

## THE SEVENTY-FIVE PER CENT RULE FOR SUBSPECIES

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Now that most species of birds have been described, avian taxonomists have turned their attention largely to the study of variation within the species. The adoption of trinomial names for subspecies was a direct and, in general, valuable result of this trend.

The usefulness of the subspecific concept decreases when subspecies are described on the basis of distinctions that prove to be either non-geographic or too slight to permit satisfactory separation of the populations in question from adjacent subspecies. Innumerable differences of opinion as to the validity of one or another subspecies cause the entire subject to be viewed with increasing dislike by non-taxonomists. Excessive splitting of subspecies may be, in the long run, equally obnoxious to the taxonomist. For example, gradual variation over a long distance (clines) is obscured by the recognition of numerous intermediate subspecies. Often minor variations have a discontinuous distribution within a species, so that too liberal application of names may result in illogical ranges and misunderstanding of the meaning of the variation. Lack (1946:63) found this to be true of the European robin and concluded: "One therefore begins to wonder whether subspecific trinomial terminology is not beginning to outlive its usefulness and validity. Certainly, in the case of *Erithacus rubecula*, it is both simpler and more accurate to describe subspecific variations in terms of geographical trends, and to omit altogether the tyranny of subspecific names." Despite these difficulties, it is unlikely that trinomials will soon be abandoned, or that they should be. Subspecific names, if conservatively used, call immediate attention to variation and incipient speciation.

Geographic variation may be so slight it can be demonstrated only by exhaustive statistical tests, or it may exceed the differences apparent between some full species. Any limit of differentiation set up for the recognition of subspecies must, therefore, be an arbitrary one. The most frequently mentioned of such criteria is the so-called "75 per cent" rule or convention. While I am uncertain who proposed this rule, it may have been the late Admiral H. Lynes who was one of its early advocates.

The 75 per cent rule has been interpreted in two quite different ways. This may be shown by the following table reproduced in part from a recent paper by Rand (1948) on the Spruce Grouse.

Table 1

Plumage type	I	II	III	IV	V	VI-VII		VII	VII-VIII		IX
						VI	VII		VIII	VIII	
<i>C. c. canadensis</i>	0	0	1	6	5	10	14	25	3	6	0
<i>C. c. osgoodi</i>	0	0	0	0	0	0	2	0	6	6	1

Rand had 70 specimens of the population of *canadensis* and 15 specimens of *osgoodi* which he distributed among nine color categories (shown by Roman numerals) as indicated. The brownest birds are in class III; they become progressively grayer through class IX. Seventy-five per cent of a sample of 70 is 52.5. Beginning at the left, classes III-VII, indicated by the upper bracket, will include 75 per cent of this sample (classes I and II were set up for other populations not considered here). Similarly for *osgoodi* 11.2 specimens are 75 per cent of a sample of 15. Beginning at the right, 75 per cent of this sample fall in the last three classes (lower bracket). Since these 75 per cent segments of *canadensis* and *osgoodi* do not overlap, the brownest 75 per cent of *canadensis* are browner than the grayest 75 per cent of *osgoodi*, at least in these samples. Rand concluded that *osgoodi* is subspecifically distinct from *canadensis*. (He has since told me that he now would prefer a separation of about 90 per cent from 90 per cent.) This

method of separation by equal percentages does not tell us directly what part of any population can be individually identified. We do not know how far the 75 per cent segments thus separated are overlapped by the remaining 25 per cent segments.

The other method of applying the 75 per cent rule is to insist that 75 per cent of a population must be separable from all (100 per cent) of overlapping populations before granting subspecific status. For statistical reasons this is better expressed as 99+ per cent rather than 100 per cent (see beyond). Applying this method to table 1, it is

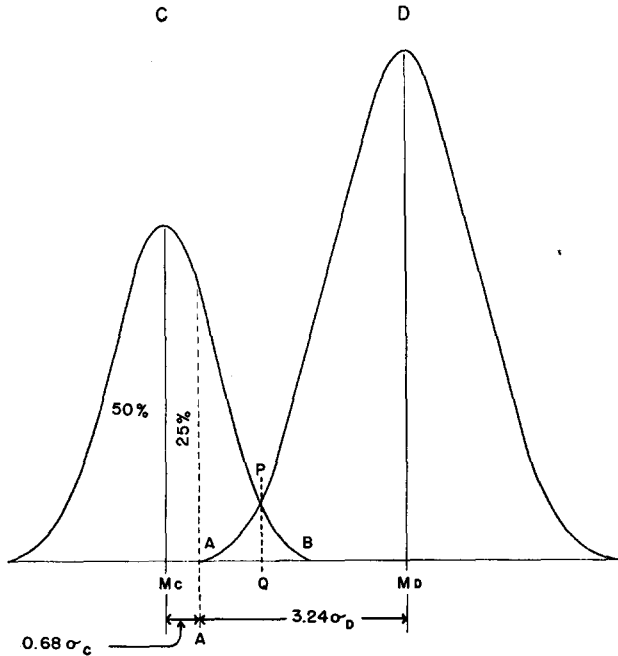


Fig. 50. Distribution curves for two series of overlapping measurements. For explanation see text.

evident that 22 of the 70 specimens of *canadensis* (31 per cent) and only 1 of the 15 specimens of *osgoodi* (7 per cent) are outside the limits of variation of the other population. According to the criterion of 75 per cent from 99+ per cent, *osgoodi* is far below the level of differentiation needed to separate it subspecifically from *canadensis*, if these samples are at all typical.

If smoothed distribution curves for two such series of overlapping measurements are drawn, the results will be similar to figure 50. A line P-Q drawn vertically through the point P where two such curves intersect gives the minimum overlap of the two upon each other. According to the first interpretation of the 75 per cent rule mentioned above, at least 75 per cent of one curve must be separable from 75 per cent of the other by this line of minimum overlap or, to state it conversely, maximum separation. The second interpretation demands that 75 per cent of each curve must be separable from 99+ per cent of the other as determined by upper or lower limits of the curves (see beyond), such as the points A and B of figure 50.

Either of these interpretations, as thus stated, might be adopted. Since the amount of differentiation necessary to give 75 per cent separation by the first is much less than by the second method (table 1 is an example of this) a choice between them must be made. A number of ornithologists, not all taxonomists, who were asked which of these

interpretations seems preferable, preferred the second, probably because it is logical to assume that a "75 per cent rule" means that 75 per cent of the individuals in a population are separable from (all) those in other populations.

Aside from statistical difficulties, which will be considered later, the second method (separation from 99+ per cent) can be used even if some lower figure such as 50 per cent from 99+ per cent were considered preferable. There are, however, a number of reasons for believing that 75 per cent from 99+ per cent is not too rigorous a criterion. Many subspecies, particularly those differing in a number of characters, or those of insular distribution have literally 100 per cent of their individuals separable. This is true even of many continental subspecies except in geographically intermediate areas of intergradation.

It must also be remembered that most taxonomic comparisons do not permit use of all the available specimens. Usually those in immature plumage as well as adults in worn or molting plumage must be eliminated. In some species, for example the spruce grouse of table 1, or certain South American ovenbirds, only the females vary to an appreciable extent geographically.

For one or another of these reasons, comparisons must often be limited to one-half or less of the available specimens. It seems reasonable to require that 75 per cent of the comparable specimens of a population be separable from substantially all (99+ per cent) of overlapping populations before a subspecific name is applied.

Although "75 per cent from 75 per cent" does not seem to set a high enough standard of differentiation for a subspecific criterion, this method of separation by equal percentages can be used more accurately when working directly with samples than can the method of "75 per cent from 99+ per cent." It is possible to achieve equal results by the two methods if the first is modified to "97 per cent from 97 per cent" which is roughly equivalent to "75 per cent from 99+ per cent." This may be demonstrated by the methods to be outlined, which involve the fact that any portion of the area of a normal distribution curve may be expressed as a multiple of its standard deviation.

A corollary of the preceding statements is that it is possible for 75 per cent of one population to be separable from 75 per cent of another when as little as 3 per cent of each population is separable from all (99+ per cent) of the other. In such cases only 6 per cent of the individuals in the combined populations (or specimens in the samples) could be positively identified as belonging to one or the other. This further emphasizes the great difference between the two interpretations of the 75 per cent rule.

In accordance with the foregoing conclusions, the 75 per cent rule will here be defined to mean that before a population is given subspecific status at least 75 per cent of the individuals comprising it must be separable from 99+ per cent of the individuals of all other populations of the same species which may overlap with it as regards the geographically variable characters. The overlap of the populations may be inferred either from the available samples directly or, preferably, by the use of normal distribution statistics applied to the samples. An equivalent statement is that 97 per cent of one of two compared populations must be separable from 97 per cent of the other. Methods of applying this rule will now be discussed. It is hoped that these methods will prove useful even if the degree of differentiation eventually accepted as most desirable for this purpose is not precisely that advocated here.

#### 75 PER CENT FROM 99+ PER CENT

For direct work with samples it is necessary only to make a frequency distribution, such as table 1, and determine whether 75 per cent of the specimens can be identified. For example, 1 of 15 specimens of *osgoodi* (7 per cent) is grayer than any of the 70 speci-

mens of *canadensis*. Unfortunately such direct comparison of samples, unless very large ones are available, is too inaccurate to be acceptable. The limit or range of variation in such comparisons is based upon only two measurements in each sample—the two extremes. A single abnormal or freak measurement will have an entirely undeserved influence. Moreover, the range to be expected in a small sample is much less than in a large one or in the total population from which the sample was drawn. The range expected in a sample of 12, for example, is only one-half that to be expected in a sample of 1000 from the same population (Simpson, 1941:792). It is for these reasons that Simpson (*op. cit.*: 785) has described the observed range as “. . . probably the least reliable and enlightening of all available measures of variation.”

In defining subspecies we seek the characters of the population and are interested in the sample only as a means of inferring these characters. It is almost always impossible to determine the range of variation of a particular measurement in the total population but by using the statistics of normal distribution we may estimate it. Simpson (1941) has proposed to use as such an estimate 6.48 times the standard deviation ( $6.48 \sigma$ ), that is, the mean plus or minus  $3.24 \sigma$  ( $M \pm 3.24 \sigma$ ). This sets up limits that will, on the average, include 999 of every 1000 measurements (99.9 per cent). The arguments for accepting this figure, which Simpson calls “standard range” he has listed in the publication cited.

Another set of limits that has been used sometimes is  $M \pm 3 \sigma$ . About 1 measurement in 440 will fall outside limits thus established. Either of these limits would be adequate for present purposes; the use of  $6.48 \sigma$  will naturally set a slightly higher standard of differentiation for subspecies than will  $6 \sigma$ .  $6.48 \sigma$  will be used here since Simpson has worked out the application of standard error to it in terms of 1 per cent points of the standard range. Simpson and Roe (1942) also have devised a standard frequency distribution method based upon standard range, including a number of tables giving various properties of normal distributions, often in terms of standard range. The most important of these to us is one permitting a quick estimate of the standard range from the observed range and sample size. This permits a rough application of the method now to be outlined without calculating the standard deviation from the sample. This need then only be done if the differentiation seems so close to 75 per cent as to require a comparison based on direct calculation of the standard deviation and the standard range from the sample. The use of standard range ( $6.48 \sigma$ ) thus places the present work on a more convenient basis for further analysis along the lines outlined by Simpson and Roe in the papers cited.

The standard range as determined above will not be much below the true range of variation of the population. In other words, if 1000 specimens are measured, the limits thus found will change very little and slowly if more are measured. It is necessary thus arbitrarily to establish limits of variation because the normal distribution curve, based as it is on the laws of chance, theoretically has no limits short of infinity. This is obviously not true of biological variates. To give a crude example, regardless of how many sparrows are measured, one the size of an eagle will never be found. The fact that the distribution curves of figure 50 are shown as meeting the base line may be considered a modification of the normal curve for biological studies.

As regards the use of standard ranges in calculating percentages of overlap, the simplest procedure is to calculate these ranges for two samples to be compared and then find what percentage of each sample lies outside the limits thus set up.

It is better, however, to find the percentage of overlap by further use of statistical methods. The procedure for this is as follows, using figure 50 as an example.  $3.24 \sigma_a$  subtracted from  $M_a$  fixes the point A, the lower limit of the standard range of curve D. The distance from A to the mean of curve C

is found ( $A - M_c$ ) and divided by the standard deviation of C. Every such quotient  $\frac{d}{\sigma}$  corresponds to a definite percentage of the area of the normal curve which may be determined from available tables (Simpson and Roe, 1939:137). Since 50 per cent of curve C is to the left of its mean, if 25 per cent or more lies between the mean of C and the lower limits of D (= point A), then 75 per cent of C will be separable from 99+ per cent of D. A value of  $\frac{d}{\sigma}$  of 0.68 corresponds to 25 per cent of the area. Hence if the quotient is of this value or higher, the 75 per cent rule is satisfied.

If the purpose is merely to determine whether the percentage of a population separable by this method is 75 per cent or greater, it is not necessary to consult a table. Dr. J. A. Armstrong pointed out to me that the desired tests can be indicated by simple equations, as follows, retaining the designations of figure 50.

Given two samples C and D, of which C has the smaller mean for a given measurement, drawn from populations also designated as C and D, then at least 75 per cent of population C will lie below the lower limits of population D (as defined by the standard range) with respect to this measurement when

$$M_d - M_c = \text{or } > \quad 3.24\sigma_d + 0.68\sigma_c \quad (1)$$

Similarly, at least 75 per cent of population D will exceed the upper limits of C for a particular measurement when

$$M_d - M_c = \text{or } > \quad 3.24\sigma_c + 0.68\sigma_d \quad (2)$$

In practice two such overlapping series of measurements will rarely if ever have precisely the same standard deviations, first because the standard deviation is correlated with the magnitude of the measurement and will average larger in the population with larger measurements, second, because one of the populations will often be more variable than the other as regards a particular character. This affects the standard deviation and the relative percentages of two populations separable from one another. The more variable population will have a higher percentage of its individuals in the zone of overlap between the two.

The above considerations are of more theoretical than practical significance. Ginsburg (1938) has treated an essentially similar problem by taking the average of the two percentage separations (which in our case would be determined by using the above two formulas). In the rare instances where one but not the other of two compared populations is 75 per cent separable, it would perhaps be best to treat them as a single subspecies.

The standard deviation calculated from a sample will be a less accurate estimate of that of the population when the sample is small. This is reflected in the standard error of the standard deviation which varies inversely with the size of the sample. Although we are concerned with comparisons based indirectly on standard deviations, a "75 per cent rule" is at best an approximate test. Only when the samples compared are small and the differentiation near the 75 per cent limits, need the standard error be considered. The simplest method of so doing is to add to each standard deviation its standard error before finding the standard range. A more accurate method is by the determination of the one per cent points of the standard range as explained by Simpson (1941), but this refinement is perhaps never needed for our purposes.

When samples are too small to permit finding the standard deviation with reasonable accuracy (six or less measurements), the above methods can not be used. If one large and one small sample are available, the standard range of the former may be found and direct comparison employed to find if the small sample lies outside this range. If both samples are small, the naming of a new subspecies is scarcely to be considered unless the differentiation is great and encompasses many characters.

Often two populations differ in a number of variable characters no one of which provides 75 per cent separation as here used. The problem of determining whether such separation is achieved if all the characters are used in combination is difficult statistically. Various methods for "adding" characters, even when so refined as Fisher's discriminant function, do not directly tell us the percentages of two populations separable. Among the things affecting this are the variable degrees of correlation among the characters involved.

For present purposes, the best procedure would seem to be first to calculate the standard ranges for each character and then by direct comparison of samples to find how many and which specimens can be identified by each character. The number of specimens in each sample that can be identified by one character or another is then tallied and if it equals 75 per cent of the sample this can be considered as satisfying the rule. Since by this method each identifiable specimen is counted only once, although some of them may be capable of identification by more than one of the variable characters considered, the correlation of the characters will be reflected in the results, even though it is not separately calculated. This is not the case if statistical methods are used exclusively. The latter, for example, might indicate that 30 per cent of a sample are separable by wing length and 30 per cent by tail length. If these characters were perfectly correlated, the 30 per cent separable in each way would be comprised of exactly the same individuals; that is, separation would be no better by use of the two measurements than by either of them separately. Hence adding the two percentages to give 60 per cent separability would be quite erroneous. This pitfall is avoided by direct tallying of individuals as here recommended.

#### 97 PER CENT FROM 97 PER CENT

Use of this alternative method is to be preferred when comparisons are limited to the actual samples and only one character is being considered. The procedure is similar to that used by Rand in table 1, except that 97 per cent (rather than 75 per cent) segments of the samples will be bracketed to see if they overlap. In terms of distribution curves this means that, on the average, only 3 measurements in 100 can lie on the "wrong" side of the line of best separation (P-Q in figure 50). Since we cannot subdivide measurements, in samples of 16 or less all must be separable in this way, in samples of 17 to 49 all but 1, etc. (97 per cent of 17 is 16.49).

The point where two overlapping normal curves intersect tends to have the same position, regardless of the size of the samples on which the particular curves are based. This is why the method of 97 per cent from 97 per cent can be used with reasonable accuracy in direct comparison of series of measurements. Even here, however, better results may be achieved by the use of statistics.

For exact statistical determination of the percentage of two curves separated by a vertical line through the point where the curves intersect it is necessary to locate this point. The formula for this proves to be so complicated as to make the use of this method impractical for ordinary purposes (for details of formula, see Klauber, 1943:56).

Although the exact location of the line of minimum overlap is thus too laborious to be a part of a convenient measure of separation, it is possible to estimate statistically whether 97 per cent of one curve is separable from 97 per cent of another. In curve C (figure 50) 50 per cent of the area is to the left of the mean. We wish to know whether an additional 47 per cent (97 per cent minus 50 per cent) lies between the mean and the line P-Q. Appropriate tables show that  $1.88 \sigma$  above (or below) the mean correspond to 47 per cent of the area of the normal curve. Hence we add  $1.88 \sigma$  to the mean of C and subtract  $1.88 \sigma$  from the mean of D. If these points just meet or do not meet then at least 97 per cent of the areas are separable. If the points overlap, less than 97 per cent separation is (usually) possible. This may be expressed by a formula as follows:

Given two samples, C and D, drawn from corresponding populations, then at least 97 per cent of populations C is separable from 97 per cent of population D by a given measurement when

$$M_c + 1.88 \sigma_c = \text{or} < M_d - 1.88 \sigma_d \quad (3)$$

Even if the two points as thus determined coincide with each other, they will not coincide with the point of intersection of the curves unless the standard deviations of the two are identical, a con-

dition that will never be met precisely. This method might indicate that 97 per cent segments of two curves were not separable when, if the line P-Q were located exactly by use of the above-mentioned equation, they would be found separable. Since, however, we are concerned with the comparison of the same measurement in closely related populations, probably the standard deviations will rarely differ enough to introduce serious error. If the use of formula (3) indicated separation just short of the required 97 per cent, the alternative method (formulas 2 and 3) which takes into account the different values of the two standard deviations may be used.

Hubbs and Perlmutter (1942) have proposed a method essentially similar to that of formula 3 but they use  $1\sigma$  above and below the mean, instead of  $1.88\sigma$ . This measures a degree of differentiation too low, in my opinion, for subspecific separation. They suggest a method of graphic comparison that is useful in studies of this kind. Ginsburg (1938, 1940) has also discussed methods involving estimates of the percentages of two populations separable in this manner. He was working with discontinuous variates such as ray counts in fish; a type of variation rarely encountered in studies of geographic variation in birds. Moreover, Ginsburg limits himself entirely to the direct comparison of samples and does not consider the more accurate results possible by the use of the statistics of normal distribution.

The foregoing methods all assume that the variable characters in question have an essentially normal distribution. This is usually true; if it is not, the construction of frequency distribution tables or histograms will make this evident. Simpson and Roe (1942) have given careful consideration to this question in their standard frequency distribution method.

The comparison of variation in color, so frequent in work with birds, can utilize the above statistical formulas if it is possible to group the specimens into a number of numerical color categories such as those of table 1. The mean and standard deviation can then be found. If this is not feasible, it is still possible to arrange the specimens in a rough sequence according to color and then to estimate whether 97 per cent of the specimens in one of the samples is separable from 97 per cent of those in the other.

#### EXAMPLE

Use of the formulas will be illustrated by analyzing wing lengths of Turkey Vultures (*Cathartes aura*). This example is not ideal in as much as in one instance the differentiation is well above and in the other well below the required 75 per cent from 99 per cent, but the material will serve to show the use of the formulas and the relation between observed and standard ranges.

The three currently recognized races of Turkey Vulture in North America are: (1) *C. a. aura*, West Indies and Panamá north to the Mexican-United States border, including the Brownsville area of Texas. (2) *C. a. teter*, western United States and southwestern Canada. (3) *C. a. septentrionalis*, eastern United States (except Florida) and southeastern Canada.

Friedmann (1933) described *teter* as having a long tail like *septentrionalis* but short wings like *aura*. After calculating the tail to wing ratio in the specimens tabulated here, it was evident that, while there is a slight tendency for the values of this ratio to be higher in larger individual specimens or in populations made up of larger individuals, the overlap is tremendous. This variation is of little or no help in defining subspecies. The series of *aura* measured by Friedmann showed a range of variation of only 15 millimeters in tail length as compared with twice that in the two other populations. This difference did not exist in the specimens measured by me. It would seem that this sampling accident is responsible for much of the over-emphasis upon variation in proportions in this species.

Geographical variation in color of plumage or soft parts in the North American Turkey Vultures also awaits confirmation. Variation seems to be chiefly in general size of which wing length is the best available measure.

Measurements given in table 2 were taken by the writer at New York and at Cambridge (courtesy Mr. J. L. Peters). Dr. A. R. Phillips sent me measurements of Arizona specimens. Measurements in the literature published in form that permitted calculation of the standard deviation were also used; such sources are marked with an asterisk in the literature cited.

Table 2  
Wing Length (chord) of *Cathartes aura* in Millimeters

Population	Number of specimens	Observed range	Standard range (grouped about mean)	Mean	Standard deviation
<i>aura</i>	23	470-505	463-517	490	8.22
<i>teter</i>	11	486-520	470-538	504	10.53
<i>septentrionalis</i>	14	530-557	523-571	547	7.55

Since *teter* is the intermediate population as well as the last one to be named, it is best to find whether 75 per cent of this group is separable from each of the other two. Using formula 1 to determine whether 75 per cent of *teter* are below the lower limits of *septentrionalis* in wing length:

$$547 - 504 = \text{or } > 3.24 (7.55) + 0.68 (10.53)$$

$$43 = \text{or } > 24.5 + 7.2$$

$$43 > 32$$

As the left member is greater, more than 75 per cent of *teter* are thus separable from *septentrionalis*.

To determine what this percentage actually is, the deviation between the lower limit of the standard range of *septentrionalis* (523) and the mean of *teter* (504) is found (19) and divided by the standard deviation of *teter* (10.53). This quotient (1.8) is equivalent to 46 per cent of the area of the curve (above the mean). When added to the 50 per cent below the mean it indicates that 96 per cent of the population *teter* will have shorter wings than the shortest winged *septentrionalis*. It is not surprising that no overlap in this measurement was found in the relatively few specimens measured.

By using equation 2 it may be shown that 89 per cent of *septentrionalis* will exceed the upper limits of *teter* in wing length. *Teter* is a somewhat more variable, intermediate population with a higher standard deviation than *septentrionalis*. This is why only 89 per cent of the latter is separable from *teter*, while 96 per cent of *teter* is separable from *septentrionalis*.

Formula 2 may also be used to determine what percentage of *teter* may be expected to exceed the upper limits of *aura* in wing length. Since the upper limit of the standard range of *aura* (517) is above the mean of *teter* (504), it is less than 50 per cent. The deviation is 13 (517 - 504); this divided by the standard deviation of *teter* is 1.2, which corresponds to 38 per cent of the area of the curve. All those *teter* with wing length below the mean (50 per cent) and 38 per cent of those above the mean are overlapped by *aura*. This leaves only the 12 per cent with longest wing length that can be separated from *aura* by this measurement. Hence *teter* would appear a synonym of *aura*, the trend toward larger size upon which it is based being too slight for subspecific recognition.

The use of formula 3, to see if 97 per cent of *septentrionalis* is separable from a like percentage of *teter* is as follows:

$$504 + 1.88 (10.53) = \text{or } < 547 - 1.88 (7.55)$$

$$524 < 533$$

Hence more than 97 per cent of either population is separable from 97 per cent of the other. Similarly it may be shown that less than 97 per cent of *aura* is separable from *teter*.



Several individuals have given me helpful advice during the preparation of this paper, in particular Drs. J. A. Armstrong, E. Mayr and A. L. Rand.

#### SUMMARY

Frequent disagreement as to the validity of one or another subspecies of bird makes it desirable to establish a criterion of differentiation that must be met before a population is named or recognized as a subspecies. One such standard, already in partial use though with frequent ambiguities, is the 75 per cent rule. This is here defined to mean that 75 per cent of a population must be separable from all (99+ per cent) of the members of overlapping populations to qualify as a subspecies. An equivalent statement is that 97 per cent of one of two overlapping populations must be separable from 97 per cent of the other. This expression of the rule, 97 per cent from 97 per cent, is more accurate than the other when comparisons are based directly on specimens (or their measurements) and do not involve use of normal curve statistics.

Better results, and with relatively little labor, may be achieved by the use of such statistical methods. For this purpose either 75 per cent from 99+ per cent or 97 per cent from 97 per cent may be used, with the former perhaps preferable. Formulas for using either method are given. Related problems are discussed and an example is given. It is hoped that the methods proposed will prove useful even if the exact degree of differentiation here advocated is modified.

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