THE AMOUNT OF OVERLAP ALLOWABLE FOR SUBSPECIES

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THE present tendency toward finer and finer subdividing of species into subspecies or geographical races, with formal trinomial nomenclature, is regarded from different viewpoints, both approving and disapproving. Agreement or at least a clarification of the principles to be followed in the applying of subspecific names is to be hoped for. The present paper is a contribution toward the clarification and stabilization of taxonomic practice in regard to lightly defined subspecies.

VARIATION IN THE SPECIES

Every individual bird differs somewhat from every other bird; any local population is at least slightly different from any other, while in appearance some populations differ widely from others of the same species.

These different degrees of variation are illustrated by such examples as the introduced House Sparrow, *Passer domesticus*, in North America in which Lack (1940) found very little geographical variation (Calhoun's (1947) study on the same subject produced more positive results, but his methods do not inspire confidence); the Lincoln's Sparrow, *Melospiza lincolnii*, in which, within the named subspecies, there is much geographical variation below the level at which it is useful to name further races (Miller and McCabe, 1935); the Field Sparrow, *Spizella pusilla*, in which a distinct eastern and western race occupy considerable areas with a broad area of intergradation between (Wetmore, 1939: 240), and such complexes as that of the Sapsucker, *Sphyrapicus varius*, in which some students still prefer to retain the three very distinct types as species.

SETTING THE LIMITS OF THE SUBSPECIES

Subspecies are subdivisions of a species; each has an exclusive geographical range, and characters which separate it from every other subdivision. The limits of subspecies are subjective, in many cases entirely depending on the judgment of the individual taxonomist (Mayr, 1942: 106). To paraphrase—the subspecies (like the genus and family) of the taxonomist is his own creation, and not a natural unit, though based on a natural phenomenon. There are a limited number of borderline cases in which the results of geographical variation grade from subspecies to species, with the development of biological discontinuity (Mayr, 1942). But the border line at the other

extreme, at which subspecies grade into non-namable populations, is marked by no biological phenomena. The taxonomist makes an arbitrary decision. This, being subjective, naturally varies with the taxonomist. In non-mensurable data it may depend on such factors as the personal acuity of color perception (Moreau, 1948: 109); and Taverner (1940: 540) wrote that common practice is to decide "with the assistance of intuition based on experience and personal equation."

However, though most taxonomists have not formulated the principles they follow, a body of convention has grown up, but with wide diversity in practice.

General Practices

It is generally agreed that subspecies may be separable on average characters. Populations, not individuals, are the units involved. A certain amount of overlap caused by individual variation is permitted without invalidating the subspecies; this is aside from the intergrading populations situated in intermediate areas.

Of course the racial characters used may be apparent only in one sex or in one age group. For example, Rand (1948a) used only the females in his study of the Spruce Grouse, *Canachites canadensis;* and in the northern races of the White-crowned Sparrow, *Zonotrichia leucophrys*, while the adults are quite distinct, the immature birds can not be distinguished (Rand, 1948b).

Huxley (1942: 405), Mayr (1943) and Tucker (1946) asked for a rather broad concept of the subspecies that may include many smaller, slightly differing populations. At the other extreme are such workers as Clancey (1946) who claimed that the validity of a form should rest solely on the measure of constancy of its imputed criteria and not on degree of separability. Apparently he believed that any demonstrable difference is sufficient.

Tucker (1946) has ably pointed out the horrible results of accepting Clancey's principles. He wrote, "any population can be shown to be genetically different from any other, provided only that the technique of analysis is sufficiently delicate and precise. If, then, a demonstrable difference is to be the only criterion, the logical and unavoidable conclusion which follows from this demonstration is that at least in the case of fairly sedentary birds—names should ultimately be given to the populations of every moderately isolated area of woodland, moor or marsh—it is merely a matter of the delicacy of the analytical technique applied to them." This is a *reductio ad absurdum*. A halt must be called at some point.

Tucker suggested that the point at which a halt should be called is

where the multiplication of names begins to retard and confuse the study of geographical variation, a point of view probably acceptable to most taxonomists.

DISSATISFACTION WITH TRINOMIALS

The principle of applying trinomials to populations has been attacked from both sides. On one side Lack (1946) has suggested that subspecific trinomial nomenclature has outlived its usefulness. On the other hand, Harrison (1945) thought that our present trinomial system is inadequate for indicating intergrades and suggested also employing a bifid system. The example he gave, for the population of jays in southeastern England is

Garrulus glandarius < *G. g. rufitergum* / *G. g. glandarius*

indicating the birds are most similar to *G. g. rufitergum* with a tendency toward *G. g. glandarius*. The idea is not new and is more clumsy than the usual method of indicating it as *Garrulus glandarius rufitergum* $\gtrless$ *glandarius*. This is of course a convention, does not alter our basic trinomial system, and is a sound auxiliary method of referring to specimens.

Huxley (1942), to designate a cline, had advanced another useful adaptation of our trinomial system, which for our Yellow-shafted Flickers would read thus: *Colaptes auratus* cl. *auratus-luteus*, indicating that from one end of the range of the species, where the birds are called *C. a. auratus* to the other end of the range where the birds are called *luteus* there is a gradual change in characters.

Toxopeus in 1930 suggested another adaptation to express relationships, which is in effect a quadrinomial system with one of the names in brackets; van Bemmel (1948: 326–327) thought this could be used to advantage for birds. But Mackworth-Praed (1943) viewed with disfavor the whole business of four or even five names to express finer "splitting" and suggested we might get such a combination as *Troglodytes troglodytes troglodytes troglodytes indigenus* for a "poor little wren whose distinctiveness is disputed."

There may be, in time, a system evolved for designating finer distinction or more effectively portraying relationships than our trinomial system, but at present our trinomial system is the only satisfactory one. The tendency to go on naming lightly differentiated populations is rendering it less useful, and, as Tucker (1946) said, such practice would result in a situation which "would be a stultification of the whole principle of trinomial nomenclature."

PRESENT CONVENTIONS ON SEPARABILITY

It seems advisable to accept a criterion based on separability as the final test of the validity of a subspecies. Probably most taxonomists use some such test, but what they use is not always apparent from their work, and few have formulated the principles they follow. The most common seem to be:

(1) the average of one subspecies separable from the average of the other subspecies.
(2) 75 per cent of one separable from all of the other.
(3) 50 per cent of one separable from all of the other.
(4) 75 per cent of one separable from 75 per cent of the other.
(5) the means of the two forms separable by the sum of their standard deviations (= 84 per cent from 84 per cent).

Before going on to discuss each of these, it is advisable to clear up a number of points.

Range of variation and size of sample.—Though museum taxonomists work with series, these are but samples of populations, and the results of the studies, including the names, are meant to apply to populations. In this connection it is important to remember that the size of the sample tends to determine the range of variation represented. Simpson (1941) has emphasized a point of great importance; in comparing samples, *the observed variation increases with the size of the sample.* For example, the observed variation in a series of 10 birds is only about half that to be expected in a population of 500 birds, and the observed range in five birds is only about half that to be expected in 75 birds. This means that small samples may show no overlap, while the populations from which they are drawn show considerable overlap. In separating subspecies, not only the observed range must be considered, but also the probable total range of variation of the population from which the sample came. The total range can be computed statistically for measurements, but for color the personal element intrudes in ordinary practice.

Assuming a sample of five as having a range of variation represented by the factor 1, the increased range of variation to be expected in the larger sample is shown (approximately) by the following factors.

Size of sample	*Factor*
5	1.0
10	1.3
20	1.6
30	1.7
40	1.8
50	1.9
75	2.0

Size of sample	*Factor*
100	2.1
150	2.2
200	2.3
500	2.6
1000	2.7

(Adapted from Table I of Simpson, 1941: 790)

The above are based on averages. Thus, a sample of 75 has, on the average, about twice the range of variation of a sample of five, but this will not be exactly true for every sample.

Overlap.—It is generally agreed that between two subspecies overlap through individual variation may occur without invalidating the subspecies; this is aside from intermediate geographical populations that are intermediate in character. To the question of separability, the number of specimens in the region of overlap is very important.

Ordinarily, one end of the range of variation of one subspecies overlaps one end of the range of the other; this shows a partial overlap. It may be illustrated by the hypothetical example listed below.

Postulated character	*Subspecies A*	*Subspecies B*
Wing greater than 180 mm.	95 per cent	0 per cent
Wing between 175–180 mm.	5	5
Wing less than 175 mm.	0	95

In this example, 95 per cent of one subspecies can be definitely and accurately identified and separated from 100 per cent of the other, with 5 per cent unidentifiable or in the zone of overlap. This is an ideal, easy type to work with. With greater or lesser extent of overlap, this is the type of variation usually assumed. It permits working with and identifying positively some percentage of the individuals.

However, in some cases there may be complete overlap in characters, but in frequency of occurrence there is great geographical variation. Almost all the individuals of one subspecies are readily separated from almost all of the other, but a few are indistinguishable. This is illustrated by the following hypothetical example.

Postulated character	*Subspecies A*	*Subspecies B*
White-lored	95 per cent	1 per cent
Grey-lored	4	4
Black-lored	1	95

Ninety-five per cent of A is separable from 99 per cent of B, but no percentage of A is separable from 100 per cent of B. In identifying a mixed collection by the characters, one would identify all white-lored birds (96 per cent) as A, and all black-lored birds (96 per cent) as B; four per cent of the birds one would class as intermediates; 95 per cent of the birds would be correctly identified (one per cent would be incorrect), but one would not know which ones.

An approach to this type of overlap probably occurs more often than is realized. Rand (1948c) has summarized a number of cases in which an individual of one subspecies looked more like another. Chapman (1928: 19) in reviewing the variation in the Barbet, *Capito auratus*, repeatedly found individuals in the range of one form which could not be distinguished from specimens of another and quite different form. These he considered as members of the subspecies in whose range they occurred.

DISCUSSION OF CONVENTIONS

Average separable from average.—This seems to be the criterion most commonly in actual use and seems indicated by such statements as:

"Averaging larger than"
"wing usually between 160 and 170 mm."
"wing usually less than 126 mm."
"averages slightly paler than"
"85% different, as a rule, from"
"that certain extreme measurements overlap does not invalidate the distinction."

The conclusions reached are backed by greater or lesser amounts of experience in handling recognized subspecies and in identifying specimens to subspecies. Since these methods have worked for so long, they undoubtedly have value. But, that does not mean they cannot be improved. Such statements as Deignan's (1946: 382) in his review of the Striated Grass Warbler, *Megalurus palustris*, based on 35 usable skins from the study of which he recognized three races; "While it is possible to recognize three geographical forms, this can be done only by a close study of the coloration of the upperparts when the birds are laid out in series; single examples of any population may be racially unidentifiable without reference to the label" make one wonder what percentage are racially unidentifiable.

Would it not remove some of the personal element and contribute toward standardization to state at least what percentage are separable and what are not? Or more simply, state how many of the specimens in the sample are different, and how many overlap and are inseparable.

Seventy-five per cent from all.—The impression one gets from much recent discussion is that the current practice with most taxonomists is to require 75 per cent of one subspecies to be separable from all of another. Actually, many practicing, outstanding taxonomists do not follow this. A. H. Miller does not (see under "75 per cent from 75 per cent), and E. Stresemann does not (see under "50 per cent from all"). An examination of much current work and checking on samples

of some North American races indicates that in much work lower standards are maintained. This is particularly evident when size is the criterion and the average of the one form falls close to or within the range of variation of the other. It is quite evident from the following example that Ridgway in his classical 'Birds of Middle and North America' did not use as strict a criterion.

Ridgway (1916) characterized *Coccyzus americanus occidentalis* as similar to *C. a. americanus* but averaging decidedly larger. The measurements in millimeters he gave (pp. 13, 17) are:

americanus ♂; wing, 135–154 (av. 143.6); tail, 133.5–150 (140.7)
occidentalis ♂; wing, 143.5–154.5 (av. 149.6); tail, 140–155 (av. 147.1)
americanus ♀; wing, 138.5–151 (av. 146.4); tail, 139–151 (av. 145.5)
occidentalis ♀; wing, 144–156.5 (av. 150.4); tail, 133.5–156 (147.2)

The fineness of the distinctions between some North American races is emphasized by Friedmann (1930: 182), who, while rejecting a proposed Madagascar race of *Himantopus himantopus* stated, "It must be admitted, however, that not a few races of North American birds are based on just such vague general differences."

There is one aspect of the "75 per cent from all" convention that is well illustrated by Dunn (1934: 170). In discussing a salamander, *Plethodon cinereus*, he pointed out that 100 per cent of those west of the Mississippi are red-backed, while east of the Mississippi 50 per cent are red-backed and 50 per cent are black-backed. He stated that, if the proportions in the East were altered to 75 per cent black, the two populations might appropriately be given different racial names. This would make 75 per cent of the eastern form (those with black backs) separable from all individuals of the western form (all with red backs) but not even one per cent of the western form (all red-backed) from all individuals of the eastern form (in which 25 per cent would have red backs). Thus, the definition must be worded as 75 per cent of one separable from all of the other, and the converse; else, one gets the anomalous situation of A being separable from B, but B not separable from A. This is illustrated by tabulating the data thus:

	Subspecies A	*Subspecies B*
Red-backed	75 per cent	0 per cent
Black-backed	25	100

Seventy-five per cent of A is separable from all of B, but not even one per cent of B is separable from all of A. To be logical, the criterion should enable both A and B to be valid, as many taxonomists would consider them. Note that even if the 75 per cent were carried to 98 per cent the same difficulty would arise.

It can be argued that the "75 per cent from 100 per cent" can be con-

verted by statistics to equal "96 per cent from 96 per cent." However, this would mean that one would have to have 25 specimens of each form before one would expect overlap to the extent of one specimen (that is, 24 out of 25 different). Obviously, much work is done on smaller samples, and overlap is permitted in these smaller samples. Thus, to consider much current work now admitted as valid, the convention would have to be less selective.

Fifty per cent from all.—This criterion that 50 per cent of one population be separable from all of another is advocated by Stresemann (1943) and it or standards similar to it are probably widely used, judging by studies of current workers.

This "50 per cent from all" has the same advantages and disadvantages of any "per cent from all," as mentioned under the preceding section.

It can be shown by statistics, that "50 per cent from 100 per cent" practically equals "93 per cent from 93 per cent." It appears surprisingly little different from "75 per cent from 100 per cent." It makes more allowance for the few extreme specimens. Using this, in samples one would not expect any overlap until 14 specimens of each were compared.

This is more practical, and much nearer current usage than "75 per cent from all."

Seventy-five per cent from 75 per cent.—This convention is that 75 per cent of one subspecies be separable from 75 per cent of the other. Also, 75 per cent of a mixed series will be correctly identified. This means that 100 per cent of a mixed series will be identified, with only a 25 per cent error, but one will not know which specimens are incorrectly identified. The identification has shifted from the individual to the population (quite properly), and the sample is identified by the percentage of different characters in it.

Rand used this in his Spruce Grouse, *Canachites canadensis*, study (1948). Miller also used it, or something very close to it in his Junco study (1941: 264). Miller recognized the race of Junco, *J. o. shufeldti*, as different from the race *J. o. montanus* on the basis of size. He said males of *shufeldti* are usually (75 per cent) less than 77 millimeters in wing length; males of *montanus* usually (85 per cent) more than 76 millimeters in wing length. The corresponding figures for the females are 66 and 85 per cent. Miller stated that by using these measurements, one can separate 75 to 80 per cent of the individuals of the two geographic groups.

In applying this criterion of "75 per cent from 75 per cent," it demands that only three out of every four specimens be separable.

Eighty-four per cent from 84 per cent.—This is similar to the "75 per cent from 75 per cent" convention but more selective. It was used by Brodkorb (1944) in separating the Black Vultures into races. This percentage was chosen because of a statistical principle; if the averages of two samples differ by the sum of their standard deviations, at least 84 per cent of one form will be separable from 84 per cent of the other, a degree of difference "usually accepted as the minimum for subspecific separation."

A sample of seven birds (actually 6.2) must be examined before any overlap should be expected.

Ninety-three per cent from 93 per cent.—This would correspond with the degree of difference of those who advocate a "50 per cent from 100 per cent" separation. A series of 15 birds (actually 14.2) would be necessary before any overlap should be expected.

Ninety-six per cent from 96 per cent.—This would correspond with the degree of difference demanded by those who advocate a "75 per cent from 100 per cent" separation. A series of 25 birds must be compared before any overlap is to be expected.

In considering a given percentage of one population separable from the same percentage of another, the following shows the smallest series of each form that can be used with each percentage and any overlap expected.

75 per cent	= 4 birds (that is, 3 out of 4 birds)
84	= 6.2 (7)* birds (6 out of 7)
90	= 10 birds (9 out of 10)
93	= 14.2 (15)* birds (14 out of 15)
96	= 25 birds (24 out of 25)

* As one can not use 0.2 of a bird, the next largest number must be used.

"A percentage from all" versus "a percentage from a percentage."—Each system has its advantages, and its disadvantages. The "percentage from all" has the advantage that a given percentage of specimens can be positively identified as individuals. The main criterion here is not average difference but is the non-occurrence of certain characters.

The disadvantages are that, in defining races, definite limits are set to the "zone of overlap," both upper and lower limits, on the basis of the samples. But as variation is greater in large samples this "zone of overlap" will vary with the size of the sample, and in larger samples individuals will occur outside the originally defined limits and may even resemble more closely the neighboring subspecies. Various methods have been used to explain the presence of such individuals. Some taxonomic treatment may obscure their occurrence, especially in North America where migration is pronounced, by treating them as

wanderers or migrants (Rand, 1948c). Another way of treating this type of phenomenon has been to consider each type as representing different species. This was often done with the two races of White-crowned Sparrows, *Zonotrichia leucophrys leucophrys* and *Z. l. gambelii*. Over most of the range of *Z. l. leucophrys* the species has black lores, and it has been customary to identify only white-lored specimens as *gambelii*.

Yet another way to treat this embarrassing type of overlap is to call such specimens freaks and not include them in the data. This is illustrated by Rogers' (1939) treatment of measurements when he described the White-throated Swift, *Aeronautes saxatilis sclateri*. The difference is in size, especially that of the wings—wings of male *sclateri* range from 143 to 151 and average 146.3 millimeters; *saxatilis*, 128 to 145 and average 139.15. However, in a footnote it is stated that one specimen of *saxatilis* measured 147 millimeters. Apparently this was omitted as an exceptional measurement, although only two millimeters greater than the next largest, because, otherwise, the average of the larger form would have fallen within the range of variation of the smaller. This is a quite unjustified treatment. The more extreme specimens are unusual or "freaks" simply because they occur less often. As such they affect averages little, but they are part of the population.

Another way of avoiding embarrassing overlap was used by Oberholser (1914): "The specimens used in the average measurement under each subspecies, and with which comparisons are made, are taken just as far as possible from typical specimens—that is, from specimens best exhibiting the differential characters." This sounds like rigging the evidence and is inexcusable.

Working with species showing such overlap it is no longer possible to identify individual specimens with absolute certainty, but it is still possible to identify populations by their composition. It is necessary to revise our thinking. We identify 100 per cent of a mixed collection and 95 per cent may be correctly identified; we can't tell which five per cent is incorrectly identified but that does not matter.

The "percentage from a percentage" has the advantage that it deals with populations. When the dividing point between two subspecies is properly set, with moderate sized samples the proportions above and below this line will remain constant with increase of sample size.

The disadvantage is that a situation could occur in which no individual can be identified with certainty. This is inherent in the problem; we are dealing with populations with average differences, and any

population, or sample of it, can be analyzed to see in what proportions the characters exist and can be identified accordingly. This can even be done in zones of geographical overlap, or in winter range; see Rand and Traylor (1949) for use in Catbird.

A SUGGESTION

From the cases examined it appears that the separability often used is less than 75 per cent from 100 (or 96 per cent from 96 per cent) which is sometimes implied in discussion. It seems that some standard of about 80 to 90 per cent of one race separable from about 80 to 90 per cent of the other would actually correspond with much current conservative practice. Perhaps this would be the most practical.

But even more important would be the practice of stating clearly the number of the specimens examined that actually were different and the number that showed overlap.

APPENDIX

To illustrate the degree of separability exhibited by some North American races the three following analyses of species with more or less lightly defined subspecies are given.

(1) The Mourning Dove, *Zenaidura macroura*, is currently considered as divisible into two lightly differentiated races in the United States, *carolinensis* (Wisconsin and Iowa to the Gulf Coast and eastward) and *marginella*, larger and paler, farther west. The distinctions between the two races are usually considered slight. The material in the Chicago Natural History Museum from Saskatchewan to British Columbia south to California and Arizona was considered to represent *marginella*, and material from Wisconsin to Connecticut and south to Florida, *carolinensis*, in making the following comparisons (only males used).

Wing-length (measured flat)	*144*	*5*	*6*	*7*	*8*	*9*	*150*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*160*	*1*	*2*	*3*	*4*	*165 millimeters*
	75 per cent																					
carolinensis (10 birds)	1	1		2			1		1	1	1	1	1	75 per cent								
marginella (12 birds)												3	3		1	1	1		1		2	

The averages of these two series, 149.8 and 157.3 millimeters, are farther apart than those recorded in a recent study of this species by Pitelka (1948: 121).

Color was estimated by laying out the summer, worn birds in a graded series from dark to light. For tabulation purposes this series, in which the graduation appeared uniform, was divided into eight nearly equal parts. The results are:

	Dark				*Light*			
	I	II	III	IV	V	VI	VII	VIII
carolinensis (11 birds)	4	3	1	1	1	0	1	
	75 per cent				75 per cent			
marginella (14 birds)	0	0	2	2	3	2	3	2

To reduce the possibility of wear and fading being greater in the more arid west, fall and winter birds in unworn plumage from Connecticut, Georgia and Florida representing *carolinensis*, and birds from Oregon, New Mexico and California representing *marginella* were compared after being placed in nearly uniformly graded series and this series divided into five units. The results:

	Dark			*Light*	
	I	II	III	IV	V
carolinensis (9 birds)	2	3	2	1	1
	75 per cent			75 per cent	
marginella (4 birds)			1	1	2

In this species it would appear that the recognized subspecies are separable on about a "75 per cent from 75 per cent" convention.

(2) *Ceryle alcyon:* Rand (1948b: 31ff) showed that the difference between the eastern and the western races was one of size, and that it was more apparent in the female. His measurements are as follows:

Wing-length in females:	*148*	*9*	*50*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*160*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*170*	*171 millimeters*
alcyon (18)	1	0	0	0	1	1	2	2	1	1	2	1	4	0	1	0	1							
caurina (10)																		5	1	1	0	2	0	1

In the sample itself 100 per cent of *alcyon* is below 165; 100 per cent of *caurina* is above 164 millimeters. On the basis of this sample, of 18 and 10 birds, it would appear that the separability in the population was greater than "90 per cent from 90 per cent", since no overlap occurs in two series of at least 10 specimens each, but the distribution of the measurements in *caurina* is unusual and more smaller birds would be expected.

Adding to the above figures those of the females in the Chicago Natural History Museum, one gets, as expected, a greater range of variation in *alcyon* where the greater increase in number of specimens was made, and none in the *caurina* sample where few were added. The combined figures for wing-length in females are:

	148	*9*	*150*	*151*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*160*	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*170*	*171 millimeters*
alcyon (44 birds)	1	0	2	0	1	1	3	1	4	4	4	3	7	1	5	0	2	4	0	0	0	0	1	
	90 per cent																							
caurina (12 birds)																		5	1	3	0	2	0	1
																		90 per cent						

In this sample, 88 per cent of *alcyon* is separable from 90 per cent of *caurina*, but not 20 per cent of *caurina* can be separated from all of *alcyon*. On a "75 per cent from 100 per cent" convention *caurina* does not qualify; on a "90 per cent from 90 per cent" *caurina* just fails to qualify (88 per cent instead of 90 per cent). Undoubtedly, more measurements of *caurina* would add to the overlap.

(3) Brown Thrasher, *Toxostoma rufum:* The Western Brown Thrasher has been recognized as *Toxostoma rufum longicauda* on the basis of size (Wetmore, 1939). The measurements given below are for our Chicago Natural History Museum material.

Wing, male adult, millimeters	*98*	*99*	*100*	*101*	*102*	*103*	*104*	*105*	*106*	*107*	*108*	*109*	*110*	*111*	*112*	*113*	*118*
	60 per cent																
Maine to Dist. Columbia	1	1	1	3	3	3	3	6	5	4	2	2					
Ill., Ind., Wis.				1	3	0	3	2	2	0	1	0	0	1			
										60 per cent							
Alta., Sask., Mont., Col.							2	1	1	1	0	1	0	0	3	0	1
Man. and N. Dak.								1	3	0	0	0	0	0	1		

Tail, male adult, millimeters	*112–113*	*114–115*	*116–117*	*118–119*	*120–121*	*122–123*	*124–125*	*126–127*	*128–129*	*130–131*	*132–133*	*134–135*	*136–137*	*138–139*	*140–141*
Me. to Dist. Col.			2	0	2	1	7	7	5	4	2	0	2	1	1
					60 per cent										
Ind., Ill., Wis.	2	0	0	1	4	2	2	0	1	0	0	0	1		
Man. and N. Dak.					1	0	0	3	0	1					
										60 per cent					
Alta., Sask., Mont., Colo.					1	0	1	1	1	1	2	0	1	2	

On this data on wing-length, comparing east coast thrashers with those of Alberta, Saskatchewan, Montana and Colorado, slightly over 60 per cent of one is separable from 60 per cent of the other. On tail-length the separability is a bare 60 per cent, and the race fails to qualify by any criterion discussed.

SUMMARY

Subspecies are subjective, though based on natural phenomena, and treatment varies as to the fineness of distinctions used in recognizing subspecies. Some workers claim any constant difference is enough; at the other extreme are those who ask that 75 per cent of the individuals of one subspecies be separable from all of another. Size of sample must be allowed for in making comparisons. With subspecies, overlap may be partial, or it may be complete but of rare occurrence. Current conventions are discussed. As subspecies are often based on average differences, rather than on non-occurrence of characters, a "percentage from a percentage" rather than a "percentage from all"

convention is advisable. A conservative value is suggested—80 to 90 per cent of one subspecies separable from 80 to 90 per cent of another before they be recognized. In any case, the degree of separability should be given in discussing races.

Three examples are given of the application of this treatment to more or less lightly defined races.

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WILFRED HUDSON OSGOOD, 1875–1947

BY KARL PATTERSON SCHMIDT

WILFRED HUDSON OSGOOD was one of the leaders of his generation in the zoological exploration of the two Americas and one of the most influential of museum curators in an era of phenomenal expansion of museums of natural history. He was a survivor of a golden age of systematic zoology in North America, and even through the radical changes of emphasis in modern zoology he commanded the respect of his colleagues in universities as well as in museums. American zoology was enriched by his thoughtful and permanently useful contributions, some of which have had a long-continuing influence in ecology and genetics. Even his short papers describing new species were organized and reflective of sound judgment based on command of the whole range of systematic mammalogy. It becomes those of his successors who knew him best to reflect on his career, to examine its meaning, and to subject it to thoughtful analysis for the lessons derivable from it. It is not the purpose of this essay to attempt a critical evaluation of the man and of his influence, which will find an appropriate place in a history of American natural history museums, when that is written. Though his reputation was mainly in mammalogy, he could by no means forget his first love—ornithology—and from his election as a Fellow of the American Ornithologists' Union,