

## GLIDING FLIGHT OF THE WHITE-BACKED VULTURE *GYPSS AFRICANUS*

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### INTRODUCTION

The object of the experiments described in this paper was to obtain a glide polar for the African white-backed vulture *Gyps africanus* by the glide comparison method. A glide polar is a graph of vertical sinking speed versus forward speed in straight, unaccelerated gliding flight. The glide comparison method entails measuring the difference between the bird's vertical and forward speeds and those of the glider, whose own glide polar has previously been determined by calibration flights. The method was first applied to birds by Raspet (1950*a, b*), who used it to obtain a polar for the American black vulture *Coragyps atratus*.

### METHOD

#### *Equipment*

The glider used for the comparison flights was a Schleicher ASK-14 powered sailplane, which was flown by the author. This aircraft is basically a motorized development of the well-known K-6E sailplane, and is powered by a 26HP Hirth two-stroke engine, which is used for take-off and the initial climb. Once thermal or other lift is encountered, the engine is switched off and the propellor feathered, and in this condition the ASK-14's gliding performance is hardly inferior to that of the K-6E.

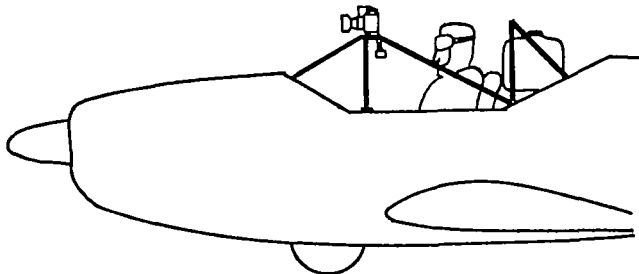


Fig. 1. The ASK-14 cockpit with canopy removed, showing the camera mounted on a special stand in front of the pilot. The rangefinder is suspended below the camera from a ball-and-socket mount.

For glide-comparison flights the ASK-14 was flown without its cockpit canopy. A Nikon F camera, fitted with a 55 mm Micro-Nikkor lens and an F 250 motor back (taking 10 m lengths of 35 mm film), was mounted in front of the pilot, looking forward over the nose (Fig. 1). The camera was driven from the aircraft's 6 AH accumulator,

which was charged sufficiently often to keep it between half and full charge at all times. Beneath the camera mount a Wild optical rangefinder of 25 cm base was suspended from a ball-and-socket mount, in such a way that the pilot could aim it with his left hand at a bird ahead of the glider, whilst flying the aircraft with his right, and operating the camera by means of a switch attached to the control column. An alcohol-in-glass photographic thermometer was attached to the rangefinder for measuring the air temperature.

The glider's instrument panel included a PR-2508 airspeed indicator made by P.Z.L., and a Kelvin Mk. XIVc (P) three-handed sensitive altimeter calibrated in feet.

#### *Measurement procedure*

Before flight the motor Nikon was set to run automatically at its 'M2' setting, which meant that as long as the camera switch was held 'on' the camera would continue to take photographs at intervals of either 0.354 or 0.363 s, depending on whether or not the mirror was locked. The interval was checked several times during the measurements by photographing a stop-watch.

The rangefinder was permanently set to a range of 50 m.

Having located a bird which appeared to be gliding in a straight line at about the same height as the glider, the procedure was to manoeuvre round and gradually approach it from directly behind. Owing to the ASK-14's excellent performance, the airbrakes generally had to be used during this initial approach phase in order to prevent the glider from getting above the bird, but they were, of course, closed during the final approach and the actual measurement. In the final stage of the approach, the rangefinder was trained on the bird, and when the images fused (at the pre-set range of 50 m), the camera button was depressed and held 'on'. The range could be closed to 25–30 m before turning aside to avoid a collision, and 8–12 photographs were usually obtained before initiating this manoeuvre.

After each observation, the following data were recorded, using a Philips cassette tape recorder.

- (1) species,
- (2) glider's air speed, read from the air speed indicator while the camera was running,
- (3) pressure altitude,
- (4) air temperature.

The photographs were taken on Kodak Plus-X film, exposed at 1/1000s at either  $f8$  or  $f11$ , depending on the lighting conditions. The negatives were developed either in Paterson 'Acutol' or Johnson 'Definol', the latter being found to give sharper and clearer images.

#### *Analysis of photographs*

The negatives so obtained were projected on to a sheet of graph paper placed on the baseboard of a Leitz 'Focomat' enlarger, the magnification ratio being determined on each occasion by measuring the spacing of the images of the perforations along the edge of the film.

The first negative in any series was taken at the known range  $R_1$  pre-set on the rangefinder, and  $b_1$  was the wing span of the image of the bird on this negative (after

Allowing for the magnification of the enlarger). From this the actual wing span  $B$  of the bird could be determined, since

$$B = b_1 \frac{R_1}{f}, \quad (1)$$

where  $f$  is the focal length of the camera lens.

The ranges at which subsequent negatives were taken were initially unknown, but the wing span  $B$  was now known, assuming that this did not change during the brief duration of the measurement – usually about 3 s. If  $b_i$  was the span of the image on the  $i$ th negative, then the range  $R_i$  at which it was taken is given by

$$R_i = f \cdot \frac{B}{b_i}. \quad (2)$$

An estimate of range was thus obtained for each negative in a series, separated by a constant time interval. A regression of range on time was then calculated, and the regression coefficient was taken as an estimate of the bird's speed relative to the glider, i.e. the closing speed  $V_x$ .

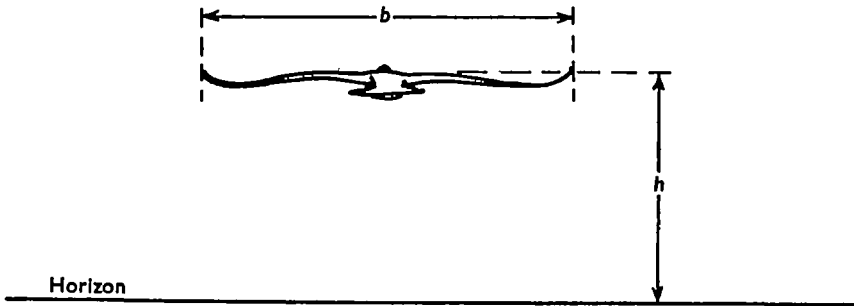


Fig. 2.  $h$  is the height of the image of the bird on the negative above that of the horizon, and  $b$  is the span of the image. The ratio  $h/b$  is the bird's height above the glider expressed in units of the wing span, and once the span is known, the actual height can be found.

A second measurement made on each negative was the distance  $h_i$  of the bird's image above that of the horizon. Since the bird's wing span  $B$  was already known, it can be seen from Fig. 2 that the bird's actual height  $H_i$  above the glider is given by

$$H_i = h_i \cdot \frac{B}{b_i}. \quad (3)$$

The regression coefficient of the bird's height  $H$  above the glider against time thus gives an estimate of the bird's vertical speed  $V_v$ , relative to the glider.

A complication now arises in that the closing speed  $V_x$ , being directly measured, is a *true* speed, whereas the speed  $V_o$  read from the glider's air speed indicator is its equivalent air speed. The glider's true air speed  $V_{to}$  is related to its equivalent air speed by the formula

$$V_o = V_{to} \sqrt{\frac{\rho}{\rho_0}}, \quad (4)$$

where  $\rho$  is the ambient air density and  $\rho_0$  the air density at sea level in the I.C.A.O. standard atmosphere. All measurements of horizontal and vertical speeds have to be

reduced to some common standard, and the usual practice is to reduce them to sea level in the standard atmosphere – that is, to convert the observed speeds to the values which would have been obtained had the whole operation been carried out at sea level.

The bird's equivalent air speed was obtained in two steps as follows: first the bird's true air speed was found by adding the true closing speed  $V_x$  to the glider's true air speed (the latter being found by reversing equation (4)), and this was then converted to the bird's equivalent air speed  $V_b$ , using equation (4). Thus

$$V_b = \sqrt{\frac{\bar{\rho}}{\rho_0}} \left( V_x + V_g \sqrt{\frac{\bar{\rho}_0}{\rho}} \right). \quad (5)$$

The conversion factor  $\sqrt{(\rho/\rho_0)}$  was read directly from a published chart (Fig. 6 of von Mises, 1945), using the pressure altitude and temperature recorded at the time of the observation.

The analysis of the data involved some 350 regression calculations based on 2000-odd negatives. This large volume of arithmetic was expediently handled by an Olivetti Programma 101 Desk-Top Computer.

#### *Errors in horizontal speed measurements*

##### (1) *Rangefinder error*

The rangefinder was allegedly accurate to within about  $\pm 2\%$  at a range of 50 m, but  $\pm 5\%$  would perhaps be a realistic guess at the accuracy actually attained. An error in the assumed range at which the first photograph was taken leads to a proportionate error in the estimated wing span: this in turn leads to proportionate errors in the range estimates from each of the subsequent photographs, and hence in the estimate of the closing speed  $V_x$ . A 5% error in  $V_x$  would appear as a  $1-2\frac{1}{2}\%$  (say 2%) error in the bird's true air speed, since  $V_x$  generally accounted for 20–50% of the latter.

##### (2) *Other instrument errors*

The glider's air speed indicator was calibrated in knots (1 knot = 0.515 m/s). It could be read to the nearest knot at speeds between 37 and 50 knots, giving a proportional error in the region of  $2\frac{1}{2}\%$ . The accuracy of the air speed indicator itself was checked against a paraffin inclined manometer, and was found to be within 1 knot throughout the range within which measurements were made. The instrument was operated from a pitot-static probe mounted on top of the fin, and according to information received from the manufacturer of the glider, position error should be negligible in the relevant speed range. Since the glider's air speed was normally about 1.2 times that of the bird, this source can be considered to contribute about another  $\pm 3\%$  to the error in the latter.

Pressure altitude was read from the altimeter (set to a reference pressure of 1013 mb) to the nearest 100 ft (30 m), and is unlikely to have been as much as 100 m out; the thermometer could be read to better than 1 °C. Errors of this magnitude would lead to an error of only about 0.5% in the ratio  $\sqrt{(\rho/\rho_0)}$ , and can safely be neglected.

##### (3) *Errors in the analysis of photographs*

The wing spans of the larger vultures are in the region of 2 m in flight, and the span of the *projected* image of the first photograph in a series was generally between 2 and

cm; this was measured to the nearest 0.1 cm, giving an error in the bird's estimated wing span of 3-5%. As in the case of rangefinder error this contributes an error of 3-5% in the estimate of the closing speed, and hence of  $1-2\frac{1}{2}\%$  in the estimate of the bird's air speed.

Errors in measuring the span of later photographs get proportionately smaller as the wing span of the image gets larger. Also the regression calculation on the range estimates should even these errors out, so that they are unlikely to make any further contribution to the error in the bird's estimated air speed.

#### (4) *Overall error of air speed estimate*

Since the errors from the above three sources are additive, the combined error should amount to the square root of the sum of the squares of the contributions from each source, that is, between 4 and 5%.

An additional source of error which cannot easily be allowed for is the possibility that the bird may alter its wing span during the course of the observations, which is most likely to happen if the bird is flying in turbulent air, or is changing speed at the time of the observation. Although very few of the series of photographs showed any detectable change of wing shape, it is possible that appreciable errors may have occurred in some observations from this cause.

Allowing for an element of guesswork in the estimation of some errors, it would seem that  $\pm 10\%$  would represent a generous estimate for the overall error of the air speed estimates for the birds.

### *Errors in vertical speed measurement*

#### (1) *Air movements*

It is implicit in the principle of glide comparison that there is assumed to be no relative motion between the air in which the glider is flying and that in which the bird is flying. The horizontal separation between glider and bird never exceeded 50 m during an observation, so that errors would only be introduced by variations of vertical air velocity over distances of 50 m or less - no error in the measured relative speed results from larger scale vertical air movements, which carry both bird and glider up or down together.

For practical reasons the majority of the measurements had to be made in strong thermal conditions, when errors from this cause were inevitable. If the method could be applied in smooth slope lift or (better) wave lift, the scatter of the measurements would undoubtedly be greatly reduced, but this was unfortunately not practicable in the present case.

#### (2) *Unsteady flight by glider or bird*

The glider's polar was measured in smooth air, when the speed could be accurately maintained and sideslip avoided. When making measurements on birds the air was often far from smooth, and the difficulty of flying accurately was aggravated by the need to follow any manoeuvres which the bird might make during the approach. If the glider's speed were decreasing during a measurement, its sinking speed would be less than that taken from the measured polar, giving an apparent increase in the bird's sinking speed, and vice versa. Other inaccuracies, such as sideslip or excessive control

deflection, would increase the glider's sinking speed, so apparently reducing that of the bird.

The bird can also introduce errors by flying unsteadily or by actively increasing its sinking speed. If a bird encounters lift when gliding straight, it will usually react by pulling up at the expense of a loss of air speed, and a measurement made during such a manoeuvre gives an erroneously low sinking speed. On the other hand a vulture patrolling in search of food will normally take steps to avoid being carried above about 700 m above the ground, and will actively increase its sinking speed if it happens to pass through a thermal. Sometimes this is done by lowering the feet, which are used as airbrakes (PennyCUICK, 1971), and this may be apparent in the photographs, but it would appear that sinking speed can also be increased by changes of wing shape which are not readily detected from a viewpoint behind the bird (Hankin, 1923; PennyCUICK, 1971).

### (3) *Error in locating the horizon*

If the horizon is incorrectly identified on the negatives, the effect is to estimate the bird's relative vertical speed in relation to a sloping plane instead of to a horizontal one. In some negatives distant hilltops were sharply defined, and gave a good horizontal reference, but in many the horizon was obscured by haze. In this case some ground feature lower down in the picture had to be used as a primary reference, the measurements being then corrected by a fixed amount to make them relate to the approximate position of the real horizon. Some errors must have resulted from this procedure; but there are no firm grounds for estimating their magnitude.

### (4) *Error in glider's measured polar*

The error in the glider's estimated sinking speed is the only one of the vertical errors which is accessible to estimation. The curve in Fig. 3 represents a regression equation of the type discussed below, and limits of one standard error above and below the curve are marked. It will be seen, however, that the theoretical curve gives a characteristically poor fit at the lowest speeds.

### (5) *Overall error of vertical measurement*

It can be seen that the bird's estimated sinking speed can be affected by a number of errors over which the experimenter has little or no control, and whose magnitude cannot readily be estimated. Since all the known sources of error can affect the final estimate in either direction, there are no grounds for supposing the results to be biased, and the only practicable course is to fit a theoretical polar curve through a large number of measured points, in the hope that the errors will even out.

It may be noted that the scatter in the measurements is due mainly to errors in the vertical rather than the horizontal speed.

### *Calibration of glider's polar*

The glider's polar was determined from fifty-one partial glides carried out on four different days to the east and south of Seronera in Tanzania, where the ground is relatively flat. All the flights were started soon after first light, and were completed before 08.00 h.

The principles of the partial glide method for estimating glide polars are set out at some length by Merklein (1963), and the method used here was basically a much-simplified version of his procedure. After stopping the engine at about 900 m above the ground, the time taken to descend 300 ft (91·4 m), as measured by the altimeter, which was continuously tapped, was measured with a stopwatch. This was repeated at different speeds down to a height of 150–200 m above the ground, when the run was ended either by landing or by restarting the engine and climbing up for another run. The flights were arranged to give three observations at each forward speed. After reducing the measured sinking speeds to sea level, the three observations in each group were averaged to give the seventeen points plotted in Fig. 3.

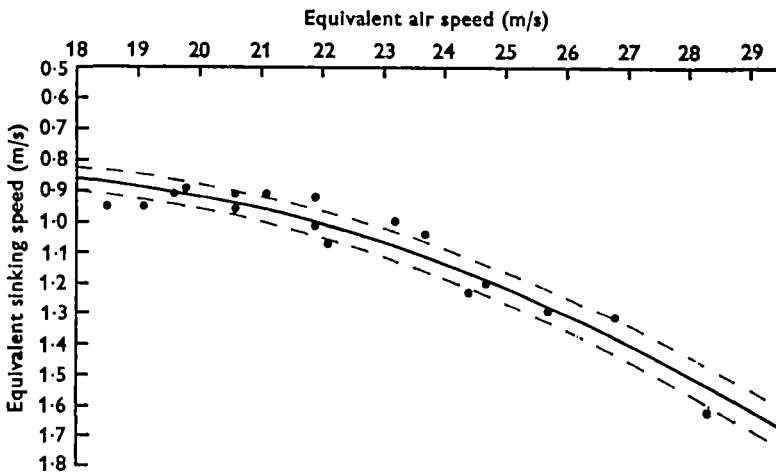


Fig. 3. Gliding performance of the ASK-14, measured with the canopy removed and the tracking camera in place. The solid curve is the regression equation  $V_s = (10.0/V) + (5.20 \times 10^{-5})V^2$ , and the dotted curves represent one standard error of the estimate of  $V_s$  above and below the curve.

The measurements were made with the canopy removed and the tracking camera in place, and in this condition the best glide ratio was found to be 22:1, and the minimum sinking speed 0.91 m/s. This is, of course, considerably inferior to the ASK-14's normal performance with the canopy fitted, when the best glide ratio is 28:1 and the minimum sinking speed 0.76 m/s (see also p. 25).

MATERIAL AND OPERATIONS

The general observations in this paper are based on eighty-eight flights in the ASK-14 totalling 240 h. Most of these were over the Serengeti National Park, Tanzania, but flights were also made over the Gregory Rift Valley from Mt. Suswa to the Gol Mountains and Oldoinyo Lengai, and eastwards to Amboseli and the east side of Kilimanjaro. The actual glide comparison measurements were made during eighteen flights totalling 65 h (included in the above totals), most of which were made during December 1969 and August 1970, when the glider was based at the Serengeti Research Institute, near Seronera. Some flights were also made from the Magadi Soda Company's airstrip at Magadi in Kenya.

Measurements were made indiscriminately on any bird which presented a target but the subsequent analysis refers only to the white-backed vulture *Gyps africanus*, since 94 of the 177 usable observations obtained were on this species. The rest of the observations were distributed among nine other species (Table 1). Although the results obtained on the other species did not in any way conflict with those on the white-backed vulture, the numbers of observations were too small, and the scatter too large for detailed analyses to be attempted.

Table 1. *Numbers of observations on different species*

Species	No. of observations
White-backed vulture, <i>Gyps africanus</i>	94
Rüppell's griffon vulture, <i>Gyps rüppellii</i>	19
Lappet-faced vulture, <i>Torgos tracheliotus</i>	19
Tawny eagle, <i>Aquila rapax</i>	13
Marabou stork, <i>Leptoptilos crumeniferus</i>	12
White-headed vulture, <i>Trionocephs occipitalis</i>	10
Secretary bird, <i>Sagittarius serpentarius</i>	2
Martial eagle, <i>Polemaëtus bellicosus</i>	6
Long-crested hawk eagle, <i>Lophoaëtus occipitalis</i>	1
Bataleur eagle, <i>Terathopius ecaudatus</i>	1
Total	177

The method of operation was to take off as soon as strong thermals were well established (usually between 10.30 and 12.00 h), stop the engine as soon as possible, and soar until birds were met with. It was found best to fly first to an area where game animals were concentrated, since the vultures and other scavenging birds appeared to follow the migrating herds. This meant that in the first study period most observations were made in the southern Serengeti between the Moru Kopjes and Lake Ndutu, whilst in the second the Kogatende area and the Western Corridor proved most productive.

A week was spent in August 1969 on the eastern escarpment of the Gol Mountains, where 500–1000 pairs of Rüppell's griffon vultures nest, in the hope of making measurements on birds soaring in slope lift along the cliffs. Unfortunately this plan was frustrated by the behaviour of the birds, which spent much of their time flying about the nesting cliffs in close formation in groups of two to seven, and reacted to the glider in the same way as to other members of their own species. Thus vultures, sometimes in considerable numbers, would readily fly close alongside or behind the glider, but it proved impossible to approach a bird from behind. Similar behaviour was occasionally seen at other times in white-backed vultures *Gyps africanus* and hooded vultures *Necrosyrtes monachus*.

Vultures patrolling in search of food or travelling across country were more amenable to measurement, and in these circumstances they usually paid little attention to the glider's approach, although a few individuals took evasive action which made measurement impossible. Tawny eagles *Aquila rapax* and martial eagles *Polemaëtus bellicosus* seemed to be attracted by the glider, and on several occasions approached within 2–3 m of the cockpit in a somewhat menacing fashion. Marabou storks *Leptoptilos crumeniferus* were apprehensive of the glider, but when gliding straight could be approached carefully from directly behind, as their lookout appeared to be poor in



that direction. On catching sight of the glider turning away a few metres behind them, however, they would often take violent evasive action, and one even rolled on to its back and dived 100 m or more. White storks *Ciconia ciconia*, yellow-billed storks *Ibis ibis* and white pelicans *Pelecanus onocrotalus* were all very nervous of the glider, and it was not possible to get usable measurements on any of these species.

RESULTS AND DISCUSSION

The ninety-four observations of sinking speed and forward speed obtained for the white-backed vulture are plotted in Fig. 4. There are theoretical grounds (Welch, Welch & Irving, 1955) for expecting a glide polar to approximate to the form

$$V_s = \frac{\beta}{V} + \gamma V^3, \tag{5a}$$

where  $V_s$  is the equivalent sinking speed,  $V$  is the equivalent forward speed, and  $\beta$  and  $\gamma$  are constants representing the contributions of induced drag and other sources of drag respectively to the sinking speed. In practice this equation gives a satisfactory

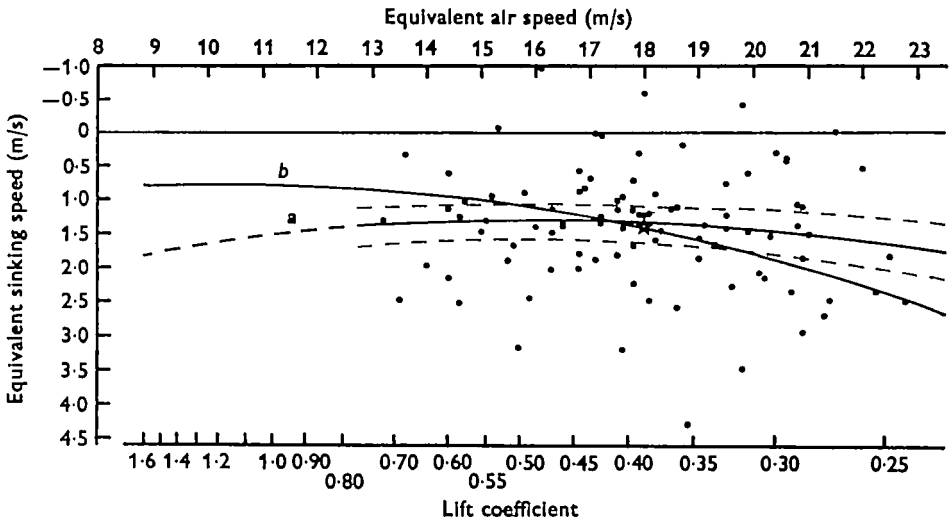


Fig. 4. Measured points for the white-backed vulture. The solid curve (a) is the regression equation  $V_s = (15.6/V) + (8.40 \times 10^{-5})V^3$ , and the dotted curves on either side of it represent one standard error of the estimate of  $V_s$  above and below the curve. Curve (b) is the equation  $V_s = (5.79/V) + (1.85 \times 10^{-4})V^3$ , the derivation of which is explained in the text. The star marks the average forward and sinking speeds of all the measured points.

fit to most glide polars derived from measurements on gliders, except at speeds in the region of the stall, where the actual curve falls away more steeply than the theoretical one. As a first attempt at analysing the data, a curve of this form was fitted through the measured points by the least-squares method (Bailey, 1959), and the result was

$$V_s = \frac{15.6}{V} + (8.40 \times 10^{-5})V^3. \tag{5b}$$

This curve is also plotted in Fig. 4, and is marked 'a'. The dotted curves on either side

of it represent one standard error of estimate above and below the calculated curve for each value of  $V$ , their ordinates are given by

$$V_s \pm \sqrt{\{(s_\beta/V)^2 + (s_\gamma V^3)^2\}},$$

where  $s_\beta$  and  $s_\gamma$  are the standard deviations of  $\beta$  and  $\gamma$  respectively, whose calculated values were 3.52 and  $3.09 \times 10^{-5}$ .

Like any regression calculation, the curve-fitting method used here is strictly valid only if the values of the independent variable ( $V$ ) are known exactly, without error. Although this condition is not met in the present case, the use of the method was thought justifiable since there are grounds (explained above) for believing that the error in measuring  $V$  was much less than that in measuring  $V_s$ .

#### *Plausibility of fitted curve*

In the theory of the glide polar presented by Welch *et al.* (1955), it is shown that the curve should obey the equation

$$V_s = \left( \frac{2kW}{\pi A \rho_0 S} \right) \cdot \frac{1}{V} + \left( \frac{C_{D0} \rho_0 S}{2W} \right) V^3, \quad (5c)$$

where  $k$  is the 'span efficiency factor' (of which more below),  $W$  is the bird's weight,  $A$  is its aspect ratio,  $S$  is its wing area,  $\rho_0$  is the air density at sea level in the standard atmosphere, and  $C_{D0}$  is the drag coefficient at zero lift, based on the wing area;  $C_{D0}$  represents the sum of the profile drag coefficients of the wings and body, the term 'profile drag' being understood to include skin friction in this context. Comparing equations (5a) and (5c), one would anticipate that the two regression constants can be interpreted thus:

$$\beta = \frac{2kW}{\pi A \rho_0 S}, \quad (6a)$$

$$\gamma = \frac{C_{D0} \rho_0 S}{2W}. \quad (6b)$$

Taking equation (6a) first, numerical values are available for all the quantities in the equation except the 'span efficiency factor'  $k$ , as follows:

$$W = 52.8 \text{ N},$$

$$A = 6.90,$$

$$S = 0.690 \text{ m}^2,$$

$$\rho_0 = 1.22 \text{ kg m}^{-3}.$$

The weight and wing area are derived from a sample of thirty-four individuals collected by Mr D. C. Houston, to whom I am indebted for the information, while the figure for the aspect ratio was derived from a detailed planform tracing of one individual shot by the author. Substituting the above values in equation (6a) gives

$$k = 2.7,$$

$k$  is a correction factor which gives the ratio of the induced drag obtained in practice to that expected from theory, assuming the optimum case of elliptical spanwise lift distribution. If the latter condition were fulfilled,  $k$  should be unity, but in practical aeroplane wings of reasonably efficient design, values of about 1.1 or 1.2 for  $k$  are typical. Some authors, notably Raspé (1960) and Cone (1962) have suggested that the

splayed primaries at vultures' wing tips may actually reduce the induced drag below the theoretical minimum for elliptical lift distribution, in other words that  $k$  may be less than 1 for this type of wing. However that may be, a value of 2.7 for  $k$  represents an inconceivably inefficient wing, and is an implausible result, so that one can conclude that the calculated value of the first coefficient  $\beta$  in the regression equation is most probably wrong.

(It should be noted that the definition of span efficiency factor used here, whilst following Welch *et al.* (1965), differs from that used by some other authors, including Tucker & Parrott (1960) and Cone (1962*c*), whose span efficiency factor, or equivalent quantity, is the reciprocal of  $k$  as defined here.)

A probable reason for the poor estimate of  $\beta$  can be seen by marking in lift coefficients on Fig. 4, on the assumption of average weight and fully extended wing area, hence a wing loading of 76.5 N m<sup>-2</sup>. On this basis the lowest vulture equivalent air speed measured, 13.2 m/s, corresponds to a lift coefficient of 0.720.

It is not likely that the vulture's maximum lift coefficient is really as low as this. Pennycuik (1968) measured a maximum lift coefficient of 1.3 (based on combined wing and tail area) in wind-tunnel experiments on the gliding pigeon *Columba livia*, whilst Tucker & Parrott (1970) measured 1.6 (based on wing area alone) in similar experiments on the laggar falcon *Falco jugger*. Both these species have rather pointed wings with little splaying of the primaries in gliding flight, and some ornithologists (the writer included) suspect that the main function of the 'wing-tip slots' of vultures may be to increase the maximum lift coefficient in gliding. Whether or not this is so, it seems unlikely that the vulture's maximum lift coefficient would be less than the laggar falcon's 1.6.

A lift coefficient of 1.6 corresponds to an equivalent air speed of 8.85 m/s in straight flight. If this is indeed the white-backed vulture's minimum gliding speed, then it can be seen from Fig. 4 that there is a large speed range, from this speed to 13.2 m/s, within which no measurements have been obtained. Now the induced drag, and the component of sinking speed resulting from it, is greatest at low speeds, and approaches zero asymptotically at very high speeds, so that measurements of sinking speed at the lower end of the speed range are crucial for the accurate estimation of this component. The absence of these particular measurements would account for the poor estimate of  $\beta$  in the regression equation.

A low probability of getting observations in the neighbourhood of the minimum gliding speed seems to be inherent in the method of measurement. Since measurements were only made in straight lines, the majority of vultures observed would be proceeding from one thermal to the next, when they would (like glider pilots) fly at or above the speed for best gliding angle. One would expect a vulture searching for lift to reduce speed on finding it, and indeed they did so; however, the rapid change of speed, high closing speed, and sudden climb associated with this manoeuvre made accurate following in the glider impossible. Also, since the manoeuvre was normally initiated in response to a sharp gradient in the vertical speed of the air, any measurements of sinking speed obtained in these circumstances would be more than usually suspect (p. 18). It is possible that good measurements at very low speeds could be obtained on vultures soaring in slope or wave lift, but unfortunately no suitable opportunities occurred to try this.

Turning now to equation (6*b*) numerical values are given above for all the variables except  $C_{D0}$ , which can thus be estimated as

$$C_{D0} = 0.0105.$$

The component of this due to body drag can be estimated from wind-tunnel measurements made by Pennycuick (1971) on the frozen body of a Rüppell's griffon vulture, which is similar in shape to the white-backed vulture, but larger. The drag coefficient measured on the 'clean' body (i.e. with neck and feet retracted) was 0.43, based on the cross-sectional area at the widest part of 0.0300 m<sup>2</sup>. This cross-sectional area, if scaled in proportion to the two-thirds power of the mass, would become 0.0255 m<sup>2</sup> for the white-backed vulture. If this drag is regarded as a component of a combined profile drag coefficient based on a wing area of 0.690 m<sup>2</sup>, as in Welch *et al.* (1955) formulation, its contribution to  $C_{D0}$  would be

$$0.43 \times \frac{0.0255}{0.690} = 0.0159.$$

As this is more than the value of  $C_{D0}$  calculated above from the coefficient  $\gamma$  of the regression equation, which is supposed to include contributions from the wing as well as the body, one must conclude that the estimate of  $\gamma$  is also implausible, being too low.

#### *Amended glide polar*

In the absence of any measurements of sinking speed at lift coefficients between 0.72 and 1.6, the only practicable expedient is to estimate  $\beta$  on the basis of some reasonable assumption about  $k$ . It will be assumed that

$$k = 1.$$

This may be regarded as a compromise between experience with aeroplane wings, where  $k$  is generally found to be somewhat greater than 1, and the prediction of Cone (1962) who suggests on the basis of a two-dimensional electrical analogue that  $k$  could be less than 1, perhaps as low as 0.75, in gliding birds with splayed primaries. The value of  $\beta$  calculated on this assumption from the data listed above is

$$\beta = 5.79 \text{ m}^2 \text{ s}^{-2}.$$

The value of  $\gamma$  is determined mainly by the high-speed end of the polar, where the measured points are concentrated. Since only one constant is now required, the simplest possible method of analysis should suffice, and with this end in view an average equivalent air speed  $\bar{V}$  and an average equivalent sinking speed  $\bar{V}_s$  were found by calculating the means of all the measured points. The results were

$$\bar{V} = 18.0 \text{ m/s},$$

$$\bar{V}_s = 1.40 \text{ m/s}.$$

The point so defined is the 'centre of gravity' so to speak of all the measured points, and a new value of  $\gamma$  was now chosen so as to make the polar pass through it. Since the polar should be convex upward throughout its length, this procedure will tend to overestimate  $\gamma$  slightly, but in view of the wide scatter of the points it was not thought worthwhile to attempt a correction for this. The new estimate of  $\gamma$  was

$$\gamma = 1.85 \times 10^{-4} \text{ m}^{-2} \text{ s}^2.$$

Substituting this value in equation (6*b*) gives

$$C_{D0} = 0.0232.$$

Assuming as before that the drag of the body contributes 0.0159 to this total, the remainder, 0.0073, would represent the profile drag coefficient of the wing. Whilst this is still a low value, it is comparable with minimum profile drag coefficients which have been measured on wing sections of 'non-laminar' type (Abbott & von Doenhoff, 1959), and is certainly less implausible than the previous estimate based on the regression calculation.

The equation of the amended glide polar can now be written

$$V_g = \frac{5.79}{V} + (1.85 \times 10^{-4})V^3. \quad (7)$$

This curve is marked 'b' in Fig. 4. It can be seen that over the speed range 15.6–20.0 m/s it falls within one standard error of estimate from the original regression curve. It falls within the 95% fiducial limits over the entire speed range within which measurements were obtained (13.2–22.8 m/s), and thus cannot be said to differ significantly from the regression curve in the statistical sense.

The amended polar of equation (7) gives a minimum sinking speed of 0.76 m/s at a forward speed of about 10 m/s and a maximum glide ratio of 15.3:1 at 13 m/s. The minimum sinking speed is the same as that of the ASK-14 in its normal condition with the canopy fitted, but the glider attains this at a much higher forward speed (20–21 m/s). With the canopy removed for tracking birds, the ASK-14's minimum sinking speed is somewhat higher, 0.91 m/s. The glider's best glide ratio is, of course, much better than that of the birds, 28:1 with the canopy fitted, and 22:1 with it removed.

Table 2. *ASK-14 polar. Regression constants and aerodynamic quantities estimated from them*

	Clean aircraft	Canopy removed
$\beta$ ( $m^3 s^{-3}$ )	9.34	10.0
$\gamma$ ( $m^{-3} s^3$ )	$3.50 \times 10^{-8}$	$5.20 \times 10^{-8}$
$k$	1.09	1.17
$C_{D0}$	0.0152	0.0226

In order to check the general soundness of the reasoning used above, it was applied to two sets of performance measurements on the ASK-14, the set shown in Fig. 3, which was made by the writer with the canopy removed and the vulture-tracking camera in place, and a set made by the aircraft's designer, Hr. Dipl.-Ing. R. Kaiser, in the normal soaring configuration with the canopy fitted. The regression equation (5*a*) was fitted through the data, and the constants  $\beta$  and  $\gamma$ , and estimates of  $k$  and  $C_{D0}$  calculated from them, are listed in Table 2. The main difference is in  $C_{D0}$  as would be expected. Removing the canopy would not be expected to have any effect at all on  $k$ : the difference between the two estimates of  $k$  seems to be due to the fact that Hr Kaiser's measurements extend only down to a forward speed of 20.0 m/s, whereas the minimum speed is about 18.5 m/s, and this appears to have resulted in a slight underestimate of the induced drag. However, the values given in Table 2 are entirely plausible as they stand.

*Circling performance*

Thermals, on which vultures and several other kinds of birds mainly depend for remaining airborne and for travelling across country, are areas of rising air of limited horizontal extent, and are usually best exploited by gliding in steady circles. The theory of circling flight in thermals has been understood for many years, and the principles are explained by Welch *et al.* (1955). Some of the main conclusions are summarized below in order to provide a basis for the subsequent estimates of the vulture's circling performance. Climbing performance is determined partly by the properties of the bird or glider, and partly by the structure of the thermals in which it flies, a general

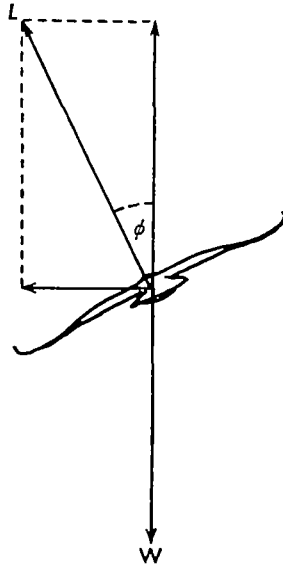


Fig. 5. A bird gliding in steady circles must bank its wings at an angle to the horizontal. The weight ( $W$ ) must be balanced by the vertical component of the lift ( $L$ ), while the horizontal component of the lift balances the centrifugal force.

account of which is given by Wallington (1961). The very detailed analysis given by Cone (1961, 1962*a, b*) needs to be interpreted with some caution, as real thermals are highly variable, and cannot be relied upon to conform closely to any particular mathematical model.

When a bird or glider is flying in steady circles, the wings must be banked at some angle to the horizontal (Fig. 5). The lift force, which is inclined at the same angle to the vertical, can be resolved into a vertical component  $L \cos \phi$  which must balance the weight, and a horizontal component  $L \sin \phi$  which balances the centrifugal force. From Fig. 5, it can easily be shown that the radius of turn  $r$  is

$$r = \frac{V_c^2}{g \cdot \tan \phi}, \quad (8)$$

where  $V_c$  is the forward speed in the turn and  $g$  is the acceleration due to gravity. It can also be seen from Fig. 5 that

$$L = \frac{W}{\cos \phi} \quad (9)$$

so that the lift coefficient  $C_L$  is

$$C_L = \frac{2W}{\rho V_c^2 S \cos \phi} \quad (10)$$

Equation (10) can be rearranged to give

$$V_c^2 = \frac{2W}{\rho S C_L \cos \phi} \quad (10a)$$

and if this expression for  $V_c^2$  is substituted in equation (8), the turning radius can be expressed in terms of the lift coefficient, the wing loading, and the angle of bank

$$r = \frac{W}{S} \cdot \frac{2}{\rho C_L g \sin \phi} \quad (11)$$

Hence for a given lift coefficient and angle of bank the turning radius is directly proportional to the wing loading; birds with low wing loadings can fly in smaller circles than those with higher wing loadings. A limiting minimum value for the turning radius can be found by substituting the maximum lift coefficient  $C_{L_{\max}}$  and the maximum value (unity) for  $\sin \phi$  in equation (11)

$$r_{11m} = \frac{W}{S} \frac{2}{\rho g C_{L_{\max}}} \quad (12)$$

$r_{11m}$  can never be reached in practice, since it requires vertical bank and infinite lift, but it is approached asymptotically at very high angles of bank.

To decrease the radius of turn, the angle of bank has to be increased, and because this is turn calls for an increase in lift (Fig. 5), the speed also has to be increased if the lift coefficient is to be kept constant. The result is that the smaller radius of turn is achieved at the expense of an increased sinking speed, until at the limiting radius of turn  $r_{11m}$ , the sinking speed would be infinite. At the other extreme, as the radius of turn approaches infinity (straight flight), the sinking speed approaches the minimum value shown on the straight-flight polar. The curve relating minimum sinking speed to radius of turn is the envelope of the family of curves shown in Fig. 6, and is referred to as the 'circling envelope'. It is of crucial importance to soaring birds and gliders since it determines the rate of climb in thermals, which in turn is the most important factor contributing to achieved cross-country speed. From another point of view, this curve determines the minimum radius and strength of thermal in which soaring is possible, an especially important consideration in vultures and some birds of prey, which rely on thermals just to remain airborne (as opposed to travelling across country) when patrolling in search of food.

#### *Construction of circling performance curves*

The problem of predicting circling performance from a straight-flight glide polar has been investigated in some detail by Haubenhofer (1964) who points out that the forward speed and sinking speed in a turn are related to those obtained in straight flight *at the same lift coefficient* as follows:

$$V_c = \frac{V}{\sqrt{(\cos \phi)}}, \quad (13)$$

$$V_{sc} = \frac{V_s}{\sqrt{(\cos^3 \phi)}}, \quad (14)$$

where  $V_c$  and  $V_{\infty}$  are respectively the forward speed and sinking speed in the turn while  $V$  and  $V_s$  (which are related to each other by the straight-flight glide polar) are the corresponding straight-flight values. Combining equation (13) with equation (8), the relation between the radius of turn and the *straight-flight* forward speed is

$$r = \frac{V^2}{g \cdot \sin \phi}. \quad (15)$$

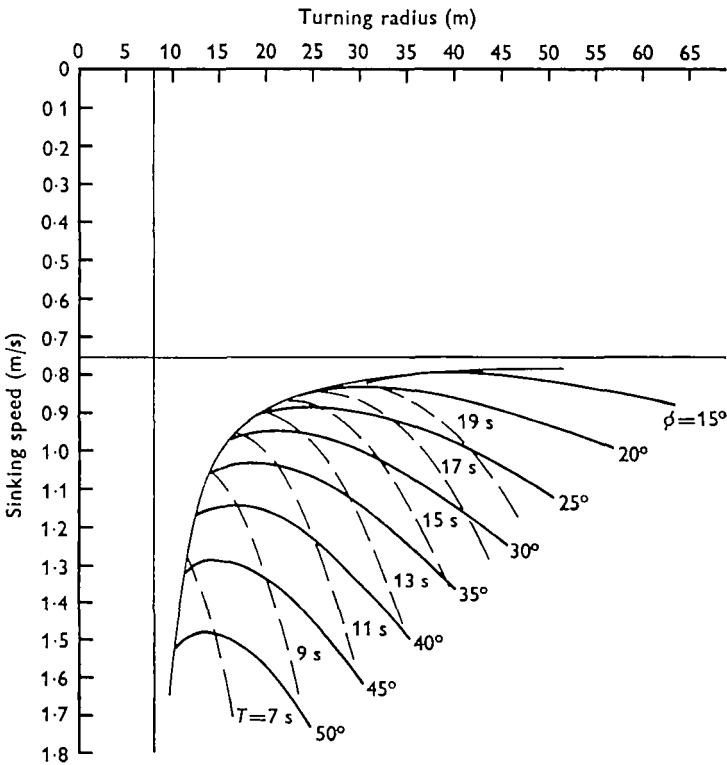


Fig. 6. Circling curves derives from curve (b) of Fig. 4. The solid curves show the relationship between sinking speed and turning radius with angle of bank ( $\phi$ ) as parameter, while the dotted curves show the same relationship, but with the time to complete one circle ( $T$ ) as parameter. The envelope of the curves defines the optimum combination of speed and angle of bank at any radius. Its asymptotes (thin straight lines) are the straight-flight minimum sinking speed (0.76 m/s) and the limiting radius of turn (8.0 m).

The family of curves shown in Fig. 6 was constructed as follows. A value of  $\phi$  was first selected as parameter for one curve of the family. Successive values of  $V$  (each corresponding to a particular lift coefficient) were then selected, and the radii of turn were calculated from equation (15). The straight-flight sinking speeds were obtained from equation (7), and converted to circling sinking speeds by means of equation (14). Each curve of Fig. 6 is thus a plot of sinking speed versus turning radius for one angle of bank, and each point on the curve corresponds to a different speed. The speeds are not marked, but the lowest speeds are to the left (smaller radii), and the left-hand end of each curve stops when the maximum lift coefficient is reached.

This method of calculating circling performance from the straight-flight polar was



Applied by Merklein (1966) to the measured polars of several different types of gliders. He also tested the validity of the method by making actual circling measurements on a K-8 glider, whose straight-flight polar had previously been determined, and obtained results showing a satisfactory agreement with theory.

*Implications of the circling curves*

It can be seen from the envelope in Fig. 6 that at low angles of bank, around 15°–20°, a small increase in angle of bank results in a substantial reduction of turning radius, with only a slight increase of sinking speed. Above about 35° of bank, however, further steepening of the bank produces only a small reduction of the turning radius, at the expense of an increasingly dramatic increase in the sinking speed.

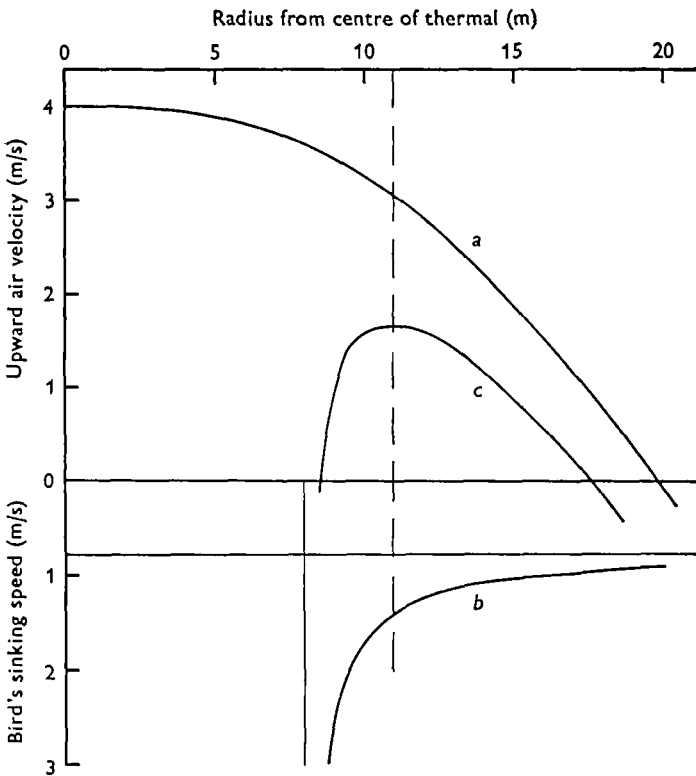


Fig. 7. Curve (a) is an arbitrary velocity profile for an imaginary narrow thermal, and curve (b) is a bird's circling envelope as in Fig. 6. Curve (c) is the achieved rate of climb (i.e. the difference between the upward air velocity and the bird's sinking speed). It reaches a maximum at the point where the slopes of curves (a) and (b) are equal and opposite (vertical dotted line).

The angle of bank which maximizes rate of climb in a particular thermal depends on the velocity profile of the thermal, that is, on the distribution of upward air velocity with distance from the centre of the thermal. Goodhart (1965) has pointed out that in general the optimum circling radius is that at which the slope of the glider's circling envelope and the thermal profile are equal and opposite (Fig. 7). In a strong but very narrow thermal, i.e. one in which the upward velocity is high at the centre but falls

steeply to zero at some small radius from the centre, it may be profitable to bank very steeply in order to remain in the narrow 'core' – lessening the angle of bank in this case would reduce the sinking speed (relative to the air), but take the bird's circle right outside the area of rising air. Normally, however, one may anticipate from Fig. 6 that angles of bank in the range  $20^\circ$ – $40^\circ$  should be best for circling in small thermals. Another reason for avoiding the higher angles of bank is that the air speed for optimum performance becomes increasingly critical. It can be seen from the slopes of the curves in Fig. 6 that at low angles of bank an increase of speed over the optimum results in an increase of circling radius with little change of sinking speed, whereas increase of speed at the steeper angles of bank produces a sharp increase of sinking speed as well.

#### *Circling in radial and circumferential air flow*

The above reasoning applies to circling in still air, or in a mass of air which is moving bodily upward with no internal flow. Real thermals contain both radial and rotary components of flow, which modify the argument somewhat. In the lower part of a thermal of the 'vortex-ring' type, or near the ground in one of the columnar or 'dust-devil' type, there is a radial component of flow inwards towards the centre of the thermal. Goodhart (1956) has shown that in such a convergent radial field of flow, a reduction of sinking speed  $\Delta V_s$  may be expected, such that

$$\Delta V_s = U_r \cdot \tan \phi \quad (16)$$

where  $U_r$  is the convergent radial air velocity. It is therefore helpful to bank rather more steeply in these circumstances than would otherwise be advisable, in order to maximize the gain from this component of the flow.

Columnar thermals rotate rapidly about their vertical axes, and a reduction of circling radius can (in principle) be obtained by circling against the direction of flow. The radius of turn in this case would be

$$r = \frac{(V_c - U_t)^2}{g \cdot \tan \phi} \quad (17)$$

where  $U_t$  is the tangential component of air velocity. Equation (17) represents a practicable manoeuvre only when  $U_t$  is substantially less than  $V_c$ , but comparison with equation (8) suggests, nevertheless, that it should be possible for a bird to sidle in very close to the axis of a rotating column by circling carefully at rather a shallow angle of bank. Whether birds in fact do this, or whether the profiles of columnar thermals would make it profitable to do so, are other questions which cannot be answered at present.

#### *Observations on circling birds*

It is difficult to make direct measurements on circling birds, but two types of simple measurements were tried to test the plausibility of Fig. 6.

In the first place an attempt was made to measure angles of bank by filming vultures circling at low altitude with a 16 mm cine camera mounted on a levelled tripod. A 75 mm lens was used, which allowed the film to be taken at long range with the camera nearly horizontal. The film was later back-projected, frame by frame, on to squared paper, and the angle of bank measured at the points when the bird was facing directly towards or away from the camera. In this way thirteen observations were obtained

In the lappet-face vulture, a somewhat larger bird than the white-backed vulture (mass 6.6 kg) but with a lower wing loading ( $63 \text{ N m}^{-2}$ ). The results ranged from  $23^\circ$  to  $43^\circ$  (mean  $34^\circ$ ). A further nineteen observations on vultures which were not positively identified gave a mean angle of bank of  $29^\circ$ , with a range of  $20^\circ$ – $40^\circ$ . These results, as far as they go, suggest that vultures climbing in small thermals prefer angles of bank between  $20^\circ$  and  $40^\circ$ , as one would expect from Fig. 6.

Secondly, vultures flying in thermals at low altitude were timed round one circle with a stopwatch. Thirteen observations on white-backed vultures ranged from 9.2 to 18.0 s (mean 13.8 s).

Since the calculation represented by Fig. 6 connects forward speed with radius of turn, the results can equally well be plotted using the time to complete one circle, instead of the angle of bank, as parameter, and some curves of this type have been added to the diagram. It can be seen that if the diagram is correct, and if the bird is using optimum combinations of speed and angle of bank, then the shortest observed time of 9.2 s would correspond to a turn of about 15 m radius, with about  $30^\circ$ – $35^\circ$  of bank, while the longer times would correspond to flatter angles of bank which would be appropriate to somewhat wider thermals.

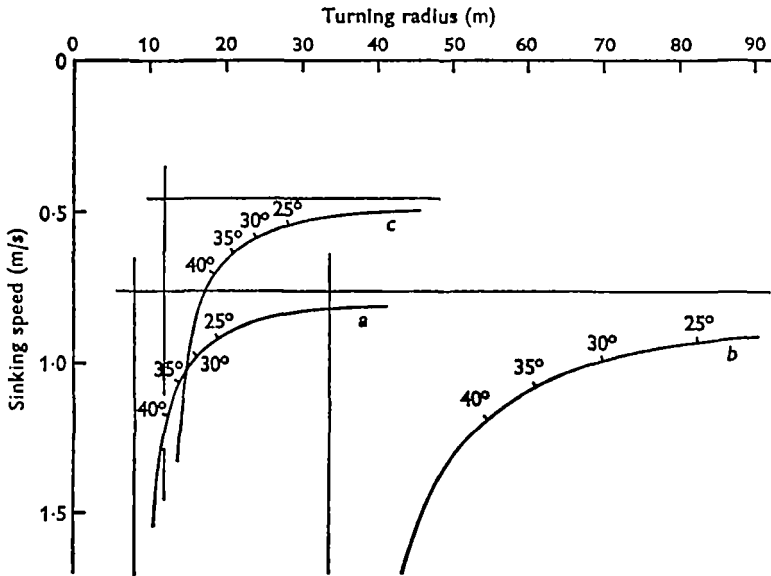


Fig. 8. Circling envelopes compared for (a) the white-backed vulture, (b) the ASK-14 with its canopy on, and (c) the 'albatross-shaped vulture'. Angles of bank from  $25^\circ$  to  $40^\circ$  are marked on each curve. The horizontal and vertical lines are the asymptotes of each curve: the sinking speed asymptote for the white-backed vulture happens to be the same as that for the ASK-14 ( $0.76 \text{ m/s}$ ).

*Comparison between the vultures and the glider*

In Fig. 8 the circling envelope calculated for the bird (a) is compared with one for the ASK-14 (b), based on data for the 'clean' aircraft with canopy fitted. The minimum sinking speed in straight flight is the same for both,  $0.76 \text{ m/s}$ . However, because the glider's wing loading ( $265 \text{ N m}^{-2}$ ) is about 3.5 times that of the vulture

( $76.5 \text{ N m}^{-2}$ ), its radius of turn at any given angle of bank would also be 3.5 times as great if its maximum lift coefficient were the same (equation 11); in fact because the glider's wing sections have been chosen for low drag rather than high lift, its maximum lift coefficient is about 1.3 (as compared to 1.6 assumed for the bird), so that its radius of turn is actually 4.3 times that of the bird at any given angle of bank.

In a typical turn designed to exploit a small thermal, say at  $35^\circ$  of bank, the bird should be able to circle at a radius of 14 m, and would require an upward air velocity of 1.06 m/s in order to maintain height, whereas the glider needs about the same upward air velocity at a radius of 61 m. Thus although the upward air velocity needed by the glider is no greater than that for the bird, the rising air has to cover about 18 times the area (i.e.  $4.3^2$ ), and the solar energy required to initiate the thermal is correspondingly greater.

The East African vultures make conspicuous use of their ability to glide in very small circles, especially early in the day when thermal convection is just beginning. In the course of the calibration flights which were made from Seronera to measure the glider's polar (p. 18), it was found that convection was inhibited in the early morning by a marked temperature inversion at about 600–700 m above the ground. As the sun started to heat the ground, small scale convection started below the inversion, resulting in small patches of lift too narrow for the glider to circle in. Only after about 10.30 h did the thermals break through the inversion and grow to a size big enough to sustain the glider. Vultures, however, could be seen circling persistently in tiny (and often transient) patches of lift as early as 08.30 h, and by 09.30 h they were often flying in thermals successfully at heights of 300 m or more above the ground.

Later in the day, when vultures and glider were able to fly in company at higher levels, the birds could usually remain in the strongest lift in the core of a thermal, while the glider, flying in bigger circles around them, was obliged to use somewhat weaker lift further from the centre. The birds could therefore normally outclimb the glider quite rapidly, except in very large thermals, where it was sometimes possible to keep up with them. It was also possible to maintain height relative to birds when flying straight in linear thermals ('thermal streets') which are common over the Serengeti, but in this case the glider, because of its higher wing loading, would steadily overhaul the bird, and occasional circles had to be flown in order to remain in company with it.

When flying straight between thermals in cross-country flight, the vultures would increase speed to 20 m/s or so, and it was then possible to maintain station with them horizontally, but because of the glider's far superior glide ratio in this speed range, the airbrakes had to be used more or less continuously to maintain station vertically.

The vulture's low wing loading is helpful in thermals, but this same feature leads to slow speeds and a poor glide ratio in the straight glides between thermals. Because of this the vultures' cross-country speeds in thermals are typically low in spite of their superior climbing ability; average speeds of 40–50 km/h are typical, whereas the glider could easily average 60–70 km/h in convection of moderate strength.

*Adaptive significance of the shape of the vulture wing*

Vultures, and other birds which use thermal soaring as their main means of locomotion, such as storks (Ciconiidae) and eagles, typically have wings of very low aspect ratio, 7 or even less being usual. Gliders, which are mostly designed for the same type of flight, typically have aspect ratios of 16 upwards (16.2 for the ASK-14). There cannot be any anatomical prohibition against birds having high aspect ratio wings, since albatrosses (Diomedidae) have aspect ratios comparable with those of gliders. For example, Greenewalt (1962) lists a wandering albatross *Diomedea exulans* of 8.5 kg mass, as having a span of 3.41 m, and an aspect ratio of 18.7. In order to see what effect on soaring performance would be expected if the white-backed vulture were to develop similar body proportions to the wandering albatross, performance estimates have been made for an imaginary 'albatross-shaped vulture', which has the above proportions scaled to the white-backed vulture's mass of 5.38 kg. The aerodynamical quantities  $k$ ,  $C_{D0}$ , and  $C_{Lmax}$  (defined above) are assumed to remain unchanged. The data used in the calculation, and some of the main results are listed in Table 3, and the calculated circling envelope for the albatross-shaped vulture is plotted in Fig. 8 along with those of the white-backed vulture and the ASK-14.

Table 3. *Data and assumptions for comparisons of circling performance*

	White-backed vulture	Albatross- shaped vulture	ASK-14
Mass (kg)	5.38	5.38	340
Span (m)	2.18	2.93	14.3
Aspect ratio	6.9	18.7	16.2
Wing loading (N m <sup>-2</sup> )	76.5	115	265
$C_{Lmax}$	1.6	1.6	1.3
$k$	1.00	1.00	1.09
$C_{D0}$	0.0232	0.0232	0.0152
Min. sinking speed (m/s)	0.76	0.47	0.76
— at forward speed (m/s).	10	11	20-21
Max. glide ratio	15	24	28
— at forward speed (m/s)	13-14	12-13	22-23
Turn radius at 35° bank (m)	14	21	61
— at sinking speed (m/s)	1.06	0.63	1.07

The wing area of the albatross-shaped vulture is two-thirds that of the white-back, and its wing loading (and turning radii) would therefore be 1.5 times as great. In other respects, however, a dramatic improvement in gliding performance is to be expected, the minimum sinking speed being reduced from 0.76 to 0.47 m/s, and the best glide ratio increased from 15 to 24. It can be seen from Fig. 8 that in thermals of any radius above about 17 m, the albatross-shaped vulture should climb better than the real white-back, and this combined with the much better glide ratio and higher speed between thermals, would result in far higher average speeds when travelling across country. The albatross-shaped vulture would be inferior in one respect only, that is, in its ability to remain airborne in thermals with radii between 14 and 17 m.

It would thus be an error to suppose that the characteristic wing shape of thermal-soaring birds is an adaptation to thermal soaring as such, since there is no doubt that an albatross-shaped vulture, once airborne, would soar superbly in thermals, and would far outdistance storks and eagles on migration.

The reason for the large area and low aspect ratio of the wings of vultures and storks is not clear at present. In the case of vultures it is possible that the ability to soar in very small thermals is crucial, allowing them to start patrolling earlier in the morning than would otherwise be possible. However, it is difficult to believe that this would be more important to a white stork *Ciconia ciconia* than the higher speed on migration which would result from a higher wing loading and aspect ratio. It is perhaps more probable that the low-aspect-ratio wing is adapted to the requirements of take-off from the ground or trees, which may be assumed to call for more wing area than taking off from the crest of a wave or from a sea cliff.

#### *Raspet's experiments*

Raspet (1950*a, b*), whose comparative glide measurements on the black vulture *Coragyps atratus* (Cathartidae) were the first of their kind, credited this creature with a best glide ratio of 23:1. Tucker & Parrott (1970), reviewing estimates of measured glide ratios reported by different authors, regard this figure as anomalously high, and profess themselves sceptical of its accuracy. It is therefore appropriate to reconsider Raspet's results in the light of experience with the present experiments.

Raspet's method was the same in principle as that used here, but differed in detail in that no horizontal closing speeds were measured. Instead, the glider was flown in such a way that its distance behind the bird (judged by eye) remained constant, and the bird's equivalent air speed was then taken to be equal to the glider's indicated air speed. The bird's height above or below the glider's horizon was measured visually by the pilot using an optical device which appears to have been based on the same principle as the one used here. A single observation lasted a matter of minutes, the pilot reporting his speed and the bird's relative height at intervals by radio to an assistant on the ground, who timed them and wrote them down. Afterwards, the glider's speed and the bird's relative height during the observation were plotted against time, and average values for the bird's speed and relative sinking speed were determined graphically.

The high best glide ratio which Raspet attributed to *Coragyps* is especially hard to understand since it considerably exceeds that which he measured on his glider (18.5:1), and it would have been extremely difficult to approach and follow birds if they had really had as big a performance margin as this over the glider. It is perhaps more probable that in the rather long, straight glides required for his observations the birds were able to gain gradually on the glider by slowing down slightly in patches of lift and speeding up in sink, without this being apparent to the pursuing pilot. This method of flattening a glide is well known to glider pilots, but can be applied by birds in patches of lift which are far too small for a glider to benefit from. Certainly the East African vultures are adept at exploiting such effects, and Raspet's technique could not be applied to them except in very calm air (in which they do not fly) for this reason.

In a later analysis of his results Raspet (1960) compared performance curves for *Coragyps* flying straight as opposed to circling, and concluded that the induced drag was reduced in the circling configuration (wing-tip slots open), relative to that seen in fast, straight flight with the slots closed. Because Raspet's technique involved flying at the same speed as the bird, no observations could be made at speeds less than the glider's

Minimum speed. The absence of observations at the lower end of the bird's speed range was therefore even more pronounced than in the present experiments, and this limitation makes the accurate estimation of induced drag impracticable for the reasons explained above (p. 23). Secondly, the glide comparison method cannot be applied in circling flight because bird and glider inevitably circle at different radii, and therefore in different (often very different) upward air velocities. Even apart from this, the rates of sink in circling flight could not be directly compared unless the speeds and angles of bank of both the glider and the bird were accurately known, an impossible condition to meet in practice.

These criticisms should not be taken to imply that Raspet's interpretation of the function of the wing-tip slots is necessarily wrong. It has been argued by Cone (1962*c*) that such an effect is theoretically possible, and the question must be regarded as still open pending further experimental evidence.

LIST OF SYMBOLS

$A$	Aspect ratio.
$B$	Wing span.
$b$	Wing span of image of bird on negative.
$C_{D0}$	Drag coefficient at zero lift.
$C_L$	Lift coefficient.
$f$	Focal length of camera lens.
$g$	Acceleration due to gravity.
$H$	Height of bird above glider.
$h$	Height of image of bird above horizon on negative.
$k$	Span efficiency factor.
$L$	Lift force on bird's wing.
$R$	Range from glider to bird.
$r$	Radius of turn.
$S$	Wing area.
$s_\beta, s_\gamma$	Standard deviations of regression constants $\beta$ and $\gamma$ .
$U_r$	Radial air velocity in a thermal.
$U_t$	Tangential air velocity in a thermal.
$V$	Equivalent air speed.
$V_b$	Bird's equivalent air speed.
$V_c$	Equivalent air speed in a turn.
$V_g$	Glider's equivalent air speed.
$V_{tg}$	Glider's true air speed.
$V_v$	Difference of true vertical speed between glider and bird.
$V_x$	Difference of true horizontal speed between glider and bird.
$V_s$	Equivalent sinking speed.
$V_{sc}$	Equivalent sinking speed in a turn.
$\beta$	Coefficient of $1/V$ in glide polar regression.
$\gamma$	Coefficient of $V^3$ in glide polar regression.
$\phi$	Angle of bank.
$\rho$	Air density.
$\rho_0$	Air density at sea level in standard atmosphere.

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#### SUMMARY

1. Glide-comparison measurements were made on ten species of East African soaring birds using a Schleicher ASK-14 powered sailplane. Horizontal and vertical speed differences between bird and glider were measured by a photographic method, and used to estimate the bird's horizontal and vertical speeds relative to the air. The analysis refers to the white-backed vulture, since by far the largest number of measurements was obtained on this species.

2. A regression analysis using a two-term approximation to the glide polar yielded an implausibly high estimate of induced drag, which was attributed to a lack of observations at lift coefficients above 0.72. An amended glide polar was constructed assuming elliptical lift distribution and a maximum lift coefficient of 1.6 to define the low-speed end, while the high-speed end was made to pass through the mean horizontal and sinking speeds of all the experimental points. This curve gave a minimum sinking speed of 0.76 m/s at a forward speed of 10 m/s, and a best glide ratio of 15.3:1 at 13 m/s. It did not differ significantly (in the statistical sense) from the original regression curve.



3. In comparing the estimated circling performance, based on the amended glide polar, with that of the ASK-14, it was concluded that the rates of sink of both should be comparable, but that the glider would require thermals with radii about 4.3 times as great as those needed to sustain the birds. The conclusions are consistent with experience of soaring in company with birds.

4. In an attempt to assess the adaptive significance of the low-aspect-ratio wings of birds specializing in thermal soaring, the white-backed vulture's circling performance was compared with that of an 'albatross-shaped vulture', an imaginary creature having the same mass as a white-backed vulture, combined with the body proportions of a wandering albatross. It appears that the real white-back would be at an advantage when trying to remain airborne in thermals with radii between 14 and 17 m, but that the albatross-shaped vulture would climb faster in all wider thermals; on account of its much better maximum glide ratio, it should also achieve higher cross-country speeds. It is concluded that the wing shape seen in vultures and storks is not an adaptation to thermal soaring as such, but is more probably a compromise dictated by take-off and landing requirements.

5. The doubts recently expressed by Tucker & Parrott (1970) about the results and conclusions of Raspet (1950*a, b*; 1960) are re-inforced by the present experience.

*Note added in proof*

Parrott (1970) has recently estimated the maximum lift coefficient of *Coragyps atratus* to be 1.1. If this unexpectedly low value were to apply to the white-backed vulture, the effect would be to increase all the above estimates of circling radii by a factor of 1.45.

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