GEOGRAPHIC VARIATION OF THE PIGEONS OF THE GENUS *COLUMBA*[1]

BY RUSSELL W. CUMLEY

DURING the past hundred years, numerous studies have been made of the relationship of body dimensions to the geographic distribution of animal species. From these investigations, two important generalizations have been derived. The first, known as Bergmann's Rule, states that warm-blooded individuals or races which inhabit cooler regions have larger general body dimensions than do those forms of the same species that live in the warmer climates (Bergmann, 1847). The other, known as Allen's Rule, is less generally applicable but states that, in the hotter regions, animals exhibit a *relative* increase in certain peripheral parts, such as the length of the tail and bill in birds, and the ears, tail, or feet in mammals (Allen, 1876, 1883, 1905). It has long been known that the cold-blooded animals tend to be larger in the warmer regions—their optimum habitat. Much evidence for the existence and operation of these rules has been submitted by Rensch (1929, 1933, 1936), whose work has been briefly summarized by Dobzhansky (1937), Robson and Richards (1936) and Huxley (1939).

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MATERIALS AND METHODS

In most older studies, a single species was examined—that is, the individuals, races, or subspecies within a species were compared. The present study extends beyond this category and considers the dimensions within a genus. The genus *Columba* was chosen because it has a nearly world-wide distribution. The measurements used in this work were taken from specimens in the collections of Field Museum of Natural History and from the literature, most of which was examined in the Ayer Library of the Feld Museum of Natural History. Naturally, data so derived are subject to errors of many different sorts.

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The measurements of the birds are assumed to be representative of the species, but these measurements could never be considered accurate unless they were taken from a large sample of the population; as a matter of fact, a relatively small sample is usually used in determining the measurement of a given species. There is, further, some size variation among the races or subspecies of a species. For example, Griscom (1935) studying the races of *Columba fasciata,* found that there was a definite size gradient operating in terms of geographic distribution. Thus, the individuals or races in the United States were larger than those in Mexico which, in turn, were larger than those in Nicaragua. Size steadily decreased southward. In the present paper, it has often been impossible to obtain measurements of the representatives of a given species that inhabit a particular area. Frequently, for example, the measurement of a South American bird was plotted as representative of the dimension of the Central American form. Obviously, such a procedure is fraught with error, particularly in the light of Griscom's experience and that of others. But since measurements of the Central American forms, in this case, were not available, it became necessary to use the other value. Migration of species introduces error. Some species migrate little, if any, while others migrate thousands of miles every year. Furthermore, some individuals of a species migrate great distances, while other individuals of the same species do not. For this reason the measurements of a given bird, supposedly inhabiting a particular area, are not necessarily measurements that should be taken as representative of the species of that region. Naturally, this is a source of error difficult or impossible to eliminate.

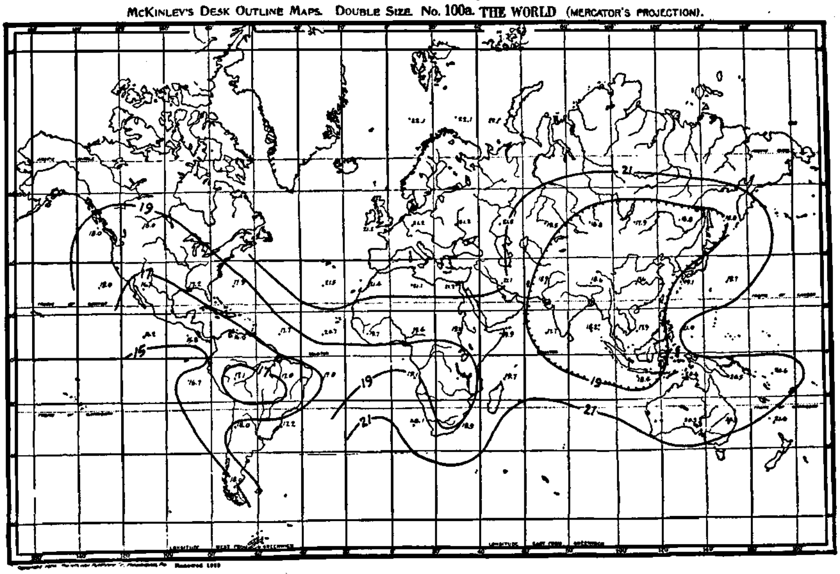
The geographic distributions of the various species and subspecies of *Columba* were plotted on outline maps of the world. These distributions, as well as the taxonomic determinations of genus, species, and subspecies, were taken largely from Peters (1937). Supplementary data as to distribution were derived from various sources when necessity required. One should recognize that distributions, as reported in the literature, seldom reveal the exact range of a species. At best, they tell us where the bird has been found. Hence, in formulating physiological principles on the basis of such data, one must always bear in mind that there probably are errors inherent in the method, which may have considerable influence on the nature of the conclusions.

The outline maps of the world on which the distributions were plotted are based on Mercator's projection. In a Mercator projection, the lines of latitude are parallel as likewise are the lines of longitude, and these together thereby describe a rectangle or quadrangle. Twenty degrees of latitude and twenty degrees of longitude, near the Equator, approximate a square. Toward the poles the same dimensions appear as an elongate rectangle with its greatest length north and south. The length exceeds the breadth by two or three times. These features may be observed in the several maps presented below.

Many of the species of *Columba* overlap in their ranges and inhabit the same regions. Therefore, in plotting the geographic distribution of the species, it was found that from one to a dozen species may live within any single quadrangle defining 20° of longitude and latitude. If there is a correlation between size of the organism and its geographic distribution, such as is implied in Allen's or Bergmann's rules, then the species of *Columba* which inhabit a quadrangle defining 20° of longitude and latitude near the Equator should be appreciably different from those species which live within a similar rectangle nearer to one of the poles. But, as a matter of fact, any given quadrangle is usually inhabited by large, medium-sized, and small species. Hence, obvious exceptions to any application of Bergmann's or Allen's rules become apparent or even striking.

Averages were taken of the measurements of each of several different body parts of species inhabiting the same 20° quadrangle. This was repeated for all the 20° quadrangles through which the *Columba* species ranged. Some of the quadrangles were represented by only one species, others by as many as a dozen. It was reasoned that if there was a correlation between environment and differences in total length, let us say, of the species of *Columba,* then such a correlation should become apparent by the method herein employed.

The body parts considered were: (1) total length of the bird; (2) wing length; (3) tail length; (4) length of culmen; and (5) tarsal length. The average measurement of all the species in a given quadrangle was placed beside a point in the center of that quadrangle. For example, the following species of *Columba* with their respective culmen lengths, were found to occur in latitude 0°–20° N., longitude 40°–60° E.:—*albitorques,* 20 mm.; *oliviae,* 22 mm.; *arquatrix,* 19 mm.; *delegorguei,* 17.3 mm.; *guinea,* 22.3 mm.; and *livia,* 19 mm. The average of all these measurements is 19.9 mm., which is the datum which may be observed in the center of the rectangle 0°–20° N., 40°–60° E. In this manner, the various points and values shown in Text-figure 1 were produced. Since these points were placed in the centers of the rectangles of longitude and latitude, many points will

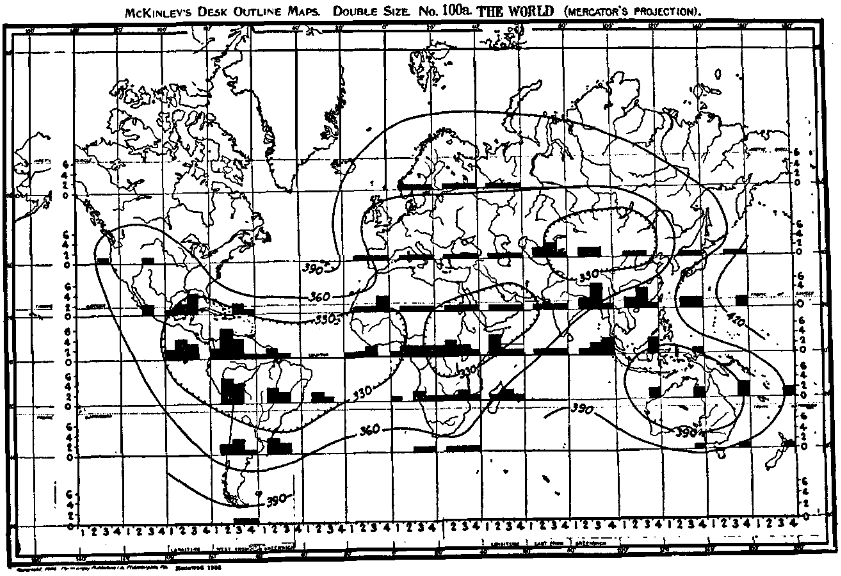


TEXT-FIGURE 1.—CULMEN LENGTH OF *Columba* SPECIES.

Contour Interval: 2 mm. of culmen length.

be observed to occur in the oceans, adjacent to continents or islands. This practice is not without undesirable features, but it was followed mainly because of the resulting regularity and ease of delineation. The points could be placed on the mainland, where the birds actually occur, rather than in the oceans, which would present a more accurate picture, but this would introduce technical difficulties not easily overcome. For example, where would the point be placed in latitude 0°–20° S., longitude 40°–60° E.? In this rectangle four species occur. One of them, *C. pollenii,* is found in the Comoro Islands, while the other species, *arquatrix, delegorguei,* and *guinea,* are found on the nearby African mainland. Obviously, if the point were placed on the mainland, the curve would be unreasonably distorted,—even as would be the case if the point were on the islands. Similarly, the geographic center of the land surface that exists in any given rectangle of latitude and longitude would have to be computed in order to determine logically just where the point should be placed. For these reasons, it was thought desirable to put the points in the center of each rectangle, irrespective of where they actually fell with reference to land surface.

When all the values were plotted for average culmen length, isometric lines were drawn, connecting points of equal value. Thus, in Text-figure 1, the 17 mm. isometric line crosses southern California between values 16.7 and 18.0, crosses Texas between 16.7 and 17.2, and enters South America between values 16.0 and 17.7. The other isometric lines were drawn in a similar manner. Values greater than the isometric value remain on the same side of the line in all cases, and lesser values remain on the other side. For example, between the 15 mm. and 17 mm. isometric lines there are no values greater

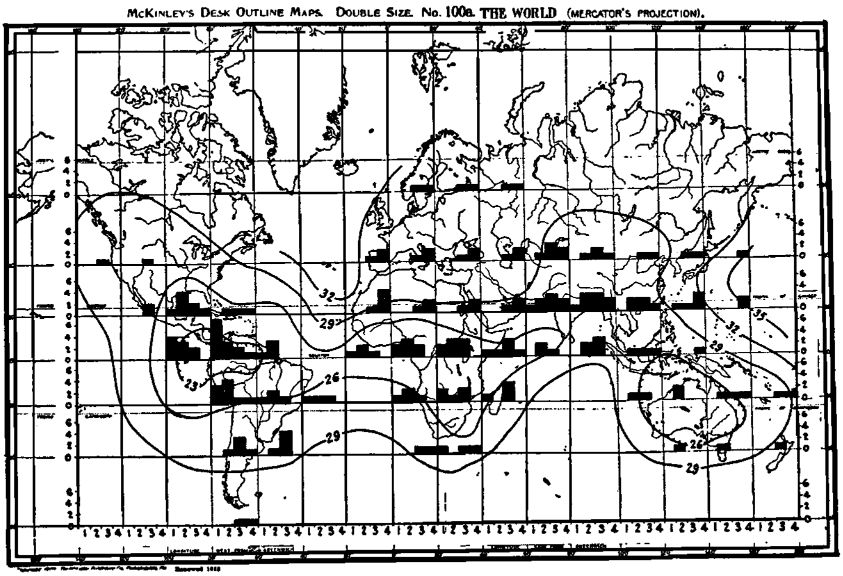


TEXT-FIGURE 2.—TOTAL LENGTH OF *Columba* SPECIES.

Block Graphs.—The ordinates in each quadrangle represent the number of species; the abscissas, the measurements, as follows: 1st Quartile: 275 mm. or less, total length; 2nd Quartile: 276–325 mm.; 3rd Quartile: 326–375 mm.; 4th Quartile: 376 mm. or over. Contour Interval: 30 mm. of total length.

than 17 nor less than 15. Therefore, the direction and disposition of an isometric line are reasonably controlled; and, given the same values, any two investigators would be compelled to map a region in much the same way. The contours of Text-figures 1–3, inclusive, were made in this way.

The averages shown in Text-figure 1, for culmen length, are not to be taken too literally. Similar figures have been omitted from Text-figures 2 and 3, so as not to convey an erroneous impression. They were included in Text-figure 1 merely to demonstrate how the isometric lines on all the maps were determined. These average values, as was pointed out earlier, are crude values and were not weighted in terms of variability or frequency of the species inhabiting a given quadrangle. For example, *livia* and *delegorguei* both inhabit the quadrangle 0°–20° N., 40°–60° E. However, let us assume that *livia* is represented in this quadrangle by 100 individuals, while *delegorguei* is represented by only ten individuals. It is unsound to give these two species the same weight in computing the average. In



TEXT-FIGURE 3.—TARSAL LENGTH OF *Columba* SPECIES.

Block Graphs.—The ordinates in each quadrangle represent the number of species; the abscissas, the measurements, as follows: 1st Quartile: 24.0 mm. or less, tarsus length; 2nd Quartile: 24.1–26.0 mm.; 3rd Quartile: 26.1–28.0 mm.; 4th Quartile: 28.1 or over. Contour Interval: 3 mm. of tarsus length.

the quadrangle 0°–20° N., 60°–80° W. there were fourteen species, of which the smallest had a total length of 258 mm. and the largest had a total length of 404 mm. This represents a wide range of values; similar variability was observed in many of the quadrangles. One wonders if the variability among the species within a given quadrangle would not be as great as, or greater than, the variability between quadrangles. No entirely adequate statistical method of determining the reliability of these averages could be found. Hence it was thought desirable to illustrate the range of variability of the species within a given quadrangle, along with the trend of the genus as a whole.

Variability of the species within each quadrangle was represented by the block graphs in Text-figures 2 and 3. In these graphs the abscissas, representing measurements of length, are subdivided into four quartiles; and the ordinates are subdivided in terms of the number of species. The value of each quartile is given with the legend to each of the figures. Thus, in Text-figure 2, quadrangle 0°–20° S., 60°–80° W. is inhabited by five species of average total length of 276–325 mm., and four species of 326–375 mm.

In Text-figures 2 and 3, therefore, one may observe the trends in the isometric lines and at the same time gain an understanding of the variability of the species, by observing the block graphs.

Results

Before discussing the positive results of this work, the materials upon which the results must necessarily be founded should be considered. The validity of any conclusions presented herein is obviously dependent upon the quality of the original data. Above, I have pointed out errors inherent in this study. I wish to emphasize further the difficulties and incongruities with which one must cope in an investigation of this sort.

Let us analyze some of the data presented in the "Total length" map, Text-figure 2. For convenience, we shall consider the quadrangles 0°–20° S., 60°–80° W., and 20°–40° S., 60°–80° W. The species that inhabit these quadrangles, together with their respective total lengths, are as follows: Quadrangle 0°–20° S., 60°–80° W.: *albilinea,* 345 mm.; *picazuro,* 348 mm.; *oenops,* 343 mm.; *plumbea,* 313 mm.; *goodsoni,* 292 mm.; *maculosa,* 368 mm.; *subvinacea,* 295 mm.; *speciosa,* 315 mm.; *rufina,* 319 mm.; average of all species, 327 mm. Quadrangle 20°–40° S., 60°–80° W.: *albilinea,* 345 mm.; *picazuro,* 348 mm.; *araucana,* 409 mm.; *maculosa,* 355 mm.; *speciosa,* 315 mm.; *rufina,* 324 mm.; average of all species, 349 mm. The difference in the averages for the two quadrangles is 22 mm. and the standard deviation of the difference is 16.5.

One may readily observe that there is great variability among the species within a given quadrangle. Thus, in the quadrangle 0°–20° S., 60°–80° W., the smallest form is 292 mm. long, and the largest 368 mm., a difference of 76 mm. Similarly, there is a difference of 94 mm. between the smallest and largest species in the quadrangle farther south. Since this variability *within* a quadrangle is so great, it becomes evident that the variation *between* quadrangles is necessarily of doubtful validity. Furthermore, the averages presented are, in reality, more or less fictitious since an average, to be worth anything at all, must imply somewhat of a regular dispersion of the population. In the present case, it is obvious that there is an irregular dispersion of values over a broad range. The standard deviation of the difference between the two averages further emphasizes that there is greater variation among the species within a quadrangle than between the species of the two adjacent quadrangles. The difference between the two averages is only 22 mm., while the standard deviation of this difference is 16.5; hence the difference is statistically insignificant. A similar analysis may be made of other quadrangles, with similar results. Thus we are prone to view the results presented herein more in terms of their "trends," rather than in terms of their statistical significance. For a set of figures may well reveal a trend without having statistical significance.

Let us now examine the data in another manner, considering the species that inhabit the quadrangles 0°–20° S., 20°–40° S., and 40°–60° S., all longitude 60°–80° W. The measurements of the *Columba* species found in the first two quadrangles have already been presented. In the quadrangle 40°–60° S., 60°–80° W., only two species have been found,—*araucana,* 409 mm., and *maculosa,* 355 mm. in total length. The average of these values is 382 mm. Now if we examine the data for all three quadrangles, we find that the smallest species, *goodsoni* (292 mm.) and *subvinacea* (295 mm.), occur near the Equator. Some of the larger species such as *maculosa* (368 mm.) and *picazuro* (348 mm.) also occur in this region. As we go farther south, away from the Equator, the smaller species drop out, leaving the larger. *Columba goodsoni, subvinacea, plumbea,* and *oenops* are found in latitudes 0°–20° S., but not in latitudes 20°–40° S. With the exception of *oenops,* all of these are smaller forms. An additional species, *araucana,* inhabits latitudes 20°–40° S. but is not found in the more equatorial regions. Passing on farther south, other species drop out, and only *araucana* and *maculosa* live in latitudes 40°–60° S. Both of these species are relatively large. Thus, the equatorial forms are usually numerous and of great variability, whereas nearer the poles the species are considerably fewer and are most often of large size. One might reasonably inquire whether, if there were as many species in Tierra del Fuego as at the Equator, there might not be just as diverse a group at the Cape as there is farther north. It is apparent that we have larger average sizes of birds at the Cape mainly because the smaller forms, which inhabit equatorial regions, do not extend their ranges into the colder countries. We have no way of knowing what their size would be if they did range southward to Cape Horn.

However, the studies of Rensch, Bergmann, and others have demonstrated that within many species there is a climatic gradient in which the larger subspecies occur in the colder regions, and vice versa. It should be remembered that Rensch and others have reported a high percentage of exceptions to Bergmann's Rule. Obviously, among subspecies and even higher categories, this rule is hardly empirical.

TOTAL LENGTH OF *Columba* SPECIES

Figure 2 demonstrates variations in total length of the *Columba* species. This map suggests that a larger proportion of the smaller forms are to be found in a belt which extends along the Equator in Central and South America, and in Central Africa; thence it deflects northeastward into Asia. In the region that embraces Mongolia, East Turkestan, northern Tibet, and northwestern China, there is a greater proportion of small forms. In the Americas, as we go farther and farther from the Equator, only large species are found. Thus, the equatorial forms occur within the 330 mm. isometric lines whereas the species more distant from the Equator extend even beyond the limits of the 360 mm. line. Similarly, there is a greater proportion of large African species distant from the Equator than in the equatorial districts. From northern Africa to the Scandinavian countries the change is more gradual, but nevertheless the Scandinavian forms include more large species than do the African. The Gobi Desert species are much smaller than the European in the same latitudes. To the east of Mongolia the species are larger, and attain their greatest lengths in the Bonin Islands, southeast of Japan. The Australian species, and those in the nearby islands to the north, likewise are of large size.

If one observes the block graphs that occur between the meridians 60° W. and 80° W. longitude, the size trend of the species is further illustrated. Thus, between 20° and 40° N. latitude the species all fall into the third and fourth quartiles. Between the Equator and 20° N., and the Equator and 20° S. latitudes most of the species fall in the second or first and second quartiles. Farther south, the bulk of the species that are represented occur again in the third and fourth quartiles. Similar analyses may be made of any group of block graphs, although, obviously, the results will not always be as striking as those mentioned here.

It is apparent, therefore, that length of the pigeon species is broadly related to their geographic distribution. Seemingly, the hotter the clime, the shorter the species. Table 1 presents data relating to this correlation. In this table the average lengths and their standard

TABLE 1

Mean Annual Temperature	*No. of Species*	*Total length (average)*	*Body length (computed average)*	*Wing length (average)*	*Tail length (average)*	*Tarsus length (average)*	*Culmen length (average)*
60°–70° F.	22	376.0±8.8	232.4±5.6	222.4±3.7	138.2±3.4	29.1±0.60	19.3±.47
80° F.+	33	338.3±8.1	211.1±5.9	202.0±4.8	127.6±3.1	25.6±0.76	17.9±.54
Difference		37.7	21.3	20.4	10.6	3.5	1.4
S.D. (difference)		11.96	8.78	6.06	4.58	.96	.72

deviations are recorded for all the species inhabiting regions of two different mean annual temperatures.

In order to arrive at these figures, the ranges of the various species were superimposed on a temperature map of the world. This map, taken from Davis (1902), featured isothermal lines of 10° intervals, showing the mean annual temperature of the globe in degrees Fahrenheit. On Davis's map, the 80° F. isothermal line roughly parallels the Equator and rarely extends as much as 20° of latitude north or south of it. Other isothermal lines more or less parallel the 80° isotherm, and thereby define broad temperature belts, extending east and west. The 50° F. isotherm passes along the U. S.-Canadian border, thence eastward to the south of England, the northern part of the Caspian Sea, and intercepts Japan at about the 40° parallel of latitude. It more or less follows the 40° parallel across the Pacific. In the Southern Hemisphere, the 50° F. isotherm crosses South America between 45° and 50° S. latitude, thence almost due eastward to the southern tip of New Zealand, thence east to South America.

The ranges of the various species, then, were superimposed on the temperature map. If a species ranged entirely within the 80° F. isotherm, is was tabulated accordingly. If it ranged between the 50° F. and the 80° F. isotherm, it was tabulated in the 50°–60°, the 60°–70°, and the 70°–80° F. categories. In order to construct Table 1, an average was taken of all the values for total length, let us say, that occurred in the 60°–70° F. category. Similar calculations were repeated for the 80° F. + category and each of the other body measurements.

In Table 1, only the two temperature increments, "80° F. +" and "60°–70° F.," were tabulated. This was because very few species live at mean annual temperatures lower than 60° F. Furthermore, the measurements of the birds inhabiting the 60°–70° F. regions were not significantly different from those of the birds living at 70°–80° F. Likewise, the 70°–80° F. birds did not differ significantly from those living at 80° F. +. This was because there was considerable overlap of ranges, many of the birds living at 80° F. + also living in regions of 70°–80° F. mean annual temperature, etc. Hence, the increment 70°–80° F. was omitted.

In the table one may observe that the average total length of the birds living in regions of mean annual temperature 60°–70° F. was 37.7 mm. greater than the average length of those birds inhabiting the hot equatorial regions. The standard error of this difference is somewhat less than three times the difference, hence we may assume that these calculations reveal a fairly significant correlation between temperature and the total length of the birds in a given habitat. However, one must understand that any general consideration of temperature, as in the present work, necessarily leaves much room for error. For example, we have used the mean annual temperature as expressed in terms of broad geographic belts, defined by isotherms. Naturally, in any selected area there is likely to be great deviation from this value, which might render insignificant this mean, as we use it here. Therefore, we must view our temperature data in much the same manner as we do our measurements, i. e., not to be taken too literally.

WING LENGTH OF THE SPECIES OF *Columba*

Because of space limitations, no map is presented here of the variations in wing lengths of the species of *Columba*. However, such a map would have many features in common with Text-figure 2. That is, the smaller wing lengths are found in the equatorial regions of South America and Africa, just as were the smallest total lengths. But it is in South America that the shortest wings occur, the average lengths being less than 180 mm. In equatorial Africa these lengths do not fall below 200 mm., while in the equatorial East Indies the values approach 220 mm. As in the case of the total lengths, the shorter-winged birds most often do not live at great distances north and south of the Equator. Thus, the wing lengths of American species of *Columba* average 174 mm. at the Equator, 209 mm. in the northwestern United States, and 210 mm. at the southern end of South America. Similarly, in the Old World the wings are longer in those species at a distance from the Equator than are the wings of the equatorial forms. Between northern Africa and the Arctic Circle the species remain rather constant in respect to their wing lengths, whereas in the New World, in the same latitudes, there is considerable diversity. The species inhabiting Japan, Australia, and the islands adjacent thereto possess the greatest wing lengths, just as they possess the greatest total lengths.

Again from Table 1, we may see that the species inhabiting those latitudes where the mean annual temperature is less than 70° F., have wing lengths greater than 220 mm., whereas those species living in hotter regions have their wing lengths reduced to much nearer 200 mm. These figures appear to reveal significant differences. It would seem, therefore, that the wing length, just as the total length, is correlated with temperature. Perhaps we should mention here that there is undoubtedly a high degree of correlation between general body size and size of the appendages. Therefore, the correlation of wing length or tail length, etc., with temperature may be in reality an expression of the correlation of these body parts with the general body size of the bird. In this case, the temperature correlation would be but incidental.

Tail Length

With regard to tail length of *Columba,* we again find a larger proportion of the small species inhabiting the equatorial regions of South America and Africa. A map featuring the geographic variation of tail length would be quite similar to the map of total length. As we go south of the Equator in Africa and South America, the long-tailed species become more common, the average tail length increasing from less than 110 mm. at the Equator to over 130 mm. at Cape Horn and Cape of Good Hope. Likewise, there are more long-tailed species in North America, the average length being nearly 140 mm. in the state of Washington and southwestern British Columbia. Variations in length are irregular through Europe and western Asia, and the longest-tailed species inhabit eastern China, Japan, Australia, and the adjacent islands. In Table 1, one may observe that the species inhabiting regions of mean annual temperature less than 70° F. have tails exceeding 135 mm. in length, whereas those in regions with mean annual temperature higher than 80° F. have tail lengths less than 128 mm. These differences are hardly significant, and serve only to show a trend.

Tarsal Length

The tarsal lengths show much the same geographic variations as do the previously mentioned measurements, as one may observe in Text-figure 3. Birds in equatorial South America obviously have the shortest tarsi, and those in equatorial Africa have the shortest tarsi of the African and European species. In Australasia the smallest tarsi occur in Australia, and the longest in all the world are to be found in the birds of the Japanese Islands and the other islands of the western Pacific. A predominance of species with a long tarsus occurs in the Americas and in Africa as distance north and south of the Equator increases. Thus, birds in Venezuela have an average tarsal length of 23.5 mm., whereas the average tarsal length of birds in southern South America is nearly 30 mm. Similar relationships may be observed in North and Central America, Africa, and Europe.

Referring again to Table 1, we see that the birds living in habitats with the mean annual temperature below 70° F. have tarsal lengths averaging more than 29.0 mm., and those living at 80° F. or higher have average tarsal lengths of 25.6. These differences are significant. Consequently, it seems evident that there is a positive correlation between temperature and tarsal length.

CULMEN LENGTH

The geographic variation in the culmen length of *Columba* species is shown in Text-figure 1. It seems evident that the culmen length is not correlated in the same manner as are the other characters, with environmental forces. In only one particular does the culmen-length map agree with the other maps; in all of them the largest species are in Europe and Asia, and the smallest species occur in the Americas. However, when we analyze the species in terms of the mean annual temperature of their habitats, we find that the culmen length varies more or less as do the other factors that have been presented. Thus, in Table 1, we see that the average culmen length at 60°–70° F. is 19.3 mm.; and it decreases to 17.9 mm. at 80°–90° F. These differences, nevertheless, do not have as much statistical significance as do the values for other characters.

An attempt was made to break down the data to include smaller and perhaps more pertinent geographic units. For example, all the species inhabiting the 80° F. + mean-annual-temperature belt in the New World were compared with the species which are found in the 60°–70° F.-temperature belt. Similarly, the European and African species were compared, as well as those of Australasia. For convenience, the species inhabiting the Old World west of the 60th meridian of longitude east of Greenwich were arbitrarily considered in Europe and Africa, while those species to the east of the 60th meridian were considered in Australasia. The more significant data derived from these comparisons are presented below.

Those of the New World species that inhabited regions with temperatures ranging from 80° F. upward, had the following measurements: total length, 327.0 mm.; body, 203.5 mm.; wing, 188.0 m.; tail, 123.0 mm. The species that lived in the 60°–70° F. regions were always somewhat larger, on the average, their measurements being as follows: total length, 355.3 mm.; body, 256.7 mm.; wing, 201.0 mm.; tail, 127.0 mm. Essentially the same relations were observed among the European and African forms. The species inhabiting the 80° F. + regions had the following measurements: total length, 328.5; body, 208.2; wing, 208.7; tail, 120.3. Those living in the 60°–70° F. region were larger, measuring: total length, 373.0 mm.; body, 233.7; wing, 225.4; tail, 139.3.

Since the number of species included in any one of the geographic units was usually quite small (most often, less than a dozen), it is evident that the differences are of questionable significance. None of the differences found among the species of Australasia was significant; hence their averages are not considered. Of those that are considered, several are of questionable significance. The measurements of which we can be reasonably certain are the total length, wing, and body measurements taken from the New World species. All these measurements reveal that a greater proportion of distinctly larger species inhabit the cooler regions.

Allen's Rule

Are the lengths of the appendages *relatively* smaller, when compared with body size, in the cold than in the hot regions? In order to make an accurate study of this problem, we should have available a reliable body measurement exclusive of feathers. But in the literature such a character is seldom or never reported. 'Total length' and 'tail length,' however, are almost always given. Hence, although one is unable to determine accurately the 'body' lengths of the many species, computed measurements might well show much the same ratios, with reference to Allen's Rule, as would the accurately measured body lengths. With this in mind, the tail length was subtracted from the total length, and the remainder assumed to be approximately the 'body' length. This calculated body length was then compared with the lengths of other parts, with the view to determining whether the derived relations obeyed Allen's Rule. Table 2 presents the ratios of body length to length of other parts. These ratios are arranged in terms of the mean annual temperature of the habitat of the various species measured, just as in Table 1.

In Table 2, one may observe that the culmen of those species inhabiting warmer regions is somewhat longer (relative to body length) than is the culmen of species living in cooler districts. Similarly, the

TABLE 2

Mean Annual Temperature	*Culmen: Body*	*Wing: Body*	*Tail: Body*	*Tarsus: Body*
50°–60° F.	.081 : 1.000	.95 : 1.00	.59 : 1.00	.125 : 1.000
60°–70° F.	.083 : 1.000	.95 : 1.00	.59 : 1.00	.125 : 1.000
70°–80° F.	.085 : 1.000	.96 : 1.00	.62 : 1.00	.124 : 1.000
80°–90° F.	.085 : 1.000	.96 : 1.00	.60 : 1.00	.121 : 1.000

wing and tail lengths are relatively greater in warmer than in cooler regions. Tarsal length, however, apparently varies in the opposite direction, the relative length of the tarsi being greater in cool climates. In all these ratios, the differences are small, and their statistical significance questionable. Therefore, these data do not appear adequate to confirm Allen's Rule.

OTHER GEOGRAPHIC VARIATION GRADIENTS

Another directional variation may be observed in this genus, which does not coincide with any climatic gradient that the author is able to recognize. In earlier sections mention has been made of the tendency of the American species to be smaller than the European, African, or Australasian forms. Especially large are the forms along the eastern coast of China and in the nearby islands of the Pacific. If we arrange our measurements in three categories—(1) Australasia, (2) Europe and Africa, and (3) New World—we find a graded series from east to west.

Table 3 presents averages of the several measurements, arranged in terms of the habitat of the various species in one of the three regions mentioned above. There is a distinct increase in size as we proceed east from the Americas. Thus, in average total length, the birds

TABLE 3

Geographic location	*Total length*	*Body length (computed)*	*Wing length*	*Tail length*	*Tarsus length*	*Culmen length*
New World	332.0	206.7	189.0	126.0	25.6	16.3
Europe and Africa	342.0	210.3	212.0	131.0	27.5	20.1
Australasia	380.0	233.2	227.0	146.0	28.5	19.1

increase from 332 mm. in the Americas to 342 mm. in Europe and Africa, and thence to 380 mm. in Asia—a total increase of 13%. Similarly, the average wing length of New World species is 189 mm.

while in European and African forms it is 212 mm., and in Asiatic species it has increased to 227 mm.—a total increase of 17%. In practically all these measurements, the differences between the New World species and those of Europe and Africa are of questionable significance, whereas the differences between the Australasian forms and those either of the New World or of Europe and Africa have significance. The culmen length is the only morphologic factor herein considered in which there is not a steady increase in length as we go from west to east, from America to Asia. In the case of the culmen, the greatest average length appears in the European and African species, although the difference between these and the Asiatic forms certainly is not great and is insignificant.

There are yet other features in the figures that deserve mention. The species that occur in Mongolia, East Turkestan, and Tibet seem to be somewhat smaller, on the average, than the birds in adjacent regions in any direction. This feature may be observed to some extent in any of the several maps, particularly Text-figure 2, which relates to the total length of the species. There are only eight species of *Columba* in these regions, some of which are restricted to this region, while others range westward to the British Isles. Unless these species have adapted themselves to the aridity that characterizes the region of the Gobi Desert, it is difficult to explain why they should be smaller here than to the west, east, and southeast. It is possible that they have become so adapted. Some of the driest regions in the world are to be found in the belt of country extending from the western edge of the Sahara eastward to the Red Sea, thence through Arabia, on northeastward into the Trans-Caspian regions, and finally into the Gobi Desert. From the Caspian Sea westward across Europe, the mean annual precipitation increases more or less steadily.

Comparing these precipitation differences with size differences in the species of *Columba,* we find small species in the Gobi Desert region, and as we proceed from this vicinity westward toward Europe, into more humid countries, the birds have longer wings, tarsi, tails, culmens, and total lengths. To the east of the Gobi, in the humid regions along the Chinese coast and in the islands of Japan, the species generally are of larger dimensions. These observations are insufficient, of course, to enable us to draw any definite conclusions. All that can be said is that there is a possible correlation between precipitation and size differences in the genus *Columba.* More extended studies are needed to elucidate this correlation.

In some regions, there is great variability in size, while in others the average measurements of species are much the same over wide areas. Thus, the average wing length increases from less than 180 mm. in the vicinity of Panama to over 200 mm. in northern Mexico. This is a relatively abrupt change and is quite different from the gradient in Europe and western Asia, where the wing length remains quite constant. No satisfactory explanation can be given for these differences in geographic variability, since there are no recognizable geographic gradients that could be applied here.

Discussion

Several explanations have been offered for Bergmann's and Allen's rules. Reinig has suggested that variation gradients are associated with species dispersion and that genetic factors have dropped out of the gene complex of the species during the dispersion process (see Huxley for discussion of Reinig's views). This explanation hardly accords with the concept of Rensch, who believes the size-variation gradients of animals to be adaptively correlated with environmental gradients. Certainly there is abundant evidence in favor of Rensch's analysis, whereas Reinig's hypothesis is difficult to entertain. Dobzhansky has considered the view that Bergmann's Rule is concerned with the temperature regulation of the animal—that is, a large body size is correlated with a *relatively* smaller body surface, and vice versa. In a cool region, it would perhaps be to an animal's advantage to have a relatively smaller body surface, because this would enable the animal to have a more limited loss of heat. In a warm country, the small-bodied species would exhibit relatively greater body surface and thereby experience greater heat loss. This would seem especially desirable in the exceptionally humid regions along the Equator in South America and Africa, and it is in these places that the smallest birds, with the relatively largest body surfaces, are to be found. This might be a reasonable view, except for the fact that most of the measurements employed in this study are measurements of feather length. These are dead structures and certainly do not have the heat regulatory function of the tail, let us say, of mammals. Therefore, it is difficult to see just how this explanation would apply. Furthermore, the species of *Columba* that inhabit the colder regions often migrate toward warmer regions during the winter months, whereas many of the species near the Equator are more restricted in their ranges. The value of longer feathers as heat regulators is accordingly open to question.

From Table 3 it is evident that there is a large-scale size-variation gradient correlated with the continents, the New World species being smaller than European and African forms, and these, in turn, smaller than the Asiatic birds.

CONCLUSIONS

A study of the species of genus *Columba* suggests that a greater proportion of the species having shorter average total length, wing length, tail length, and tarsal length, inhabit the warmer regions of the earth. In the cooler regions there is a preponderance of the large forms. Thus, Bergmann's Rule, or more likely a modification thereof, may be applied to the species of genus *Columba.* Allen's Rule cannot be confirmed by these data. Evolution within the genus *Columba,* in the characteristics studied, appears to have proceeded primarily from south to north or vice versa, though with some evidence of progressive differentiation from east to west.

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University of Wisconsin
Madison, Wisconsin