advocated by Wilson and Brown (1953), which tells us neither the characters of the population nor its relationships to other populations, to say nothing of being less concise and less manageable. Substitution of geographic symbols or descriptions for subspecific names, as urged by these authors, is patently absurd, particularly in the case of open-ring forms and still more pointless in the case of erratic wanderers such as *Loxia* as well as the wholly or partly migratory birds, of which up to five subspecies may be found in the same place at one time or another, though normally not in the breeding season.

DELIMITING SPECIES AND SUBSPECIES

Since evolution is a continuous process, we may expect to find a number of border-line cases between species and subspecies at any given time. The most obvious cases are the so-called "Open-Ring Forms"; here certain populations occur together in more or less complete reproductive isolation but are connected by a chain of intergrading subspecies elsewhere. These cases are now considered to represent a single species. To satisfy our definition of the species, a population need only interbreed freely with *one* other population within the common pool of genes.

Often populations are variably intermediate, in characters and geography, between two well-marked subspecies. Thus, the still-standard method of writing one subspecific name on the label of every specimen only courts error and postulates false migration routes. Drawing sharp lines on maps, to separate two intergrading subspecies barely if at all distinguishable, certainly does violence to the facts of Nature; yet this is common practice (see Grinnell and Miller, 1944; Pitelka, 1951; and review by Phillips, 1952). Intermediate and undifferentiated populations *exist*, and a good study should present all the facts.

A case of subspecific variation in color, more

²*cf.* Pitelka. 1951:378-379, for a contrary view.

³The suggestion that subspecies be named to the point where the multiplication of names begins to retard and confuse the study of geographic variation (Tucker, 1946) is impractical; some people are too easily confused, even by only two names. Confusion is a mental affliction that affects many on the slightest provocation. ⁴Even if these differences are genetic.

extreme than even such celebrated cases as the Song Sparrow (*Melospiza melodia*) and wagtails (*Motacilla* spp.), is the unappreciated case of the Rufous-sided Towhee (*Pipilo erythrophthalmus*, including "ocai"). Its many well-known races, from southern Canada to central Mexico, have black heads and upperparts (brown in females northeastwardly), rufous from sides to crissum, and white spotting on tail, wings, and (westwardly) back. In parts of the west, it is sympatric with the Green-tailed Towhee (*P. chlorurus*), an unspotted greenish bird with rufous crown, white throat, and dull olivaceous sides and flanks (belly white in both species). This last color-pattern is almost exactly duplicated in the "ocai" races of southwestern Mexico, which overlap the range of a "normal" black, spotted race of *erythrophthalmus* in Oaxaca without known hybridization (unless the type of *P. chlorosoma* really came from there). Small wonder that old-fashioned taxonomists unanimously call "ocai" and *erythrophthalmus* distinct species. But their calls, behavior, and juvenal plumages are very similar, and elsewhere one type grades insensibly into the other. A lengthy paper on their "species formation" [=adult external morphology] (Sibley, 1950) maintains the two as "species" by drawing an arbitrary line east of Morelia, Michiocán, and ignoring the population at Teziutlán, Puebla (Traylor, 1949). Sibley talks of "hybrid swarms" in Jalisco and "an example of the F₁ generation" in Puebla, but neither "parent" occurs in the areas concerned. Persistence of Linnaean thinking is especially obvious on p. 145: "Teziutlán is included [in the range of *ocai*] because the hybrid *P. complexus* came from there." In brief, these two dissimilar types of towhee meet in five regions (not four, as stated by Sibley, 1950:152); in three, there is complete mixing; on Mt. Orizaba there is partial but incomplete segregation; while in Oaxaca there may be full reproductive isolation. Open-minded biologists will hardly acquiesce in Sibley's Line and postulate a history of isolation to bolster recognition of two species "for practical nomenclatural purposes" (italics Sibley's) where but one exists in Nature.

Pre-Darwinian ornithologists often postulate such dubious histories to justify their recognition of unnatural "species." The two arrays of subspecies theoretically had "a period of separate existence as related polytypic species" which "are regarded as secondarily in junction" (A.O.U. 1955:6, 10); but they admit (p. 11) that the amount of morphological variation is a function, *not* of the history of the population, but of the paucity (and absence of linkage) of the genes involved and the absence of selection.

Nor will competent biologists agree that these extraordinarily dissimilar subspecies are figments of a taxonomist's imagination, derived from a theoretical "concept," as claimed by Wilson and Brown (1953). Many subspecies have a reality nearly as obvious as the species', regardless of whether this is susceptible

of easy verbal definition; many were first described as species. Had we no trinomials, these and many others would be re-elevated to binomials, destroying the clear delineation of the most obvious reality in Nature, the biologic species.

While the limits of some of the subspecies may be susceptible to modification by the taxonomist, the species' limits are decided by the animals. The *animals* decide the reproductive isolation which, if not absolutely essential to define the species, is still the most important factor maintaining them. Genetic or not, this isolation is normally psychological. The animal decides which others are suitable as mates. There has been much effort to deny that psychological factors operate in other animals than man; non-human animals are pictured as chemical creatures of rigid instinct, while man alone possesses (but seldom uses) a thinking mind. The evidence for this distinction does not greatly impress me. Psychological factors include behavioral traits such as voice, movements, and perhaps ecological factors, as well as colors of soft parts (gape, etc.) varying from group to group.

Essentially the same characters that differentiate species, morphologically, differentiate subspecies *within* the species, or even the sexes. Such characters include size, proportions, coloration, shapes of the tips of the primaries, and the wing-formula (relative lengths of primaries). But subspecific differences in color-pattern, and perhaps in colors of mouth, tarsi, and toes, are rare. The number of primaries notched or "cut out" seems, however, to be constant within the species, not racially variable; this number varies little even between full species. No competent taxonomist will agree with Wilson and Brown (1953) that equal importance should be attached to the welter of insignificant variations possible in animals as to the few conservative, taxonomically important variations.

Ornithology has an enormous literature. Anyone who does not believe in subspecies should visit a library and spend a week thumbing through the many classic volumes of Ridgway and Friedmann's "Birds of North and Middle America"; Cory, Hellmayr, and Conover's "Catalog of Birds of the Americas"; Hartert's "Vögel der Paläarktischen Fauna"; and the various recent Check-Lists of birds of many parts of the world, besides Peters' "Check-List of Birds of the World." Then go to a good museum, and finally spend a month afield collecting in Mexico and the Southwest.

TRENDS IN RECENT TAXONOMIC WORK

Most subspecies of birds newly named today are based on series of specimens, but there is still room for improvement. Even recently races have been named, based on one or two newly taken specimens (possibly accidental where taken, and usually of dubious age and sex) that differ from two or three old museum skins. Examples are "*Neochloe brevipennis browni*" (Miller and Ray, 1944), "*Xenospiza*

baileyi sierrae" (Pitelka, 1947), and "*Otophanes mcleodii rayi*" (Miller, 1948).

More widespread is the stubborn resistance to biological species concepts. Within this century some authors persisted in naming as "species" forms which could not be shown to intergrade (or on islands), even though their morphologic differences were negligible. (Cf. "*Vireo mailliardorum*" Grinnell, 1903; "*Carpodacus mutans*" Grinnell, 1911 and 1912, and see J. Phillips, 1912). Grinnell steadily rejected the biological species concept, arguing in his last paper (1939) that, in some cases at least, binomials should indicate recognizable groups of subspecies within the genus, even though these groups intergrade with other such groups and show no biological differences. This hyper-conservatism persists in such recent University of California publications as Sibley's, discussed above. Miller (1941:147) emphasizes "intergradation, either geographic or morphologic, . . . in arbitrarily defining species and subspecies"; the A.O.U. (1955:4-5) still questions the unity of *Sphyrapicus varius* and calls its three main types "near species," though they have no known differences in voice or behavior and interbreed more or less (certainly far more than does any of them with their sole congener, the widely sympatric *S. thyroideus*, with which only two hybrids are known). Miller maintains (1949) that no matter how numerous the "hybrids" between two forms, this does not prove "full or even partial breakdown of reproductive isolation and hence racial status" (as opposed to the two forms being distinct species). Surely this tortured reasoning is incompatible with modern species concepts. Only the worst swivel-chair taxonomists today "in large measure for practical reasons fall back on the morphologic evidence" (A.O.U. 1955:3) and ignore calls, songs, tendencies to associate or remain aloof, mating, life history, juvenal plumages, etc. For a century, despite their inability to find good morphologic differences, ornithologists have recognized several species of *Empidonax* and *Contopus* flycatchers; and they are slowly learning that sharply defined (morphologically) forms of *Colaptes*, *Sphyrapicus*, *Junco*, etc., are merely subspecies. Despite the resistance in high quarters, the modern biological concept is steadily gaining. "Lumping" has even gone too far, in some cases, simply because two species are allopatric, or thought to be so. Examples are the treatment of *Centurus uropygialis* by Peters (1948) and of *Progne dominicensis*, *Campylorhynchus gularis*, *Melanotis hypoleucus*, *Ergaticus versicolor*, and *Melospiza bicaratum* by Hellmayr (1934-1938); neither author was personally familiar with the living birds.

Distressed by the uneven differentiation of subspecies, an occasional ornithologist has proposed a *quadrinomial* nomenclature with the third (next to last) term representing a *group* of similar races. This would more logically express Grinnell's idea (1939). But trinomials are unwieldy enough, with-

out having to decide whether connecting race "c" is more like "b" or "a."

Recent fashions are (1) needless statistical treatments of measurements and (2) artificial categories of coloration, or both. The A.O.U. (1955:18) strongly urges statistical procedures. Authors often omit the actual range of measurements, or ignore females. But living things are not dead marbles; even if the same statistical curves apply, the weakened extremes may be absent from adult populations. Misused statistics produced erroneous results in their lone applications to *Empidonax* (Mengel, 1952) and *Dumetella* (Rand and Traylor, 1949). Inflexible color standards misled Miller (1941:275) into erroneously recording a subspecies of *Junco* at several extralimital points. Birds should be compared only with *series of comparable birds*; ornithologists should concentrate on, and present, full measurements of birds of *known* ages and sexes, and, where required, a minimum statistical analysis. Laziness is the only reason for consistently measuring only one wing in a series of skins (as is often done), if the chord is measured; flattening the wing may damage the specimen, and rarely increases the accuracy of the measurement.

OPEN-RING FORMS

An apparent "open-ring form" in North America (not yet properly investigated) is the Mallard and Black Duck, *Anas p. platyrhynchos* and allies. Female and eclipse plumages, voice, and ecology, at least, are very similar throughout the group. The main morphological gap between the supposed species is in New Mexico, where the familiar green-headed Mallard drake becomes a hen-feathered male (*diasi*) much like a female Mallard. There is little or no good evidence of reproductive isolation in the Albuquerque region and northward, where a careful study is needed; breeding experiments should also be conducted to expose the genetic basis. Farther southeast and east we have *maculosa*, north of which nests the Black Duck, *rubripes*, partially overlapping the breed range of *A. p. platyrhynchos*, with only limited hybridization. The open ring thus surrounds the unoccupied Great Plains area.

Differences between this case and the famous one of the Herring and Lesser Black-backed Gulls (*Larus argentatus*)⁵ are: (1) the step from *platyrhynchos* to *diasi*, in males, is steep phenotypically; and (2) reproductive isolation of the overlapping ends is incomplete. Bent (1923:41) says: "The Mallard seems to be more inclined to hybridism than any other species [of duck], particularly with its near-relative, the Black Duck. Numerous specimens of hybrids between these two species have been collected, showing various grades of mixed blood; they freely interbreed in captivity and their offspring are perfectly fertile." Such crosses or back-crosses probably

⁵*Larus* is poorly understood; other open-ring forms may exist.

account for alleged strays of *diazi* and *maculosa* south of the zone of overlap in fall and winter.

Other open-ring forms in America are in the geese (*Branta* spp.), probably, and perhaps also in wrens (*Troglodytidae*), whose taxonomy is very crude at all levels. Wrens badly need a biological classification, such as was urged for *Tyrannidae* by Ihering (1904) and Meise (1949). A whole bevy of allopatric Middle American "species" of wrens are now in a heterogeneous genus *Thryothorus*. Some would doubtless be reduced to subspecies if we knew which represented which. Two sympatric west-Mexican species, *sinaloa* and *felix*, sing and nest very similarly, yet quite differently from the northeastern *T. ludovicianus*. Clearly, we must know songs, nests, plumage sequences, internal structure, colors of soft parts, etc., to classify these wrens properly and to determine the presence of open-ring forms, which also may occur in House Wrens (*Troglodytes*). The plain-colored lowland *Troglodytes musculus* overlaps (in El Salvador, at least) the bright highland forms, with patterned head, flanks, and crissum. These forms are replaced, northwest of the Isthmus of Tehuantepec, by less brightly-colored races with longer bills and (northward) tails. Yet a principal break in characters, in southern Arizona, is only subspecific (Marshall, 1956); we may suspect the same status at the Isthmus of Tehuantepec in the highland series. Thus, if *musculus* is conspecific with the far-northern forms which it much resembles (cf. Paynter, 1957a), we may have an open-ring form in *Troglodytes*.

Other possible American open-ring forms are *Amazilia beryllina* and *cyanura*, and *Anthracothorax thalassinus* [= "*prevostii*"] and *nigricollis* (see Dickey and van Rossem, 1938). *Cassidix mexicanus* now seems to be forming a new ring around the Sierra Madra Occidental; two races have overlapped in southern Arizona since these grackles were last reviewed (by Phillips, 1950). Three cases of overlapping, reproductively isolated subspecies (*Pica*, *Parus*, *Phylloscopus*) in Asia are cited by Vaurie (1955); the case of *Parus major*, cited by him, has been subsequently reported as denied by Prof. Portenko (in Vaurie and Snow, 1957:42).

Were there but four points of contact, we could regard the case of *Pipilo erythrophthalmus* as an open ring around the Río Balsas basin; but the intermediate Teziutlán population obstructs this simple viewpoint.

VALUES OF SUBSPECIES

Subspecies have practical uses, too. By careful studies of series of specimens I have traced the times and routes of the migrations of numerous populations of birds (most of the data remain unpublished; cf. Phillips, 1951). No other method is as profitable in western North America, where many well-marked subspecies are migratory. The amount and distribution of geographic variation is a clue to the length of occupancy, by the species, of different regions, and to their past isolation. Subspecies, or even popu-

lations that are not distinct morphologically, must be considered by such workers as experimental zoologists and game managers (cf. Aldrich, 1946).

INTERSPECIFIC HYBRIDIZATION⁶

Two genuine species of North American birds regularly hybridize: the Blue- and Golden-winged Warblers (*Vermivora pinus* and *V. chrysoptera*). This occurs freely in the relatively large part of their restricted breeding ranges that overlaps, but does not blur the species' boundaries. The exact per cent has not been determined. Parkes (1951) considers the striking differences in coloration between the two species as due to only three gene pairs, and reviews the literature. In the related genus *Dendroica*, *townsendi* and *occidentalis* hybridize rather regularly, as first shown by Jewett (1944); and *D. coronata* and "*auduboni*" cross still more often,⁷ but are probably conspecific.

Despite a voluminous literature of supposed hybrids (partly reviewed by Cockrum, 1952), real interspecific hybrids in North American birds are largely limited to ducks (*Anatinae*), Galliformes, hummingbirds (*Trochilidae*), and wood warblers (*Parulidae*), with only a very occasional case in other groups (most of these in *Picidae* and "*Fringillidae*"). "Hybrids" listed by the A.O.U. (1955:4-5) are almost all between artificial species; in one case, *Junco oreganus* and "*aikeni*," one supposed "parent" is absent from the area! The one positive exception is in *Lophortyx*, and I do not believe that one of every 44 quail *anywhere* is a hybrid.⁸ Certain interbreeding forms of orioles (*Icterus*), buntings (*Passerina*), etc., on the Great Plains are dubiously distinct species (cf. Sutton, 1938).

GENERAL TENDENCIES, CLINES AND CONCORDANCE

Geographic variation is often clinal. More than one cline may be involved, and certain clines appear rather frequently in unrelated species. Thus, size often reaches a maximum in the southern Rocky Mountains or on the northern Sierra Madre Occidental, or a minimum in marshes of San Francisco Bay or northward; insular or peninsular birds may show large bills; hole-nesting species have small races among the cardons and saguaros of the Gulf of California region. Eastern sparrows (*Emberizinae*) are darker, with deeper bills, than their relatives on the Great Plains and west, but smaller and darker forms often occur again west of the Cascade Mountains, and they are represented by dark populations

⁶The word "hybrid" should be restricted to crosses between two organisms that are believed to be true species, such as the mule, in its classic meaning. Its use for crosses *within* the species can only result in destruction of its meaning, so rarely are two organisms exactly alike.

⁷Though some alleged "hybrids" reported, as by Packard (1945), are merely molting "*auduboni*".

⁸Both in collecting and in preserving specimens, collectors select the unusual, such as real hybrids, and often neglect the common.

(if at all) in Mexico. Northeastern, migratory races may have slightly more pointed wings than those that perform shorter, or no migrations; this is probably true of southern hemisphere migrants also (*cf.* Meise, 1949). The brightest, yellowest races of some *Parulidae* are along the Pacific coast, but this cline runs southward in *Dendroica aestiva* (= *petechia*, part, of much recent literature) and eastward, exactly reversed in *Vireo belli*, at least.

Miller claims (1956:265) that the pattern of the Song Sparrow (*Melospiza melodia*), of whose many races over half are restricted to the Pacific coast area or islands from Alaska to Baja California, "can be repeated in lesser or greater degree over and over in terrestrial vertebrates." The A.O.U. (1931, 1957) offers some support to this claim, as regards birds. But a number of the recognized Californian subspecies have no validity; several, based on post-mortem color changes, end neatly at the Baja California border. Such Californian Song Sparrows as "*mailliardi*" are surely not comparable to the Mexican races (see Marshall, 1948; Phillips and Dickerman, 1957). Only objective studies of abundant new material of all species can decide to what extent California exceeds other regions in subspeciation and to what extent in its quality of ornithology.

The western United States and Mexico, with their wealth of diverse, isolated habitats and shortened migrations, naturally produce more subspecies than the relatively uniform north and east of North America. The main geographic variations, in a number of species, are limited (or chiefly so) to Mexico and, in some, Middle America. Examples are *Accipiter striatus*, *Colinus virginianus*, *Dendrocoptes scalaris* and *stricklandi* (including "*arizonae*"), *Myriarchus* spp., *Empidonax difficilis*, *Contopus sordidulus*, *Tachycineta thalassina*, *Stelgidopteryx*, *Progne* spp., *Auriparus flaviceps*, various wrens (*Troglodytes*, *Campylorhynchus*, *Cistothorus*, *Catherpes*, *Salpinctes*), *Mimus* (probably), *Poliophtila* spp., *Vireo gilvus* and probably *griseus*, *Parula* (see Parkes, 1954; Paynter, 1957b), *Geothlypis* spp., *Sturnella magna*, *Icterus spurius* (including *fuertesi*) and *cucullatus*, *Cassidix* spp., *Pyrrhuloxia* (including "*Richmondensis*"), *Carpodacus mexicanus*, *Aimophila* spp., and "*Amphispiza*" *bilineata*.

Clines need not run parallel; indeed they may cross perpendicularly. Thus, in the Great Basin region, clines in *Melospiza melodia* toward long wing and dark color northward cross clines toward short wing, large bill, and heavy breast-spotting westward. In *Oporornis tolmiei* (see Phillips, 1947), the usual east-west cline of increasingly bright dorsum is short and not striking, though obvious in unworn plumages; it crosses a north-south cline of lengthening tail; while slightly farther north (and eastward) is the closely related *O. philadelphia*, separable in immature plumages only by its shorter tail. Thus this cline runs through two species, if they are really distinct.

All variations, then, need not be concordant geographically; but geographic variations are usually or always concordant in the two sexes. That is, the area where the color or proportions of the female changes is also where the male changes, if at all. Another frequent concordance is between the geography of many subspecies in quite unrelated species, which tend to be delimited along very close lines, such as the crest of the Cascade Mountains.

PATTERNS OF GEOGRAPHIC VARIATION

Geographically variable birds show at least five general patterns. Pattern 1 is *Clinal or convergent variation*. This usually involves one species, but may cover two as in *Petrochelidon*, *Oporornis*, *Sturnella*, and *Junco* (and more than two could conceivably be involved). Thus, *Sturnella magna* gradually becomes paler, with less black that becomes broken into bars, as it approaches its original zone of contact with *S. neglecta*, whether from east or south. The resulting *S. m. lilianae* is just like *neglecta* in general coloration and broadly sympatric with it. Conversely, *Junco hyemalis* and *J. phaeonotus* are allopatric.

Where two species are involved, a common fallacy is that the convergence is due to hybridization. Thus, hybrid origin of the southernmost race of *Junco hyemalis* (*dorsalis*) was suggested by Dwight (1918) and later Miller (1941:379; 1956:268). This infers that the original *Junco* stock first diverged, then overlapped and produced a fertile hybrid population, and then both parents withdrew or were selected against and lost. How much simpler to believe that, in a simple cline, mutations and behavioral differentiation isolated the two Arizona forms (*dorsalis* and *palliatius*) reproductively as well as geographically. Miller also calls the northernmost Arizona birds a "hybrid swarm" between *dorsalis* and *J. b. caniceps* (1949:340). By this sort of logic, practically all forms of *Junco* are hybrids between *carolinensis* of the Appalachian Mountains and *alticola* of Guatemala, if not *vulcani* of Costa Rica. Coues (1866:83) remarked facetiously, but all too prophetically, "How convenient it would be if we could, with dignified imperturbability, accept a broad theory of hybridization as the correct solution of these constantly recurring and vexatious problems!" Once well differentiated, a species is not particularly apt to hybridize, much less to alter the characters of neighboring populations.

Pattern 2 is the *Open-ring form*, a single species or superspecies; here the cline encircles a wholly unoccupied region, and its overlapping ends are more or less isolated reproductively. This is discussed above.

Pattern 3 is *Broken-ring forms or divergent variation*. Here pattern 2 breaks up still further, producing two species which are quite similar except where they approach each other. They become more distinct morphologically where they overlap. Assuming that Rock Nuthatches (*Sitta neumayer* and *tephronota*) once inhabited parts of Russia north of their present

range, and ranged thence east past Tibet, we can account for the similarity of the races east and west of the present zone of overlap in Iran (*cf.* Vaurie, 1950). The case would then have been comparable to that of *Larus argentatus*, except that the hiatus contained inland seas and high mountains instead of the Arctic Ocean.

Pattern 4 is *Parallel variation*. At least two species are involved, and the other patterns may occur concurrently. Besides the "general tendencies" above, conspicuous examples are the different species of *Dendrocopos* woodpeckers. Both *D. villosus* and *D. pubescens* have reduced white spotting in the west, plus darker underparts in the Pacific northwest, and size varies in a parallel manner.

Pattern 5 is *Non-clinal or random variation*. Geographic variations occur irregularly. Among the purely gray forms of Plain Titmice (*Parus inornatus*), larger, somewhat darker birds occur in the White Mountains, California, but also in Colorado; small birds occur in the Southwest, but also in Idaho; while the central (Utah) populations are normal or undifferentiated. Naming of these random variations seems pointless. Color variation in the *plumbeus* group of the Bush-Tits (*Psaltriparus minimus*) in the same region (and south to latitude 30° N.) likewise seems not to be clinal.

Similarly, Lincoln's Sparrow (*Melospiza lincolni*) shows slight variations in size (none of importance in color) away from the Pacific northwest, where it has a small race with a rich buff overcast anteriorly. The wing (chord) averages variously from 61.2 to 63.2 mm. in males of the northern interior. Males average 65.2 to 65.9 mm. from Colorado to central California. On this basis Miller and McCabe (1935) named a southern race "*Passerella lincolni alticola*" without any diagnosis nor stated summer nor winter range. They admitted that topotypical *lincolni* (of Labrador) averages 63.8 mm., while the southernmost California males average only 64.3. Six of my twelve breeding males from Arizona measure less than 64 mm. Clearly, there is no cline or nomenclatural value here.

Exclusive again of the Pacific coastal area, the Poor-will (*Phalaenoptilus nuttalli*) shows several pronounced color types; at least one, *hueyi* of the Yuma region (Arizona and California), is well-marked and locally dominant. But alongside these birds occur, not infrequently, normal individuals, just like ordinary Poor-wills elsewhere. These are now called "migrants," yet some were taken in late May, after migration has probably ended (there are no helpful annotations on the labels). Mutations and natural selection in this open-ground-dwelling bird are producing local color phases; but until these become more exclusive, individual variation is too great to recognize useful subspecies. Similar cases are the random size variations of *Cacatua*, *Psittichas*, etc., in the New Guinea area (Mayr, 1942:37).

REPRODUCTIVE ISOLATION WITHIN THE SPECIES

Reproductive barriers within a species occur in the open-ring forms, and probably in Traill's Flycatcher (*Empidonax traillii*), whose two eastern subspecies are barely distinguishable morphologically. Yet they have distinct habitats, songs, and nests (Snyder, 1953; Aldrich, 1953). To complicate an already difficult matter, the race of the southern Great Plains has now spread eastward over part of the other race's original range. Naturally we cannot easily determine the amount of interbreeding between two forms that hardly differ except in voice and behavior; but these are just the differences that do maintain reproductive barriers between the species of *Empidonax*. Even if the barrier were complete in *E. traillii*, however, few ornithologists would recognize two species in the absence of divergence in size, structure, or pattern, and with such minute differences in color.

In other cases where two subspecies overlap with little or no known interbreeding, they differ usually in size, not behavior. Examples are: the Red Crossbill (*Loxia curvirostra*) in the western United States and the Great Lakes area; the Brown-headed Cowbird (*Molothrus ater*) in a belt from Owens Valley, California, east to northwestern New Mexico, but excluding southwesternmost Utah; and the Boat-tailed Grackle (*Cassidix mexicanus*) in places, at least in southern Arizona (though the situation here may now be simply another open ring). Unfortunately, the first two are especially unsuitable subjects for study; the crossbill nests in winter, and few nests have yet been found, while the cowbird does not nest at all, being parasitic. Still we could study the amount of mingling of the races, their reproductive condition and mating behavior, local distribution, regularity or irregularity in the zone of overlap, and the frequency of genuine intermediates. Even complete reproductive isolation locally would not demonstrate full species rank here, either. (Opening forms have been discussed above.)

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SUMMARY AND CONCLUSIONS

Birds, like other groups, show a wide variety of patterns of speciation. The taxonomist must always consider every point, and avoid complete reliance on any one point, especially where the bulk of the evidence is at variance. Speciation is *not* merely a matter of adult external morphology, as often misconceived, but includes voice, behavior, life history (including juvenal plumages and molts), and at times other aspects of ecology. Because of this wide variety, we must especially beware the author who bases a general argument on a few carefully selected

examples, chosen strictly to prove his narrow and preconceived point of view.

Despite the very poor quality of ornithological collections, birds are today the best-known major group of animals. Their speciation and migrations are often correlated. Species, and often subspecies, are perfectly obvious entities; each of the two ranks contains both well-marked forms and others difficult to distinguish, though the latter are naturally far more numerous among subspecies than among species. Reproductive isolation, while not 100 per cent reliable in distinguishing the two categories, is of maximum importance and is normally a psychological (ethologic) problem. The "open-ring form" is a case in point, and other examples are cited.

Recent trends are toward a biological species concept (in spite of stubborn resistance) and a constant increase of the number of subspecies recognized, with a gradual decrease in the number of species. Attempts are made herein to define the species and the subspecies, and to describe and classify the main patterns of geographic variation in birds.

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