# Recent Statistical Methods for Orientation Data

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IN THE AREAS of animal orientation and navigation, directions are measured in various ways. Animals are either kept in cages and their movements or preferences with respect to a reference direction recorded, or they are released and at certain points of their path the bearings are measured. The purpose of a statistical analysis is to establish preferred directions and to compare them with geographical lines such as directions to breeding places, homeward directions, valleys, mountain ranges, shore lines, and the like. It is also important to find significant differences between experimental and control groups.

A comprehensive account of statistical methods in the analysis of directions for biologists was published in reference 1. In the past five years, there was considerable interest in this area by both theoretical and applied research workers. A host of new results and methods is available today.

This paper explains and illustrates those methods that are immediately useful for biologists. No attempt is made to review results that are of purely theoretical interest no matter how important they may be for future statistical research. We will restrict ourselves to the two-dimensional or circular case and omit the three-dimensional or spherical case.

An exhaustive bibliography is found at the end of this paper for the reader whose interest goes beyond the rather limited scope of this account. Only those publications are listed that are not already quoted in Batschelet, 1965 (ref. 1). Recent papers of basically mathematical interest can be found under such names as Ajne, Beran, Downs, Maag, Mardia, Rao, Schach, Stephens, and Watson. For the spherical case we refer the reader to Bingham (1964), Downs (1966, 1970), Downs and Gould (1967), Savary (1965), Selby (1964), Stephens (1967, 1969), Watson (1965, 1966, 1967, 1970).

## NOTATIONS

We will use the same notations as in reference 1. Let $\alpha_1, \alpha_2, \cdots, \alpha_n$ be a *sample* of independent angles taken from a certain theoretical distribution. Without loss of generality we choose the positive $x$ axis as zero direction and associate the positive sign with a counter-clockwise rotation (see fig. 1).

It is convenient to introduce unit vectors, that is, vectors of unit length pointing in the directions given by the angles $\alpha_i$ $(i = 1, \cdots, n)$. The tips of these unit vectors are located on the circumference of the unit circle.
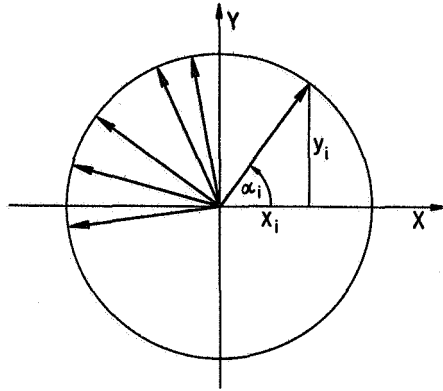
**FIGURE 1.** Circular sample represented by unit vectors.



**FIGURE 2.** Circular sample represented by unit masses and their center $C$ of gravity.

In a rectangular $x,y$-coordinate system the components of the unit vectors are

$$x_i = \cos \alpha_i, \quad y_i = \sin \alpha_i \quad (i = 1, \cdots, n) \quad (1)$$

When a preferred direction or a mean direction is to be defined, we associate with each direction a unit mass which we locate at the tip of the corresponding unit vector (fig. 2). Then we calculate the coordinates of the center of gravity by

$$\bar{x} = \frac{1}{n} \Sigma x_i = \frac{1}{n} \Sigma \cos \alpha_i, \quad \bar{y} = \frac{1}{n} \Sigma y_i = \frac{1}{n} \Sigma \sin \alpha_i \quad (2)$$

Denote the center of gravity by $C$. The vector which points to $C$ is called the mean vector, whose components are $x$ and $y$.

The length of the mean vector is denoted by $r$ and may be calculated from

$$r = (\bar{x}^2 + \bar{y}^2)^{1/2} \quad (3)$$

An alternative way of calculating $r$ uses vector addition. Consider again the unit vectors with components $\cos \alpha_i$, $\sin \alpha_i$ ($i = 1$, $\cdots$, $n$). The sum of these vectors, also called the resultant vector, has components
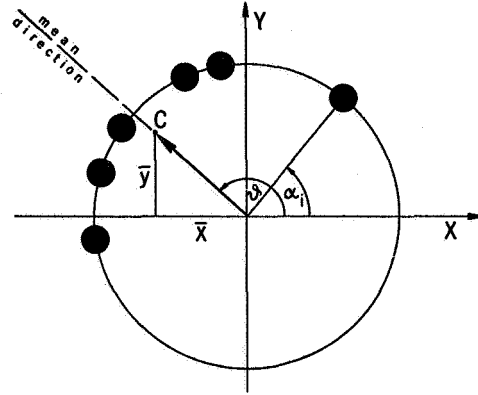
$$V = \Sigma \cos \alpha_i, \quad W = \Sigma \sin \alpha_i \quad (4)$$

The length of the resultant vector is

$$R = (V^2 + W^2)^{1/2} \quad (5)$$

Then the length $r$ of the mean vector is simply

$$r = \frac{1}{n} R \quad (6)$$

If the population center of gravity falls into the origin, then no single preferred direction exists. This may be the case where all directions are equally likely, which is referred to as uniform distribution. Another possibility occurs with certain multi-modal distributions, for instance, when two opposite directions are equally probable.

We should also consider the influence of chance fluctuations. A sample may have a non-zero mean vector even if the underlying theoretical distribution has its center of gravity in the origin. It is therefore desirable to test whether $r$ differs from zero significantly. Such tests will be presented in the following five sections.

Assume now that the length of the mean

vector is significantly different from zero and that the sample points are concentrated around a single preferred direction. Then we have good reason to introduce a mean direction, which is defined to be the direction of the mean vector. We denote its angle by $\vartheta$ (Greek theta) and call it the mean angle (fig. 2). This angle is calculated by solving the equations

$$x = r \cos \vartheta, \bar{y} = r \sin \vartheta \qquad (7)$$

or

$$V = R \cos \vartheta, W = R \sin \vartheta \qquad (8)$$

## RAYLEIGH TEST AND MODIFICATION

The Rayleigh test is presented in reference 1, p. 28. For reasons that are explained there, the Rayleigh test should be used only in the unimodal case. The null hypothesis states that the theoretical distribution is uniform. As a test statistic we may use the length $r$ of the mean vector. When $r$ exceeds a certain critical value, the null hypothesis is rejected.

For the presentation of a table of critical values it is better to consider the test statistic

$$z = nr^2 \qquad (9)$$

instead of $r$ itself. A short table of critical values adapted from work by Greenwood and Durand was published in reference 1. Now it is possible to enlarge this table (table 1) considerably by adapting tables published in reference 2 and by using an unpublished table kindly submitted by W. T. Keeton, Cornell University.

The Rayleigh test is most powerful if the alternative to the uniform distribution is a circular normal distribution (ref. 3).

Recently, a modification of the Rayleigh test has proved to be most useful.[1]

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[1] I am indebted to Keeton for drawing my attention to the $V$ test.

It may occur that a particular direction is expected to be the preferred direction in advance of the experiment. For instance, when pigeons are released at a test site, the home direction is known in advance. The null hypothesis that we are going to test is randomness, which means that the angles of the sample are independent observations from a uniform circular distribution. For a test of the null hypothesis, it would be a loss of information when the knowledge of a predicted direction were abandoned. Indeed, by using this direction we obtain a more powerful test.

Let $\theta_0$ be the angle of the predicted direction, and let $R$, $\vartheta$ be defined as above. When making the predicted directions to a new $X$-axis, then the $X$-component of $R$ is

$$V' = R \cos (\vartheta - \theta_0) \qquad (10)$$

as shown in figure 3. By means of formula (8) we also get

$$V' = V \cos \theta_0 + W \sin \theta_0 \qquad (11)$$

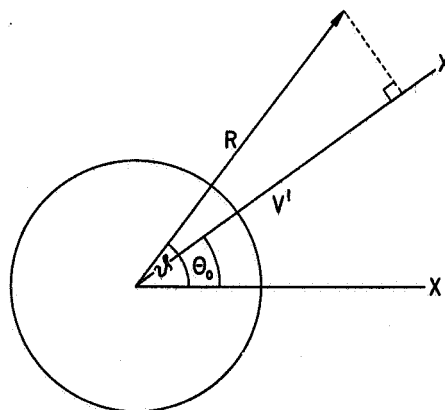which is more practical for numerical calculations.



FIGURE 3. The $V'$ component of $R$ as used in the $V$ test.

TABLE 1.—*Critical Values of the Test Statistic* z *of the Rayleigh Test*

| $n$ | $P=10\%$ | 5% | 2.5% | 1% | 0.1% |
|---|---|---|---|---|---|
| 4 | 2.36 | 2.87 | 3.28 | 3.69 | .................. |
| 5 | 2.29 | 2.84 | 3.34 | 3.86 | 4.91 |
| 6 | 2.29 | 2.86 | 3.40 | 4.08 | 5.30 |
| 7 | 2.29 | 2.88 | 3.45 | 4.16 | 5.56 |
| 8 | 2.29 | 2.90 | 3.48 | 4.20 | 5.74 |
| 9 | 2.29 | 2.91 | 3.50 | 4.25 | 5.88 |
| 10 | 2.29 | 2.92 | 3.52 | 4.29 | 6.00 |
| 11 | 2.29 | 2.93 | 3.54 | 4.32 | 6.06 |
| 12 | 2.29 | 2.93 | 3.55 | 4.34 | 6.16 |
| 13 | 2.29 | 2.94 | 3.57 | 4.36 | 6.22 |
| 14 | 2.29 | 2.94 | 3.58 | 4.38 | 6.27 |
| 15 | 2.29 | 2.95 | 3.59 | 4.40 | 6.32 |
| 16 | 2.29 | 2.95 | 3.59 | 4.41 | 6.35 |
| 17 | 2.29 | 2.95 | 3.60 | 4.42 | 6.39 |
| 18 | 2.29 | 2.95 | 3.60 | 4.43 | 6.42 |
| 19 | 2.29 | 2.96 | 3.61 | 4.44 | 6.45 |
| 20 | 2.30 | 2.96 | 3.61 | 4.45 | 6.47 |
| 21 | 2.30 | 2.96 | 3.61 | 4.46 | 6.49 |
| 22 | 2.30 | 2.96 | 3.61 | 4.46 | 6.51 |
| 23 | 2.30 | 2.96 | 3.62 | 4.47 | 6.53 |
| 24 | 2.30 | 2.96 | 3.63 | 4.48 | 6.54 |
| 25 | 2.30 | 2.97 | 3.63 | 4.48 | 6.56 |
| 30 | 2.30 | 2.97 | 3.64 | 4.49 | 6.62 |
| 35 | 2.30 | 2.97 | 3.64 | 4.51 | 6.66 |
| 40 | 2.30 | 2.98 | 3.65 | 4.52 | 6.69 |
| 45 | 2.30 | 2.98 | 3.65 | 4.53 | 6.72 |
| 50 | 2.30 | 2.98 | 3.66 | 4.54 | 6.74 |
| $\infty$ | 2.31 | 3.00 | 4.06 | 4.61 | 6.90 |

In an experiment of homing, $V'$ denotes the so-called homeward component (ref. 1, p. 19), if $\theta_0$ is the angle of the homeward direction.

The basic idea of the test is to consider the size of $V'$. If $V'$ is small there is no evidence that the animals are oriented in the predicted direction with angle $\theta_0$. If $V'$ is relatively large, however, there must be some concentration of the directions around the predicted bearing. The larger the component

$V'$ is, the better chance there is of rejecting the null hypothesis of randomness. Therefore, we may choose $V'$ as our test statistic. For this reason the test is called the $V$ test (ref. 4).

*The* V *test leads to significance only if there is sufficient clustering around the predicted direction. In contrast the Rayleigh test is less powerful in this case but remains powerful for clustering on any part of the circle.*

For preparing a numerical table of criti-

TABLE 2.—*Critical Values of the Test Statistic* u *of the Modified Rayleigh Test* (V *Test*)

| n | $P=0.10$ | 0.05 | 0.01 | 0.005 | 0.001 | 0.0001 |
|---|---|---|---|---|---|---|
| 5 | $u=1.3051$ | 1.6524 | 2.2505 | 2.4459 | 2.7938 | 3.0825 |
| 6 | 1.3009 | 1.6509 | 2.2640 | 2.4695 | 2.8502 | 3.2114 |
| 7 | 1.2980 | 1.6499 | 2.2734 | 2.4858 | 2.8886 | 3.2970 |
| 8 | 1.2958 | 1.6492 | 2.2803 | 2.4978 | 2.9164 | 3.3578 |
| 9 | 1.2942 | 1.6486 | 2.2856 | 2.5070 | 2.9375 | 3.4034 |
| 10 | 1.2929 | 1.6482 | 2.2899 | 2.5143 | 2.9540 | 3.4387 |
| 11 | 1.2918 | 1.6479 | 2.2933 | 2.5201 | 2.9672 | 3.4669 |
| 12 | 1.2909 | 1.6476 | 2.2961 | 2.5250 | 2.9782 | 3.4899 |
| 13 | 1.2902 | 1.6474 | 2.2985 | 2.5290 | 2.9873 | 3.5091 |
| 14 | 1.2895 | 1.6472 | 2.3006 | 2.5325 | 2.9950 | 3.5253 |
| 15 | 1.2890 | 1.6470 | 2.3023 | 2.5355 | 3.0017 | 3.5392 |
| 16 | 1.2885 | 1.6469 | 2.3039 | 2.5381 | 3.0075 | 3.5512 |
| 17 | 1.2881 | 1.6467 | 2.3052 | 2.5404 | 3.0126 | 3.5617 |
| 18 | 1.2877 | 1.6466 | 2.3064 | 2.5424 | 3.0171 | 3.5710 |
| 19 | 1.2874 | 1.6465 | 2.3075 | 2.5442 | 3.0211. | 3.5792 |
| 20 | 1.2871 | 1.6464 | 2.3085 | 2.5458 | 3.0247 | 3.5866 |
| 21 | 1.2868 | 1.6464 | 2.3093 | 2.5473 | 3.0279 | 3.5932 · |
| 22 | 1.2866 | 1.6463 | 2.3101 | 2.5486 | 3.0308 | 3.5992 |
| 23 | 1.2864 | 1.6462 | 2.3108 | 2.5498 | 3.0335 | 3.6047 |
| 24 | 1.2862 | 1.6462 | 2.3115 | 2.5509 | 3.0359 | 3.6096 |
| 25 | 1.2860 | 1.6461 | 2.3121 | 2.5519 | 3.0382 | 3.6142 |
| 26 | 1.2858 | 1.6461 | 2.3127 | 2.5529 | 3.0402 | 3.6184 |
| 27 | 1.2856 | 1.6460 | 2.3132 | 2.5538 | 3.0421 | 3.6223 |
| 28 | 1.2855 | 1.6460 | 2.3136 | 2.5546 | 3.0439 | 3.6258 |
| 29 | 1.2853 | 1.6459 | 2.3141 | 2.5553 | 3.0455 | 3.6292 |
| 30 | 1.2852 | 1.6459 | 2.3145 | 2.5560 | 3.0471 | 3.6323 |
| 40 | 1.2843 | 1.6456 | 2.3175 | 2.5610 | 3.0580 | 3.6545 |
| 50 | 1.2837 | 1.6455 | 2.3193 | 2.5640 | 3.0646 | 3.6677 |
| 60 | 1.2834 | 1.6454 | 2.3205 | 2.5660 | 3.0689 | 3.6764 |
| 70 | 1.2831 | 1.6453 | 2.3213 | 2.5674 | 3.0720 | 3.6826 |
| 100 | 1.2826 | 1.6452 | 2.3228 | 2.5699 | 3.0775 | 3.6936 |
| 500 | 1.2818 | 1.6449 | 2.3256 | 2.5747 | 3.0877 | 3.7140 |
| 1000 | 1.2817 | 1.6449 | 2.3260 | 2.5752 | 3.0890 | 3.7165 |

cal values, it is more practical to use the related test statistic

$$u = (2/n)^{\frac{1}{2}} V' \qquad (12)$$

A chart of critical values published in reference 4, p. 234, satisfies most practical purposes. The more accurate numerical table (table 2) was submitted by Keeton.

For applications of the V test see references 5 and 6. The following examples were also suggested by Keeton:

*Example 1.* Assume a random sample of directions as shown in figure 4. Despite an apparent clustering to the left, the Rayleigh test does not lead to significance ($z = 2.86$, $P > 0.5$). But when we learn that the home direction has azimuth $\theta_0 = 279°$, the prospect improves. Let us apply the V test. The azimuths $\alpha_i$, listed in increasing order of magnitude, are 0°, 175°, 195°, 225°, 240°, 240°, 260°, 295°, 330°, 340°, and 345°. With $n = 11$ we get, from formulas (4), (5),
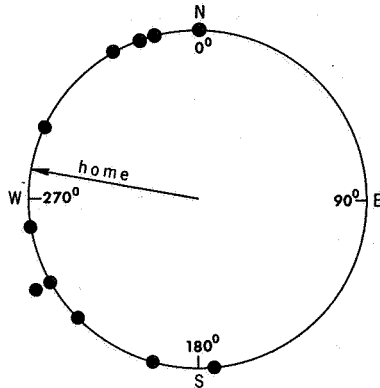
**FIGURE 4.** Home direction is used as predicted direction in application of $V$ test.
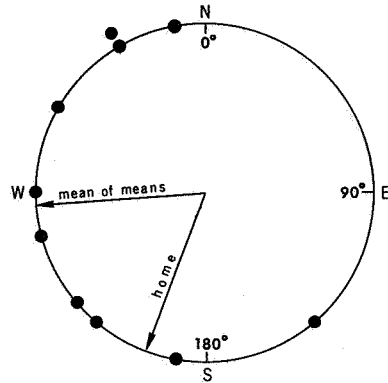


**FIGURE 5.** Long experienced mean direction serves as predicted direction in application of $V$ test.

and (8), $V = + 0.3514$, $W = — 5.6026$, $R = 5.614$, and $\vartheta = 274°$. Then it follows from formulas (11) and (12) that $V' = + 5.589$ and $u = 2.38$. For $n = 11$, table 2 reveals that $P < 0.01$. Hence the hypothesis of randomness can be rejected, whereas the Rayleigh test was too weak in our case.

*Example 2.* At a test site near Castor Hill, N. Y., it was observed in a long series of releases that the mean bearing of homing pigeons always deviated by roughly the same angle from the homeward direction. Figure 5

depicts the situation. The sample shown was collected under special experimental conditions that tend to increase the scatter of the bearings. The azimuths are 140°, 190°, 220°, 230°, 255°, 270°, 300°, 330°, 330°, and 350°. If we are interested in rejecting randomness, we may accept the long-experienced mean direction with azimuth $\theta_0 = 267.4°$ as a predicted direction. The test statistic of the $V$ test is $u = 2.21$. Thus the $V$ test leads to significance with a $P$ value of less than 5 percent, whereas the Rayleigh test would fail again since $P$ turns out to be nearly 10 percent $(z = 2.45)$.

## TEST BY HODGES AND AJNE

Hodges (ref. 7) proposed a bivariate sign test that later turned out to be quite useful in the analysis of directions.

Assume that two quantities are measured on each individual or experimental unit. Denote the two measurements by $x$ and $y$ and assume that the measurements are repeated $n$ times. Thus we get the pairs

$$(x_i, y_i) \qquad i = 1, 2, \cdots, n$$

If the experiment is performed with the same individuals under different conditions, we get another sample consisting of $n$ pairs, say

$$(x_i', y_i') \qquad i = 1, 2, \cdots, n$$

The null hypothesis states that the two samples were taken from the same bivariate distribution. To test this hypothesis we form the differences

$$x_i' — x_i, \; y_i' — y_i, \qquad i = 1, 2, \cdots, n$$

and plot these differences in a rectangular $x$, $y$-diagram. Thus we get $n$ vectors with
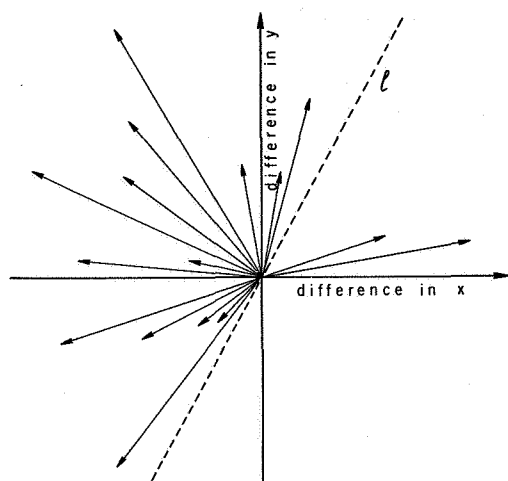
**FIGURE 6. Hodges' test for paired bivariate samples.**

components $x_i' - x_i$ and $y_i' - y_i$, respectively (fig. 6). If the null hypothesis is true, we would observe vectors pointing in all directions. If, on the other hand, the null hypothesis is wrong, the vectors should point to one sector of the $x$, $y$-diagram more frequently than to the rest of the plane.

To get a suitable test statistic we may draw a straight line $l$ through the origin and count how many of the vectors point to one or the other side of $l$. Now we rotate $l$ around the origin until we minimize the number of vectors on one side. This minimum is the test statistic. We denote it by $K$. If $K$ is small enough compared with the sample size $n$, the null hypothesis can be rejected. Critical values for $K$ can be found in table 3, which is adapted from tables in references 3 and 7. Hodges' test may be interpreted as an extension of the sign test to bivariate data.

*Example 3.* In figure 6 the sample size is $n = 16$, and the minimum number of vectors on one side of a straight line $l$ is $K = 2$. The null hypothesis states that the measure-

ments $(x_i, y_i)$ and $(x_i', y_i')$ belong to the same distribution.

Table 3 yields $P = 0.044$. Hence we can reject the null hypothesis at a 5-percent level of significance.

*Example 4.* In the paper in these proceedings entitled "Satellite and Ground Radio Tracking of Elk," F. C. Craighead et al. study the deviations between the actual location of an individual elk and the points tracked by a satellite. The errors of location are recorded as vectors in a horizontal plane in their figure 5.

Do the vectors indicate any preferred directions? Applying Hodges' test, we obtain $n = 17$ and $K = 6$. Table 3 yields a $P$-value greater than 0.500 or 50 percent. Hence we have no reason to assume a preferred direction.[2]

Notice, however, that east-west errors seem to be larger than north-south errors. To test significance of this kind we would need another test. Hodges' test is not sensitive to changes of variance.

*Example 5.* When tracking a single animal, a question frequently arises: Is the movement of the animal oriented or is it random? Consider figure 7 where the track of an animal is recorded. At a glance it appears that the animal is generally headed north and that it only occasionally deviates strongly from his course.

In the light of probability theory, the track may be considered as a realization of a stochastic process. It is very likely that consecutive sections of the track are dependent on each other. We want to show that the animal reorientates himself toward the north over and over again.

Present-day statistics is not able to

TABLE 3.—*Critical Values of Test Statistics* K *in Relation to the Significance Level* P *and the Sample Size* n

| n | K=0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|---|
| 8 | P=.063 | .375 | | | | | | | |
| 9 | .035 | .246 | | | | | | | |
| 10 | .020 | .156 | | | | | | | |
| 11 | .011 | .097 | .376 | | | | | | |
| 12 | .006 | .059 | .258 | | | | | | |
| 13 | .003 | .035 | .171 | .489 | | | >.500 | | |
| 14 | .002 | .021 | .111 | .355 | | | | | |
| 15 | .001 | .012 | .070 | .250 | | | | | |
| 16 | | .007 | .044 | .171 | .444 | | | | |
| 17 | | .004 | .027 | .114 | .327 | | | | |
| 18 | | .002 | .016 | .075 | .233 | | | | |
| 19 | | .001 | .010 | .048 | .163 | .399 | | | |
| 20 | | | .006 | .030 | .111 | .296 | | | |
| 21 | | | .003 | .019 | .074 | .213 | .466 | | |
| 22 | | | .002 | .012 | .049 | .151 | .356 | | |
| 23 | | | .001 | .007 | .032 | .104 | .265 | | |
| 24 | | | | .004 | .020 | .071 | .193 | .413 | |
| 25 | <.001 | | | .003 | .013 | .048 | .137 | .315 | |
| 26 | | | | .002 | .008 | .031 | .096 | .235 | .466 |
| 27 | | | | | .005 | .020 | .066 | .172 | .364 |
| 28 | | | | | .003 | .013 | .045 | .124 | .278 |
| 29 | | | | | .002 | .008 | .030 | .087 | .208 |
| 30 | | | | | .001 | .005 | .020 | .061 | .153 |
| 35 | | | | | | | .002 | .008 | .026 |
| 40 | | | | | | | | | .003 |

prove that such a track is oriented. Nor is statistics able to deal with random walks. However, the following modest approach is possible: Let us play the role of a devil's advocate and assume that from time to time the animal chooses new directions "at random." The directions would be taken from a uniform circular distribution. We call this assumption the null hypothesis. We consider the points $P_1$, $P_2$, $\cdots$ reached by the animal at time 1 hour, 2 hours, $\cdots$ , respectively, after release at $P_0$. (The time interval depends on the frequency of new decisions. In our example, we assume that a new decision is made at intervals smaller than an hour.) Now we form the vectors $\overrightarrow{P_0P_1}$, $\overrightarrow{P_1P_2}$, $\overrightarrow{P_2P_3}$, $\cdots$ . Under the null hypothesis these vectors have random directions. We plot these vectors with a common base 0 and draw a line $l$ that minimizes the number of vectors on one side of $l$. Applying Hodges' test to the vectors of our example, we get $n = 13$, $K = 1$. Table 3 yields $P = .035$. Hence we are able to reject the null hypothesis of randomness at a level of $P = 5$ percent.

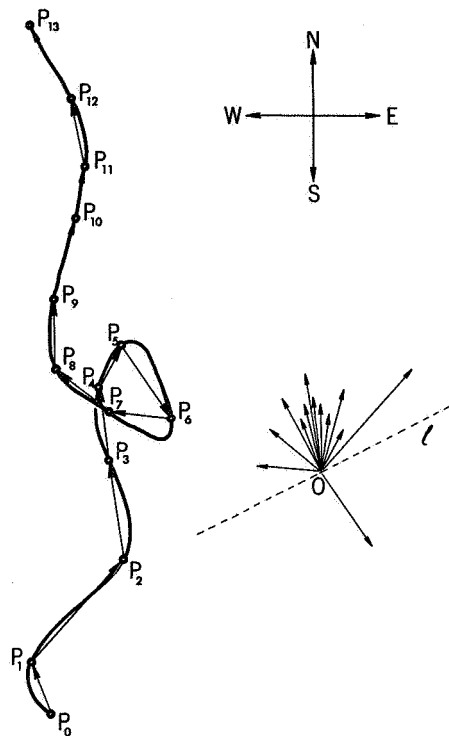Ajne (ref. 3) proposes a circular one-

**FIGURE 7.** Track of an animal and a test for randomness.

sample test. The problem is the same as for the Rayleigh test discussed previously. Consider a sample from a unimodal circular distribution. Can a preferred direction be established statistically? The null hypothesis is a uniform distribution.

The test procedure is very simple once a circular plot is provided. We draw a straight line $l$ through the center of the circle and count the number of sample points on each side of $l$. Then we rotate $l$ and minimize the number of sample points on one side of $l$. This minimum number is denoted by $K$ and used as a test statistic. If $K$ is small relative to the sample size $n$, the null hypothesis of a uniform distribution is rejected.

We slightly modified the original formulation of Hodges' and Ajne's tests. Thus it

becomes obvious that Ajne's test is a special case of Hodges' test. This connection was discovered by Bhattacharyya and Johnson (ref. 8). Ajne's test is powerful if the alternative to the uniform distribution is a rather narrow unimodal distribution (high degree of concentration around the mean direction).

*Example 6.* Homing pigeons were released singly. They disappeared at directions measured by the following azimuths (arranged in increasing order): 115°, 120°, 120°, 130°, 135°, 140°, 150°, 150°, 150°, 165°, 185°, 210°, 235°, 270°, and 345°. Sample size is $n = 15$. The line $l$ can be drawn in such a way that the minimum number of sample points on one side of $l$ is $K = 1$ (fig. 8). From table 3 we get $P = .012$. Hence the null hypothesis of a uniform distribution can be rejected at a 2-percent level of significance.

## AJNE'S SECOND TEST

Ajne (ref. 3) proposes a further method for testing the null hypothesis of a uniform distribution. Consider again the straight line $l$ in figure 8. If the theoretical distribution were uniform, we would expect an equal
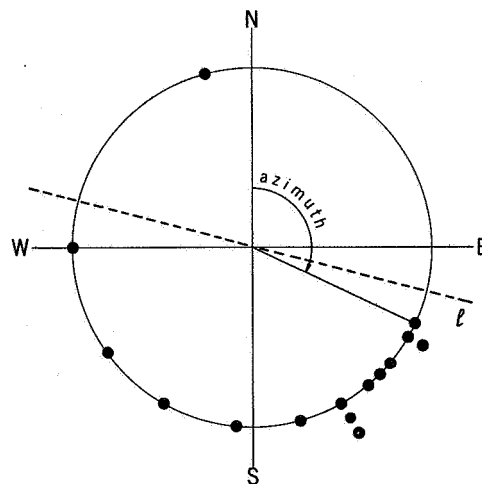


**FIGURE 8.** Ajne's test applied to an orientation problem.

TABLE 4.—*Critical Values for Ajne's Test Statistic* A *in Degrees*

| $n$ | $P=10\%$ | $5\%$ | $2.5\%$ | $1\%$ | $0.5\%$ |
|---|---|---|---|---|---|
| 5 | A = 185 | 227 | 262 | 301 | 324 |
| 6 | 184 | 227 | 268 | 314 | 343 |
| 7 | 184 | 228 | 269 | 318 | 354 |
| 8 | 184 | 229 | 271 | 322 | 359 |
| 9 | 184 | 230 | 272 | 326 | 364 |
| 10 | 185 | 231 | 274 | 329 | 369 |
| 11 | 185 | 231 | 275 | 332 | 372 |
| 12 | 185 | 232 | 277 | 334 | 375 |
| 13 | 185 | 232 | 277 | 336 | 377 |
| 14 | 185 | 232 | 278 | 337 | 379 |
| 15 | 185 | 232 | 278 | 338 | 381 |
| 16 | 185 | 233 | 279 | 339 | 383 |
| 17 | 185 | 233 | 279 | 340 | 385 |
| 18 | 185 | 233 | 280 | 341 | 386 |
| 19 | 185 | 233 | 280 | 341 | 386 |
| 20 | 185 | 233 | 281 | 342 | 387 |
| 30 | 186 | 234 | 283 | 346 | 393 |
| 40 | 186 | 235 | 284 | 347 | 395 |
| 50 | 186 | 235 | 284 | 349 | 397 |
| 100 | 186 | 235 | 285 | 351 | 400 |
| 200 | 186 | 236 | 286 | 352 | 402 |
| ∞ | 185 | 236 | 287 | 354 | 404 |

number of sample points on each side of $l$, that is, $n/2$ sample points. A small deviation from $n/2$ may be due to chance fluctuation. A large deviation, however, indicates that the uniform distribution is not the proper hypothesis. When we rotate $l$ around the center, the deviation from $n/2$ varies. Ajne chooses a suitably defined average of this deviation as a test statistic.

A rather lengthy mathematical analysis leads finally to the following procedure (ref. 9). Let $\alpha_1$, $\alpha_2$, $\cdot$ $\cdot$ $\cdot$ , $\alpha_n$ be the observed angles in degrees and assume that they are arranged in ascending order. Thus

$$\alpha_1 \leqq \alpha_2 \leqq \alpha_3 \leqq \cdots \leqq \alpha_n \qquad (13)$$

Calculate the differences

$$m_{12} = \alpha_2 - \alpha_1, \; m_{13} = \alpha_3 - \alpha_1,$$
$$m_{23} = \alpha_3 - \alpha_2, \cdots$$

If one of them exceeds $180°$, take the complementary value by subtracting it from $360°$. For instance, if $\alpha_{10} - \alpha_1 = 205°$, take $m_{1, 10} = 360° - 205° = 155°$. The differences may be arranged as follows:

$$m_{12} \; m_{13} \quad m_{14} \; m_{15} \; \cdot \; \cdot \; \cdot \; m_{1,n}$$
$$m_{23} \; m_{24} \; m_{25} \; \cdot \; \cdot \; \cdot \; m_{2,n}$$
$$m_{34} \; m_{35} \qquad \vdots$$
$$m_{45} \qquad\qquad \vdots$$
$$m_{n-1,n} \; (14)$$

Then form the sum of all these $n(n-1)/2$ differences, that is,

$$Z = \sum_{j=2}^{n} \sum_{i=1}^{j-1} m_{ij} \qquad (15)$$

With this sum the test statistic can be written in the form

$$A = n \cdot 90° - \frac{2}{n} Z. \qquad (16)$$

The null hypothesis of a uniform distribution is rejected if $A$ exceeds a certain critical value. A table of critical values was published by Stephens (ref. 9); our table 4 is an adaptation of it.

Ajne's second test is especially powerful if the alternative to the uniform distribution is a unimodal distribution with a large angular deviation (low degree of concentration).

*Example 7.* We apply Ajne's test to the same data as in example 6. Here $\alpha_1 = 115°$, $\alpha_2 = 120°, \cdots, \alpha_{15} = 345°$. The differences in degrees arranged in the scheme (equation 14) are

```
5   5  15  20  25  35  35  35  • • •
    0  10  15  20  30  30  30  • • •
       10  15  20  30  30  30  • • •
            5  10  20  20  20  • • •
                5  15  15  15  • • •
                   10  10  10  • • •
                        0   0  • • •
                            0  • • •
```

Notice that $\alpha_{15} - \alpha_1 = 345° - 115° = 230°$, but $m_{1,15} = 360° - 230° = 130°$. Formula (15) yields $Z = 6660°$. Hence, we get from formula (16)

$$A = 15(90°) - \frac{2}{15} 6660° = 462°$$

This value is larger than any critical value in table 4. Therefore, we can reject the null hypothesis of a uniform distribution at a 0.5-percent level of significance.

## TEST BY LAUBSCHER AND RUDOLPH

Sometimes tests are required that are not necessarily powerful but are quick to apply. When testing uniformity versus a unimodal alternative on the circle, such a test could be quite useful. This was proposed by Laubscher and Rudolph (ref. 10) and also investigated by Rao (ref. 11).

Let $R$ be the length of the smallest arc on the circle that contains all sample points. $R$ may be called the range of the sample. A sufficiently small value of $R$ indicates that the sample was not taken from a uniform distribution. Therefore, $R$ can be chosen as a test statistic. If $R$ is below a certain critical value, the null hypothesis of a uniform distribution can be rejected. A table of critical values follows (table 5) which is part of a table published in Laubscher and Rudolph (ref. 10).

*Example 8.* Six different migrating birds kept in cages moved toward average directions with the following azimuths: 122°, 93°, 158°, 67°, 85°, and 145°. Is the concentration of directions significant?

All six angles are between 67° and 158°. Hence the range is $R = 158° - 67° = 91°$. The critical value of $R$ for a significance level of 1 percent is 100.2° (table 5). The sample range is below the critical value. Hence the null hypothesis of a uniform distribution can be rejected. The concentration of directions is indeed significant.

## RAO'S TEST

The previous sections have dealt with the same topic—testing whether a circular sam-

TABLE 5.—*Critical Values n Degrees of the Range* R *of a Circular Sample*

| $n$ | $P = .005$ | 0.01 | 0.025 | 0.05 | 0.10 |
|---|---|---|---|---|---|
| 4 | R = 38.8 | 48.9 | 66.3 | 83.6 | 105.3 |
| 5 | 64.0 | 76.1 | 95.7 | 113.8 | 135.4 |
| 6 | 87.2 | 100.2 | 120.3 | 138.2 | 158.7 |
| 7 | 107.6 | 120.8 | 140.8 | 158.0 | 177.3 |
| 8 | 125.5 | 138.5 | 157.9 | 174.4 | 192.5 |
| 9 | 141.1 | 153.8 | 172.5 | 188.1 | 205.1 |
| 10 | 154.7 | 167.1 | 185.0 | 199.8 | 215.8 |
| 11 | 166.8 | 178.7 | 195.9 | 209.9 | 225.0 |
| 12 | 177.4 | 189.0 | 205.4 | 218.7 | 233.0 |
| 13 | 187.0 | 198.1 | 213.8 | 226.5 | 240.0 |
| 14 | 195.5 | 206.2 | 221.3 | 233.4 | 246.2 |
| 15 | 203.2 | 213.5 | 228.0 | 239.5 | 251.7 |
| 16 | 210.2 | 220.1 | 234.0 | 245.1 | 256.7 |
| 17 | 216.6 | 226.2 | 239.5 | 250.1 | 261.2 |
| 18 | 222.4 | 231.6 | 244.5 | 254.7 | 265.3 |
| 19 | 227.7 | 236.7 | 249.0 | 258.8 | 269.1 |
| 20 | 232.7 | 241.3 | 253.2 | 262.7 | 272.5 |
| 21 | 237.2 | 245.6 | 257.1 | 266.2 | 275.6 |
| 22 | 241.4 | 249.5 | 260.7 | 269.4 | 278.6 |
| 23 | 245.4 | 253.2 | 264.0 | 272.5 | 281.3 |
| 24 | 249.0 | 256.7 | 267.1 | 275.3 | 283.8 |
| 25 | 252.5 | 259.9 | 270.0 | 277.9 | 286.1 |
| 26 | 255.7 | 262.9 | 272.7 | 280.4 | 288.3 |
| 27 | 258.7 | 265.7 | 275.2 | 282.7 | 290.4 |
| 28 | 261.5 | 268.3 | 277.6 | 284.8 | 292.3 |
| 29 | 264.2 | 270.8 | 279.8 | 286.9 | 294.1 |
| 30 | 266.7 | 273.2 | 281.9 | 288.8 | 295.9 |

ple is taken from a uniform distribution. All of these tests are restricted to the situation where the alternative is a unimodal distribution.

However, multimodal distributions occur frequently in biology.[3] They have two or more preferred directions. When we apply one of the aforementioned tests to such data, the test loses most of its power; that is, it

frequently fails to reject the null hypothesis of a uniform distribution even though the existence of modes is strongly suggested.

A test that is powerful in unimodal as well as multimodal situations was recently proposed by Rao (ref. 11). Its application is easy. Assume that the angles of a random sample are arranged in increasing order:

$$\alpha_1 \leqq \alpha_2 \leqq \alpha_3 \leqq \cdots \leqq \alpha_n$$

Then we calculate the length of all $n$ arcs

---

[3] We will omit here the special treatment of multimodal distributions with strict symmetry.

TABLE 6.—*Critical Values for the Test Statistic* U *in Degrees*

| n | P=0.01 | 0.05 | 0.10 |
|---|---|---|---|
| 4 | U=221.0 | 186.5 | 171.7 |
| 5 | 212.0 | 183.6 | 168.8 |
| 6 | 206.0 | 180.7 | 166.3 |
| 7 | 202.7 | 177.8 | 164.9 |
| 8 | 198.4 | 175.7 | 163.4 |
| 9 | 195.1 | 173.5 | 162.4 |
| 10 | 192.2 | 172.1 | 161.3 |
| 11 | 189.7 | 170.3 | 160.2 |
| 12 | 187.6 | 169.2 | 159.2 |
| 13 | 185.8 | 167.8 | 158.4 |
| 14 | 184.0 | 166.7 | 157.7 |
| 15 | 182.2 | 165.6 | 157.0 |
| 16 | 180.7 | 164.9 | 156.6 |
| 17 | 179.6 | 164.2 | 155.9 |
| 18 | 178.2 | 163.1 | 155.2 |
| 19 | 177.1 | 162.4 | 154.8 |
| 20 | 176.0 | 161.6 | 154.4 |
| 25 | 171.9 | 158.9 | 152.7 |
| 30 | 168.8 | 156.7 | 151.4 |
| 35 | 166.4 | 155.0 | 150.3 |
| 40 | 164.4 | 153.6 | 149.5 |
| 45 | 162.7 | 152.4 | 148.7 |
| 50 | 161.2 | 151.4 | 148.1 |
| 100 | 152.8 | 146.8 | 143.7 |
| 200 | 146.8 | 142.6 | 140.4 |

between consecutive sample points on the circle. We denote these arc lengths by $T_i$.

$$T_1 = \alpha_2 - \alpha_1,$$
$$T_2 = \alpha_3 - \alpha_2,$$
$$\cdots$$
$$T_{n-1} = \alpha_n - \alpha_{n-1},$$
$$T_n = 360° + \alpha_1 - \alpha_n \qquad (17)$$

Notice that we always have

$$\Sigma \, T_i = 360° \qquad (18)$$

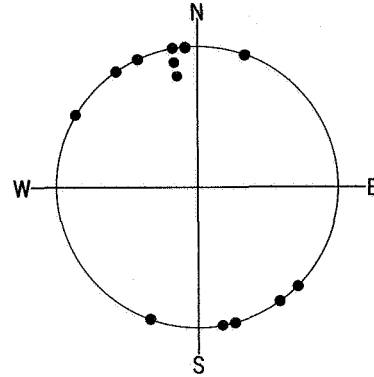If the theoretical distribution is uniform,



FIGURE 9. Testing a bimodal sample using Rao's test.

we expect that the $T_i$ differ only slightly from each other. They fluctuate around their mean value $360°/n$. On the other hand, if the $T_i$ differ sufficiently from $360°/n$, this indicates that the theoretical distribution is not uniform but rather unimodal or multimodal. Rao introduces the sum of deviations as test statistic; more specifically

$$U = \frac{1}{2} \sum_{i=1}^{n} \left| T_i - \frac{360°}{n} \right| \qquad (19)$$

If $U$ exceeds a certain critical value, the null hypothesis of a uniform distribution is rejected. The following (table 6) is a table of critical values for the $U$ statistic. It is partly based on a table in reference 11.

*Example 9.* Homing pigeons were released singly in the Toggenburg Valley under subalpine conditions.[4] The birds did not adjust quickly to the homing direction but preferred to fly in the axis of the valley (fig. 9). The vanishing points are given by the angles arranged in ascending order: 20°, 135°, 145°, 165°, 170°, 200°, 300°, 325°, 335°, 350°, 350°, 350°, and 355°. Sample size is $n = 13$.

TABLE 7.—*Critical Values of the Test Statistic* $K = \sqrt{n} \ (D^+ + D^-)$

| $n$ | $P=10\%$ | $5\%$ | $1\%$ | $0.1\%$ |
|---|---|---|---|---|
| 4 | K = 1.428 | 1.536 | 1.728 | 1.874 |
| 5 | 1.458 | 1.565 | 1.764 | 1.970 |
| 6 | 1.473 | 1.584 | 1.793 | 2.018 |
| 7 | 1.484 | 1.598 | 1.815 | 2.051 |
| 8 | 1.493 | 1.609 | 1.830 | 2.076 |
| 9 | 1.501 | 1.618 | 1.842 | 2.096 |
| 10 | 1.507 | 1.625 | 1.853 | 2.112 |
| 11 | 1.512 | 1.632 | 1.862 | 2.126 |
| 12 | 1.518 | 1.637 | 1.869 | 2.140 |
| 14 | 1.527 | 1.647 | 1.882 | 2.155 |
| 16 | 1.534 | 1.656 | 1.892 | 2.168 |
| 18 | 1.540 | 1.662 | 1.901 | .................... |
| 20 | 1.546 | 1.665 | 1.908 | .................... |
| 30 | 1.562 | 1.684 | 1.930 | .................... |
| 40 | 1.571 | 1.695 | 1.941 | .................... |
| 50 | 1.577 | 1.701 | 1.949 | .................... |
| 60 | 1.582 | 1.705 | 1.955 | .................... |
| 70 | 1.585 | 1.708 | 1.959 | .................... |
| 80 | 1.588 | 1.711 | 1.962 | .................... |
| 100 | 1.590 | 1.716 | 1.967 | .................... |
| ∞ | 1.620 | 1.747 | 2.001 | 2.303 |

Does a uniform distribution fit these data? To test this possibility we apply Rao's $U$ statistic. From formulas (17) we obtain

$T_1 = 115°$    $T_5 = 30°$    $T_9 = 15°$
$T_2 = 10°$    $T_6 = 100°$    $T_{10} = 0°$
$T_3 = 20°$    $T_7 = 25°$    $T_{11} = 0°$
$T_4 = 5°$    $T_8 = 10°$    $T_{12} = 5°$
                               $T_{13} = 25°$

As a check of computation we get $\Sigma T_i = 360°$.

Since $360°/n = 27.7°$, we obtain from formula (19)

$$U = \frac{1}{2}(87.3 + 17.7 + 7.7 + 22.7 + 2.3 + 72.3 + 2.7 + 17.7 + 12.7 + 27.7 + 27.7 + 22.7 + 2.7) = 162°$$

For $P = 0.05$ we get from table 6 the critical value 167.8°; our $U$ value from the sample is somewhat below this. Thus we were not able to establish significance at a 5-percent level. However, a slightly higher sample size, say $n = 15$, would probably have yielded the desired result.

## KUIPER'S GOODNESS-OF-FIT TEST

In reference 1, Kuiper's test was described in detail. The test could serve the same purpose as the previous tests, that is, to decide if a circular distribution is uniform.

Stephens (ref. 12, table 1) slightly corrected the table of critical values for the test statistic and enlarged it considerably. Table 7 is based on Stephens' findings.

Kuiper's test can be used in the unimodal and the multimodal case. A test related to Kuiper's test is Watson's $U^2$ test. It is described in reference 1 (p. 27). In samples occurring in biology, Watson's test is at least as powerful as Kuiper's test.

*Example 10.* We apply Kuiper's test to the data of example 9. Following the test procedure as explained in reference 1, p. 26, we obtain figure 10. From this figure we read

$D^+ = .023$ and $D^- = .369$. Hence

$$K = \sqrt{n}(D^+ + D^-) = \sqrt{13}(.023 + .369)$$
$$= 1.414$$

From table 7 we obtain the critical value $K = 1.642$ at a 5-percent level of significance.

Our $K$ value from the sample is smaller. Therefore, we cannot claim a significant deviation from the uniform distribution. The result is consistent with our findings based on Rao's test.

## CONFIDENCE INTERVALS FOR THE MEAN ANGLE

In the case of a unimodal distribution, it is convenient to work under the hypothesis of circular normal distribution introduced by von Mises in 1918. The probability density function is

$$f(\alpha) = Ce^{\kappa(\alpha-\theta)} \tag{20}$$

where $\theta$ denotes the mean angle, $\kappa$ the parameter of concentration, and $C$ a numerical constant depending on $\kappa$. More details, charts, and tables are given in reference 1.

If we are given a sample of $n$ independent angles $\alpha_1, \alpha_2, \cdots, \alpha_n$, it is often demanded to estimate the parameters $\theta$ and $\kappa$. As a point estimate of $\theta$, we take the mean angle $\vartheta$ calculated from the sample (formula 7).

In addition, the research worker wants to know the reliability of this estimate. The
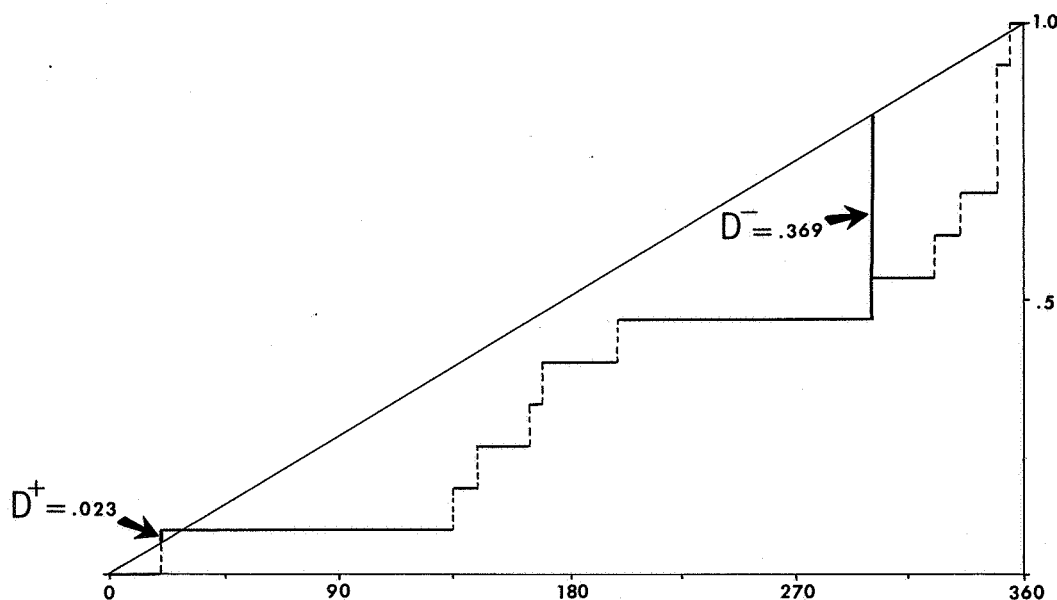


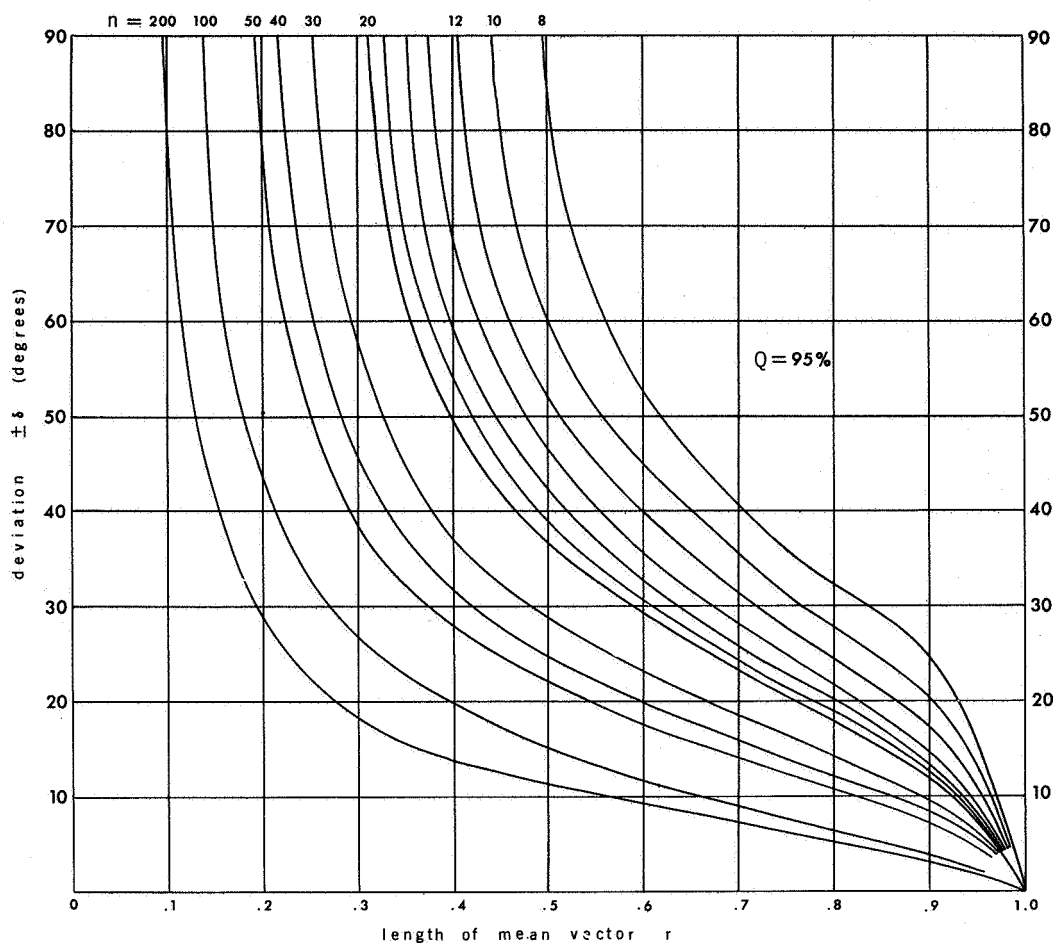FIGURE 10. Application of Kuiper's test to a circular sample.

**FIGURE 11.** Chart for determining a confidence interval of the mean angle with a 95 percent confidence coefficient.

question is then to find an interval around $\vartheta$ in which the unknown parameter $\theta$ falls with a preassigned probability $Q$, called the confidence coefficient.

In reference 1 a confidence interval of the form

$$\vartheta \pm \delta \qquad (21)$$

was presented. However, the method to determine the deviation $\delta$ is somewhat sophis-

ticated. It was therefore a good idea (ref. 13) to search for a direct graphical approach. Brown and Mewaldt present a chart from which the deviaton $\delta$ can be read as a function of the sample size $n$ and the length $r$ of the mean vector. Their chart was prepared for only $Q = 99$ percent and is fairly sketchy. It seemed worthwhile to follow their idea and to draw accurate charts. Figures 11 and 12 yield $\delta$ for confidence coefficients $Q = 95$ percent and $Q = 99$ percent, respectively.
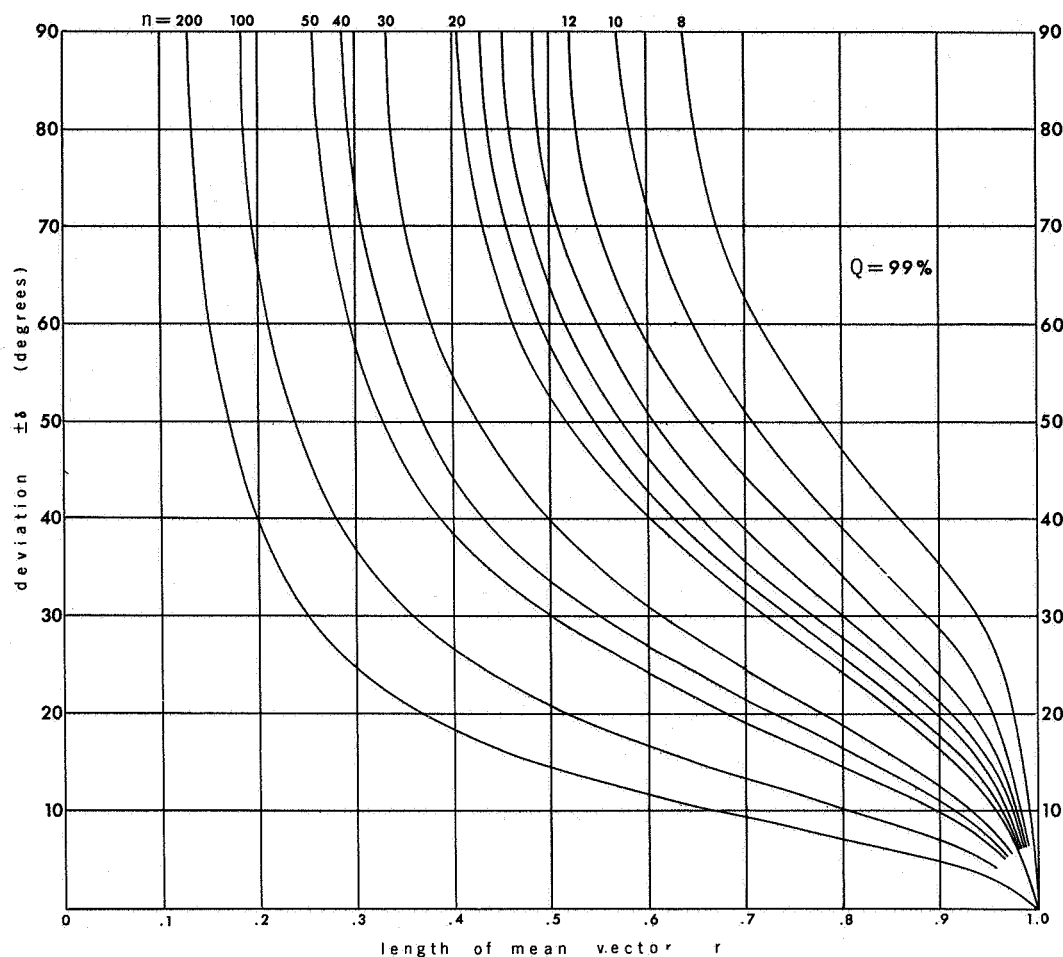
**FIGURE 12.** Chart for determining a confidence interval of the mean angle with a 99 percent confidence coefficient.

*Example 11.* In example 6 the null hypothesis of a uniform distribution was rejected. It is reasonable to assume that the sample was taken from a circular normal distribution with unknown mean angle $\theta$ and unknown parameter $\kappa$ of concentration.

To estimate $\theta$ we first determine the center of gravity following the instructions given in the second section of this paper. We get

$$\Sigma \cos \alpha_i = - 8.5723,$$

$$\bar{x} = \frac{1}{15}(- 8.5723) = - .5715,$$

$$\Sigma \sin \alpha_i = + 3.8478,$$

$$\bar{y} = \frac{1}{15}(3.8478) = + .2565,$$

$$r = (\bar{x}^2 + \bar{y}^2)^{\frac{1}{2}} = .6264,$$

$$\cos \vartheta = \frac{x}{r} = - .9123,$$

$$\sin \vartheta = \frac{y}{r} = + .4095,$$

$$\vartheta = 155.8°$$

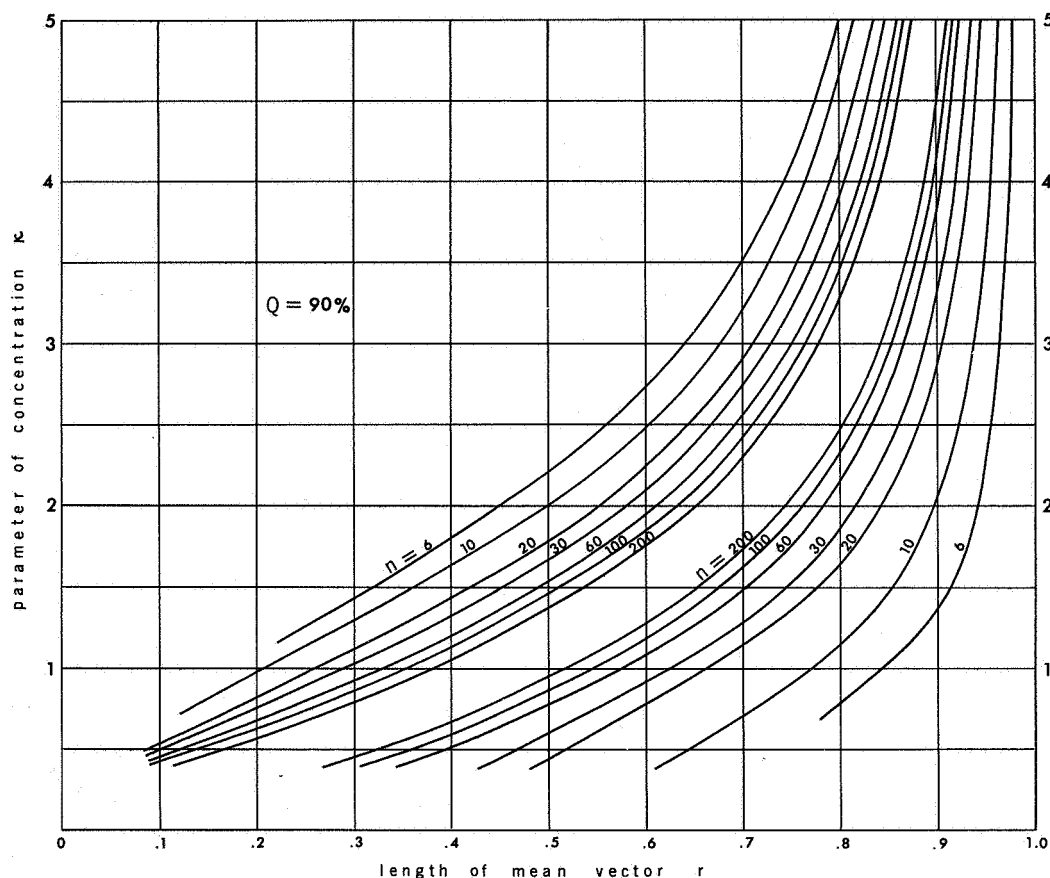Now we choose $Q = 95$ percent as con-

**FIGURE 13.** Chart for determining a confidence interval of the parameter of concentration with a 90 percent confidence coefficient.

fidence coefficient. In figure 11 we find lines for sample sizes $n = 14$ and 16. Our sample size is $n = 15$ so that we have to interpolate. At $r = .6264$ we find $\delta = 30.6°$ for $n = 16$ and $\delta = 33.4°$ for $n = 14$. Hence $\delta = 32.0°$ fits our purpose. Using formula (21) our confidence interval for $\theta$ turns out to be

$$155.8° \pm 32.0°$$

## CONFIDENCE INTERVALS FOR PARAMETER OF CONCENTRATION

As in the previous section, we assume that the theoretical distribution is a circular normal distribution with probability density function (20). Our purpose is to estimate the parameter $\kappa$.

Values of $\kappa$ range from 0 to $\infty$. The particular value $\kappa = 0$ indicates that the distribution is uniform. The higher the value of $\kappa$, the stronger is the concentration about the mean direction. Usually $\kappa$ has to be estimated when the mean angle $\theta$ is unknown. The estimation is based on the length $r$ of the mean vector, which was defined in formula (3). For a point estimate of $\kappa$, we use table B in the appendix of reference 1.
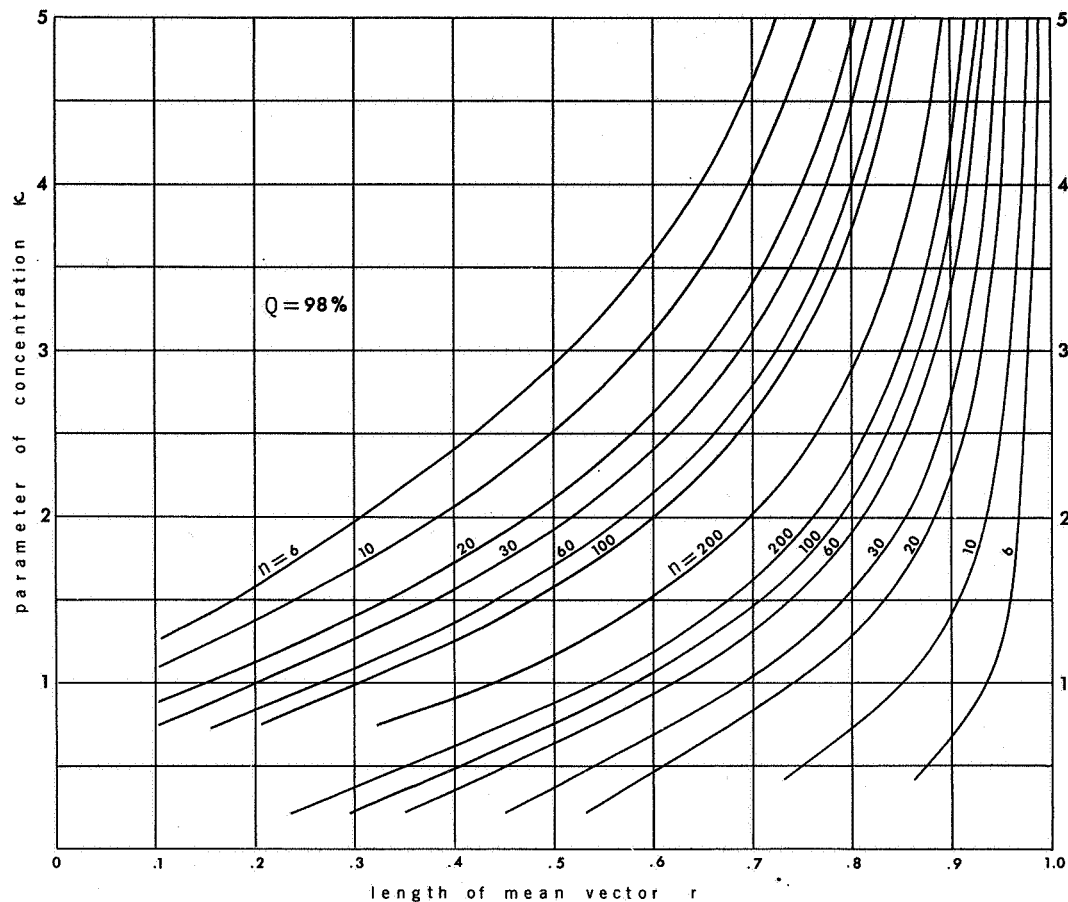
FIGURE 14. Chart for determining a confidence interval of the parameter of concentration with a 98 percent confidence coefficient.

There $r$ ranges from 0 to 1 in steps of 0.01. The estimate of $\kappa$ can be read in the third column.

Stephens (ref. 14) studied the theoretical distribution of $r$ for a variety of circular normal distributions where $\kappa$ ranges from 0 to 5. Based on his table 2, the following charts were drawn: Figures 13 and 14 give upper and lower confidence limits for $\kappa$ for various sample sizes $n$ and for the confidence coefficients $Q = 90$ and 98 percent, respectively. The use of the charts is explained in example 12.

We denote the lower limit by $\kappa_l$ and the upper limit by $\kappa_u$. Thus the confidence interval is

$$\kappa_l < \kappa < \kappa_u \qquad (22)$$

Notice that sometimes the lower confidence limit is zero so that there is no uncertainty on the lower side of the interval. In this case the confidence coefficient has to be raised approximately from 90 to 95 percent and from 98 to 99 percent, respectively.

*Example 12.* We return to example 11.

There $n = 15$ and $r = .6264$. To get a point estimate of $\kappa$, we use table B in the appendix of reference 1. For $r = .62$ we find $\kappa = 1.60044$. For $r = .6264$ we get by linear interpolation $\kappa = 1.629$.

For confidence limits of $\kappa$, we choose $Q = 90$ percent as our confidence coefficient. In figure 13 we find curves for $n = 10$ and $n = 20$. For our own sample with $n = 15$ we will have to interpolate. For the lower limit we read from the lower curves at $r = .6264$

$$n = 10, \qquad \kappa_l = 0.44,$$
$$n = 20, \qquad \kappa_l = 0.88.$$

By linear interpolation for $n = 15$ we obtain

$$\kappa_l = 0.66$$

Similarly for the upper limit we read from the upper curves at $r = .6264$

$$n = 10, \qquad \kappa_u = 2.62,$$
$$n = 20, \qquad \kappa_u = 2.40.$$

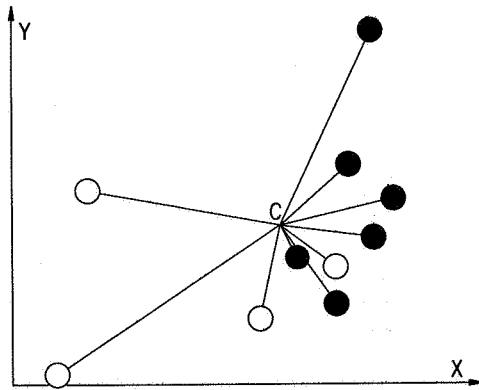Linear interpolation for $n = 15$ leads to



**FIGURE 15.** Testing two bivariate samples. One sample is represented by open circles, the other sample by filled circles. (Mardia's test).

$$\kappa_u = 2.51$$

Hence with probability 90 percent we conclude that

$$0.66 < \kappa < 2.51$$

Notice that the point estimate $\kappa = 1.629$ does not fall exactly into the center of this interval.

## TWO-SAMPLE TEST BY MARDIA, WATSON, AND WHEELER

Wheeler and Watson (ref. 15) proposed a test procedure for comparing two circular samples. This test is nonparametric and powerful; for both reasons the test should be favored by research workers.

Mardia (ref. 16) has shown that Watson's and Wheeler's test is a special case of a bivariate test proposed by Mardia (ref. 17). Mardia also provided tables of critical values for the test statistic. Therefore, it seems to be appropriate to attribute the circular test to all three authors and to name it the Mardia-Watson-Wheeler test. In this section we will first explain Mardia's bivariate test and later consider the special case for circular samples.

We consider a sample of bivariate observations

$$(x_i, y_i), \qquad i = 1, \cdots, m.$$

and a second sample

$$(x_j', y_j'), \qquad j = 1, \cdots, n.$$

We want to know whether the two samples belong to the same bivariate population. To explain the test procedure we plot the sample points (fig. 15). The sample points $(x_i, y_i)$
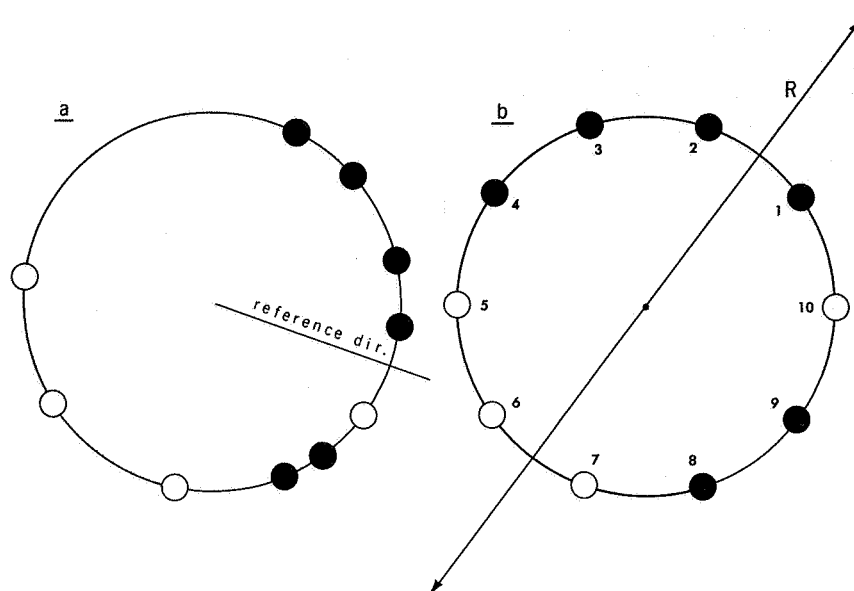
FIGURE 16. (a) Reduction of bivariate samples to circular samples. (b) Generation of equidistant sample points (Mardia-Watson-Wheeler test).

of the first sample are plotted by filled circles and the sample points $(x_i', y_i')$ of the second sample by open circles. The second sample is located slightly to the left and below the first sample. Is this shift due to chance only or were the samples drawn from different populations?

To find a statistical answer to this question we pool the two samples and calculate the coordinates of the common center $C$ of gravity using the formulas

$$\bar{x} = \frac{\Sigma x_i + \Sigma x_j'}{m + n}, \quad \bar{y} = \frac{\Sigma y_i + \Sigma y_j'}{m + n} \quad (23)$$

The center $C$ of gravity is marked in figure 15.

From $C$ we draw vectors to all $m + n$ sample points and consider their directions. Mardia's test is based on these directions only; thus the test reduces the bivariate case to the circular case (fig. 16a).

Now we rank the $m + n$ directions with numbers $1, 2, 3, \cdots, m + n$ by starting at any reference direction and by rotating counterclockwise. Let

$$r_1, r_2, \cdots, r_m$$

be the ranks of the first sample, and

$$r_1', r_2', \cdots, r_n'$$

the ranks of the second sample. In figure 16a we see that $r_1 = 1$, $r_2 = 2$, $r_3 = 3$, $r_4 = 4$, $r_5 = 8$, $r_6 = 9$ and $r_1' = 5$, $r_2' = 6$, $r_3' = 7$, $r_4' = 10$. We have tacitly assumed that there are no intersample ties.

As a next step we introduce $n + m$ equally spaced dots on the circumference of the unit circle and mark them in the same order as the dots of the original samples (fig. 16b). If the dots of one sample are sufficiently separated from the dots of the other sample,

we conclude a significant difference between the samples. To define a test statistic we concentrate on one of the two samples. The choice is irrelevant. Then we calculate the length $R$ of the resultant vector using formulas (4) and (5). When choosing the first sample, the angles are

$$\beta_i = \frac{360°}{n + m} \cdot r_i \qquad i = 1, 2, \cdots, m \quad (24)$$

Hence

$$V = \sum_{i=1}^{m} \cos \beta_i, W = \sum_{i=1}^{m} \sin \beta_i,$$
$$R = (V^2 + W^2)^{1/2} \quad (25)$$

In figure 16b the angles $\beta_i$ are plotted with the horizontal direction as zero line:

$$\beta_1 = 36°, \quad \beta_2 = 72°, \quad \beta_3 = 108°,$$
$$\beta_4 = 144°, \quad \beta_5 = 288°, \quad \beta_6 = 324°$$

Hence $V = 1.118$, $W = 1.539$, $R = 1.902$.

This length $R$ can be used as a test statistic. If $R$ is sufficiently large, the dots of the first sample are concentrated around a preferred direction and thus more or less separated from the dots of the second sample. This argument is very similar to the procedure of the Rayleigh test (see the third section). Thus, in a certain sense, the two-sample test is reduced to a one-sample test, an idea which was successfully applied to other tests (ref. 18).

Instead of $R$ itself, Mardia uses the following function of $R$ as a test statistic

$$B = R^2 \quad (26)$$

If $B$ exceeds a certain critical value, we reject the null hypothesis that the samples were taken from the same population.

The Mardia-Watson-Wheeler test can be safely used only if there are no intersample ties, that is, if no angle of the first sample coincides with an angle of the second sample. When the test leads to significance, this does not necessarily imply that the two samples differ in location. It could well occur that the main reason for significance is a difference in dispersion. This property is typical for most nonparametric tests. For a discussion see reference 1 (p. 34, especially figure 23.1).

Table 8 of $B$ values is based on table 1 of reference 17.

For $N > 17$, Mardia (ref. 17) gives the following approximate distribution:

The quantity

$$U = \frac{2(m + n - 1)}{m\,n} R^2 \quad (27)$$

is approximately distributed as $\chi^2$ with two degrees of freedom. Using a table of critical $\chi^2$ values, it is easy to find critical values for $U$.

In our illustrative example of figures 15 and 16 we got $R = 1.902$. Hence, $B = R^2 = 3.62$. For $n + m = N = 10$ and $n = 4$, the critical value is 9.47 at a 5 percent level of significance. Our $B$ value is smaller. Thus we cannot claim significance.

For a biological example see Mardia (ref. 16, p. 189).

## WATSON'S $U^2$ TEST

A nonparametric two-sample test attributed to Cramér, von Mises, and Smirnov was adapted for the circular case by G. S. Watson. The test was explained and exemplified in reference 1 (pp. 35 and 36). The test statistic is denoted by $U^2_{n,\,m}$ where $n$ and $m$ are the two sample sizes.

The lack of critical values of $U^2_{n,\,m}$ has prohibited the use of this test in the beginning. Now tables of critical values are avail-

TABLE 8.—*Critical Values of the Test Statistic B. (The Two Samples Are of Size* m *and* n, m $\geq$ n, N = m + n.)

| $N$ | $n$ | $P=0.001$ | 0.01 | 0.05 | 0.10 |
|-----|-----|-----------|------|------|------|
| 8 | 4 | | | | 6.83 |
| 9 | 3 | | | | 6.41 |
|   | 4 | | | | 4.88 |
| 10 | 3 | | | | 4.62 |
|    | 4 | | | 9.47 | 6.24 |
|    | 5 | | | 10.47 | 6.85 |
| 11 | 3 | | | | 5.23 |
|    | 4 | | | 10.42 | 7.43 |
|    | 5 | | | 12.34 | 6.60 |
| 12 | 3 | | | 7.46 | 5.73 |
|    | 4 | | | 9.71 | 7.46 |
|    | 5 | | 13.93 | 10.46 | 7.46 |
|    | 6 | | 14.93 | 11.20 | 7.46 |
| 13 | 3 | | | 7.68 | 6.15 |
|    | 4 | | | 9.35 | 7.03 |
|    | 5 | | 15.26 | 10.15 | 7.39 |
|    | 6 | | 17.31 | 10.42 | 8.04 |
| 14 | 3 | | | 7.85 | 6.49 |
|    | 4 | | 12.34 | 9.30 | 7.60 |
|    | 5 | | 15.44 | 10.30 | 7.85 |
|    | 6 | | 15.59 | 12.21 | 7.94 |
|    | 7 | | 16.39 | 11.65 | 8.85 |
| 15 | 3 | | | | 6.78 |
|    | 4 | | 12.78 | 8.74 | 7.91 |
|    | 5 | | 14.52 | 10.36 | 7.91 |
|    | 6 | | 17.48 | 11.61 | 9.12 |
|    | 7 | 22.88 | 16.14 | 11.57 | 9.03 |
| 16 | 3 | | | 7.81 | 5.83 |
|    | 4 | | 13.14 | 9.44 | 7.38 |
|    | 5 | | 15.55 | 10.44 | 9.03 |
|    | 6 | 22.43 | 16.98 | 11.54 | 9.11 |
|    | 7 | 25.27 | 18.16 | 12.66 | 9.78 |
|    | 8 | 26.27 | 18.89 | 13.14 | 9.44 |
| 17 | 3 | | | 8.01 | 6.14 |
|    | 4 | | 13.10 | 9.74 | 7.64 |
|    | 5 | 18.86 | 16.44 | 11.03 | 8.76 |
|    | 6 | 23.73 | 17.76 | 12.21 | 9.41 |
|    | 7 | 27.40 | 17.98 | 12.63 | 10.11 |
|    | 8 | 29.37 | 19.11 | 13.36 | 10.15 |

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TABLE 9.—*Critical Values for Watson's* $U^2_{n,m}$. *(The Two Samples Are of Sizes* n *and* m, n $\geq$ m*)*

| n,m | P=10% | 5% | 1% | 0.1% | n,m | P=10% | 5% | 1% | 0.5% |
|---|---|---|---|---|---|---|---|---|---|
| 10, 6 | .153 | .182 | .243 | .266 | 20, 4 | .151 | .178 | .231 | .251 |
| 10, 7 | .153 | .183 | .246 | .270 | 20, 6 | .152 | .182 | .245 | .270 |
| 10, 8 | .153 | .183 | .248 | .273 | 20, 8 | .152 | .183 | .251 | .278 |
| 10, 9 | .153 | .184 | .249 | .275 | 20, 12 | .153 | .185 | .256 | .285 |
| 10, 10 | .153 | .184 | .250 | .277 | 20, 16 | .153 | .185 | .258 | .289 |
| 12, 6 | .153 | .182 | .244 | .268 | 20, 20 | .153 | .185 | .259 | .290 |
| 12, 7 | .153 | .183 | .247 | .272 | 25, 5 | .151 | .180 | .240 | .263 |
| 12, 8 | .153 | .184 | .249 | .275 | 25, 10 | .152 | .184 | .254 | .283 |
| 12, 9 | .153 | .184 | .251 | .278 | 25, 15 | .153 | .185 | .258 | .289 |
| 12, 10 | .153 | .184 | .252 | .279 | 25, 20 | .153 | .186 | .260 | .291 |
| 12, 11 | .153 | .184 | .253 | .280 | 25, 25 | .153 | .186 | .261 | .293 |
| 12, 12 | .153 | .184 | .253 | .282 | 30, 5 | .150 | .179 | .240 | .263 |
| 14, 6 | .153 | .182 | .244 | .269 | 30, 10 | .152 | .184 | .254 | .284 |
| 14, 8 | .153 | .184 | .250 | .276 | 30, 15 | .152 | .185 | .259 | .290 |
| 14, 10 | .153 | .184 | .253 | .281 | 30, 30 | .153 | .186 | .262 | .294 |
| 14, 12 | .153 | .185 | .254 | .283 | 40, 5 | .150 | .179 | .240 | .263 |
| 14, 14 | .153 | .185 | .255 | .285 | 40, 10 | .152 | .184 | .254 | .284 |
| 16, 4 | .151 | .178 | .231 | .251 | 40, 15 | .152 | .185 | .259 | .290 |
| 16, 6 | .152 | .182 | .244 | .269 | 40, 20 | .152 | .186 | .261 | .293 |
| 16, 8 | .153 | .183 | .250 | .277 | 40, 40 | .152 | .186 | .263 | .296 |
| 16, 10 | .153 | .184 | .253 | .282 | 50, 5 | .150 | .178 | .239 | .263 |
| 16, 12 | .153 | .185 | .255 | .284 | 50, 10 | .151 | .183 | .254 | .284 |
| 16, 14 | .153 | .185 | .256 | .286 | 50, 15 | .152 | .185 | .259 | .290 |
| 16, 16 | .153 | .185 | .257 | .287 | 50, 20 | .152 | .185 | .261 | .293 |
| | | | | | 50, 25 | .152 | .186 | .262 | .295 |
| | | | | | 50, 50 | .152 | .186 | .264 | .298 |
| | | | | | $\infty, \infty$ | .1517 | .1869 | .2684 | .3035 |

able. Burr (ref. 19, p. 1094) published a table for all pairs $m, n \geq 4$, $m + n \leq 17$, and $P < 0.01$. Later Stephens (ref. 20), extended the table for large values of $n$ and $m$ up to $m = n = 50$.

Watson's $U^2_{n, m}$ test is sensitive for all kinds of deviations between two populations. Table 9 is adapted from reference 20.

#### $V_{n,m}$ TEST

Another nonparametric two-sample test, Kuiper's modification of a test by Smirnov, is now known as the $V_{n,m}$ test. It is described in detail in reference 1 (p. 35). Maag and Stephens (ref. 29) have provided tables for the critical values of the test statistic. They range from $n = 3$ to $n = 10$ and from $m = 3$ partly up to $m = 20$.

#### MULTISAMPLE TESTS

In orientation problems, sometimes more than two samples have to be compared with each other. Tests designed to discover differences among several samples are often called tests of homogeneity.

A test for comparing the mean directions of several circular samples was proposed by Watson and Williams (ref. 21). It is assumed that $q$ samples of sizes $n_1$, $n_2$, . . . , $n_q$, respectively, are taken from $q$ circular normal

(or von Mises') distributions with the same unknown parameter $\kappa$ of concentration.

The null hypothesis states that the mean directions of the $q$ normal distributions are the same. To test the null hypothesis we calculate for each sample the length $R_i$ of the resultant vector using formulas (4) and (5). We also pool the $q$ samples and calculate for all

$$N = n_1 + n_2 + \cdots + n_q \qquad (28)$$

observations the length $R$ of the resultant vector. Then the test statistic is

$$F = \frac{(N - q)(\Sigma R_i - R)}{(q - 1)(N - \Sigma R_i)} \qquad (29)$$

If $F$ exceeds a certain critical value, the null hypothesis of equal mean directions is rejected. The test statistic $F$ is approximately distributed as Fisher's $F_{q-1, N-q}$ with $q - 1$ and $N - q$ degrees of freedom. Critical values of $F$ can be found in any table of the $F$ distribution, e.g. in the well-known table by Fisher and Yates (ref. 22) on pages 47, 49, 51, 53, 55. There $F$ is denoted by $e^{2z}$.

For the rationale of the test and for a biological example see reference 1 (section 22).

A modification of Watson's and Williams' test was recently proposed by Stephens (ref. 23). For the two-sample case, Stephens' test is exact. In the multisample case, the accuracy is improved by the introduction of a factor $C$ that depends on $R/N$.

These tests are parametric; that is, they are based on strict assumptions on the underlying distributions. They are certainly powerful, but the power may be outweighed by doubts about the basic assumptions. It is therefore desirable to apply nonparametric tests whenever we have no evidence of unimodal distributions with the same degree of concentration. A nonparametric multisample test was proposed by Maag (ref. 24). It is an extension of Watson's $U^2$ test (see the previous section). Unfortunately the test cannot yet be applied since a table of critical values for the test statistic is not available.

A generalization of the Mardia-Watson-Wheeler test to the multisample case will soon be published. For this test critical values of the test statistic will be available (see refs. 25 and 26).

### COSINOR METHOD

In the statistical analysis of biological rhythms a method has been developed that is strongly connected to circular distributions. If the period $T$ of a cyclic phenomenon is known, it is natural to associate the quantity measured with a circle. As the time increases by one period, we rotate once around the circle. As a rule, there will be a time instant when the quantity reaches a maximum. This time instance corresponds to the mean direction of a unimodal circular distribution.

To be more specific, we consider the data in figure 17.[5] The interperitoneal temperature of a rat is measured at various times during the 24 hours of a day, not necessarily at regular time intervals. The data suggest the following model:

$$z_i = C_0 + C \cos (\omega t_i - \varphi) + e_i \qquad (30)$$

where $t_i$ $(i = 1, \ldots, k)$ are the time instants at which the measurements $z_i$ were taken. $C_0$ denotes the mean level of $z_i$, $C$ the amplitude, $\omega = 2\pi/T$ the known angular frequency, and $\varphi$ the so-called acrophase, that is, the phase at which the peak of the quantity $z$

$F(t) = C_o + C \cos(\omega t + \phi)$

Key:

$C_o$ = mean level, in °C
$C$ = amplitude, in °C
$\omega$ = angular frequency, fixed at
 360°/24h = 15°/h
$t$ = time, in hours
$\phi$ = computative acrophase, in degrees from $00^{00}$

SE = standard error

SE" = .07 °C

$C$ = .86 °C

$C_o$ = 37.62 °C $\}$ SE' of $C_o$ = .05 °C

$\phi$ = -109° → CI of $\phi$ = -100° to -118°

$\varphi$ = -199° → CI of $\varphi$ = -190° to -208°

CI = $\phi \pm (SE''/C \times 112.31)$ = 95 % confidence interval

Lighting Regimen:

| Clock hour (GMT): | $18^{00}$ | $00^{00}$ | $06^{00}$ | $12^{00}$ | $18^{00}$ | $24^{00}$ |
|---|---|---|---|---|---|---|
| Degrees { from $00^{00}$ | | 0 | -90 | -180 | -270 | -360 |
| { from mid-L: | 0 | -90 | -180 | -270 | -360 | |
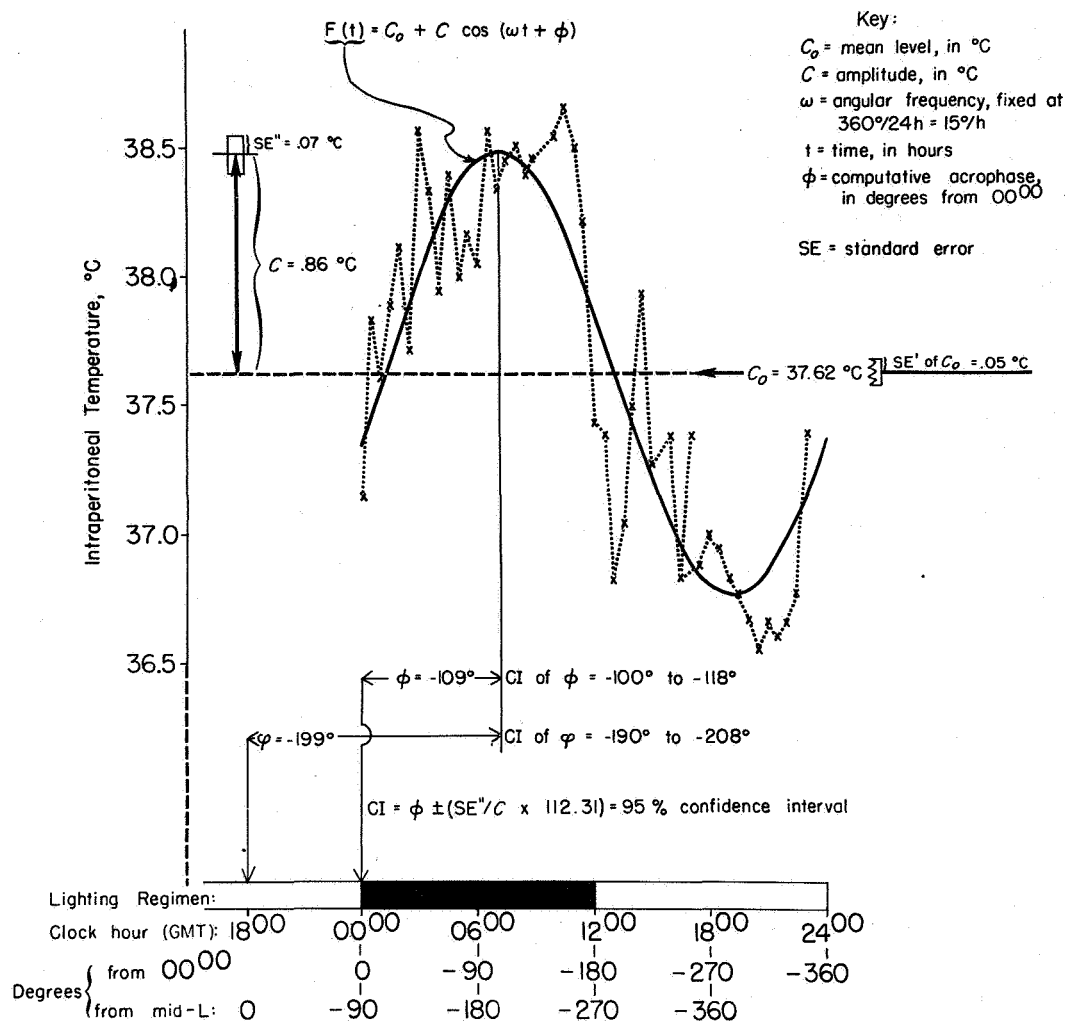
FIGURE 17. Application of the Cosinor method to telemetric measurements of intraperitoneal temperatures of adult female rat. Rat is subjected to special lighting regimen which influences the acrophase. Data were obtained in preparation for a space shot.

occurs theoretically. Finally $e_i$ is the error term.

In order to apply the standard technique of least squares estimation we assume that the errors $e_i$ are independently distributed normal variates with mean zero and common variance $\sigma^2$.

The model is not linear in the unknown parameter $\varphi$, but it can be linearized by rewriting

$$C \cos(\omega t_i - \varphi) = C \cos \omega t_i \cos \varphi + C \sin \omega t_i \sin \varphi \qquad (31)$$

and by substituting

$$C \cos \varphi = x, \quad C \sin \varphi = y \qquad (32)$$

Thus $C$ and $\varphi$ are replaced by new parameters $x$ and $y$. Notice that $x$ and $y$ can be interpreted as rectangular components of a vector of length $C$ and polar angle $\varphi$.

It is not the place here to present the method of least squares estimation. We mention only that we get minimum variance estimates $\hat{x}$, $\hat{y}$, $\hat{C_0}$ for the unknown parameters and an estimate $s^2$ for the unknown variance $\sigma^2$ of the error term.

Estimates for $C$ and $\varphi$ are found by solving the equations (32) with $x$ and $y$ replaced by $\hat{x}$ and $\hat{y}$, respectively.

If measurements are not only taken from one individual but from $n$ comparable individuals independently, we obtain a sample of estimates

$$\hat{C}_{0j}, \ \hat{C}_j, \ \hat{\varphi}_j \qquad j = 1, \ldots, n \qquad (33)$$

The biological interest usually focuses on the amplitude and the acrophase. It is then natural to plot the $n$ vectors with polar coordinates $C_j$, $\varphi_j$ or corresponding rectangular coordinates $x_j$, $y_j$ in an $xy$-coordinate system. If our bivariate sample is roughly unimodal, it makes sense to calculate the components of the sample mean vector:

$$\bar{x} = \frac{1}{n} \Sigma \hat{x_j}, \ \bar{y} = \frac{1}{n} \Sigma \hat{y_j} \qquad (34)$$

This mean vector in turn defines a mean amplitude and a mean acrophase for the sample.

Let $\mu_x$ and $\mu_y$ denote the rectangular coordinates of the true but unknown mean vector. We may then be interested in a confidence ellipse that covers the point $(\mu_x, \mu_y)$. For this purpose we follow again a standard technique and determine the sample correlation coefficient $r$ and the standard errors $S_x$ and $S_y$ of $\hat{x_j}$ and $\hat{y_j}$. Then the point $(\mu_x, \mu_y)$ satisfies the inequality

$$\left( \frac{\bar{x} - \mu_x}{S_x} \right)^2 - 2r \left( \frac{\bar{x} - \mu_x}{S_x} \right) \left( \frac{\bar{y} - \mu_y}{S_y} \right)$$

$$+ \left( \frac{\bar{y} - \mu_y}{S_y} \right)^2 \leq (1 - r^2) \frac{2(n-1)}{n-2}$$

$$\cdot F_{2, n-2} \qquad (35)$$

Here $F_{2, n-2}$ denotes Fisher's $F$ for a preassigned confidence coefficient. The inequality (35) defines the desired confidence ellipse.

The confidence ellipse informs the research worker to what extent he can rely on the estimated mean amplitude and mean acrophase. If, for instance, the confidence ellipse does not cover the point $(0,0)$, we conclude statistically that the amplitude is significantly different from zero.

Conversely if the confidence ellipse covers the point $(0,0)$, then we have no reason to assume that there exists a nonzero amplitude. In this case, periodicity of the quantity $z$ cannot be established.

This method and related techniques, proposed by Halberg and coworkers, have become known as Cosinor method. For a more detailed account see reference 27. It is expected that the Cosinor method will not only be useful in the area of biological rhythms as hitherto but also in some problems of orientation.

There are other statistical methods which also deal with biological rhythms. For a remarkably clear treatment of periodic regression, see reference 28 (chapter 17).

## DISCUSSION

WILLIAMS: A number of us have been going to extremes to get not only the point on the circle or

vanishing point but also to develop a statistic that will express the degree of orientation of a track. The problem essentially is this: Given two sets of radiating lines, radiating in some primary direction, other than just plotting where they intersect a circle, how can one determine whether these represent two different populations? Secondly, how can we develop a statistic that will express the straightness of the plot?

BATSCHELET: To express the degree of orientation we may subdivide the track into a moderate number of sections, each of them with the same flying time. We replace each section of the track by a straight line and represent their directions by unit vectors. Then we calculate the mean vector as usual. Its angle serves as mean angle, and its length $r$ is a measure of concentration. We may also use the angular deviation $s = [2(1-r)]^{1/2}$ as a measure of dispersion.

Since each radiating line can be replaced by a straight line with a certain mean angle, a set of radiating lines can be considered as a circular sample. If such a set is a random sample from a population, circular tests can be applied. Likewise for two sets, circular two-sample tests are applicable.

The straightness of a plot can be statistically expressed in many different ways. One such way is using the length of the mean vector as described before. Another statistic or index would be the maximum deviation from a straight line joining initial and end points of a track. Whatever statistic we use, we have to keep in mind that we lose some information and that there will be no definition that serves all purposes.

Special difficulties arise if the animal follows a geographic line or is watching for a food source. Under variable atmospheric conditions the track could also be the result of a learning process.

CARR: What do you think about that series of 10-minute duty-cycle heading reports mentioned by Mr. Baldwin this morning? You suggested that these could not be evaluated statistically because the animal had perhaps learned something between each successive heading. I don't understand this. Why can't each reported heading be considered in the same light as a single sally of an experimental bird in an orientation arena and regular circular statistics applied?

BATSCHELET: A statistic for the "straightness" of a track could be quite suitable to express how well an animal is keeping a certain direction. However, the question may be more demanding: Is the animal heading for a particular destination or can

the track be explained otherwise, say by random movements? With one single animal this question cannot be solved by today's statistical methods. We should first create appropriate models for animal migration. Such models would belong to the large area of stochastic processes. Then statistical methods would have to be developed to test whether an observed track fits the model. A random sample of a few animals seems to be the easiest method to solve the problem of how well the animals are motivated.

WATERMAN: We are all very concerned with these problems of experimental design and data analysis for orientation. One great difficulty is that we know almost nothing about the dynamics of orientation, consequently we do not really know what endpoints to use. We can take as many observations ad lib, but are they really independent?

Another problem which is prominent in our research on polarotaxis is multiple peak orientation. It is difficult to decide how many significant orientation peaks you really have. In addition, we are also interested in knowing the location of these peaks and estimating the significance of their differences.

BATSCHELET: Multiple peak orientation occurs quite frequently. It is essential in each experiment to find out the reasons for this behavior before statistical methods are applied. Once the theoretical peak directions are defined, statistics is able to test the goodness of fit or to decompose a multimodal distribution into unimodal distributions. However, counting peaks without a biological or physical model is a hopeless statistical enterprise.

CARR: Suppose you put out a mechanical turtle with a built-in orientation system and you want to answer the question, Is the machine orienting or travelling at random? Is there no statistical way for evaluating its capacity simply to hold a course? Is there no test for significance for a segment of a course, in terms of its adherence to a straightline or to some regular modification of a straight line?

BATSCHELET: In principle it can be solved, but in the graphs I have seen, it cannot be handled that way.

BALDWIN: What is your opinion of the validity of comparing the paths of two turtles released simultaneously, assuming that there is no communication between them?

BATSCHELET: Whether two turtles released at the same time move independently of each other cannot be tested by statistical methods.

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