

## AERODYNAMICS OF GLIDING FLIGHT OF A BLACK VULTURE *CORAGYPS ATRATUS*

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### INTRODUCTION

Although aerodynamicists have used wind tunnels for over half a century, biologists have only recently studied the aerodynamics and physiology of live birds flying in tunnels (see Tucker & Parrott, 1970; Pennycuick, 1968; Greenewalt, 1960, for aerodynamic work; and Tucker, 1968, 1966; Eliassen, 1963, for physiological studies). The wind tunnel provides a controlled aerial environment that allows one to obtain aerodynamic data of known accuracy. In addition, the aerodynamic and gravitational forces of gliding can be simulated in a tunnel without the movement of a bird relative to an observer. Under these conditions measurement of glide angle (angle between horizontal and a bird's glide path relative to air) is facilitated and a gliding bird can be studied over a selected range of air speeds and glide angles.

Prior to wind tunnel studies on live birds, aerodynamic data for gliding birds were obtained either from wind tunnel tests on frozen, stuffed or model birds (see e.g. Naylor & Simmons, 1921; Feldmann, 1944), or from field studies on naturally gliding birds (see e.g. Raspet, 1950; Pennycuick, 1960). Models may not simulate the surface features of a live bird and cannot assume the various configurations of a flying bird. Measurement of a bird's glide angle under natural conditions is difficult because an observer on the ground must know both the motion of the bird relative to the ground and the motion of the air relative to ground to determine glide angle.

I have circumvented these difficulties by training a black vulture to fly freely in the working section of a wind tunnel. The black vulture is a common cathartid of the south-eastern United States, where it can often be seen soaring for many minutes on motionless wings.

### METHODS AND MATERIALS

#### *Calculations and definitions*

This paper is concerned with the aerodynamics of equilibrium gliding, i.e. non-flapping flight without acceleration. In practice this meant that the vulture was moving less than 0.01 m/s relative to the wind tunnel. In equilibrium gliding the lift ( $L$ ) and drag ( $D$ ) forces, which are respectively perpendicular and parallel to the glide path, are balanced by components of the weight of the aircraft (see Jones, 1950, for a discussion of gliding flight). The following relations were used in this study

$$D_T = W \sin \theta, \quad (1)$$

$$L = W \cos \theta, \quad (2)$$

$$L/D = \cot \theta, \quad (3)$$

where  $W$  is the weight,  $D_T$  is total drag and  $\theta$  is the glide angle. All units are in the mks system. For angles less than  $8^\circ$ ,  $\cos \theta$  is within 1% of unity so  $W$  approximates to  $L$ .

For equilibrium gliding in still air  $L/D$  corresponds to the ratio of horizontal distance travelled to altitude lost per unit time. Sinking speed is related to glide angle and air speed by the equation

$$\text{sinking speed} = V \sin \theta, \quad (4)$$

where  $V$  is air speed. For angles less than  $10^\circ$ ,  $\sin \theta$  is nearly equal to  $\tan \theta$  so that

$$\text{sinking speed} = \frac{V}{L/D}. \quad (5)$$

Lift coefficients ( $C_L$ ) were calculated from the standard equation

$$C_L = \frac{L}{\frac{1}{2}\rho S V^2}, \quad (6)$$

where  $\rho$  is air density ( $1.17 \text{ kg/m}^3$  in this study) and  $S$  is wing area, defined as the plane projected area of both wings, including the area intercepted by the body. Intercepted area is that part of the body bounded by lines joining the points where the leading and trailing edges of the wings contact the body. I determined wing areas from enlarged photographs with a planimeter. Right and left areas were measured separately and added to intercepted area to obtain total wing area. A scale factor was determined by measuring the width of a wing's base on each picture. I estimate that wing areas are accurate to 5%.

The total drag of an aircraft is composed of induced drag and parasite drag. Induced drag ( $D_i$ ) was calculated from the equation

$$D_i = \frac{L^2}{\pi \frac{1}{2}\rho (bVM)^2}, \quad (7)$$

where  $b$  is wing span (tip to tip distance) and  $M^2$  is the Munk span factor. For an elliptical distribution of lift across the span, the induced drag is a minimum and  $M^2$  is 1. For non-elliptical distributions the span factor is less than 1. Most wings have a  $M^2$  between 0.9 and 0.95 (von Mises, 1959) and I used a value of 0.9 in this study.

Parasite drag ( $D_p$ ), which is caused by skin friction and pressure drag, is the part of total drag that is not associated with lift production. I obtained parasite drag by subtracting the calculated induced drag from the measured total drag. Parasite drag coefficients ( $C_{Dp}$ ) were calculated from the equation

$$C_{Dp} = \frac{D_p}{\frac{1}{2}\rho S_w V^2}, \quad (8)$$

where  $S_w$  is wetted area (total surface area of an aircraft).

I calculated body area by assuming that the vulture consisted of a cylinder (head and neck), a frustrum (thoracic region) and a cone (abdomen). Projected wing area was multiplied by 2.05 (this factor accounted for upper and lower surfaces and curvature of the wings) to obtain wetted wing area. Total wetted area was then calculated by adding wetted wing area to body and tail area and subtracting twice the intercepted area. Body area is probably accurate to only 20%, but because body area is about 10% of the total wetted area the latter is accurate to better than 10%.

Values of Reynolds number (Re) were calculated from the formula

$$\text{Re} = \frac{cV\rho}{\mu}, \quad (9)$$

where  $\mu$  is the dynamic viscosity of air and  $c$  is the chord of the wings. For a non-rectangular wing the chord varies along the span and thus the average chord ( $S/b$ ) was used to calculate Re. The value of  $\rho/\mu$  for this study was  $6.38 \times 10^4$ . Re varied from  $1.5 \times 10^5$  to  $2.6 \times 10^5$  over the range of air speeds encountered.

#### *Wind tunnel and calibration*

The wind tunnel used for this study was of the open circuit, closed jet design and could be tilted from  $0^\circ$  to  $7\frac{1}{2}^\circ$  down from horizontal about a central pivot. The working section was 1.1 m high by 1.4 m wide by 2.3 m long and had a wire screen (0.013 m mesh) at the rear to prevent the bird from drifting close to the fan. The front of the working section opened without screen or obstruction into the entrance cone. A variable speed motor provided air speeds up to 16.8 m/s.

I calibrated the working section for air speed distribution, direction of air flow and turbulence (see Tucker & Parrott, 1970, for a description of the calibration techniques).

Air speed, determined in the region where the bird usually flew, varied  $\pm 5\%$  from the mean.

Direction of air flow varied about  $1^\circ$  across the working section. The direction of air flow with respect to the working section was independent of tunnel tilt and air speed. Mean angles, accurate to  $\frac{1}{2}^\circ$ , were used for calculations. Variation in direction of air flow resulted in drag measurements accurate to 11%.

Mean % turbulence was 0.4%, which corresponds to a turbulence factor of approximately 1.3 (Pope & Harper, 1966).

#### *Experimental animal and training procedure*

The black vulture was purchased from an animal dealer and its weight during the study was  $17.5 \text{ newtons} \pm 2\%$  (mass = 1.79 kg,  $g = 9.8 \text{ m/s}^2$ ). The wing span to tunnel width ratio was 0.97 at maximum  $L/D$ .

A perch that could be raised and lowered (when lowered, the perch did not interfere with air flow) was mounted in the front of the working section. A capacitance-discharge shocking device was employed to give the bird mild shocks. A wire ( $1.5 \times 10^{-3}$  m in diameter and 2.2 m long) was attached to each leg and a shock could be given whenever necessary. These wires also prevented the bird from entering the entrance cone.

The training procedure consisted of reward and punishment. Initially, the bird was placed on the perch and given a shock if it jumped from the perch to the tunnel floor. After a few shocks the bird learned to stay on the perch and rarely jumped to the floor. At this stage of the training I turned on the motor and lowered the perch. If the bird remained in the air for a few seconds no shock was given and the perch was raised. The bird was then rewarded by being allowed to sit on the perch for 15–30 s before the next flight. If the bird landed, instead of remaining in the air, a shock was given and the bird was placed back on the perch. By giving shocks whenever the bird landed and by gradually lengthening the time that the perch was lowered, the vulture

was trained to glide for up to 30 min at a time. The entire training procedure took about 4 weeks with sessions at least every other day.

I was able to train the vulture to glide in the desired part of the working section by giving mild correctional shocks whenever the bird drifted back into the screen or bumped into the ceiling or side walls. Characteristically, the bird would drift back when the perch was lowered and then glide to the front portion of the section. After remaining nearly motionless there for 10–30 s, the vulture would slowly drift back about 1 m and then glide forward again.

At air speeds less than 13.9 m/s and glide angles greater than 6°, the vulture usually held its feet down perpendicular to the air flow. The feet were progressively retracted with increasing air speed and/or decreasing angle.

### *Experimental procedure*

I photographed the vulture when it was in the region where the calibrations had been made and when neither of its wing tips was touching the side walls. Photographs were taken from above the working section through the Plexiglass ceiling with a motor-driven 35 mm camera that tilted with the tunnel. An electronic flash illuminated the bird from above.

Glide angle and air speed were systematically varied, and about six pictures were obtained for each combination of speed and angle. The normal procedure was as follows. The bird was flown for a few minutes until its flight pattern was consistent (the vulture usually flapped vigorously and was erratic at the beginning of each session). Then the tunnel was tilted down to  $7\frac{1}{2}^\circ$  and the tunnel speed set. After pictures were taken, the tunnel was tilted back  $\frac{3}{4}^\circ$  and the bird was photographed at the new angle. This procedure was continued until an angle (minimum glide angle,  $\theta_{gr}$ ) was found below which the bird would no longer maintain its position without flapping. I then tilted the tunnel to  $7\frac{1}{2}^\circ$  again and selected a higher speed.

Photographs were obtained over a range of air speeds and glide angles from 9.9 to 16.8 m/s and from  $4.8^\circ$  to  $7.9^\circ$ , respectively. Below 9.9 m/s the vulture would not remain airborne without flapping.

### *Corrections: drag due to wires*

The drag of the training wires was measured and found to be about 10% of the total drag of the bird at maximum  $L/D$  (the wires were twisted together except for the last 0.15 m.). Drag was measured by attaching a fine thread to the wires and running the thread over a pulley mounted in the region where the bird flew. The thread passed through a hole in the floor of the working section and was tied to a weight (mass =  $m$ ) on a top-loading Mettler balance. Tension ( $T$ ) in the wires was determined by the equation

$$T = g(m - R), \quad (10)$$

where  $R$  is the balance reading (in kg) at various air speeds. At each air speed I used a protractor to measure the angle ( $\phi$ ) between the direction of air flow and the wires (tunnel tilt was  $6^\circ$ ). Drag of the wires, equal to  $T \cos \phi$ , was subtracted from the total drag of the vulture. Corrections ranged from 0.14 N at the lowest speed to 0.19 N at the highest.

*Corrections: tunnel interference effects*

Wind tunnel boundaries cause the flow pattern around an object in a tunnel to differ from the pattern in free air and measurements may have to be corrected for this boundary interference (Pope & Harper, 1966).

The wake and solid blockage correction for lift and drag, horizontal buoyancy correction for drag and streamline curvature correction for lift were each about 1% or less and I did not correct data for these effects.

The downwash correction to drag was 29% at the lowest speed and diminished to 8% at the highest speed. Drag values were corrected according to the equation

$$D = D_M + \frac{\rho(SC_L V)^2}{16C}, \quad (11)$$

where  $D_M$  is the measured drag and  $C$  is the cross-sectional area of the working section ( $1.5 \text{ m}^2$ ).

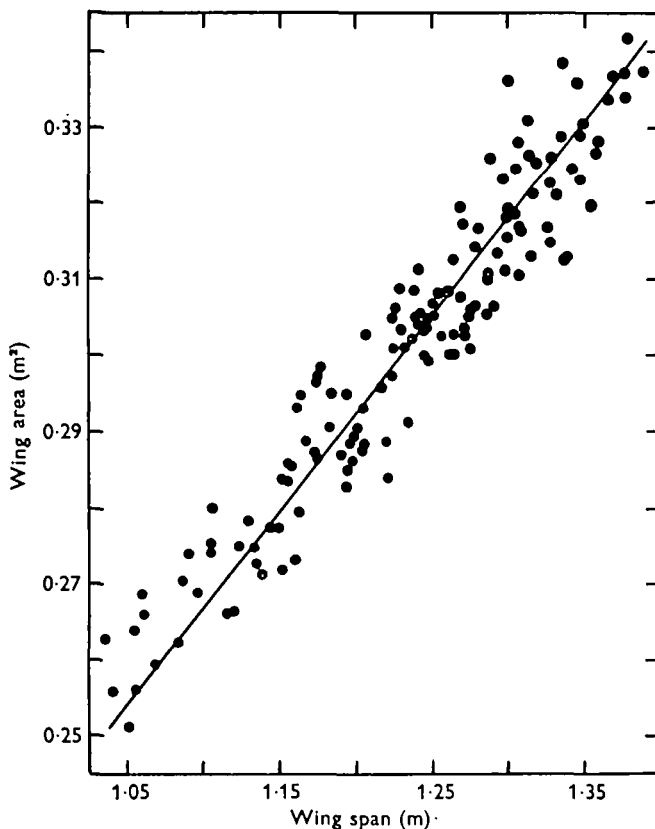


Fig. 1. Wing area of the vulture at different wing spans. The equation for the linear least-squares regression line is  $S = 0.255b - 0.013$  ( $N = 142$ , standard error of estimate is  $0.0062$ ).

## RESULTS

Wing span and wing area were linearly related (Fig. 1). Air speed and glide angle influenced wing area (Fig. 2). The variation of wing area with air speed depended on glide angle. At a given air speed wing area decreased as glide angle increased.

Lift coefficients calculated for the vulture ranged from 0.3 to 1.1. At a particular air speed,  $C_L$  was largest for a glide angle of  $7.9^\circ$  (Fig. 3). Maximum  $C_L$  for the vulture is smaller than that calculated for the falcon (Tucker & Parrott, 1970) and for the pigeon (Pennycuik, 1968), which have maximum  $C_L$ 's of 1.6 and 1.3, respectively. Raspet (1950) calculated a maximum  $C_L$  of 1.57 for the black vulture.

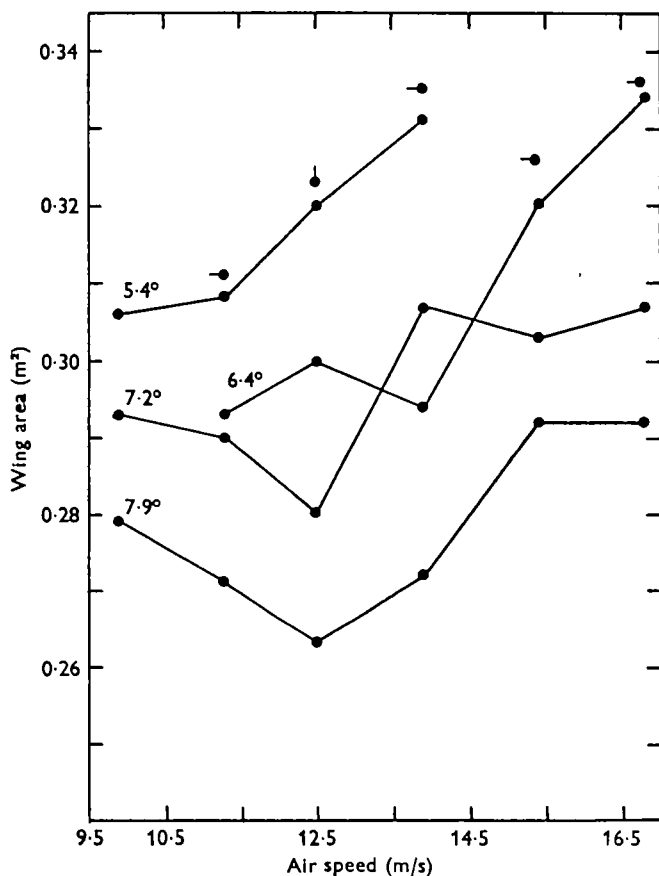


Fig. 2. Mean wing area of the vulture at various air speeds and glide angles. Wing area at minimum glide angles (except at 9.9 m/s) is given by the following symbols: (●), wing area extrapolated from curve below point; (◐), wing area measured. The minimum glide angles at which these areas were observed are given in Fig. 4. Mean sample size for each point (except ●) is 6. Mean standard deviation is 0.008.

Table 1. *Summary of basic data for the vulture at minimum glide angles*

Air speed (m/s)	Wing area (m <sup>2</sup> )	Wing span (m)	Wetted area* (m <sup>2</sup> )	Total drag (N)
9.9	0.306	1.25	0.71	1.94
11.3	0.311	1.27	0.72	1.68
12.5	0.323	1.32	0.74	1.61
13.9	0.335	1.37	0.77	1.51
15.4	0.326	1.33	0.75	1.65
16.8	0.336	1.37	0.77	1.79

\* Wetted area ( $S_w$ ) was calculated by adding wetted wing area ( $2.05S$ ) to wetted tail and body areas (0.050 m<sup>2</sup> and 0.087 m<sup>2</sup>, respectively) and subtracting twice the intercepted area (0.055 m<sup>2</sup>).

Minimum glide angle for the vulture was about  $4.9^\circ$  from 11 to 14 m/s. At air speeds lower and higher than this range,  $\theta_M$  increased (Fig. 4). Basic data at  $\theta_M$  are summarized in Table 1.

The vulture's sinking speed varied with air speed (Fig. 5).  $L/D$  for an aircraft in Fig. 5 can be found at any air speed by use of equation (5). The vulture had a maximum  $L/D$  of 11.6 at 13.9 m/s.

Parasite drag coefficients for the vulture at different  $Re$  ranged from 0.0113 to 0.0179 (Fig. 6).  $K$  values (as used in Tucker & Parrott, 1970) ranged from 1.9 to 2.8.

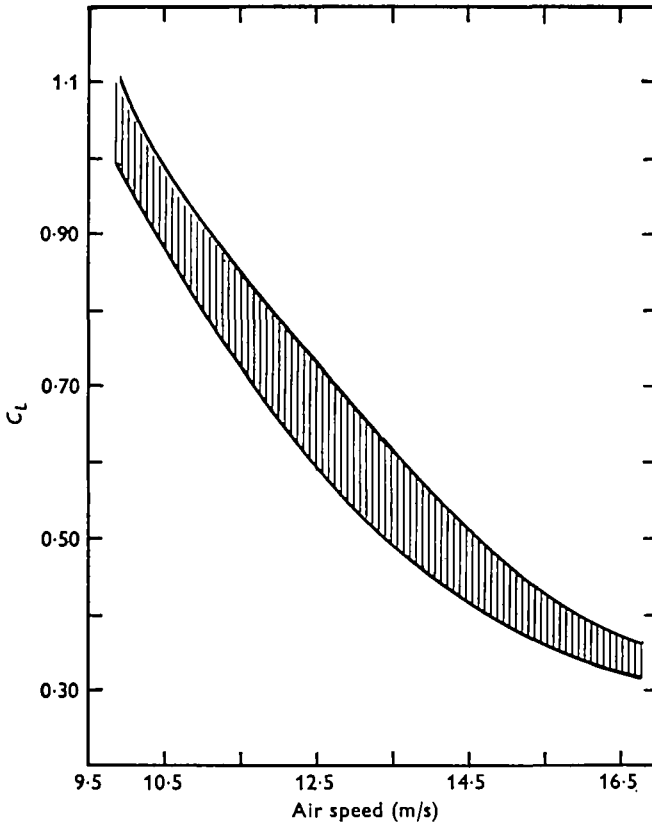


Fig. 3. Lift coefficients for the vulture at various air speeds. At a given air speed, lift coefficient was largest at  $7.9^\circ$  (upper boundary of hatched area), smallest at minimum glide angle (lower boundary) and intermediate at angles between  $7.9^\circ$  and minimum.

## DISCUSSION

### *Comparison of wind tunnel data with Raspet's data*

Raspet (1950) studied the gliding performance of black vultures in free air. He followed vultures with a sailplane and recorded their position and air speed relative to the plane. From this information he calculated the difference in sinking speed between the bird and plane. The plane's sinking speed at various air speeds in still air was known and thus the vulture's sinking speed at different air speeds could be computed.

Raspet reported maximum  $L/D$ 's of 23 and 21, respectively, for soaring and gliding vultures. The former had fully extended wings and were gaining altitude while circling. The latter had flexed wings and were descending along a fairly straight path. The vulture I studied in the tunnel had a continuously variable wing shape rather than the dichotomy described by Raspet.

Why is the maximum  $L/D$  (11.6) of the vulture in the wind tunnel so inferior to the values Raspet computed for vultures in free air? An analysis of parasite drag reveals

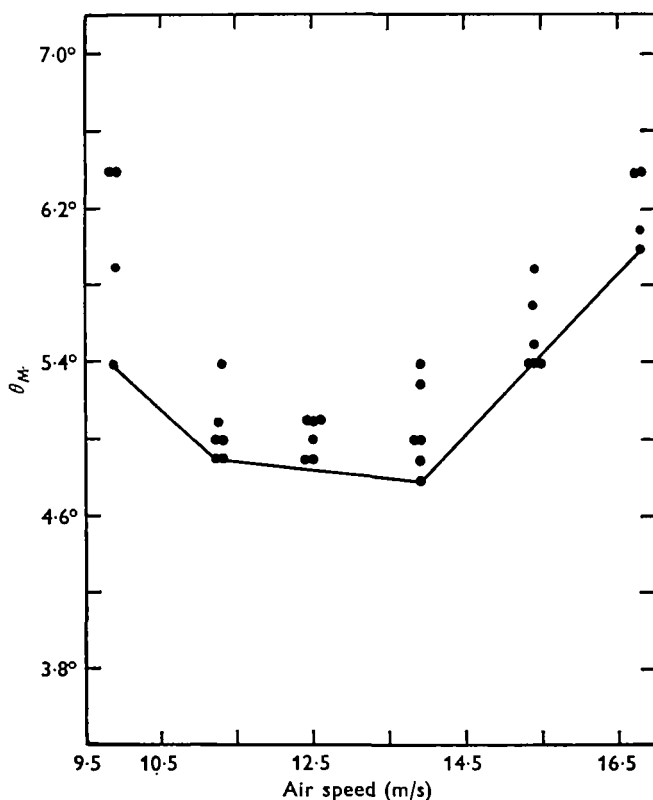


Fig. 4. Minimum glide angle ( $\theta_M$ ) of the vulture at different air speeds. The curve is drawn through the smallest angle observed at each air speed.

that Raspet's vultures, at most values of  $Re$ , apparently have a  $C_{Dp}$  less than, or similar to, that for a flat plate (parallel to air flow) at the same  $Re$  with a laminar boundary layer. The coefficients for such a plate are, however, at a theoretical minimum and this leads one to conclude that the vulture's maximum  $L/D$  is almost certainly not as large as that determined by the sailplane technique.

Parasite drag coefficients for the vulture, based on both Raspet's data and mine, are shown in Fig. 6 as a function of  $Re$ . On the same figure are shown the drag coefficients of a flat plate parallel to the air flow with a laminar boundary layer in one case and a turbulent one in the other. The values of  $C_{Dp}$  (usually called  $C_f$  for a flat plate) for the plate with laminar flow are, as mentioned previously, theoretically at a minimum (Goldstein, 1965).



Raspet (1960) presented 'average skin friction coefficients' for the vulture, none of which was below the line for a laminar plate, but he did not describe the method used to calculate the coefficients. The curves in Fig. 6 for soaring and gliding vultures were computed from Raspet's values for  $L/D$ ,  $b$  (1.44 m),  $W$  (22.5 N) and  $S_w$  (1.06 m<sup>2</sup>), using equations (7) and (8) and a  $M^2$  of 0.9. In gliding flight the vulture's minimum  $C_{Dp}$  is 17% above the line for a flat plate with a laminar boundary layer, while in soaring flight the minimum  $C_{Dp}$  is 19% below the same line.

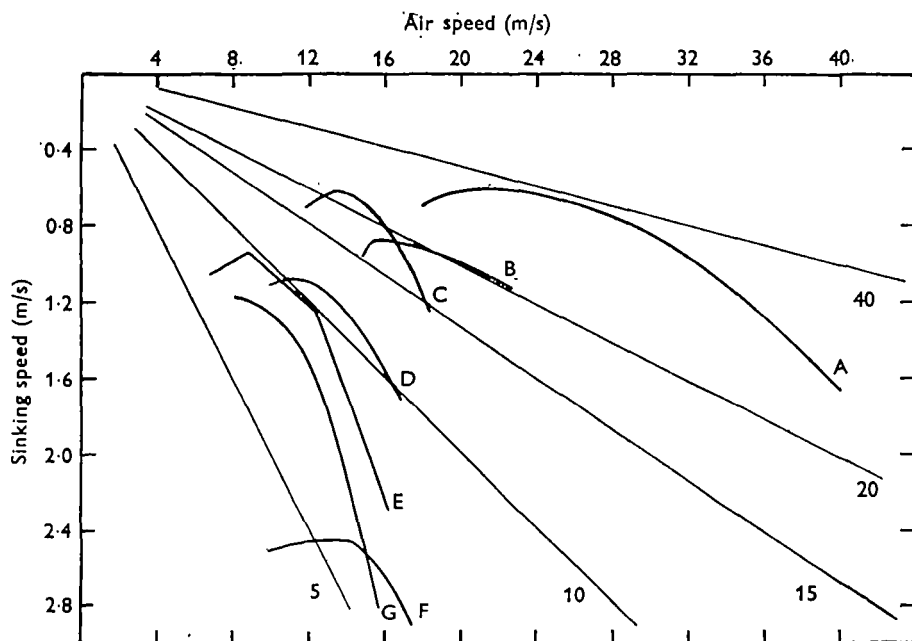


Fig. 5. Sinking speeds at various air speeds for the vulture, several other birds and a sailplane. The aircraft in the figure are at minimum glide angles and are represented by the following letters: (A) SHK sailplane (see Tucker & Parrott, 1970, for dimensions of plane); (B) gliding vulture, *Coragyps atratus* (Raspet, 1950); (C) soaring vulture, *C. atratus* (Raspet, 1950); (D) vulture, *C. atratus* (present paper); (E) falcon, *Falco jugger* (Tucker & Parrott, 1970); (F) pigeon, *Columba livia* (Pennycuick, 1968); (G) fulmar, *Fulmaris glacialis* (Pennycuick, 1960). All points falling on the diagonal lines have the  $L/D$  value indicated at the end of each line.

The curve calculated from tunnel data, by comparison, lies above the line for a turbulent flat plate and minimum  $C_{Dp}$  (which was reached at the same air speed as maximum  $L/D$ ) for the vulture is 1.9 times as large as the  $C_{Dp}$  for a turbulent plate at the same Re. Furthermore, bird-like airfoils with Re's around  $3.75 \times 10^5$  have parasite drag coefficients that are 1.6 to 5.7 times as large as  $C_{Dp}$  for the turbulent flat plate at the same Re (see Tucker & Parrott, 1970, for airfoil data).

Tucker & Parrott (1970) stated that Raspet's high  $L/D$  values were probably the result of the vultures' using some form of atmospheric energy (such as vertical currents of air or changes in the velocity of air) which the larger sailplane could not utilize. They did not, however, analyse several other possible errors that could explain the discrepancy between Raspet's data and mine: the effect of circling on sinking speed, tunnel interference effects and boundary layer transition effects.

The sinking speed of an aircraft in a turn is proportional to  $\secant(\beta)^{1.5}$  (Cone, 1964). Angle of bank ( $\beta$ ) is the angle between a line perpendicular to the mean wing plane and the vertical direction (von Mises, 1959). Raspet's data for soaring vultures were obtained when the bird and the plane were circling together and the fact that he did not correct data for the increase in sinking speed during a turn could account

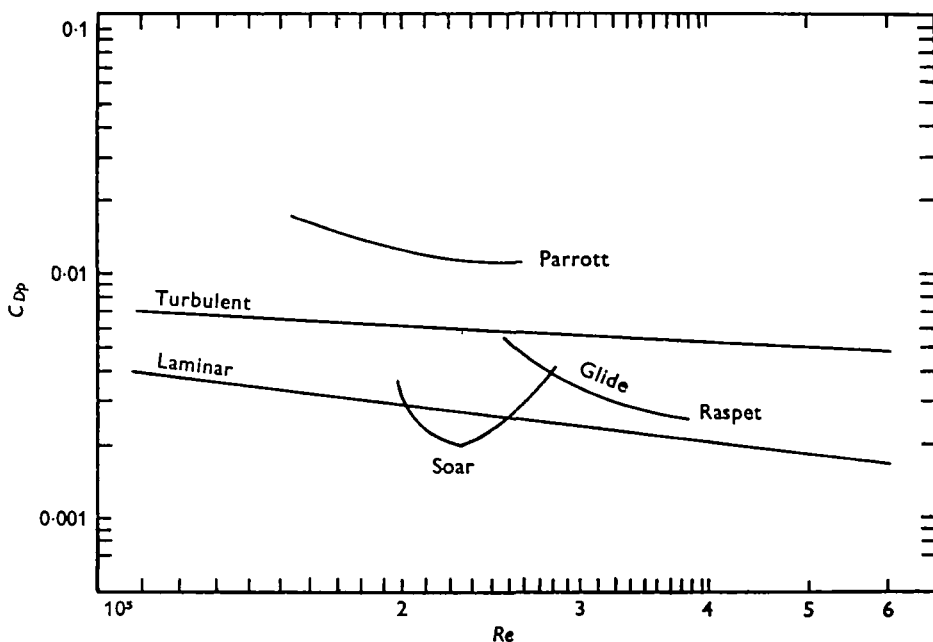


Fig. 6. Parasite drag coefficients for the vulture at various  $Re$ , based on both Raspet's data for soaring and gliding vultures and on Parrott's wind-tunnel data. The upper line for the flat plate parallel to airflow with a turbulent boundary layer is drawn from Prandtl's equation. The lower line for the laminar parallel plate is drawn from the Blasius equation (see Tucker & Parrott, 1970, for these equations).

for the larger  $L/D$  he reported for soaring vultures. If  $C_L$ , total drag coefficient and wing loading ( $W/S$ ) are the same as for level flight, then in a turn requiring a  $\beta$  of  $30^\circ$  (Raspet stated that the angle was usually less than  $30^\circ$ ), the sinking speed of the plane and bird would be increased by about 25%. The difference in sinking speed between bird and plane would be 25% larger during a turn and the sinking speed calculated for the vulture would be 25% too small. This error does not, however, resolve the difference between my data and Raspet's data for vultures gliding in a straight path.

Tunnel interference effects in this study do not seem large enough to explain the disparity between tunnel and sailplane data. Only downwash was significant and this effect caused the vulture's apparent drag in the wind tunnel to be smaller than the actual drag. Neglecting downwash corrections entirely results in a maximum  $L/D$  of 13.6, a figure considerably lower than either of Raspet's.

Transition of air flow from laminar to turbulent could explain the discrepancy if the air flow over the vulture's wings in the tunnel had not undergone transition, while that over the wings of naturally flying vultures had. Schmitz (1952) worked at lower  $Re$ 's (approximate range:  $0.2 \times 10^5$  to  $1.68 \times 10^5$ ) than most aerodynamicists and showed

that transition can double the  $L/D$  of an airfoil. This effect probably does not account for the disparity, however, since the vulture's  $Re$ , the tunnel turbulence factor and the  $Re$  (around  $7 \times 10^4$ ) at which Schmitz observed a doubling of  $L/D$  for conventional airfoils all indicate that the wings of the vulture in the tunnel had a turbulent boundary layer.

Raspet concluded on the basis of low drag coefficients for the vulture that some form of boundary layer control must operate to keep the air flow over the wings laminar and the drag low. But Tucker & Parrott (1970) pointed out that, at a given  $C_L$ , the vulture would probably have a lower  $C_{Dp}$  with a turbulent boundary layer than with a laminar one over the wings. Furthermore, Schmitz's data and the vulture's  $Re$  again indicate that the wings of vultures in free air also have turbulent boundary layers.

The wind-tunnel data I have presented, coupled with values of  $C_{Dp}$  for conventional airfoils, strongly suggest that Raspet's low drag coefficients and high values of  $L/D$  are explained by the vultures' using atmospheric energy which the plane did not, rather than by control of the boundary layer.

### *Gliding performance*

Maximum  $L/D$  for the black vulture is the largest for birds thus far tested in wind tunnels. The falcon has a slightly smaller maximum  $L/D$  of 10, while that for the pigeon is only 6 (see Fig. 5). The  $L/D$  values for these birds are small compared to the maximum  $L/D$  of 38 for the sailplane in the same figure.

Although the falcon does not achieve an  $L/D$  as large as the vulture's, it nevertheless has a lower minimum sinking speed. This is possible because sinking speed is a function of  $V$  and  $L/D$  (see equation 5) and the falcon's lower air speed more than compensates for its smaller  $L/D$ .

The vulture's air speed under natural conditions may be influenced by two possible objectives of an avian glider: covering distance over the ground toward a site and gaining altitude without flapping. In the wind tunnel the vulture achieves its minimum sinking speed at an air speed (11.3 m/s) less than that for maximum  $L/D$  (13.9 m/s). Tucker & Parrott (1970) analysed the significance of  $L/D$ ,  $V$  and time to maximizing the distance travelled or altitude gained by a naturally gliding aircraft under various aerial conditions. According to their analysis the vulture should glide at maximum  $L/D$  in still air to cover the greatest distance over the ground (from a given altitude). However, with a tail wind, the distance travelled would be maximized by gliding at minimum sinking speed. Furthermore, in an updraft greater than the vulture's sinking speed, the greatest altitude would be gained by gliding at minimum sinking speed and remaining in the updraft as long as possible.

### *Wing geometry*

Data for the pigeon, falcon and vulture (present paper) show that wing area and wing span are linearly related at all air speeds and glide angles investigated.

At a given air speed the wing area of the falcon and vulture decreases as  $\theta$  increases. At  $\theta_M$  wing area of the pigeon and falcon decreases with increasing air speed. Wing area for the vulture, however, increases slightly at  $\theta_M$  as air speed increases.

## SUMMARY

1. A black vulture (mass = 1.79 kg) gliding freely in a wind tunnel adjusted its wing span and wing area as its air speed and glide angle changed from 9.9 to 16.8 m/s and from 4.8° to 7.9°, respectively.
2. The minimum sinking speed was 1.09 m/s at an air speed of 11.3 m/s.
3. The maximum ratio of lift to drag forces was 11.6 at an air speed of 13.9 m/s.
4. Parasite drag coefficients for the vulture are similar to those for conventional airfoils and do not support the contention that black vultures have unusually low values of parasite drag.

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## REFERENCES

- CONE, C. D. (1964). The design of sailplanes for optimum thermal soaring performance. *NASA TN D-2052*.
- ELIASSEN, E. (1963). Preliminary results from new methods of investigating physiology of birds during flight. *Ibis* **105**, 234-7.
- FELDMANN, I. F. (1944). Windkanaluntersuchung am Modell einer Möwe. *Aero revue, Zurich* **19**, 219-22.
- GOLDSTEIN, S. (1965). *Modern Developments in Fluid Dynamics*. New York: Dover Publ.
- GREENEWALT, C. H. (1960). *Hummingbirds*. New York: Doubleday.
- JONES, B. (1950). *Elements of Practical Aerodynamics*. New York: Wiley and Sons.
- MISES, R. VON. (1959). *Theory of Flight*. New York: Dover Publ.
- NAYLER, J. L. & SIMMONS, L. F. G. (1921). A note relating to experiments in a wind channel with an Alsatian swift. *Aeron. Res. Comm. Reports and Memoranda*, No. 708.
- PENNYCUICK, C. J. (1960). Gliding flight of the fulmar petrel. *J. exp. Biol.* **37**, 330-8.
- PENNYCUICK, C. J. (1968). A wind-tunnel study of gliding flight in the pigeon *Columba livia*. *J. exp. Biol.* **49**, 509-26.
- POPE, A. & HARPER, J. J. (1966). *Low-speed Wind Tunnel Testing*. New York: Wiley and Sons.
- RASPET, A. (1950). Performance measurements of a soaring bird. *Aeron. Engin. Rev.* **9**, 14-17.
- RASPET, A. (1960). Biophysics of bird flight. *Science* **132**, 191-200.
- SCHMITZ, F. W. (1952). *Aerodynamik des Flugmodells*. Duisburg: Carl Lange Verlag.
- TUCKER, V. A. (1966). Oxygen consumption of a flying bird. *Science* **154**, 150-1.
- TUCKER, V. A. (1968). Respiratory exchange and evaporative water loss in the flying budgerigar. *J. exp. Biol.* **48**, 67-87.
- TUCKER, V. A. & PARROTT, G. C. (1970). Aerodynamics of gliding flight in a falcon and other birds. *J. exp. Biol.* (In Press.)