

# THE EFFECT OF THE CORIOLIS FORCE ON THE FLIGHT OF A BIRD

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**ABSTRACT.**—In Part I, a mathematical treatment is given of the various ways in which a bird could, in principle, determine its latitude from measurements of the Coriolis force. A bird flying in a horizontal plane can determine whether it is in the Northern or Southern Hemisphere and locate the meridian by seeking a flight direction in which the Coriolis force is horizontal. By flying out of the horizontal plane and seeking a flight direction in which the Coriolis force is zero, it can determine its latitude (but not its hemisphere) and locate the meridian. Its latitude, hemisphere, and meridian are determined by doing both of these experiments or by determining the direction of the Coriolis force for two different flight directions, or from one flight direction if it knows the angular speed of the Earth.

In Part II, a discussion is given of the trajectories that would be followed under the influence of the Coriolis force alone. At high latitudes, the trajectory takes the form of a loop that drifts east or west according to whether the initial latitude is greater or less than  $45^\circ$ . At low latitudes, the trajectory is a figure-eight that drifts east or west depending on the initial azimuth. *Received 11 June 1979, accepted 24 September 1979.*

THE method by which migrating birds navigate has long been one of the great mysteries in ornithology. Numerous theories have been proposed; some have been rapidly discarded, while others seem to be supported to a greater or lesser degree by observation and experiment. It seems likely that several different types of clues may give birds navigational information, or that not all species use the same method or methods.

Among the possible directional clues that have been suggested is the Coriolis force, but this has usually been dismissed as being too small and is rarely discussed today. Yeagley and Whitmore (1947) and Yeagley (1951) gave some experimental evidence in support of their idea that birds could obtain positional information from a combination of measurements of the Coriolis force and the Earth's magnetic field, although even they conceded that the Coriolis force was very small. Wilkinson (1946) and Varian (1948) especially felt that this was a fatal objection on the grounds that the Coriolis force at most would make an apparent change in the direction of local gravity of less than a minute of arc, while Slephan (1948) raised a similar objection to the magnetic field theory, on the grounds that the Lorentz force (which the bird perceives as an electric field as a result of its motion through a magnetic field) is very much less than the Earth's ambient electric field.

There are certainly good grounds for rejecting the Coriolis force as too small. As an extreme example, if a bird flies very rapidly at  $40 \text{ m}\cdot\text{s}^{-1}$  (89 mi per h) at one of the Earth's poles (where the Coriolis force is greatest), it will experience a Coriolis acceleration of only  $5.8 \times 10^{-3} \text{ m}\cdot\text{s}^{-2}$ . More realistically, for a bird flying north or south at  $15 \text{ m}\cdot\text{s}^{-1}$  (34 mi per h) at a latitude of  $45^\circ$ , the Coriolis acceleration is  $1.5 \times 10^{-3} \text{ m}\cdot\text{s}^{-2}$ .

Even the larger of these values is very small, not only compared with the gravitational-centrifugal acceleration  $g$  of  $9.8 \text{ m}\cdot\text{s}^{-2}$ , but also compared with the equator-to-pole variation in  $g$ , which amounts to about  $5 \times 10^{-2} \text{ m}\cdot\text{s}^{-2}$  (a point that particularly worried Davis, 1948). If we are to postulate that a bird *can* detect the very tiny Coriolis acceleration, then we must also admit that, in principle, it could de-

termine its latitude much more readily from the much stronger variation with latitude of  $g$ .

The purpose of this paper is not to argue that birds really do use the Coriolis effect for navigation, but to investigate, on a much firmer mathematical basis than has hitherto been published, how *in principle* a bird *might* determine its latitude and direction of flight supposing that it were capable of measuring the Coriolis acceleration. Whether a bird, in practice, can use these methods is a matter for biological study and is outside the scope of this paper. Such a study, however, will need a mathematical understanding of the principles involved and the results developed in this paper. Because my purpose in this paper is only to provide a mathematical framework, I have deliberately avoided reference to any particular bird species or any known data on bird migration routes. Nor do I advocate that the Coriolis effect is or is not used, in practice, by birds. In my Concluding Remarks, however, I do argue that the admittedly very small magnitude of the effect is by no means a fatal objection, even when other forces of much greater magnitude may be present.

In Part I, we shall see that there are several different ways in which a bird could obtain navigational clues from the Coriolis effect, and, according to the circumstances, we shall have to ascribe varying degrees of ability to the bird. For example, not only might the bird have to be able to measure its velocity and the Coriolis acceleration, but it might have to know the angular speed of the Earth, and it would usually have to be able to do mathematical calculations in flight. I shall not be concerned with *how* it makes its measurements or gains its knowledge or performs its calculations. When I show how the direction to north can be calculated from certain measurements, I am merely demonstrating that information about the direction to north is inherent in the measurements made.

In Part II of this paper, I take a rather different approach. I do not attribute any ability in the bird to measure the Coriolis acceleration or to calculate the direction to north from its measurements, but assume that the bird is totally ignorant of the Coriolis acceleration and calculate the path the bird would fly if it attempted to fly bill first without allowing for the Coriolis acceleration.

## PART I

*Velocity-acceleration relationships.*—Imagine that a bird is situated at some point  $O$  and can refer directions with respect to a coordinate system  $Oxyz$ . The  $z$  direction is vertically upwards and the  $xy$  plane is horizontal. The  $x$  direction is arbitrary, perhaps the direction to some distant landmark.

I shall make use of vector methods. A vector  $\mathbf{A}$  can be specified by its cartesian components  $A_x, A_y, A_z$ , or by its magnitude  $A$  and spherical coordinates  $\theta, \phi$  (Fig. 1A) or direction cosines  $l, m, n$ . The direction cosines  $l, m, n$  are the cosines of the angles between  $\mathbf{A}$  and the  $x$ -,  $y$ - and  $z$ -axes, respectively. The relations between the various quantities are

$$A_x = lA \tag{1}$$

$$A_y = mA \tag{2}$$

$$A_z = nA \tag{3}$$

$$l = \sin \theta \cos \phi \tag{4}$$

$$m = \sin \theta \sin \phi \tag{5}$$

$$n = \cos \theta \tag{6}$$

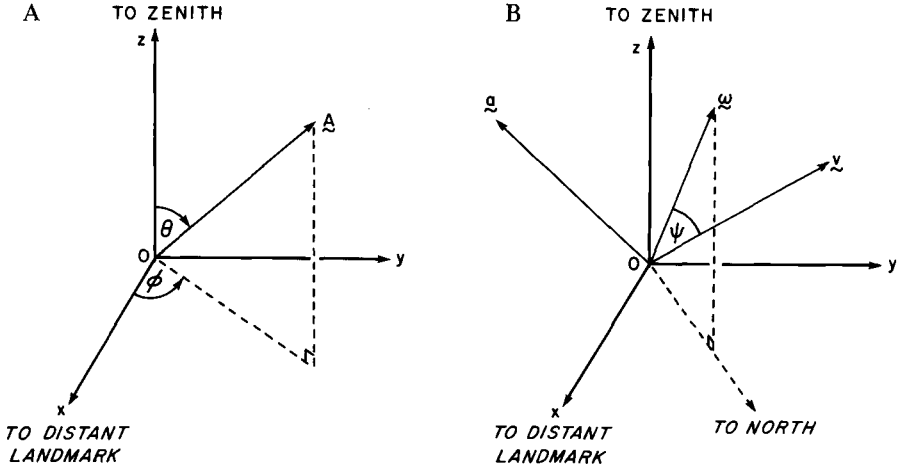


Fig. 1. A. The spherical coordinates of a vector  $\mathbf{A}$  (A). B. The relations between  $\mathbf{v}$  ( $\mathbf{v}$ ),  $\mathbf{a}$  ( $\mathbf{a}$ ), and  $\boldsymbol{\omega}$  ( $\boldsymbol{\omega}$ ).

In particular, I shall discuss the relationships between three vectors:  $\boldsymbol{\omega}$ , the Earth's angular velocity vector;  $\mathbf{v}$ , the bird's velocity vector; and  $\mathbf{a}$ , the Coriolis acceleration. The vector  $\boldsymbol{\omega}$  is parallel to the Earth's rotation axis and directed to the north celestial pole. Its spherical coordinate  $\theta$  is equal to the bird's angular distance from the Earth's north pole. The spherical coordinate  $\phi$  of  $\boldsymbol{\omega}$  is the azimuth of the north point of the horizon with respect to the  $x$  axis. Suppose that the angle between  $\mathbf{v}$  and  $\boldsymbol{\omega}$  is  $\psi$ . The Coriolis acceleration  $\mathbf{a}$  is perpendicular to the plane containing  $\mathbf{v}$  and  $\boldsymbol{\omega}$  (Fig. 1B), and is given explicitly by

$$\mathbf{a} = 2\mathbf{v} \times \boldsymbol{\omega} \tag{7}$$

From equation (7), if we know the bird's velocity  $\mathbf{v}$  and the Earth's angular velocity  $\boldsymbol{\omega}$ , we can calculate the resulting Coriolis acceleration  $\mathbf{a}$ . From the bird's point of view the problem is: given  $\mathbf{v}$  and  $\mathbf{a}$ , can it determine the direction of  $\boldsymbol{\omega}$  and hence its latitude and the direction to north? The immediate answer is negative, for  $\boldsymbol{\omega}$  is not uniquely specified by equation (7). The general solution of equation (7) is

$$\boldsymbol{\omega} = \frac{\mathbf{a} \times \mathbf{v}}{2v^2} + \lambda \mathbf{v} \tag{8}$$

where  $\lambda$  is an undetermined scalar quantity whose magnitude depends on the magnitudes of  $\mathbf{v}$  and  $\boldsymbol{\omega}$  and the angle between them, and whose dimensions are the reciprocal of length (see Fig. 2).

*Horizontal Coriolis acceleration in horizontal flight.*—An enterprising bird need not be lost, however, and by experimentation it can obtain the required information. For example, if the bird flies horizontally, it will experience a Coriolis acceleration that in general will not be horizontal. If, however, it can find a horizontal direction of flight for which it experiences only a horizontal Coriolis acceleration, then  $\mathbf{a} \times \mathbf{v}$  is a vertical vector. It follows from equation (8) that the horizontal component of  $\boldsymbol{\omega}$  must be parallel or antiparallel to  $\mathbf{v}$ . The bird is therefore flying north or south. Further, if the Coriolis force is toward the bird's right, the bird is in the Northern Hemisphere, and if it is toward the left, it is in the Southern Hemisphere. Thus, using this technique the bird can determine whether it is north or south of the

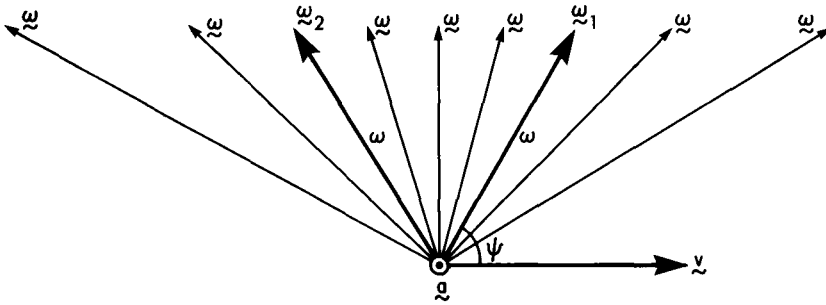


Fig. 2. Illustrating the equation  $\omega = (\mathbf{a} \times \mathbf{v})/(2v^2) + \lambda\mathbf{v}$ . The vector  $\mathbf{a}$  is directed toward the reader. Any of the vectors marked  $\omega$  satisfy the equation  $\mathbf{a} = 2\mathbf{v} \times \omega$ . The component of  $\omega$  perpendicular to the plane containing  $\mathbf{a}$  and  $\mathbf{v}$  is  $\frac{1}{2}a/v$ , but  $\omega$  may also have a component of any magnitude parallel or antiparallel to  $\mathbf{v}$ .

If the magnitude  $\omega$  of  $\omega$  is specified, however, only two solutions to  $\mathbf{a} = 2\mathbf{v} \times \omega$  are possible, indicated by  $\omega_1$  and  $\omega_2$ . They are symmetrically oriented with respect to the normal to the plane containing  $\mathbf{a}$  and  $\mathbf{v}$ ; the sum of the angles  $(\mathbf{v}, \omega_1)$  and  $(\mathbf{v}, \omega_2)$  is  $180^\circ$ .

equator and it can locate the meridian, but it cannot determine its latitude (with one exception discussed in the next paragraph), nor can it distinguish between south and north. Whether this can account for occasional instances of "reverse migration" is a question I leave open.

A special case of the above method arises if the bird is on the equator. In this case it can find *no* horizontal  $\mathbf{v}$  for which  $\mathbf{a}$  is horizontal. It can find two opposite horizontal directions for which  $\mathbf{a}$  is zero. It then knows it is on the equator and that it is flying either north or south.

*Flight out of the horizontal plane.*—If the bird is prepared to fly out of the horizontal plane, it can find its latitude. All it has to do is to locate some direction of flight for which it experiences zero Coriolis acceleration and it knows it is then flying parallel or antiparallel to the Earth's angular velocity vector  $\omega$ . The angle that its direction of flight makes with the horizontal is equal to the bird's latitude (Fig. 3). The bird does not know which hemisphere it is in nor which is the north direction and which the south. If the bird is rising, it is either in the Northern Hemisphere and flying north or in the Southern Hemisphere flying south. If the bird's height above the ground is decreasing, then it is north of the equator and flying south, or south and flying north.

Note that with this method, the bird knows its latitude but not its hemisphere, while with the first method it knows its hemisphere but not its latitude. In both cases it knows the direction of the meridian but does not know which is north and which is south.

*Combination of the two methods.*—If the bird tries *both* methods (that is, it finds a horizontal  $\mathbf{v}$  for which  $\mathbf{a}$  is horizontal and a nonhorizontal  $\mathbf{v}$  for which  $\mathbf{a}$  is zero), then it can determine its latitude and its hemisphere, and it can distinguish between south and north.

Perhaps those birds involved in "reverse migration" are those (or half of those) that used only one of these methods.

*Calculation of Earth's axis position from the directions of two Coriolis accelerations.*—The foregoing techniques require some considerable experimentation and trial-and-error as the bird seeks those elusive directions for  $\mathbf{v}$  that result in zero or

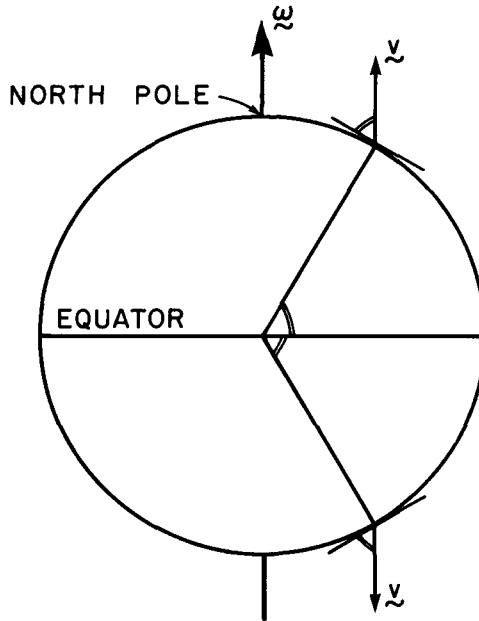


Fig. 3. A bird flying parallel to the Earth's axis experiences no Coriolis acceleration.

horizontal Coriolis acceleration. If the bird is a gifted mathematician (or has equivalent abilities), it may omit this patient experimentation. Let us consider a particular example. The Earth rotates on its axis once every sidereal day, so that  $\omega = 7.2921 \times 10^{-5} \text{ rad} \cdot \text{s}^{-1}$ . Let us suppose that the bird is in latitude  $30^\circ\text{N}$  and it selects its distant landmark that defines the  $x$ -axis such that the azimuth of the north point of the horizon is  $\phi = 20^\circ$ . The complete specification of the Earth's angular velocity is then

$\omega$ :

$$\begin{aligned} \omega &= 7.2921 \times 10^{-5}(\text{rad} \cdot \text{s}^{-1}) \\ \theta &= 60^\circ \\ \phi &= 20^\circ \\ l &= 0.81380 \\ m &= 0.29620 \\ n &= 0.50000 \\ \omega_x &= 5.9343 \times 10^{-5}(\text{rad} \cdot \text{s}^{-1}) \\ \omega_y &= 2.1599 \times 10^{-5}(\text{rad} \cdot \text{s}^{-1}) \\ \omega_z &= 3.6461 \times 10^{-5}(\text{rad} \cdot \text{s}^{-1}) \end{aligned}$$

Suppose that the bird flies with a velocity  $\mathbf{v}_1$  given by

$\mathbf{v}_1$ :

$$\begin{aligned} v &= 27.221(\text{m} \cdot \text{s}^{-1}) \\ \theta &= 81^\circ 33' \\ \phi &= 68^\circ 12' \\ l &= 0.36736 \\ m &= 0.91840 \\ n &= 0.14694 \\ v_x &= 10(\text{m} \cdot \text{s}^{-1}) \\ v_y &= 25(\text{m} \cdot \text{s}^{-1}) \\ v_z &= 4(\text{m} \cdot \text{s}^{-1}) \end{aligned}$$

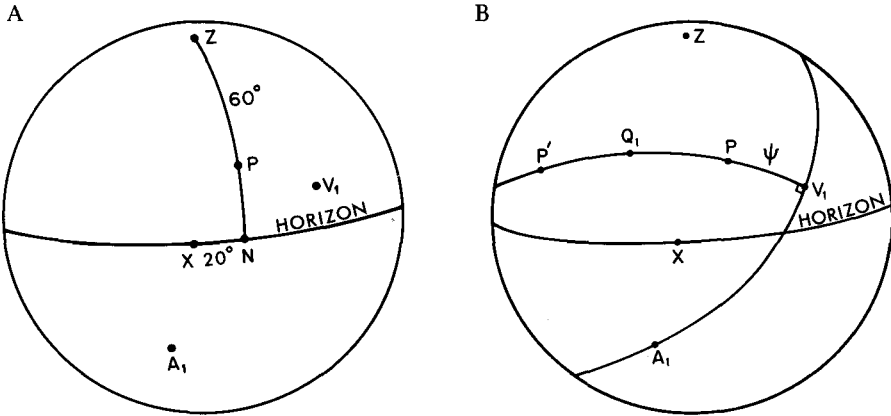


Fig. 4. A. The celestial sphere, showing a distant landmark  $X$ , the north point of the horizon  $N$ , the north celestial pole  $P$ , the zenith  $Z$ , and the points  $V_1$  and  $A_1$  to which the velocity and acceleration vectors  $\mathbf{v}_1$  and  $\mathbf{a}_1$  are directed. B.  $Q_1$  is the pole of the great circle  $A_1V_1$ . The celestial pole must lie on the great circle connecting  $Q_1$  and  $V_1$  either at  $P$  or at  $P'$ .

From our prior knowledge of  $\omega$  we can easily calculate, from equation (7), that the Coriolis acceleration  $\mathbf{a}_1$  experienced by the bird is given by

$\mathbf{a}_1$ :

$$a = 3.0356 \times 10^{-3}(\text{m} \cdot \text{s}^{-2})$$

$$\theta = 146^\circ 38'$$

$$\phi = -8^\circ 46'$$

$$l = 0.54361$$

$$m = -0.08383$$

$$n = -0.83514$$

$$a_x = 1.6502 \times 10^{-3}(\text{m} \cdot \text{s}^{-2})$$

$$a_y = -0.25447 \times 10^{-3}(\text{m} \cdot \text{s}^{-2})$$

$$a_z = -2.5352 \times 10^{-3}(\text{m} \cdot \text{s}^{-2})$$

The bird, however, with no prior knowledge of  $\omega$ , has to make do with equation (8) to try to deduce  $\omega$  from the observed  $\mathbf{v}$  and  $\mathbf{a}_1$ .

In Fig. 4 I have drawn the celestial sphere centered on the bird. The bird's zenith is  $Z$ , and  $X$  is its distant landmark.  $P$  is the north celestial pole and is the projection of  $\omega$  on the celestial sphere. The projection of  $\mathbf{v}_1$  on the celestial sphere is  $V_1$ , and the projection of the resulting acceleration  $\mathbf{a}_1$  is  $A_1$ . Because  $\mathbf{a}_1$  is always at right angles to  $\omega$ , it follows that  $A_1$  is on the celestial equator. The figures are drawn to correspond to the data of the example.

Figure 4B illustrates the information available to the bird.  $Q_1$  is the pole of the great circle connecting  $A_1$  and  $V_1$  and is situated at  $\theta = 58^\circ 54'$ ,  $\phi = -27^\circ 08'$ . It is also the projection on the celestial sphere of the vector  $\mathbf{a} \times \mathbf{v}$ .  $Q_1V_1$  is the great circle connecting  $Q_1$  and  $V_1$ ; it is also the equator of the point  $A_1$ . The angle  $Q_1V_1A_1$  is  $90^\circ$ . What equation (8) (and Fig. 2) tells the bird is that the north celestial pole is somewhere on the semi great circle containing  $Q_1$  and  $V_1$ ; this means that that great circle is the declination circle through  $V_1$ . In Fig. 4B I have drawn the north celestial pole  $P$  at an angular distance  $\psi$  from  $V_1$ . (The meaning of  $P'$  will be described later.) Although the bird can locate the great circle  $Q_1V_1$ , it cannot by equation (8) alone determine the position of  $P$  or the angle  $\psi$ .

All the bird now has to do, however, is to fly in some other direction  $V_2$  (which must not be on the great circle containing  $Q_1$  and  $V_1$ ). It will then experience a different Coriolis acceleration, directed toward another point on the celestial equator,  $A_2$ , and this in turn defines another declination circle,  $Q_2V_2$ . The celestial equator is therefore found immediately from the two accelerations, and the north celestial pole is found from the point of intersection of the two semi declination circles.

The calculation can be done as follows. Suppose the two accelerations are directed toward points  $A_1$  and  $A_2$ , with spherical coordinates  $(\theta_1, \phi_1)$  and  $(\theta_2, \phi_2)$ , respectively. Let  $P(\theta, \phi)$  be the north celestial pole (which has to be determined) and  $Z$  the zenith. Remembering that  $PA_1$  and  $PA_2$  are each  $90^\circ$ , we find from solution of spherical triangles  $PZA_1$  and  $PZA_2$  that

$$\cos \theta_1 \cos \theta + \sin \theta_1 \sin \theta \cos(\phi - \phi_1) = 0 \quad (9)$$

$$\cos \theta_2 \cos \theta + \sin \theta_2 \sin \theta \cos(\phi - \phi_2) = 0 \quad (10)$$

Elimination of  $\theta$  gives  $\phi$  from

$$\tan \phi = \frac{\tan \theta_2 \cos \phi_2 - \tan \theta_1 \cos \phi_1}{\tan \theta_1 \sin \phi_1 - \tan \theta_2 \sin \phi_2} \quad (11)$$

and  $\theta$  can then be found from (9) or (10).

For example, adding to our previous data, if the bird were to fly with velocity  $v_2$  given by

$$\begin{aligned} v_2: \quad & v = 27.203(\text{m} \cdot \text{s}^{-1}) \\ & \theta = 59^\circ 01' \\ & \phi = 30^\circ 57' \\ & l = 0.73521 \\ & m = 0.44113 \\ & n = 0.51465 \\ & v_x = 20(\text{m} \cdot \text{s}^{-1}) \\ & v_y = 12(\text{m} \cdot \text{s}^{-1}) \\ & v_z = 14(\text{m} \cdot \text{s}^{-1}) \end{aligned}$$

we can calculate, from equation (7) and our knowledge of  $\omega$ , that it will experience a Coriolis acceleration  $a_2$  given by

$$\begin{aligned} a_2: \quad & a = 0.65440 \times 10^{-3}(\text{m} \cdot \text{s}^{-2}) \\ & \theta = 148^\circ 53' \\ & \phi = 36^\circ 56' \\ & l = 0.41302 \\ & m = 0.31048 \\ & n = -0.85616 \\ & a_x = 0.27028 \times 10^{-3}(\text{m} \cdot \text{s}^{-2}) \\ & a_y = 0.20318 \times 10^{-3}(\text{m} \cdot \text{s}^{-2}) \\ & a_z = -0.56027 \times 10^{-3}(\text{m} \cdot \text{s}^{-2}) \end{aligned}$$

Thus, by flying in two different directions, the bird has experienced accelerations in the directions:

$$\begin{aligned} \theta_1 &= 146^\circ 38' & \phi_1 &= -8^\circ 46' \\ \theta_2 &= 148^\circ 53' & \phi_2 &= 36^\circ 56' \end{aligned}$$

The bird now has to recover the direction of  $\omega$  from the directions of  $\mathbf{v}_1$ ,  $\mathbf{v}_2$ ,  $\mathbf{a}_1$ , and  $\mathbf{a}_2$ .

From equation (11) we find immediately that the azimuth of  $\omega$  is  $\phi = 20^\circ$  or  $200^\circ$  and hence, from (9) or (10),  $\theta = 60^\circ$  or  $120^\circ$ . The two solutions represent the two points of intersection of the two declination circles whose poles are  $A_1$  and  $A_2$ . The ambiguity, however, is easily cleared up from the relationship between the vectors given by equation (7), and so the direction of the north celestial pole is at  $\theta = 60^\circ$ ,  $\phi = 20^\circ$ . Note that all the bird had to do was to determine the *directions* of two different Coriolis accelerations. It did not need to measure the magnitudes of these accelerations, nor its speed, nor the Earth's angular velocity. It did, however, have to fly in two different directions in order to obtain the required information.

*Calculation of Earth's axis position with prior knowledge of length of day.*— Could the bird do any better if it were able to measure the magnitudes of the Coriolis acceleration and its velocity, and if it were to have some knowledge of the magnitude of the Earth's angular velocity? Could it then locate the pole from just one direction of flight and without having to solve two simultaneous equations? It might first be asked whether it is reasonable to suppose that a bird could have any knowledge of the magnitude of the Earth's angular velocity. If  $\omega$  were a quantity that varies rapidly compared with the rate at which natural selection operates, it might be difficult for such knowledge to become incorporated in the genetic make-up of a species. From data obtained from ancient eclipses and from estimates of tidal friction, it has been estimated that  $\omega$  is decreasing at a rate of only about one part in  $10^5$  in  $10^5$  yr. That is, the length of the day increases by about 1 s in 120,000 yr. Thus  $\omega$  is changing only very slowly, and it might not be impossible for knowledge of  $\omega$  to be incorporated into the genetic make-up. But actually that is the least of the bird's problems, for if it does not already know  $\omega$ , it can easily measure it by observing the diurnal motion of the stars. If it estimates  $\omega$  from the length of the day, that is from observation of the diurnal motion of the sun, it makes an error of only one part in 366.

Assuming, then, that the bird can measure  $\mathbf{v}$  and  $\mathbf{a}$  and can measure or has innate knowledge of  $\omega$ , reference to Fig. 2 shows that there are just two possible directions for  $\omega$ . In fact, the angle  $\psi$  between  $\omega$  and  $\mathbf{v}$  is given by

$$\sin \psi = \frac{a}{2\omega v} \quad (12)$$

From our first example, with

$$\begin{aligned} \omega &= 7.2921 \times 10^{-5} (\text{rad} \cdot \text{s}^{-1}) \\ v &= 27.221 (\text{m} \cdot \text{s}^{-1}) \\ a &= 3.0356 \times 10^{-3} (\text{m} \cdot \text{s}^{-2}), \end{aligned}$$

it is easily found that

$$\psi = 49^\circ 52' \text{ or } 130^\circ 08'.$$

The two possible positions are indicated in Fig. 4B by the two points  $P$  and  $P'$ . Note that  $P$  and  $P'$  are symmetrically positioned with respect to  $Q$ , and also that  $V_1P + V_1P' = 180^\circ$ .

The parameter  $\lambda$  of equation (8) can be calculated from



$$\lambda = \frac{\mathbf{w} \cdot \mathbf{v}}{v^2} \quad (13)$$

or from

$$\lambda = \frac{a}{2v^2 \tan \psi} \quad (14)$$

or from  $\omega$  and the cartesian components of  $\mathbf{v}$  and  $\mathbf{a}$  by equating the magnitudes of the two sides of equation (8) to yield

$$\lambda^2 = \frac{\omega^2}{v^2} - \frac{1}{4v^6} [(a_y v_z - a_z v_y)^2 + (a_z v_x - a_x v_z)^2 + (a_x v_y - a_y v_x)^2] \quad (15)$$

In our example, any of these yields  $\lambda = \pm 1.7264 \times 10^{-6} \text{m}^{-1}$ .

Substitution of one of these values (actually the positive one) in equation (8) will give the correct cartesian components of  $\omega$  and hence the spherical coordinates of  $P$ . The other value of  $\lambda$  gives the spherical coordinates of  $P'$ . There is, however, no means of telling which of the two values of  $\lambda$  is the correct choice, and no means of telling, from a single flight, whether it is  $P$  or  $P'$  that is the correct pole. However, the bird can easily tell by flying horizontally toward points on the horizon with the same azimuths as  $P$  or  $P'$ . If it is flying to the true north point of the horizon it will experience a Coriolis force that is horizontal; if it makes the wrong choice the Coriolis force will have a vertical component.

It might be remarked that if the bird initially were to fly in an arbitrary direction in the horizontal plane, the two points  $P$  and  $P'$  would have the same altitude above the horizon, and therefore the bird's latitude would be immediately determined without ambiguity. This can be seen, for example, by equating the vertical components of each side of equation (8):

$$\omega \cos \theta = \frac{a_x v_y - a_y v_x}{2v^2} + \lambda v_z \quad (16)$$

If  $v_z = 0$ , the ambiguity in the sign of  $\lambda$  does not affect the calculations of  $\theta$ . There will still, however, be two solutions for  $\phi$ .

*The Ising mechanism.*—Finally, mention must be made of the remarkable mechanism suggested by Ising (1945), who showed how it was possible, in principle, for a bird to use the Coriolis effect to determine its latitude without flying at all! All that the bird had to do was to incline its head. The effect of the Coriolis force would then be to set up circulatory motions of the fluids in the semicircular canals of the bird's ear, and the bird could presumably detect this and hence determine its latitude.

As described by Ising, the effect can be described in a manner closely parallel with the more well-known phenomena of electromagnetism. For example, the Coriolis force  $2m \mathbf{v} \times \omega$  is analogous to the Lorentz force  $q \mathbf{v} \times \mathbf{B}$  of electromagnetism, and we can think of the vector  $2\omega$  as a "rotation field." The analogy goes much further. In the phenomenon of electromagnetic induction, an electromagnetic force is induced if a coil is made to rotate in a magnetic field, the magnitude and direction of the electromagnetic force being given by the laws of Faraday and Lenz. If the circuit is closed, a current will flow. Ising shows how a "hydromotive force" is induced if a toroidal tube containing a fluid is rotated in the "rotation field" of the Earth, a phenomenon he describes as "hydraulic induction."

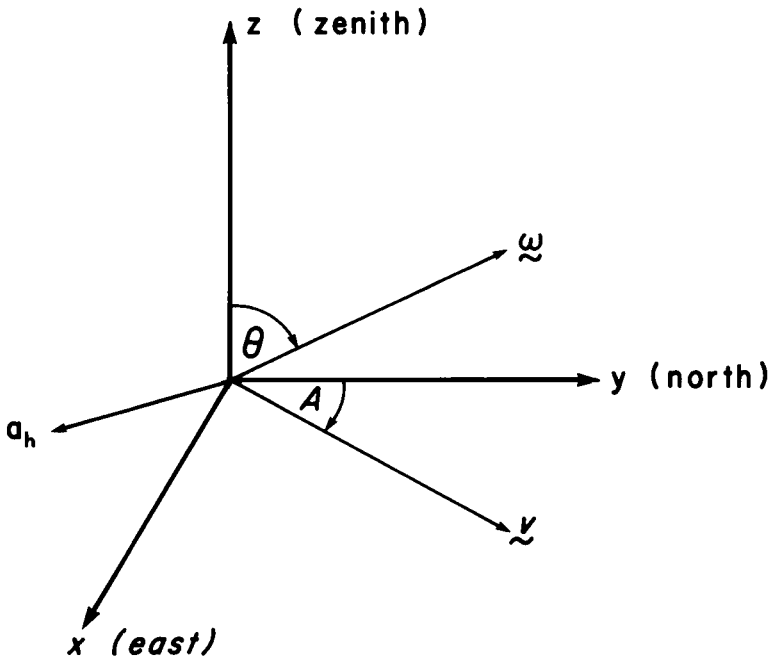


Fig. 5. The horizontal component ( $a_h$ ) of the Coriolis acceleration of a bird flying at a constant height.

Thorpe and Wilkinson (1946), Wilkinson (1946), and de Vries (1948) discussed this further and concluded that in the real bird this mechanism could be rejected on the grounds of its very small magnitude. I do not attempt any further analysis here, as the scope of this paper is specifically restricted to the effect of the Coriolis force on the *flight* of a bird, and a proper analysis demands greater knowledge of the structure of a bird's ear than I possess. It is, however, worth pointing out that, from the point of view of a physicist, such a mechanism is by no means fantastic, and, whatever might be concluded about its magnitude, the type of fluid flow described by Ising as a bird inclines its head would unquestionably take place. It is not as well known as it deserves to be, and it was not mentioned by Ising, that many decades ago the physicist A. H. Compton (1913, 1915a, 1915b) analyzed the effect mathematically and performed a remarkable series of experiments in which he determined his latitude, the direction to north, and the length of the day without looking out of the window—a feat with profound philosophical implications in connection with Mach's principle. In these experiments, Compton filled toroidal tubes with fluids and observed the circulation of the fluids when the tubes were rotated in various manners. These early papers of Compton are essential reading for any serious discussion of the Ising mechanism.

## PART II

There will be those sceptics who are conscious of the very small magnitude of the Coriolis acceleration and of the great demands we are making on the bird's ability to measure velocities and accelerations and to carry out mathematical calculations; they will find it difficult to believe that birds navigate by making use of the Coriolis

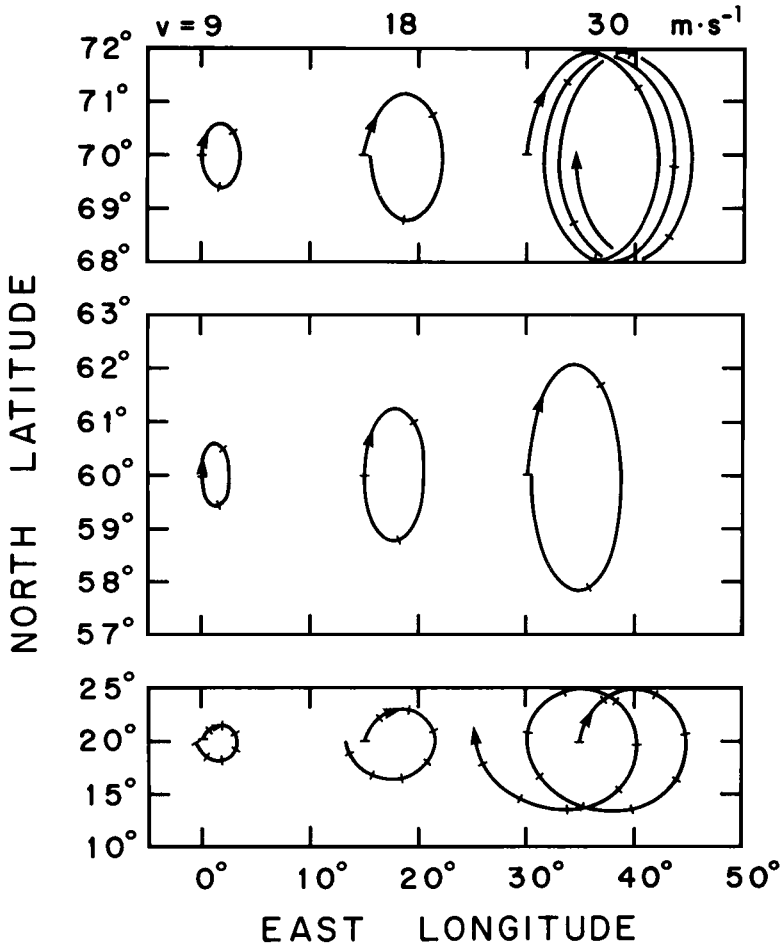


Fig. 6. Some trajectories for birds at high latitudes for different flight speeds, with tick marks every 0.2 day. The drift is toward the east or the west according to whether the latitude is greater than or less than  $45^\circ$ .

acceleration. It is to these readers that the second part of this paper is addressed. Here I assume that the bird has no knowledge of the Coriolis acceleration, cannot measure it, and would not know how to calculate its position from the acceleration. The bird does not in fact use the Coriolis acceleration for navigation. What we suppose in this part is that a bird starts to fly in some direction of its choice and after starting off it continues to fly bill first. Because of its supposed ignorance of the Coriolis effect, this policy will not result in the bird's trajectory being either a straight line or even a great circle. The trajectory will always deviate a little to the right if the bird is flying horizontally in the Northern Hemisphere, and a little to the left in the Southern Hemisphere. Small though it may be, when integrated over long distances the effect will be pronounced on the actual path flown by the bird.

In precise terms we state the problem thus: At some instant the bird is situated at colatitude (north polar distance)  $\theta$  and east longitude  $l$ . The angle  $\theta$  is measured

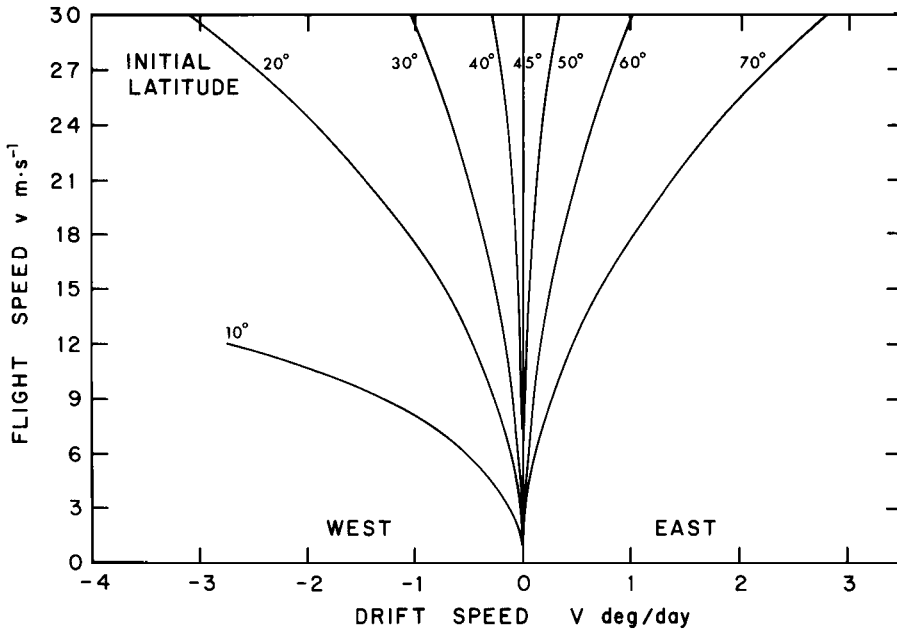


Fig. 7. Drift speed  $V$  as a function of flight speed  $v$  and latitude.

from the north pole southward from  $0^\circ$  to  $180^\circ$ ; the angle  $l$  is measured from the Greenwich meridian eastward from  $0^\circ$  to  $360^\circ$ . The bird is flying at a constant height above the ground toward an azimuth  $A$  measured from the north point of the horizon eastward from  $0^\circ$  to  $360^\circ$ . It flies at a constant speed  $v$  and its subsequent trajectory is influenced by the horizontal component of the Coriolis acceleration. Any vertical component of the Coriolis acceleration is interpreted as a local gravity anomaly, and the bird continues to fly at a constant height and speed. The problem is solved if we can calculate the colatitude and longitude of the bird at any subsequent time  $t$ .

Refer to Fig. 5. The bird is at  $O$ , and we choose axes such that  $Oy$  is directed to the north,  $Ox$  to the east, and  $Oz$  to the zenith. The Earth's angular velocity vector  $\boldsymbol{\omega}$  is in the  $yz$  plane, making an angle  $\theta$  with the  $z$  axis, where  $\theta$  is the bird's colatitude. The bird's velocity vector,  $\mathbf{v}$ , is in the  $xy$  plane, making an angle  $A$  with the  $y$  axis. The Coriolis acceleration  $\mathbf{a} = 2\mathbf{v} \times \boldsymbol{\omega}$  is at right angles to  $\mathbf{v}$  and to  $\boldsymbol{\omega}$ . In Fig. 5 I indicate only the horizontal component,  $a_h$ , of  $\mathbf{a}$ ; it, too, is at right angles to  $\mathbf{v}$ . Because  $\mathbf{a}$  is perpendicular to  $\mathbf{v}$ , the magnitude  $v$  of  $\mathbf{v}$  is constant.

By taking cartesian components of the equation  $\mathbf{a} = 2\mathbf{v} \times \boldsymbol{\omega}$ , we find the  $x$  and  $y$  components of  $\mathbf{a}$  to be

$$a_x = 2v_y\omega_z \quad (17)$$

and

$$a_y = -2v_x\omega_z \quad (18)$$

For example, suppose the bird is at latitude  $30^\circ\text{N}$  ( $\theta = 60^\circ$ ) flying toward azimuth  $A = 35^\circ$  at  $v = 15 \text{ m}\cdot\text{s}^{-1}$ . With  $\boldsymbol{\omega} = 7.2921 \times 10^{-5} \text{ rad}\cdot\text{s}^{-1}$ , we find  $a_x = 5.433 \times 10^{-4} \text{ m}\cdot\text{s}^{-2}$  and  $a_y = -7.760 \times 10^{-4} \text{ m}\cdot\text{s}^{-2}$ .

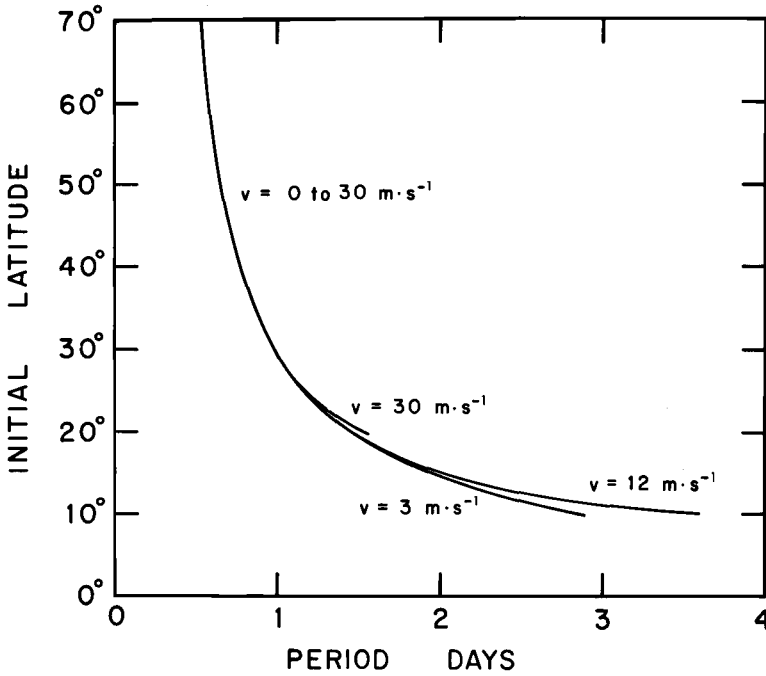


Fig. 8. Period of cycle as function of latitude. The period is almost, but not quite, independent of flight speed  $v$ .

In a short time  $\Delta t$ , the  $x$  and  $y$  displacements of the bird from its original position will be

$$\Delta x = v_x \Delta t + v_y \omega_z (\Delta t)^2 \tag{19}$$

and

$$\Delta y = v_y \Delta t - v_x \omega_z (\Delta t)^2 \tag{20}$$

The resulting displacements in colatitude and east longitude,  $\Delta \theta$  and  $\Delta l$ , will be

$$\Delta \theta = -\Delta y / R \tag{21}$$

$$\Delta l = \Delta x / (R \sin \theta) \tag{22}$$

where  $R$  is the radius of the Earth. (In this analysis I am assuming that the Earth is spherical, with radius  $R = (R_E^2 R_P)^{1/3}$ , where  $R_E$  and  $R_P$  are the equatorial and polar semidiameters of the actual geoid. Numerically,  $R = 6.3710 \times 10^6$  m. I have not investigated the effect of the Earth's asphericity on the path of the bird.)

The new azimuth  $A'$  of the bird's velocity vector is given by

$$\tan A' = \frac{v_x + a_x \Delta t}{v_y + a_y \Delta t} \tag{23}$$

where  $v_x$  and  $v_y$  are the initial velocity components. If the bird remains at the same height and continues to fly at the same speed, the new components of its velocity,  $v'_x$  and  $v'_y$ , are

$$v'_x = v \cos A' \tag{24}$$

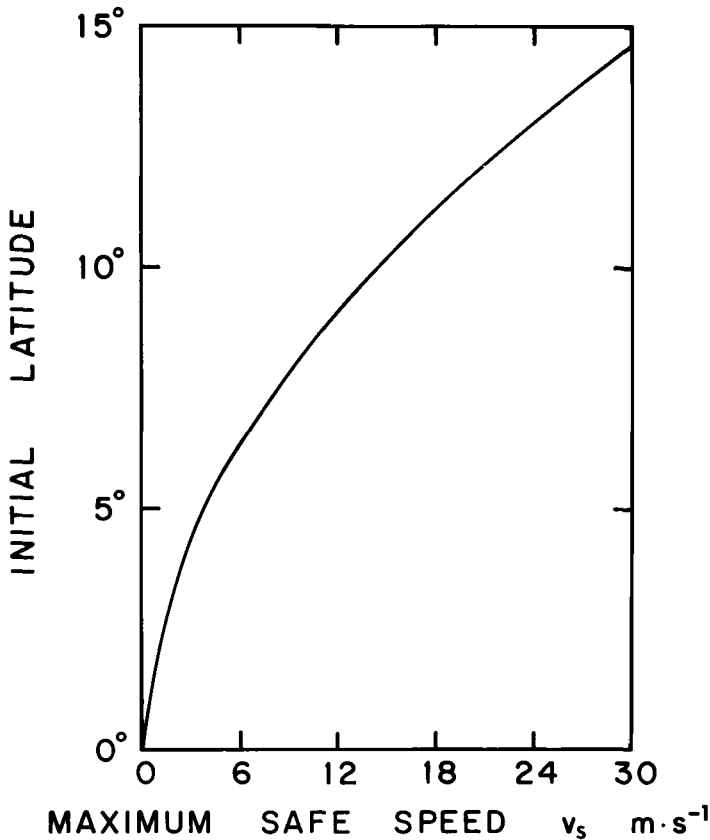


Fig. 9. A bird, starting at a given latitude and heading away from the equator, will never cross the equator if its flight speed is less than the "maximum safe speed"  $v_s$ .

and

$$v'_y = v \sin A' \quad (25)$$

Equations (19) to (25) enable us to make an instant-by-instant numerical calculation of the bird's position as a function of time, given its initial speed, direction, and latitude.

To investigate some trajectories, I integrated these equations at intervals of 0.001 day for the first 20 days of the bird's flight for 10 different speeds and 15 different initial latitudes, assuming that the initial velocity was directed either due north or due south. I also investigated the trajectories of a bird starting at the equator with 10 different velocities and 16 different azimuths. Spot checks for rounding-off errors were made by several integrations with intervals of 0.0001 day, making a total of nearly 10 million integrations in all.

A large number of trajectories are possible, far too many to show in great detail here. Their general character may be understood by realizing that the bird always deviates to the right in the Northern Hemisphere and to the left in the Southern Hemisphere. Therefore, if the bird remains in the Northern Hemisphere, it describes a roughly elliptical clockwise loop, and in the Southern Hemisphere, a roughly elliptical anticlockwise loop. The loop is not a closed loop, however, but drifts slowly

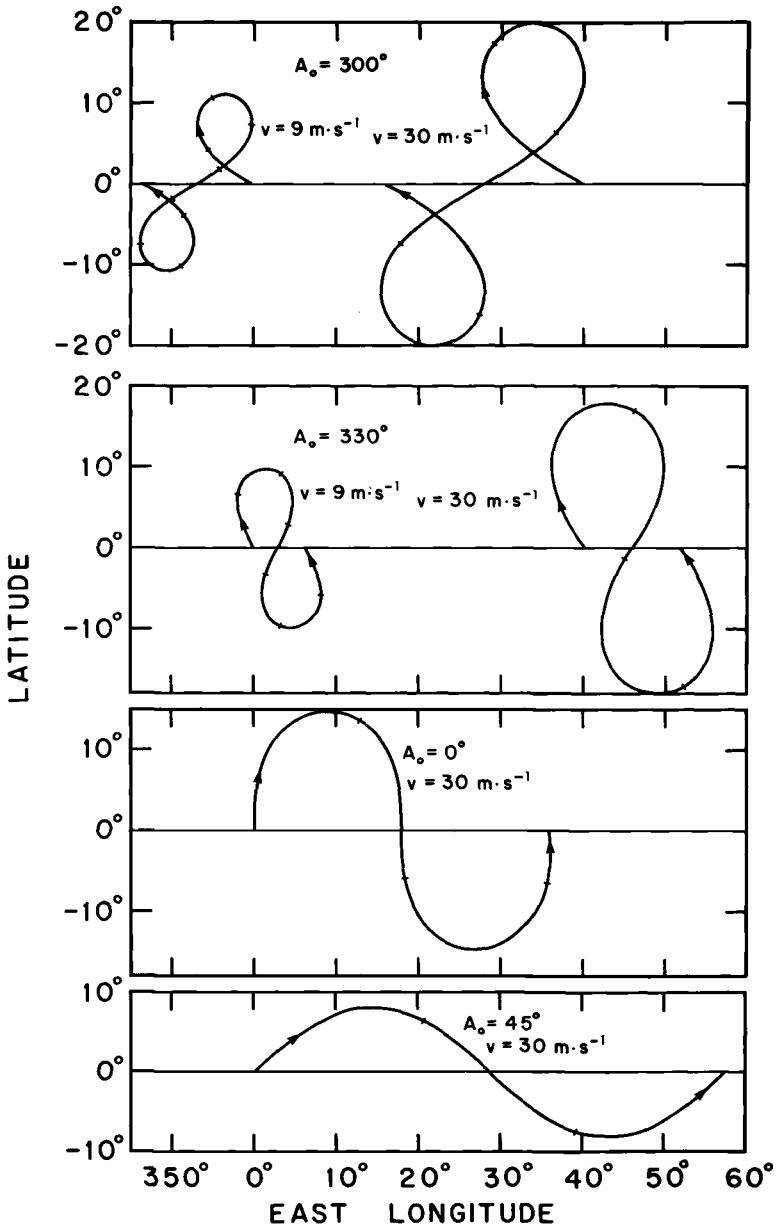


Fig. 10. Some trajectories near the equator, with tick marks every 1.0 day. The drift is toward the west if  $221\frac{1}{2}^\circ < A_o < 318\frac{1}{2}^\circ$ , and toward the east otherwise, or zero if  $A_o = 221\frac{1}{2}^\circ$  or  $318\frac{1}{2}^\circ$ .

or rapidly either east or west, depending on the flight speed and the latitude. If the bird crosses the equator, the direction of the Coriolis force changes, and the trajectory will resemble a figure-eight, which will take the bird to and fro across the equator. The figure-eight is not closed, but drifts either east or west.

Figure 6 shows the trajectories for birds starting at latitudes  $70^\circ\text{N}$ ,  $60^\circ\text{N}$ , and  $20^\circ\text{N}$ , initially heading due north at speeds of 9, 18,  $30 \text{ m}\cdot\text{s}^{-1}$ . Tick marks on the trajectories are shown at intervals of 0.2 day. Seven of the drawings show just 1

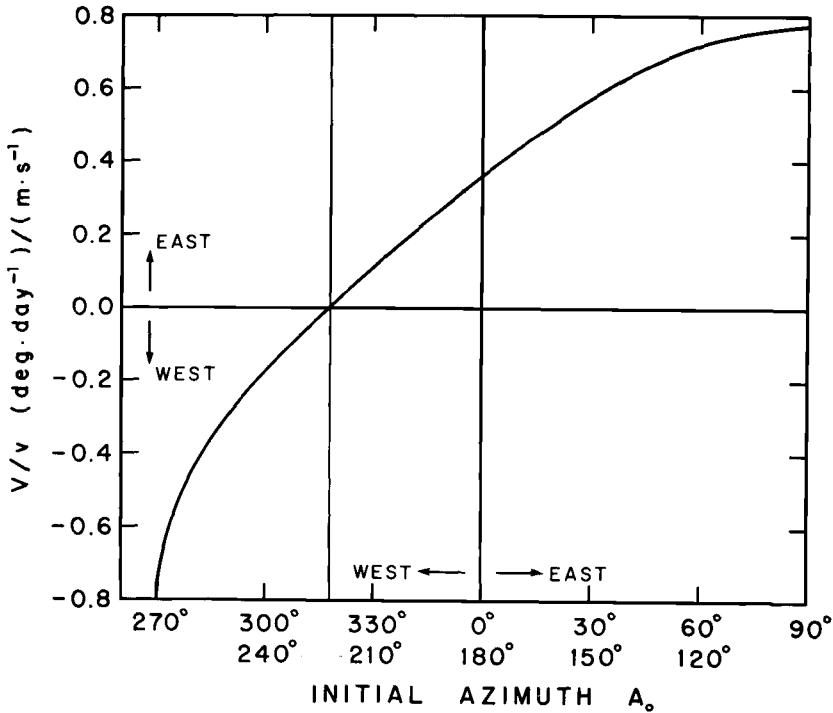


Fig. 11. Drift speed ( $V$ )/flight speed ( $v$ ) as a function of initial azimuth ( $A_0$ ) for equator-crossing paths.

cycle of the trajectory, but 1 of them shows 2 and another shows 3. The trajectories for birds at corresponding latitudes in the Southern Hemisphere are mirror images of these by reflection in the plane of the equator.

The trajectories are loops, which drift eastward for latitudes greater than  $45^\circ$  and westward for latitudes less than  $45^\circ$ . At  $45^\circ$ , the loops are closed and stationary. The drift speed  $V$ , in degrees of longitude per day, depends on the flight speed  $v$  and the latitude (Fig. 7). The amplitude in latitude becomes greater at lower latitudes. Notice the different latitude scales in Fig. 6, which are responsible for the apparent changes in shape at lower latitudes. The trajectories are not quite symmetric about the initial latitudes. At high latitudes they are nearly symmetric, but, for an initial latitude of  $20^\circ$ , the bird gets much farther south of  $20^\circ$  than north of  $20^\circ$ .

The period of each cycle depends almost entirely on the latitude and is almost independent of flight speed at a given latitude. At low latitudes, however, there is a very slight dependence of the period on the flight speed, related to the distortion close to the equator mentioned above. The variation of period with latitude (and, where detectable, on flight speed) is shown in Fig. 8.

A bird flying at  $30 \text{ m}\cdot\text{s}^{-1}$  and starting at  $20^\circ\text{N}$  approaches the equator fairly closely (Fig. 6). If the bird crosses the equator, the nature of the trajectory changes somewhat because of the change in direction of the Coriolis force. This will be discussed shortly, but before doing so it is of interest to know how fast a bird can fly, heading away from the equator at a given latitude, and *not* reach the equator. The maximum "safe" speed  $v_s$  ("safe" in this sense meaning avoidance of the equator) as a function of initial latitude is shown in Fig. 9.



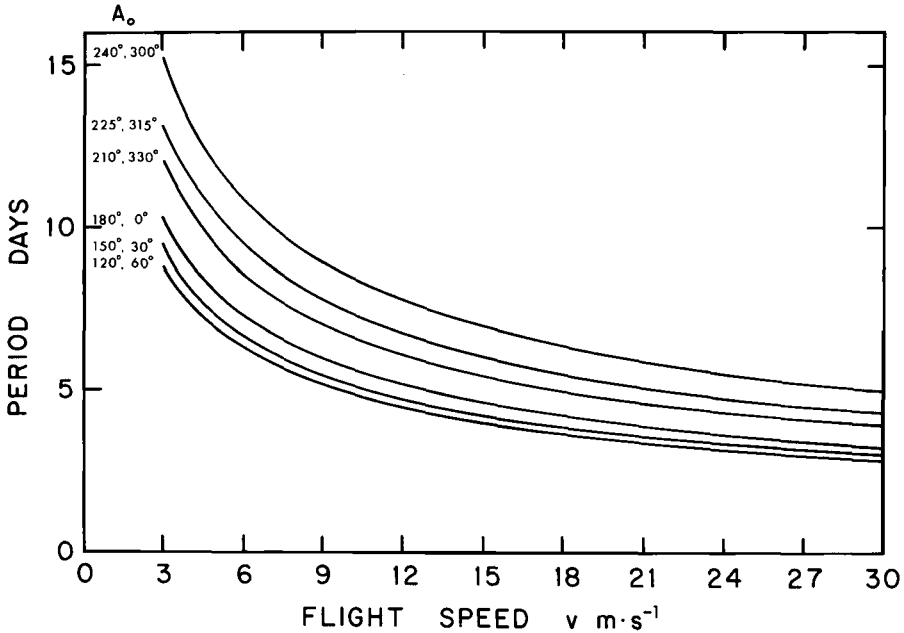


Fig. 12. Period of cycle for equator-crossing paths as a function of flight speed ( $v$ ) and azimuth ( $A_0$ ) at the equator.

If the bird crosses the equator, the trajectory becomes symmetric about the equator. It is then easier to describe the trajectories by considering the bird to start at the equator and determining how the trajectories vary as the initial azimuth of the bird's motion is changed. A sample of the main types is shown in Fig. 10. The run of these trajectory types can be followed by considering what happens to a bird, starting on the equator, as the initial azimuth of its flight varies from  $270^\circ$  (due west) through  $0^\circ$  (due north) to  $90^\circ$  (due east). The trajectories for azimuths between  $90^\circ$  and  $270^\circ$  are then easily found, as the trajectories are symmetric with respect to the equator. If the bird starts flying due west ( $A_0 = 270^\circ$ ), it continues flying west, around the equator, without deviation, because there is then no horizontal component of the Coriolis force. This equilibrium is unstable, however, and the slightest deviation to left or right will take the bird away from the equator into the Southern or Northern Hemisphere, respectively.

If the initial azimuth is not due west, but is somewhat west of due north or of due south ( $180^\circ < A_0 < 360^\circ$ ), the bird describes a sort of figure-eight, which drifts either west or east. The drift is toward the west if  $221\frac{1}{2}^\circ < A_0 < 318\frac{1}{2}^\circ$  and toward the east if  $A_0 > 318\frac{1}{2}^\circ$  or  $A_0 < 221\frac{1}{2}^\circ$ . If  $A_0 = 221\frac{1}{2}^\circ$  or  $318\frac{1}{2}^\circ$  (that is, if the initial azimuth is  $41\frac{1}{2}^\circ$  west of due south or of due north) the figure-eight is closed and stationary.

As the initial azimuth becomes more and more easterly, the figure-eight gradually opens out into a roughly sinusoidal curve, until, at  $A_0 = 90^\circ$  (due east), the bird flies without deviation eastward along the equator. This equilibrium is stable, so that if the bird deviates slightly to left or right away from the equator, the Coriolis force moves it back toward the equator.

Tick marks on the trajectories shown in Fig. 10 are given at intervals of 1 day. The drift speed  $V$  depends on the initial azimuth (or azimuth at the equator)  $A_0$  and on the flight speed  $v$ , being linearly proportional to  $V$ . The ratio  $V/v$  as a function of  $A_0$  is shown in Fig. 11. Finally, the period of each cycle as a function of flight speed and initial azimuth is shown in Fig. 12.

#### CONCLUDING REMARKS

It should be emphasized again that it has not been my purpose here to argue either that birds use the Coriolis force for navigation or that their migration routes are largely determined by the force. Neither is it the purpose to argue the contrary. Rather, the work was carried out in the belief that any opinion one way or the other concerning the role or lack of role of the Coriolis force should not be made on the basis of idle conjecture, but should be based on a study of the known facts of bird migration in conjunction with a precise mathematical analysis of the effect of the Coriolis force alone. This paper supplies the analysis on which such studies might be made.

That the Coriolis force may be small, or perhaps even very small, compared with other forces acting on a migrating bird (not least the winds, themselves influenced very strongly by the Coriolis force) is not denied. I suggest, however, that this alone should not be thought sufficient to discard the possibility that the Coriolis force might have some important influence.

Imagine, for example, the motion of electrons in a copper wire of diameter 1 mm at 20°C. Because of their small mass, the thermal motion of the electrons is much faster than that of the molecules in the air of a room. They are in fact dashing hither and thither in random directions, constantly colliding with each other or with the copper atoms, at speeds of the order of  $100 \text{ km} \cdot \text{s}^{-1}$ . Now suppose that the wire is connected to a battery so that an electric current of 1 A flows. As can be verified by a quite elementary calculation, this current means that, superimposed on the rapid thermal motion described above, there is a very slow drift of the electrons down the wire, the drift speed being only about  $1 \text{ mm} \cdot \text{s}^{-1}$ , or about  $10^{-8}$  of the thermal speed. Though the thermal motion is exceedingly rapid, the electrons nevertheless still inevitably drift down the wire in response to the electric field, which, far from being negligible, exerts a major and easily measurable influence.

Likewise, it must be borne in mind that, whatever other forces may be acting on a migrating bird and however large they may be, whenever the bird moves it inevitably experiences the Coriolis force. It cannot be neglected on the grounds of its small magnitude alone, any more than can the electric field in the example of the copper wire. For this reason I believe that the objection of Wilkinson (1946) that the bird cannot hold a "true enough course to permit of an unambiguous interpretation of the Coriolis effects" is by no means unanswerable. Small irregularities in the bird's motion will result in corresponding small irregularities in the Coriolis force; but, averaged over a long flight-path, the overall effect of the Coriolis force is not only possible, but it is certain and inevitable.

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