GLIDING BIRDS: THE EFFECT OF VARIABLE WING SPAN

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SUMMARY

1. The equilibrium gliding performance of a bird is described by the relationship between sinking speed ($V_s$) and air speed ($V$). When $V_s$ is plotted against $V$, the points fall in a 'performance area' because the wing span is changed during gliding.

2. The lowest $V_s$ for each $V$ in the performance area defines a 'maximum performance curve'. This curve can be predicted by a mathematical model that changes the wing span, area and profile drag coefficient ($C_{D,pr}$) of a hypothetical bird to minimize drag. The model can be evaluated for a particular species given (a) a linear function relating wing area to wing span, and (b) a 'polar curve' that relates $C_{D,pr}$ and the lift coefficient ($C_L$) of the wings.

3. For rigid wings, a single polar curve relates $C_{D,pr}$ to $C_L$ values at a given Reynolds number. The position and shape of the polar curve depend on the aerofoil section of the wing and the Reynolds number. In contrast, the adjustable wings of a laggar falcon (Falco jugger) and a black vulture (Coragyps atratus) gliding in a wind tunnel have $C_L$ and $C_{D,pr}$ values that fall in a 'polar area' rather than on a curve. The minimum values of $C_{D,pr}$ at each $C_L$ bound the polar area and define a polar curve that is suitable for evaluating the model.

4. Although the falcon and the vulture have wings that are markedly different in appearance, the data for either bird are enclosed by the same polar area, and fitted by the same polar curve for minimum $C_{D,pr}$ at each $C_L$ value. This curve is a composite of the polar curves for rigid wings with aerofoils similar to those found in avian wings. These observations suggest that the polar curves of other gliding birds may be similar to that of the falcon and the vulture.

5. Other polar curves are defined by $C_L$ and $C_{D,pr}$ values for the falcon and the vulture gliding at a constant speed but at different glide angles. Each speed has a different polar curve; but for a given speed, the same polar curve fits the data for either bird.

6. The falcon and the vulture gliding in the wind tunnel at a given speed were found to increase their drag by decreasing their wing span. This change increases induced drag and probably increases $C_{D,pr}$ for the inner parts of the wing because of an unusual property of bird-like aerofoil sections: wings with such sections have minimum values of $C_{D,pr}$ at $C_L$ values near 1, while conventional wings have minimum values of $C_{D,pr}$ at $C_L$ values near 0.

Key words: birds, glide polar, gliding performance, polar curve, soaring, wing span.
INTRODUCTION

During equilibrium gliding, all the forces on a glider are balanced; it neither accelerates nor decelerates. The relationship between a glider's air speed and the speed at which it sinks through the air completely describes the glider's aerodynamic performance, and can be predicted from a relatively simple theory for rigid wings (Welch, Welch & Irving, 1955; Pennycuick, 1975).

Gliding birds, however, change their wing span during flight. Anyone can observe these birds gliding slowly on fully spread wings, then progressively flexing their wings as they glide faster and faster. Hankin (1913) called this behaviour 'flex gliding'. Flex gliding influences stability (Lighthill, 1975) and gliding performance (Cone, 1964; Newman, 1958; Pennycuick, 1968; Raspet, 1960; Tucker & Parrott, 1970). In this paper, I shall analyse the relationship between lift and drag, for different wing spans, in birds gliding at equilibrium and use that relationship to predict maximum gliding performance.

THEORY

Consider a bird gliding at equilibrium at speed V along a flight path inclined at angle \( \theta \) (the glide angle) to the horizontal (Fig. 1). Only two forces have significant effects on the bird: gravitational force (the bird's weight, W) and aerodynamic force. Since the sum of these two forces is zero, the aerodynamic force on the bird equals the weight in magnitude but has the opposite direction.

The aerodynamic force has two components (Fig. 1): total drag (D), the component \( W \sin \theta \) that is parallel to the flight path, and lift (L), the component \( W \cos \theta \) that is perpendicular to the flight path (Welch, Welch & Irving, 1955; Pennycuick, 1975).

Fig. 1. Forces and velocities during equilibrium gliding. The glide path is inclined at angle \( \theta \) to the horizontal. Lift and drag are perpendicular and parallel, respectively, to the glide path. Air speed (V) is parallel to the glide path, and sinking speed (\( V_s \)) is vertical and downwards.
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$W \cos \theta$ that is perpendicular to the flight path. $\sin \theta$ and $\cos \theta$ can be replaced with expressions involving the sinking speed through the air ($V_s$) and the air speed ($V$):

$$D = W V_s / V, \quad (1)$$
$$L = W [1 - (V_s / V)^2]^4. \quad (2)$$

The total drag coefficient, $C_D$, and the lift coefficient, $C_L$, are computed by dividing the force components by $0.5 \rho SV^2$:

$$C_D = 2D / (\rho SV^2), \quad (3)$$
$$C_L = 2L / (\rho SV^2). \quad (4)$$

Air density ($\rho$) is $1.23$ kg m$^{-3}$ in this study—the value at sea level in the US standard atmosphere (von Mises, 1959), and $S$ is the projected wing area, including the area of the wings intercepted by the body.

The performance of a glider, described by the relationship between $V$ and $V_s$, depends on total drag, as can be seen by rearranging equation 1:

$$V_s = V D / W. \quad (5)$$

I shall analyse performance by dividing total drag into additive components: induced drag, profile drag and parasite drag. Many textbooks on aircraft aerodynamics describe this method in detail (see, for example, Pope, 1951).

**Induced drag**

Induced drag, $D_I$, arises whenever the wing produces lift. Lift results from a higher pressure below the wing than above, and this pressure difference induces an upward flow of air at the tips of the wing and a downward flow along the wing span. The induced downward flow causes the induced drag on the wing (see Prandtl & Tietjens, 1957, for a detailed discussion). Induced drag depends on wing span, $b$ (measured across the widest span of the wings), and is given by:

$$D_I = 2kL^2 / (\pi \rho b^2 V^2). \quad (6)$$

The induced drag factor, $k$, has a value of 1 for a wing with a straight leading edge when viewed from the front, constant downwash and an elliptical distribution of lift along its span. Actual wings typically have $k$ values in the range of 1–1.1 (Reid, 1932), and some wings theoretically may have $k$ values less than 1 (Cone, 1962; van Dam, 1987). $k$ also corrects the parasite drag of a complete aircraft at low speeds (see section on Parasite drag below). I shall follow the common practice of using a value of 1 for $k$ when dealing with isolated wings, and a value of 1.1 when dealing with a complete aircraft. Spedding (1987) found a value of $k$ of 1.04 in a gliding sparrow hawk, *Falco tinnunculus*; which is consistent with a value of 1.1 after correcting for parasite drag at low speeds. (Some authors place the induced drag factor in the denominator of equation 6, in which case it typically has values of 1 or less.)

The induced drag factor of bird wings may change during flight if the wings change their shape and span so that the lift distribution is not elliptical. There are insufficient data to account for these changes in the present theory, which assumes...
that $k$ remains constant during flight. However, the effect of increases in $k$ will be discussed qualitatively.

The induced drag is related to the induced drag coefficient, given by:

$$C_{D,i} = 2D_i/(\rho SV^2).$$  \hspace{1cm} (7)

If the right side of equation 6 is substituted for $D_i$ in the equation above, and $L$ is expressed in terms of $C_L$, one obtains a simple expression for $C_{D,i}$:

$$C_{D,i} = kC_L^2/(\pi A),$$  \hspace{1cm} (8)

where $A$ is the aspect ratio of the wing, defined as the ratio of wing span to wing chord. Wing chord is the mean width of the wing, defined as $S/b$. Therefore, $A = b^2/S$.

Profile drag

Profile drag, $D_{pr}$, is the drag on the wing in addition to induced drag. It arises from skin friction and pressure differences and is related to the profile drag coefficient, given by:

$$C_{D,pr} = 2D_{pr}/(\rho SV^2).$$  \hspace{1cm} (9)

The profile drag coefficient varies with the lift coefficient of the wing, and hence with $V$. The relationship between $C_{D,pr}$ and $C_L$ depends on the shape of the wing’s cross-section (the aerofoil section, since the wing is an aerofoil) and the Reynolds number ($Re$) of the wing, defined as

$$Re = \rho c'V/\mu.$$  \hspace{1cm} (10)

$c'$ is the wing chord calculated from maximum wing area ($S_{max}$) and maximum wing span ($b_{max}$):

$$c' = S_{max}/b_{max}.$$  \hspace{1cm} (11)

$\mu$ is the viscosity of the air. The ratio $\rho/\mu$ has the value 68 436 s m$^{-2}$ for air at sea level in the US standard atmosphere.

At a given $Re$, $C_L$ plotted against $C_{D,pr}$ for a rigid wing yields a polar curve. If the wing is not twisted along its span and has the same aerofoil section everywhere, the polar curve is nearly independent of aspect ratio (Prandtl & Tietjens, 1957) and is characteristic of the aerofoil section.

$C_{D,pr}$ at a given $C_L$ decreases as $Re$ increases, with a drop of several-fold over a narrow range of $Re$ values (Hoerner, 1965; Schmitz, 1960). The midpoint of this range is the critical $Re$, which decreases in turbulent air or if the aerofoil surface is rough. The critical $Re$ for a smooth, bird-like aerofoil section in non-turbulent air is 75 000 (the Göttingen 801 section; Schmitz, 1960; similar to the USATS 4 section in Fig. 4). Most soaring birds have $Re$ values between 75 000 and $10^6$. $C_{D,pr}$ changes gradually over this range according to the relationship:

$$F = 1.21 - 0.226 Re \times 10^{-5} + 0.0151 (Re \times 10^{-5})^2,$$  \hspace{1cm} (12)
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where $F$ is the ratio $C_{D,pr}/(C_{D,pr} \text{ at } Re \times 10^{-5} = 1)$. I derived this relationship from data in Hoerner (1965, fig. 17, pp. 6-13) and Schmitz (1960, fig. 6, p. 171) for a variety of aerofoil sections at $C_L = 0.7$.

As $Re$ changes, the polar curve shifts right or left without markedly changing shape (Schmitz, 1960). Thus, the $C_{D,pr} vs C_L$ curve can be shifted to any $Re$ between the critical $Re$ and $10^6$ by calculating a correction term for $C_{D,pr}$ at a $C_L$ of $0.7$ and adding that term algebraically to the $C_{D,pr}$ axis. Equation 12 was used to correct all polar curves and $C_{D,pr}$ values in this paper to $Re \times 10^{-5} = 1$. An example of the correction is shown in the Appendix.

**Parasite drag**

Parasite drag, $D_{par}$, is the drag on the aircraft exclusive of the drag on the wings and is related to the parasite drag coefficient, given by:

$$C_{D,par} = 2D_{par}/(\rho S_{par} V^2) .$$

In flying birds, $D_{par}$ is the drag of the head, body, tail and feet. $S_{par}$ is the cross-sectional area of the drag-producing structures.

The parasite drag on an aircraft is commonly expressed in terms of the area of a flat plate held perpendicular to the airflow. If the drag coefficient of the plate is assigned a value of 1, a plate of area $S_{par} C_{D,par}$ has the same drag as the parasite drag of an aircraft at speed $V$. The area of the plate is known as the equivalent flat plate area, $S_{fp}$:

$$S_{fp} = S_{par} C_{D,par} .$$

If $S_{fp}$ for an aircraft is known, parasite drag is given by:

$$D_{par} = 0.5 \rho S_{fp} V^2 .$$

$S_{fp}$ tends to increase at lower speeds as the tail of an aircraft drops, thereby increasing the drag of the fuselage and tail. The change in $S_{fp}$ is small, and it is common practice to compensate for it by increasing the induced drag factor slightly (Pope, 1951). $S_{fp}$ also tends to increase at lower speeds as $Re$ decreases (Goldstein, 1965).

**Speed and sinking speed**

The total drag on an aircraft is the sum of the three components:

$$D = D_i + D_{pr} + D_{par} ,$$

so, from equation 5,

$$V_s = V(D_i + D_{pr} + D_{par})/W .$$

After expanding the drag terms, this equation becomes:

$$V_s = 2kL^2/(\pi \rho Wb^2 V) + 0.5 \rho V^3 (SC_{D,pr} + S_{fp})/W .$$
Models

Equation 18 becomes a model of a glider if one allows \( b, L, C_{D,pr}, S_{fp} \) and \( V \) to vary in the same way that they do in the real glider. The simplest model (I shall call it the 'constant span' model) describes a glider with rigid wings. Speed varies, but the wing span, profile drag coefficient and the other variables on the right side of equation 18 remain constant. If sinking speed is plotted against speed for the constant span model, a curve (I shall call it the 'performance curve') results.

The performance curve is often called the 'glide polar', but I shall use the former terminology to avoid confusion with the polar curves that relate lift and profile drag coefficients for wings. Performance curves are usually drawn on a \( V \) vs \( V_s \) diagram with \( V_s \) increasing downwards and \( V \) increasing to the right (Fig. 2).

A more realistic model for birds, which I shall call the 'maximum performance' model, describes gliders with adjustable wings. Birds typically extend their wings to maximum span when gliding slowly and flex glide at higher speeds. As wing span changes, so do wing area, induced drag, and the lift and profile drag coefficients. These changes make the product \( S C_{D,pr} \) in equation 18 a function of wing span.

The relationship between sinking speed and speed calculated from equation 18 as wing span varies need not be a performance curve as is the case with the constant span model. If, at a given speed, \( b \) varies, then sinking speed varies as well. Birds can also increase sinking speed by lowering their feet to increase \( S_{fp} \) (Pennycuick, 1960, 1968, 19716). As a result, sinking speed can have a range of values at each speed, and

![Fig. 2. The performance area bounded by performance curves for a falcon, Falco jugger. Speed for maximum performance is lowest at A, where \( C_l \) is maximum at 1.87. \( V_s = V \) along line \( BC \) — i.e. descent is vertical at each speed. Vertical descent is slowest at B, where total drag = profile drag of the fully extended wings with \( C_{D,pr} = 1 \) — i.e. the wings act as flat plates held perpendicular to the airflow. Vertical descent is fastest at C, where total drag = parasite drag — i.e. the wings are fully folded. Solid lines calculated from the theory in this paper, dashed lines interpolated.](image)
the points relating sinking speed and speed fall in an area (Cone, 1964). I shall call this the 'performance area' (Fig. 2).

The 'maximum performance' model describes the upper boundary of the performance area. I shall call this boundary the 'maximum performance curve'. Maximum performance in this sense means that a bird can glide at a particular speed for the maximum time and distance through the air when it minimizes sinking speed. If one considers the motion of the bird relative to the earth, the maximum performance curve shows the minimum vertical wind velocity component required to keep the bird from losing altitude and, for a given horizontal wind, indicates the maximum distance over the ground that the bird can cover for a given loss in altitude.

The lower boundary of the performance area is the 'minimum performance curve', which describes the maximum sinking speed at each speed. At all but the lowest speeds, maximum sinking speed occurs in vertical descent when \( V_s = V \) and drag = weight. Vertical descent is slowest when the bird 'parachutes' on extended wings (Fig. 2, point B), and fastest when the bird folds its wings and dives (Fig. 2, point C).

The constant span model

In the constant span model, \( L \) is assumed to equal \( W \) (a constant); the only variable on the right side of equation 18 is \( V \). The equation for the performance curve becomes:

\[
V_s = k_1/V + k_2V^3, 
\]

where \( k_1 \) and \( k_2 \) are constants, defined as follows:

\[
k_1 = 2kW/(\pi \rho b^2), 
\]

\[
k_2 = 0.5\rho (SC_{D,pr} + S_{fp})/W. 
\]

This model is useful to glider pilots (Welch et al. 1955) because it approximates the characteristics of man-made gliders with simple wings. Such gliders can fly only at the combinations of \( V \) and \( V_s \) that fall on a single performance curve because their rigid wings have lift and profile drag coefficients that fall on a single polar curve. The glider cannot change its drag, and hence its sinking speed, without changing speed. [For manoeuvres such as landing, gliders are usually equipped with panels on the wings that may be raised to increase profile drag. Advanced gliders also have wing flaps that can change the aerofoil section of the wing during flight – see, for example, Jacobs (1986). The constant span model does not describe gliders that use these devices.]

The constant span model has been used for gliding birds (Newman, 1958; Pennycuick, 1971a,b, 1975, 1982; Blake, 1983). The simplicity of the model is attractive, but a gliding bird need not hold its wing span and the other variables on the right side of equation 18 constant at different speeds as the model requires. The constant span model describes a performance curve that may be wholly within the performance area, partly within it or wholly outside it, depending on the values assigned to \( k_1 \) and \( k_2 \) in equation 19.
The maximum performance model

In the maximum performance model, wing span, wing area and the profile drag coefficient may vary at each speed; their values are chosen to minimize sinking speed at each speed. Under these conditions, equation 18 describes the maximum performance curve.

Sinking speed may have a minimum value at a given speed when the wings are flexed to less than their maximum span. Suppose, for example, that $C_{D,pr}$ were constant. Then changes in wing span would have opposite effects on two of the drag terms in equation 17: a reduction in span would increase induced drag but decrease profile drag by reducing wing area (Newman, 1958; Pennycuick, 1968; Pennycuick & Webbe, 1959; Tucker & Parrott, 1970). Indeed, a falcon gliding in a wind tunnel at different speeds has been observed to adjust its wing span to near the theoretical values for minimum sinking speeds (Tucker & Parrott, 1970).

$C_{D,pr}$, however, varies with wing span because (1) $C_{D,pr}$ and $C_L$ are related by a polar curve in bird wings as span varies, and (2) $C_L$ is related to $S$ (equation 4), which varies with wing span. To develop the maximum performance model, I shall represent these two relationships by polynomials:

$$C_{D,pr} = C_0 + C_1 C_L + C_2 C_L^2 \quad (22)$$

and

$$S = C_3 b + C_4 \quad (23)$$
in which $C_0, \ldots, C_4$ are constants.

The wing span for minimum sinking speed at each speed can be found by making appropriate substitutions into equation 16, setting the derivative $dD/db$ equal to 0 and solving for $b$. The minimum sinking speed can then be calculated.

First the terms in equation 16 are expanded:

$$D = 2kL^2/(\pi \rho b^2 V^2) + 0.5 \rho S C_{D,pr} V^2 + 0.5 \rho S_f V^2 \quad (24)$$

For economy of notation, some of the constants in equation 24 may be combined into new constants:

$$D = k_3 L^2/(b V)^2 + k_4 S C_{D,pr} V^2 + k_5 V^2 \quad (25)$$

Before differentiation, $C_{D,pr}$ and $S$ in equation 25 must be replaced with functions of $b$. $C_{D,pr}$ is a function of $C_L$ (equation 22), so

$$D = k_3 L^2/(b V)^2 + k_4 S V^2 (C_0 + C_1 C_L + C_2 C_L^2) + k_5 V^2 \quad (26)$$

$C_L$ is a function of $S$, so from equation 4

$$C_L = k_6 L/(SV^2) \quad (27)$$

and

$$D = k_3 L^2/(b V)^2 + C_0 k_4 S V^2 + C_1 k_4 k_6 L + C_2 k_4 (k_6 L)^2/(SV^2) + k_5 V^2 \quad (28)$$

Replacing $S$ with the right side of equation 23,

$$D = k_3 L^2/(b V)^2 + C_0 k_4 (C_3 b + C_4) V^2 + C_1 k_4 k_6 L + C_2 k_4 (k_6 L)^2/[(C_3 b + C_4) V^2] + k_5 V^2 \quad (29)$$
Differentiating,
\[ \frac{dD}{db} = -2k_3L^2/(b^3V^2) + C_0k_4C_3V^2 - C_2k_4C_3(k_6L)^2/[(C_3b + C_4)V]^2 \quad (30) \]

and, replacing \( L \) with \( W[1-(V_s/V)^2] \) (equation 2),
\[ \frac{dD}{db} = -2k_3W^2[1-(V_s/V)^2]/(b^3V^2) + C_0k_4C_3V^2 - C_2k_4C_3(k_6W)^2[1-(V_s/V)^2]/[(C_3b + C_4)V]^2 \quad . (31) \]

The value of \( b \) that makes the derivative equal to 0 is the wing span \( (b') \) for minimum total drag. Replacing \( b \) with \( b' \), \( L \) with \( W[1-(V_s/V)^2] \) and \( D \) with \( WV_s/V \) in equation 25 yields
\[ V' = k_3W[1-(V_s/V)^2]/(b'^2V) + V^3(k_4SC_{D,pr} + k_5)/W , \quad (32) \]
where \( V' \) is the value of \( V_s \) used to calculate \( b' \).

The first chosen value of \( V'_s \) will probably not be a solution of equation 32 (i.e. \( V_s \) will probably not equal \( V'_s \)), and I used Newton’s method (Sokolnikoff & Sokolnikoff, 1941) to estimate a new value of \( V'_s \). This value is used to recalculate \( b' \), and the whole process is repeated until values of \( V'_s \) and \( b' \) are obtained that do satisfy equation 32. The procedure is repeated with different values for \( V \) to obtain the maximum performance curve.

The quantity \( C_0 \) in the above equations varies with \( Re \), and hence with \( V \). As \( Re \) changes, the curve (equation 22) relating \( C_{D,pr} \) to \( C_L \) shifts to the right or left by an amount related to \( F \) from equation 12. This shift is accomplished mathematically by adding \( C(F-1) \) to \( C_0 \), where \( C \) is the value of \( C_{D,pr} \) calculated from equation 22 for \( C_L = 0.7 \). (A computer program that calculates a maximum performance curve, including \( Re \) effects, is available from the author.)

MEASUREMENTS

This section describes the data that will be used to evaluate the maximum performance model and summarizes how they have been obtained. All the data have been published, and details may be found in the original publications. Curvilinear relationships between two variables are described with second-degree polynomial equations (fitted by least squares) of the form:
\[ y = a_0 + a_1x + a_2x^2 , \quad (33) \]
where \( a_0 \), \( a_1 \) and \( a_2 \) are constants.

Lift and drag

Lift and drag can be determined by measuring \( W \) and the glide angle \( \theta \), or \( V_s \) and \( V \), and then solving equations 1 and 2. In some cases, the measurements have been made on birds gliding in natural conditions by using tracking devices, mounted either on the ground or in a sailplane (Raspet, 1960; Pennycuick, 1960, 1971a), to record the position of the bird relative to the observer.

It is difficult to make accurate measurements in nature for two reasons: (1) tracking devices of sufficient accuracy are complicated and difficult to operate,
(2) not only the bird must be tracked, but the air as well. Equilibrium gliding
requires an inertial frame of reference relative to which the air does not move. The
frame may move relative to the observer (for example, if there is a wind), but its
movements must be measurable. Indeed, there may not be such a frame, for winds
often change in both speed and direction as a result of gusts and topographical
features (see McGahan, 1973, and Pennycuick, 1971a, for a discussion of these
problems).

The glide angle $\theta$ can be measured more accurately in a wind tunnel than it can in
nature. If a bird is trained to glide freely in a wind tunnel tilted at the glide angle, the
bird remains stationary relative to the observer, and the motion of the air in the wind
tunnel is known. This technique has been used with a pigeon \textit{(Columbia livia;}
Pennycuick, 1968), a laggar falcon \textit{(Falco jugger, similar in size to the more familiar
peregrine falcon; Tucker & Parrott, 1970) and a black vulture \textit{(Coragyps atratus;}
Parrott, 1970). These studies will be identified in this paper by references to 'the
pigeon', 'the falcon' and 'the vulture'.

\textbf{Wing span and area}

Wing span and area are changed in living birds during flight. Maximum wing span
$(b_{\text{max}})$ and area $(S_{\text{max}})$ can be measured on dead birds by stretching out the wings. At
lesser spans, the relationship between wing span and area was linear in the pigeon,
falcon and vulture gliding in a wind tunnel. This relationship can be estimated for
gliding birds from measurements of $b_{\text{max}}$ and $S_{\text{max}}$ (see Appendix).

\textbf{Equivalent flat plate area}

Equivalent flat plate area of a bird can be measured by placing the body on a flight
balance in a wind tunnel (Pennycuick, 1968; Tucker, 1973). $S_{\text{fp}}$ is a function of a
bird’s linear dimensions and varies with body mass (Tucker, 1973):

$$S_{\text{fp}} = 0.00334m^{0.6660}.$$  \hspace{1cm} (34)

This equation was obtained from drag measurements made at nearly constant speeds
$(11–12 \text{ m s}^{-1})$ on birds with masses between 0.025 and 6.9 kg. It therefore includes
$Re$ effects due to body size but not those due to speed. $S_{\text{fp}}$ did not change with speed in the pigeon. Variations in $S_{\text{fp}}$ with speed are ignored in the present study since the
drag due to $S_{\text{fp}}$ is a small proportion of total drag at the speeds at which birds usually
glide.

\textbf{Profile drag coefficient}

\textit{Rigid wings: polar curves for bird-like and conventional aerofoil sections}

The profile drag coefficient, $C_{D,pr}$, may be determined by measuring the total drag
of a rigid wing and subtracting the induced drag from it. The total drag can be
measured by mounting the wing on a flight balance in a wind tunnel, and induced
drag can be calculated using equation 6. Alternatively, induced drag may be.
eliminated so that profile drag equals total drag. This is accomplished by mounting
an untwisted, rectangular wing with a constant aerofoil section in a wind tunnel so
that it spans the tunnel from wall to wall (Pope & Harper, 1966). The profile drag coefficient is obtained by dividing profile drag by $0.5 \rho SV^2$.

The shapes of bird-like aerofoil sections are quite different from the shapes of conventional ones. Bird wings (for example see Nachtigall, 1985) have highly cambered upper and lower surfaces at the base of the wing and less cambered surfaces towards the tip (Fig. 3). Wings of conventional aircraft have lower surfaces that are nearly flat to convex, as in the Clark Y section (Fig. 4). This section was used in many aircraft built between 1920 and 1940, and it often appears as an example in textbooks on low-speed aerodynamics. Its aerodynamic characteristics are well-known for a range of $Re$ values, and it will be used in this paper as a reference for comparison with the less conventional, bird-like sections.

There are also differences between the polar curves of bird-like aerofoil sections and those of conventional aerofoils. Conventional sections have a minimum $C_{D,pr}$

![Fig. 3. Bird-like aerofoil sections and their polar curves. The sections progress (top to bottom) from a highly cambered section typical of the base of a bird wing to a less-cambered section typical of the tip of a bird wing. Shown for comparison are the polar curve for minimum drag (equation 35) for the falcon and the vulture, and polar curves for three different pigeon wing sections (Nachtigall, 1979). Polar curves have been corrected to a Reynolds number of $10^5$ and smoothed by fitting points to a second-degree polynomial equation. Data for the bird-like sections and their polar curves may be found in the National Advisory Committee on Aeronautics Technical Reports listed in References. The number of the Technical Report is given in parentheses: Göttingen 462 (286), RAF 19 (93), Göttingen 400 (124), Eiffel 35 (93).]
Fig. 4. The top three aerofoil sections have the same thickness and progressively less-cambered lower surfaces. The lift coefficient for the minimum profile drag coefficient decreases as the camber of the lower surface decreases. The bottom aerofoil section (Clark Y) is typical of those used in low-speed man-made aircraft flying at Reynolds numbers between $1.5 \times 10^5$ and $4 \times 10^6$. Polar curves have been corrected to a Reynolds number of $10^6$ and smoothed by fitting points to second-degree polynomial equations (except Clark Y data, which were fitted by free-hand curve). Data for these sections and their polar curves may be found in the National Advisory Committee on Aeronautics Technical Reports listed in References. The number of the Technical Report is given in parentheses: RAF 19 (93), USATS 4 (93), Durand propeller 13 (93), Clark Y (244).

value at a $C_L$ value near 0, and $C_{D,pr}$ is nearly constant for $C_L$ values between 0 and 1.0 (Clark Y, Fig. 4). Highly cambered bird-like sections such as the RAF 19 (Fig. 3) have a minimum value for $C_{D,pr}$ near a $C_L$ value of 1, and $C_{D,pr}$ increases two- or three-fold as $C_L$ drops towards 0. In addition, the minimum $C_{D,pr}$ values for bird-like sections are higher than that for the Clark Y section.

These differences are related to the amount of camber of the lower surface of the wing. The more the camber of the lower surface, the higher the $C_L$ at which the minimum $C_{D,pr}$ occurs (Fig. 4).

Not all studies of avian wing sections agree with the above description. Nachtigall (1979) investigated model wings with the same aerofoil sections as those of the pigeon wing. The polar curves for the model sections were similar to those for conventional sections in that $C_{D,pr}$ was at a minimum near a $C_L$ of 0 (Fig. 3). Also, the maximum $C_{D,pr}$ values for the model sections were several times higher than those for the bird-like or conventional sections in Figs 3, 4.

**Adjustable wings: the polar area for bird wings**

The profile drag of a wing attached to a living bird can be determined by measuring the total drag of the bird and subtracting induced drag and parasite drag.
In contrast to rigid wings, \( C_{D,pr} \) and \( C_L \) values for the adjustable wings of living birds do not fall on a single polar curve. Birds may change wing span, aerofoil sections and degree of wing twist from base to tip at a given speed. Consequently, their wings have a range of \( C_{D,pr} \) values for each \( C_L \). The points representing this range fall within an area (I shall call it the polar area) of the \( C_{D,pr} \) vs \( C_L \) diagram rather than on a curve. (Fig. 7 shows the polar area for the falcon and the vulture.)

Bird wings can have a polar curve if the bird glides under conditions that select one curve from the infinite number that comprise the polar area. For example, the pigeon, falcon and vulture wings had polar curves when the birds were gliding in wind tunnels at their shallowest glide angles (i.e. with minimum sinking speed and drag) for a given speed. These curves are the left-hand bounds of the polar areas, and I shall call them 'polar curves for minimum drag' (e.g. Fig. 5).

The falcon and vulture also glided over a range of glide angles at a particular speed. Measurements under these conditions yield polar curves that I shall call 'polar curves for constant speed'. They will be described after the next section.

**Polar curves for minimum drag**

The \( C_{D,pr} \) and \( C_L \) values for the falcon and the vulture fall on the same polar curve for minimum drag (Fig. 5) when corrected to an \( Re \) value of \( 10^5 \). The equation for the curve is:

\[
C_{D,pr} = 0.0349 - 0.0781C_L + 0.0799C_L^2. \tag{35}
\]

This curve is a composite of the polar curves for the bird-like aerofoil sections found in different regions of the wing (Fig. 3). As the wing span varies, these sections are

![Graph of polar curve for minimum drag for the falcon (open circles) and the vulture (filled circles), corrected to a Reynolds number of \( 10^5 \). \( C_L \) increases as speed decreases. Data from Tucker & Parrott (1970, table 2) and Parrott (1970, table 1).](image-url)
exposed to the airflow to different degrees, so it is not surprising that the polar curve for minimum drag shares points with the polar curves for the aerofoil sections.

The pigeon's polar curve for minimum drag has $C_{D,pr}$ values that are much greater than those for the falcon and vulture at high $C_L$ values (Fig. 6), comparable at $C_L$ values near 0-5, and lower at $C_L$ values below 0-5. Pennycuick cautions that low $C_{D,pr}$ values for the pigeon may be unreliable because of uncertainties in measuring parasite drag.

Using data from gliding vultures, obtained by tracking from sailplanes (Raspet, 1960; Pennycuick, 1971a), presumably with the vultures at minimum sinking speeds, I have constructed polar curves for minimum drag. The $C_{D,pr}$ values calculated from Raspet's data for black vultures (see Appendix) are negative (Fig. 6), probably because the vulture and the sailplane were gliding in different air masses (Tucker & Parrott, 1970; Pennycuick, 1971a).

Pennycuick (1971a) assumed that $C_{D,pr}$ was independent of $C_L$ in African white-backed vultures and estimated its value to be 0-0073 at an $Re$ value of $2.9\times10^5$. Correcting this value to $Re = 10^5$ yields 0-011, somewhat lower than the minimum $C_{D,pr}$ value of 0-018 for the falcon and the vulture (Fig. 6).

The lift coefficients and total drag coefficients for dried bird wings mounted on a flight balance in a wind tunnel have been measured for several species (Withers, 1981). A polar curve constructed from the data (see Appendix) for the one soaring
Table 1. Characteristics of different species used with the maximum performance model

<table>
<thead>
<tr>
<th>Species</th>
<th>W (N)</th>
<th>(b_{\text{max}}) (m)</th>
<th>S (m²)</th>
<th>(S/S_{\text{max}})*</th>
<th>(S_{\text{fp}}) (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Falcon</td>
<td>5·60</td>
<td>1·01</td>
<td>0·112b + 0·019</td>
<td>0·857b/(b_{\text{max}}) + 0·144</td>
<td>0·00214</td>
</tr>
<tr>
<td>Black vulture</td>
<td>17·5</td>
<td>1·37</td>
<td>0·260b - 0·020</td>
<td>1·060b/(b_{\text{max}}) - 0·060</td>
<td>0·00486†</td>
</tr>
<tr>
<td>African white-backed vulture</td>
<td>52·8</td>
<td>2·18</td>
<td>0·335b - 0·041†</td>
<td>1·060b/(b_{\text{max}}) - 0·060</td>
<td>0·0101</td>
</tr>
<tr>
<td>Fulmar</td>
<td>7·20</td>
<td>1·09</td>
<td>0·073b + 0·034</td>
<td>0·700b/(b_{\text{max}}) + 0·299</td>
<td>0·00270†</td>
</tr>
<tr>
<td>Albatross</td>
<td>85·6</td>
<td>3·03</td>
<td>0·062b + 0·425†</td>
<td>0·307b/(b_{\text{max}}) + 0·693</td>
<td>0·0140†</td>
</tr>
</tbody>
</table>

See text for references.

* Dimensionless relationship between wing span and wing area.
† See Appendix for derivation.
‡ Calculated from equation 34.

bird he investigated, the red-shouldered hawk (*Buteo lineatus*), will be used here. Although the measurements were made at one speed with a constant wing span, the results are interesting when compared with those for the wings of living birds (Fig. 6).

The hawk wing had \(C_{\text{D,pr}}\) values that are greater than the total drag coefficients of the intact falcon and the vulture. Clearly, the dried wing is not aerodynamically similar to living wings. Withers attributes the high drag of the dried wing to a low \(Re\) value (0·5 \(\times 10^5\), which is below the critical \(Re\) for smooth wings), surface roughness, fluttering of feathers and wing twist. In addition, the aerofoil sections of living bird wings during gliding can change markedly from those of anaesthetized or dead birds (Biesel, Butz & Nachtigall, 1985).

It is remarkable that the same polar curve for minimum drag describes the data for both the falcon and the vulture, as these birds are distinctly different in appearance and size. At maximum span, the falcon’s wings have pointed tips and an aspect ratio of 7·7 (calculated from data in Table 1). The vulture’s wings have square tips ending in separated primary feathers, and an aspect ratio of 5·6. The vulture weighs three times as much as the falcon.

The polar curve for these birds is also similar to curves for rigid wings with bird-like aerofoils, although it differs from the curve for the gliding pigeon. The pigeon is a flapping bird rather than a gliding bird. Perhaps measurements on other flapping birds will show that they too have different polar curves from gliding birds.

These observations suggest that polar curves for minimum drag may be similar to equation 35 in all gliding birds with highly cambered aerofoils – a hypothesis that will be interesting to test. In the absence of polar curves for minimum drag for gliding birds other than the falcon and the vulture, I shall use equation 35 to evaluate the maximum performance model for gliding birds in general.

**Polar curves for constant speed**

Both the falcon and the vulture glided in the wind tunnel over a range of glide angles at a given speed. Data for both birds fell on the same polar curve for a given
Wing span and profile drag

How do birds change their wing spans to glide at various combinations of $V$ and $V_s$ in the performance area? Either an increase or a decrease in wing span could increase drag, depending on where the bird is flying in the performance area.

The falcon and the vulture when gliding at a given speed in the wind tunnel invariably decreased their wing spans to increase drag. This change increased induced drag, but paradoxically it also increased profile drag (as calculated in this study) in both birds (Fig. 8). One might expect that profile drag would decrease with wing span because of the reduction in wing area. The lift coefficient increased with the reduction in wing area but not enough to account for the increase in $C_{D,pr}$ according to the polar curve for minimum drag (Fig. 5).

Pennycuick (1971b) offered an explanation for the increased profile drag. African vultures appear to increase drag when landing by twisting their wings so that the lift increases at the outer parts of the wing and decreases at the inner parts of the wing. Consequently, the lift distribution along the wings becomes less elliptical, and the induced drag factor ($k$ in equation 6) increases. The extra induced drag appears as profile drag, since $k$ in this study has a constant value of 1·1.
Variable wing span in gliding birds

Fig. 8. Total drag and profile drag at different wing spans for the falcon gliding at constant speeds in a wind tunnel. At a given speed, the tunnel was tipped to various glide angles. The falcon responded by decreasing its wing span to increase drag and sinking speed. Data for low speeds (8.4 and 9.1 m s\(^{-1}\)) are similar and are pooled. Data for high speeds (11.2, 12.3 and 14.1 m s\(^{-1}\)) are also similar and are pooled. Data from Tucker & Parrott (1970, fig. 5).

Twisting the wings as described above may also increase the actual profile drag of the inner parts of the wings. These parts have aerofoil sections with highly cambered lower surfaces. Polar curves for such sections have minimum \(C_{D,pr}\) values at \(C_L\) values greater than 1 (Fig. 3), and \(C_{D,pr}\) increases two-fold or more as \(C_L\) drops towards 0. If the wings are twisted so that the lift, and therefore \(C_L\) of the inner wing, drops towards 0, the profile drag of the inner wing will increase. In contrast, birds flying on the maximum performance curve adjust their wing spans and keep their \(C_L\) values high, thereby avoiding the high-drag regions of the polar curves for their wings.

Man-made gliders with simple wings have lower and lower \(C_L\) values as they fly faster and faster along their maximum performance curve. Consequently, designers of these aircraft select aerofoils that, like the Clark Y, have minimum \(C_{D,pr}\) values when \(C_L\) is near 0 (Fig. 4).

**Predictions**

*Maximum performance model*

Given equation 35, very little additional information about a bird is needed to predict a curve for maximum performance – only weight, maximum wing span and a
linear function relating wing area and wing span (Table 1). The predictions of the maximum performance model can be compared with measured performance curves of birds that presumably were gliding at the minimum sinking speed at each speed. The falcon and the vulture in the wind tunnel fit this criterion when the wind tunnel was tipped to the shallowest angles at which they would glide.

Sinking speeds were close to those predicted by the model, and wing spans showed less agreement with the predictions (Figs 9, 10). The observed sinking speeds would have been slightly lower if both birds had chosen different wing spans at some speeds. The falcon usually kept its wings too flexed, and the vulture sometimes kept its wings too flexed and at other times too spread out.

The predicted maximum performance curve for African white-backed vultures fits the data of Pennycuick (1971a), presumably obtained at minimum sinking speeds. Pennycuick used a constant span model to fit an empirical curve to the data (Fig. 11). However, the data are too variable to discriminate between the two curves.

Pennycuick (1960) estimated a performance curve for fulmars (Fulmarus glacialis) by tracking them while they soared near a cliff top. This curve is below the predicted maximum performance curve (Fig. 12), suggesting that the fulmars were not gliding at the minimum sinking speeds for their speeds.

The wandering albatross (Diomedea exulans) is one of the largest gliding birds; its pointed, high aspect ratio wings are quite different from the wings of the falcon and the vulture. The maximum performance model predicts poorer performance (Fig. 12; Table 2) for this bird than has been estimated by others. For example, Pennycuick (1982) estimated a maximum lift to drag ratio of 23.2 for the albatross, compared to 14.2 estimated by the maximum performance model. Pennycuick used a
Fig. 10. Predicted maximum performance curve and wing spans for maximum performance in the vulture. Points represent measurements made at minimum glide angles in the wind tunnel. Wing span is expressed as a fraction of maximum wing span.

Fig. 11. Bottom: predicted maximum performance curve (\(M\)), empirically fitted performance curve (\(E\)) and measured data points for the African white-backed vulture. The empirical curve assumes a constant wing span and a constant profile drag coefficient. Measured data and empirical curve from Pennycuick (1971a). Top: predicted wing spans for maximum performance. Wing span is expressed as a fraction of maximum wing span.
Fig. 12. Predicted maximum performance curves and wing spans in the fulmar and the wandering albatross. Points represent measurements on the fulmar (Pennycuick, 1960). Wing spans are expressed as fractions of maximum wing span.

constant span model and a combined drag coefficient of 0.20 for profile and parasite drag to make his estimate.

The combined drag coefficient is given by the sum $C_{D,pr} + S_{fp}/S$, and a value for it of 0.20 represents much lower profile and parasite drag values than those used in the maximum performance model. $S_{fp}$ in the maximum performance model is computed from equation 34, so $S_{fp}/S$ for the albatross is 0.023. This value alone is higher than the combined drag coefficient of 0.20. If $S_{fp}/S$ is halved to 0.012, then $C_{D,pr}$ becomes 0.008 for the constant span model, which is still less than the lowest value of $C_{D,pr}$ (0.011) used in the maximum performance model. Albatrosses certainly look streamlined in comparison with hawks and vultures and may indeed have better

<table>
<thead>
<tr>
<th>Species</th>
<th>Speed ($\text{m s}^{-1}$)</th>
<th>$V_{s,\text{min}}$ ($\text{m s}^{-1}$)</th>
<th>Speed ($\text{m s}^{-1}$)</th>
<th>$L/D_{\text{max}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Falcon</td>
<td>8</td>
<td>0.83</td>
<td>10</td>
<td>11.9</td>
</tr>
<tr>
<td>Black vulture</td>
<td>10</td>
<td>0.97</td>
<td>12</td>
<td>11.6</td>
</tr>
<tr>
<td>African white-backed</td>
<td>12</td>
<td>1.02</td>
<td>14</td>
<td>11.7</td>
</tr>
<tr>
<td>vulture</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fulmar</td>
<td>10</td>
<td>0.95</td>
<td>12</td>
<td>11.5</td>
</tr>
<tr>
<td>Albatross</td>
<td>16</td>
<td>1.17</td>
<td>18</td>
<td>14.2</td>
</tr>
</tbody>
</table>

$V_{s,\text{min}}$, minimum sinking speed for all speeds; occurs at speed shown in column immediately to the left.

$L/D_{\text{max}}$, maximum lift to drag ratio for all speeds; occurs at speed shown in column immediately to the left.
Variable wing span in gliding birds

Fig. 13. Comparison of predictions for the falcon by the maximum performance model (M) and constant span model (C). The constant span model uses a wing span of 1·01 m and a $C_{D,pr}$ of 0·02. The bottom panel shows performance curves. Other panels show the profile drag coefficient ($C_{D,pr}$), profile drag ($D_{pr}$) and induced drag ($D_i$) at different speeds.

performance than the maximum performance model predicts. Measurements on a living albatross gliding in a wind tunnel would resolve the matter.

For all of the birds mentioned above, the model predicts that the wing span should be maximum for maximum performance at all speeds up to a critical speed. Above the critical speed, wing span should decrease as speed increases. All the birds achieved their minimum sinking speed and maximum lift to drag ratio (Table 2) at speeds below the critical speed, i.e. with their wings at maximum span.

**Constant span model**

A performance curve predicted by the constant span model has a different shape from the maximum performance curve. For example, the maximum performance model predicts that the falcon will have its maximum lift to drag ratio when gliding at a speed of 10 m s$^{-1}$ (Table 2), with values for wing span and $C_{D,pr}$ of 1·01 m and 0·02, respectively. Using these values in the constant span model, the predicted performance curve is above the maximum performance curve at speeds less than 10 m s$^{-1}$ (Fig. 13). Sinking speeds are too low because profile drag is too low (Fig. 13). At speeds greater than 10 m s$^{-1}$, the sinking speeds are greater than those for maximum performance because wing span, and hence profile drag, is too high.
Induced drag is low, but not low enough to compensate for the higher profile drag (Fig. 13).

Although the constant span model is not accurate for the entire maximum performance curve, it can predict a part of it. In the falcon, for example, the predicted wing span and $C_{D,pr}$ values for maximum performance are nearly constant at speeds near $10 \text{ m s}^{-1}$ (Figs 9 and 13, respectively). At these speeds, the constant span model predicts nearly the same performance curve as the maximum performance model if one chooses the right wing span and $C_{D,pr}$ values (Fig. 13).

**APPENDIX**

Raspet's data for the black vulture

Raspet (1960) gives the following data for the black vulture: mass = 2.3 kg, weight = 22.7 N, $b = 1.44$ m, $S = 0.365$ m$^2$. He also gives sinking speeds ($V_s$) for a range of speeds ($V$) for a soaring vulture.

The profile drag coefficient ($C_{D,pr}$) before correction to $Re \times 10^{-5} = 1$ is given by:

$$C_{D,pr} = 2(D - D_1 - D_{par})/(\rho SV^2).$$

The drag terms on the right-hand side of this equation are given, respectively, by equations 1, 6 and 15. $S_{fp}$ comes from equation 34.

$C_{D,pr}$ is corrected to $C_{D,pr}$ at $Re \times 10^{-5} = 1$ by the method described below for the hawk wing. Reynolds number for Raspet's vulture is 68426$c'V$, where $c'$ is the wing chord, given by $S/b$.

Withers's data for the red-shouldered hawk wing

Withers (1981) gives the following relationship between $C_L$ and $C_D$ at $Re \times 10^{-5} = 0.5$ and aspect ratio ($A$) = 3:

$$C_D = 0.085 - 0.153C_L + 0.555C_L^2.$$

The profile drag coefficients ($C_{D,pr}$) at this $Re$ are given by:

$$C_{D,pr} = C_D - C_L^2/(\pi A).$$

To correct $C_{D,pr}$ to the equivalent profile drag coefficient ($C_{D,pr}$) at $Re \times 10^{-5} = 1$, a term must be subtracted from all $C_{D,pr}$ values. This term is $0.203(1 - 1/F)$, where 0.203 is the value of $C_{D,pr}$ at $C_L = 0.7$, and $F$ is computed from equation 12 for $Re \times 10^{-5} = 0.5$.

Wing span and area for the white-backed vulture

The relationship between wing span and wing area for the African white-backed vulture was estimated from that for the black vulture, since both birds have similar wing shapes. The dimensionless relationship between wing span and wing area for the black vulture (Table 1) is:

$$S/S_{max} = 1.060b/b_{max} - 0.060.$$
Variable wing span in gliding birds

The maximum wing area ($S_{\text{max}}$) of the white-backed vulture is 0.69 m$^2$, and $b_{\text{max}}$ is 2.18 (Pennycuick, 1971a). Multiplying both sides of the equation by $S_{\text{max}}$ and then substituting values for $S_{\text{max}}$ and $b_{\text{max}}$ yields the desired relationship:

$$S = 0.335b - 0.041.$$  

Wing span and area for gliding birds

The wings of some gliding birds are very different in appearance from those of the falcon and the vulture. For example, the wandering albatross has wings with pointed tips and an aspect ratio twice that of the falcon or the vulture. This section estimates the relationship between span and area for a simplified, hypothetical wing of any aspect ratio. The equations are then adjusted to estimate the relationship between wing span and area for actual gliding birds. For the purposes of this paper, an estimation will be made for the wandering albatross. First, consider wing span.

The hypothetical wing has three rigid, rectangular elements of lengths $r_1$, $r_2$ and $r_3$ (Fig. 14), connected by joints at the shoulder, elbow and wrist. Two sets of elements and the body width ($b_B$) make up the wing span. The maximum wing span is given by:

$$r_1 + r_2 + r_3 = b_{\text{max}}(1-k_7)/2.$$  

Expressing $b_B$ as a proportion of $b_{\text{max}}$,

$$b_B = k_7b_{\text{max}},$$

equation 36 becomes, after substitution and rearrangement,

$$r_1 + r_2 + r_3 = b_{\text{max}}(1-k_7)/2.$$  

If the angles at the wing joints remain equal as the wing flexes at angle $\alpha$,

$$b = 2(r_1 + r_2 + r_3)\sin\alpha + b_B$$

or, after substitution,

$$b = b_{\text{max}}[k_7 + (1-k_7)\sin\alpha].$$

Fig. 14. Hypothetical bird wing showing changes in wing area with flexing. See text for explanation.
Now consider the area of the wing as it flexes. The wing loses area $HIJK$ (Fig. 14) at the wrist joint as the feathers overlap, but it gains area $DEFG$ at the elbow joint as overlapped feathers are exposed. The areas lost and gained at the wrist and elbow are equal, so the net loss in area with flexing is due to overlap of the body by the base of the wing (area $ABC$). The area lost ($S'$) at the base of both wings is:

$$S' = c^2 \tan(90 - \alpha),$$

where $c$ is the wing chord at the wing base, given by:

$$c = \frac{S_{\text{max}}}{b_{\text{max}}}.\quad (42)$$

In a tapered wing, the chord at the base of the wing is larger than the value given by the above equation, and the changes in area at the elbow and wrist are no longer equal when the wing flexes. In addition, $\alpha$ may be constrained anatomically from reaching $90^\circ$ in an actual wing. For simplicity, I shall attribute the entire reduction in area of a flexed, tapered wing to overlap of the body by a wing of chord $c\cdot e$ at its base. The ‘taper factor’, $e$, is 1 for a rectangular wing with equal flex angles at each joint. Actual wings will have taper factors greater than 1, to be determined empirically. Equation 41 for actual wings becomes:

$$S' = ec^2 \tan(90 - \alpha).\quad (43)$$

The area of both wings when flexed at angle $\alpha$ is

$$S = S_{\text{max}} - e (S_{\text{max}}/b_{\text{max}})^2 \tan(90 - \alpha).\quad (44)$$

The relationship between $b$ and $S$ that results when a range of values for $\alpha$ is substituted into equations 40 and 44 is approximately linear for $b > \frac{1}{2} b_{\text{max}}$.

The above equations describe the measured relationships between wing span and wing area for the falcon and the vulture when taper factors are 1·6 and 1·5, respectively. Since the wing of the wandering albatross appears to be nearly rectangular near the wing joints, I chose a taper factor of 1·2 for it. Using $k_7 = 0·093$, $S_{\text{max}} = 0·611$ and $b_{\text{max}} = 3·03$ for the albatross (data from Pennycuick, 1982) yields the following relationship between wing span and area:

$$S = 0·062b + 0·425.\quad (45)$$

### List of Symbols

- **$A$**: aspect ratio
- **$a_0, a_1, a_2$**: constants in polynomial equation
- **$\alpha$**: angle between humerus and body
- **$b$**: wing span
- **$b'$**: temporary value of $b$ used to compute $V_s$
- **$b_B$**: body width
- **$b_{\text{max}}$**: maximum wing span
- **$C$**: constants
- **$C_{D,\text{pr}}$ at $C_L = 0·7$, $Re = 10^5$**
- **$C_D$**: total drag coefficient
- **$C_{D,i}$**: induced drag coefficient
- **$C_{D,\text{par}}$**: parasite drag coefficient
- **$C_{D,\text{pr}}$**: profile drag coefficient
- **$C_L$**: lift coefficient
- **$c$**: wing chord at base
- **$c'$**: wing chord for maximum wing span
Variable wing span in gliding birds

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
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<tr>
<td>D</td>
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<td>D_{pr}</td>
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<tr>
<td>e</td>
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<td>correction factor for Reynolds number</td>
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</tr>
<tr>
<td>m</td>
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<tr>
<td>\mu</td>
<td>viscosity of air</td>
</tr>
<tr>
<td>\pi</td>
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<td>r_1, r_2, r_3</td>
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REFERENCES


