

EMPIRICAL ESTIMATES OF BODY DRAG OF LARGE WATERFOWL AND RAPTORS

By C. J. PENNYCUICK

Department of Biology, University of Miami, PO Box 249118, Coral Gables, FL 33124, USA

HOLLIDAY H. OBRECHT III AND MARK R. FULLER*

United States Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, MD 20708, USA

Accepted 7 October 1987

SUMMARY

Measurements of the body frontal area of some large living waterfowl (Anatidae) and raptors (Falconiformes) were found to vary with the two-thirds power of the body mass, with no distinction between the two groups. Wind tunnel measurements on frozen bodies gave drag coefficients ranging from 0.25 to 0.39, in the Reynolds number range 145 000 to 462 000. Combining these observations with those of Prior (1984), which extended to lower Reynolds numbers, a practical rule is proposed for choosing a value of the body drag coefficient for use in performance estimates.

INTRODUCTION

Numerical estimates of bird flight performance are usually based on calculating the mechanical power required to fly, as a function of speed. Following the classical 'synthetic' approach of aeronautical engineering, an estimate of the total power can be built up by adding several components, each representing the power consumed for a different purpose. This paper extends the empirical basis for estimating one of these components, the 'parasite power', so named by aeronautical engineers because it represents the power required to overcome the drag of all those parts of an aircraft that do not contribute to supporting the weight. In the case of a bird in steady cruising flight, the parasite power is the power required to overcome the drag of the body, excluding the wings. The parasite power (P_{par}) depends on the speed (V) thus:

$$P_{\text{par}} = \rho AV^3/2, \quad (1)$$

where ρ is the air density. At a given speed and air density, the parasite power is determined by the 'equivalent flat-plate area' of the body (A). A is the area of a theoretical circular flat plate, transverse to the air stream, that would have the same

* To whom reprint requests should be addressed.

drag as the body. It is a composite quantity, made up by multiplying S_b , the actual frontal area of the body (i.e. its cross-sectional area at the widest point), by C_D , its drag coefficient:

$$A = S_b C_D . \quad (2)$$

The drag coefficient is a dimensionless number, less than 1, representing the degree of streamlining of the body. A well-streamlined body has a low drag coefficient, meaning that the drag is low in relation to the frontal area.

In some earlier discussions of power requirements for flight, such as that of Pennycuick (1975), parasite power was discussed in terms of equivalent flat-plate area, on the assumption that the drag coefficient could be considered the same for different birds. Tucker (1973) presented some drag measurements of bird bodies, also in terms of equivalent flat-plate area, but did not list the frontal areas and drag coefficients separately. In this paper we present measurements on two groups of birds, waterfowl (Anatidae) and raptors (Falconiformes), in which frontal area and drag coefficient are considered as two separate data sets. We present a relationship between frontal area and body mass, and a second relationship between drag coefficient and Reynolds number. When combined, these two relationships supply a basis for estimating the equivalent flat-plate area, and hence the parasite power, for an unknown bird characterized only by its mass and wing span.

Reynolds number as an independent variable

In a pioneering survey, Prior (1984) made body drag measurements on 17 species of waterfowl (Anatidae) of various sizes, ranging from the cinnamon teal (*Anas cyanoptera*) to the mute swan (*Cygnus olor*). In order to investigate the effect of changes of scale on drag, Prior followed aeronautical tradition by plotting the drag coefficient against the Reynolds number (Re), where

$$Re = Vd/\nu , \quad (3)$$

d is the body's 'diameter', defined as the diameter of a circle whose area is the same as the frontal area, and ν is the kinematic viscosity of the air, that is the ratio of its viscosity to its density. In the context of testing small-scale models, engineers use the Reynolds number as a 'similarity criterion', since the pattern of flow around two bodies having the same shape but different size is in general not similar unless the Reynolds number is the same for both. This condition may be met in model experiments by testing the smaller body at a higher speed than the larger one, or by testing it in a fluid of higher density, such as water.

Reynolds number has a different significance in the context of comparisons among related animals of different size, since smaller animals generally fly (or swim) more slowly than larger ones. It is therefore never possible to compare two species differing widely in size at the same Reynolds number, whilst also choosing speeds that both species might use for similar types of locomotion. Reynolds number cannot be used as a similarity criterion in this type of comparison, and some other criterion is needed for making tests under 'similar' conditions. For example, in birds one can

make an estimate for each species of the maximum range speed, as the speed most likely to be used on migratory flights, and make the drag measurements at or around this speed. In this case the Reynolds number at which each species is tested is different and increases in a regular manner with body size.

It follows that, in general, the pattern of flow about each body will also be different, even though the bodies may all be similar in shape. In particular, there is an increasing tendency, as Reynolds number is reduced, for the flow to separate from the surface of the body after passing the widest point, instead of converging smoothly downstream. This creates a 'dead' area of chaotic flow immediately downstream of the body, in which the pressure is less than that impinging on the upstream face of the body, and this longitudinal pressure difference results in drag. Prior (1984) observed this effect directly by inserting smoke filaments into the air stream, and indirectly by measuring higher drag coefficients at lower Reynolds numbers. He observed the effect of Reynolds number on drag coefficient partly by comparing bodies of different size, and partly by testing each body over a range of different speeds.

MATERIALS AND METHODS

Frontal area

We measured captive specimens of six species of ducks, geese and swans at the Wildfowl Trust of North America, and one species of duck and three of raptors kept at the Patuxent Wildlife Research Center, MD. All the measurements were taken on living birds in good health, whose mass was also measured at the same time. A pair of wooden calipers was used to measure the width and depth of the bird's body at the widest point. Enough pressure was applied to the calipers to flatten the feathers, but not to distort the body. To find the frontal area (S_b) from the depth (z) and width (w), we assumed that the body was elliptical in cross-section, in which case:

$$S_b = \pi wz/4 . \quad (4)$$

Preparation of wind tunnel specimens

Six bird bodies (Table 1) were used in our experiments, of which two (mallard and green-winged teal) were fresh specimens shot for the purpose, and the other four had been frozen for varying periods prior to the experiments. The wings were removed

Table 1. *Frontal areas of wind tunnel specimens*

Species	Frontal area (m ²)
<i>Anas crecca</i>	6.18×10^{-3}
<i>Anas platyrhynchos</i>	1.54×10^{-2}
<i>Chen caerulescens</i>	1.88×10^{-2}
<i>Cygnus columbianus</i>	3.51×10^{-2}
<i>Buteo platypterus</i>	7.60×10^{-3}
<i>Haliaeetus leucocephalus</i>	3.09×10^{-2}

from each body by disarticulating the shoulder joints. A 7·9 mm diameter steel rod was inserted transversely through the body in the shoulder region. A thinner (4·8 mm) steel rod was inserted through the cloaca. In the smaller species this passed forward into the neck, but in the larger species the neck was stiffened separately with a length of 6 mm diameter copper tubing. The feet were furled and fixed close under the tail, or under the flank feathers. Each body was supported in its own jig, made of foam polystyrene padding, and frozen in a posture judged to be similar to that adopted by birds in cruising flight.

The feathers were removed from a small area in the middle of each specimen's back, near the centre of gravity, and a piece of Velcro fastening material was glued to the skin. This was for attaching dummy radio-tracking transmitters, to assess their effect on the body drag. These experiments are described in a separate paper (Obrecht, Pennycuick & Fuller, 1988).

Wind tunnel and mounting of specimens

Drag measurements were made in the Glenn L. Martin Wind Tunnel at College Park, MD. This is a closed-circuit, closed-throat wind tunnel with a rectangular working section 3·36 m wide and 2·36 m high. The test specimens were mounted on the drag balance by a three-point support system (Fig. 1). The transverse rod passing through the specimen was supported at a height of 1·16 m above the floor of the tunnel, between two upright supports 0·82 m apart. These upright supports passed through the floor of the tunnel to the drag balance below. They were faired by sheet metal streamlined fairings attached to the floor of the tunnel. The exposed parts of the support rod, between the sides of the body and the upright supports, were

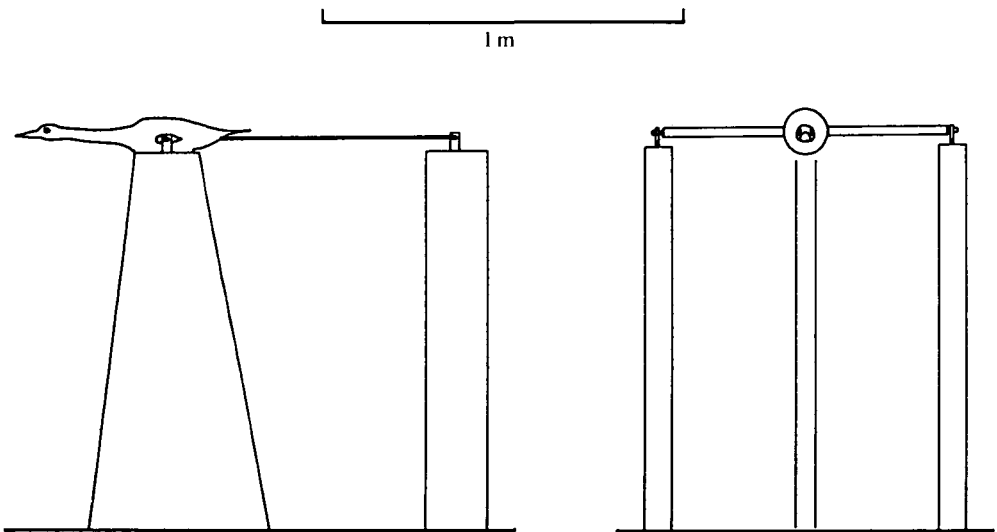


Fig. 1. Method of mounting specimens in the wind tunnel. The pillars are hollow streamlined fairings, attached to the floor. Only the ends of the support rods protrude from the fairings. They are not attached to the fairings, but pass through the floor, to the drag balance below.

faired with streamline-section steel tubing. The specimen's pitch attitude was controlled by connecting the thin steel rod projecting from its posterior end to a third upright support in the centre of the tunnel, and 0.81 m downstream of the main supports. Like the main supports, this tail support was also connected to the drag balance and was surrounded by its own streamlined fairing.

Drag of supports

Drag measurements of mounted specimens represented the total drag of the specimen plus the supports. To find the drag of the specimen alone, we had to allow for the drag of the supports. First, a measurement was made of the drag of those portions of the three upright supports that protruded from the tops of their respective fairings, with no transverse support bar. Then a transverse bar was added, faired with streamlined tubing over the full width (span) between the main supports. Thus the drag per unit span of the streamlined support bar was determined. When a specimen was in place, the body replaced the central part of the support bar. The drag was corrected in proportion to the span of that part of the support bar that was exposed to the air stream. The magnitude of the correction varied from one specimen to another, even under otherwise similar conditions, because of the variable amount of support bar exposed. With the larger specimens, the drag of the support system amounted to about 40% of the total drag.

We did not apply any correction for the horizontal part of the bar protruding from the posterior end of the specimen. As the rod was thin and aligned with the flow, we assumed its drag would be small, and the correction would in any case have been conjectural, as the rod was embedded in the chaotic wake behind the specimen.

Measurement procedure

As our intention was to determine the drag coefficients of the bodies as a function of Reynolds number, we began by pre-selecting a series of Reynolds numbers, each greater than the one below by a factor of $10^{1/6}$. The ambient air temperature and pressure were read from instruments on the control console, and the density and kinematic viscosity were calculated from formulae given by Rae & Pope (1984). The primary variable used by the tunnel operator to set the wind speed was the dynamic pressure (Q), defined as:

$$Q = \rho V^2 / 2. \quad (5)$$

Using the diameter of the specimen (as defined above) as the reference length, the speeds and dynamic pressures corresponding to the required Reynolds numbers were calculated. The tunnel operator then set the required dynamic pressure, using a remote digital indication from an electrical transducer connected to a pressure tap in the tunnel. The drag balance was also read remotely from the digital display on the operator's console, which displayed the mean and standard deviation of several measurements taken automatically over a short interval. The mean was recorded after the standard deviation had become negligible, indicating that the balance had settled down to a steady reading.

This instrumentation was not ideally suited to our purposes, because the drag balance was operating near the lower limit of its range, and at times the same may have been true of the dynamic pressure transducer. The drag balance was designed to read up to a maximum of 500 poundsforce (lbf) (about 2200 N), whereas our measurements were mostly in the region of 1 lbf (4.4 N). Although the display indicated drag to a nominal precision of 0.01 lbf, we were not able to determine the linearity or repeatability of the readings at the lower end of the measurement range. Because of this limitation, we were not able to test the smallest specimens at speeds within the range that they would be expected to use in flight. The wind tunnel used by Prior (1984) had a drag balance with a full-scale reading of 20 lbf (90 N), which enabled him to make drag measurements at lower speeds than we were able to use. We were therefore not able to duplicate the low end of the range of Reynolds numbers used by Prior.

RESULTS

Frontal area

Table 2 shows the mean mass and frontal area, as calculated from caliper measurements, for both sexes of each species in our sample. Fig. 2 is a double-logarithmic plot of frontal area against mass, with a line fitted by the reduced major-axis method as recommended for allometric plots by Rayner (1985). We have

Table 2. *Frontal areas measured on living specimens*

Species	Sex	Mass (kg)	Frontal area (m ²)	N
Waterfowl				
<i>Anas crecca</i>	♂	0.375	3.60×10^{-3}	2
<i>Anas crecca</i>	♀	0.290	3.17×10^{-3}	1
<i>Anas discors</i>	♂	0.360	4.21×10^{-3}	2
<i>Anas discors</i>	♀	0.360	3.47×10^{-3}	3
<i>Anas rubripes</i>	♂	1.19	9.40×10^{-3}	3
<i>Anas rubripes</i>	♀	1.02	9.31×10^{-3}	3
<i>Aythya americana</i>	♂	1.05	7.16×10^{-3}	1
<i>Aythya americana</i>	♀	0.910	6.62×10^{-3}	2
<i>Aythya valisineria</i>	♂	1.08	9.78×10^{-3}	2
<i>Aythya valisineria</i>	♀	1.15	8.61×10^{-3}	2
<i>Branta bernicla</i>	♂	1.37	1.22×10^{-2}	1
<i>Branta bernicla</i>	♀	1.07	1.16×10^{-2}	1
<i>Cygnus columbianus</i>	♂	8.07	2.89×10^{-2}	10
<i>Cygnus columbianus</i>	♀	6.85	2.36×10^{-2}	4
Raptors				
<i>Falco sparverius</i>	♂	0.115	2.12×10^{-3}	2
<i>Falco sparverius</i>	♀	0.136	2.29×10^{-3}	2
<i>Parabuteo unicinctus</i>	♀	0.996	7.59×10^{-3}	2
<i>Haliaeetus leucocephalus</i>	♂	3.90	2.26×10^{-2}	1
<i>Haliaeetus leucocephalus</i>	♀	4.30	2.16×10^{-2}	1

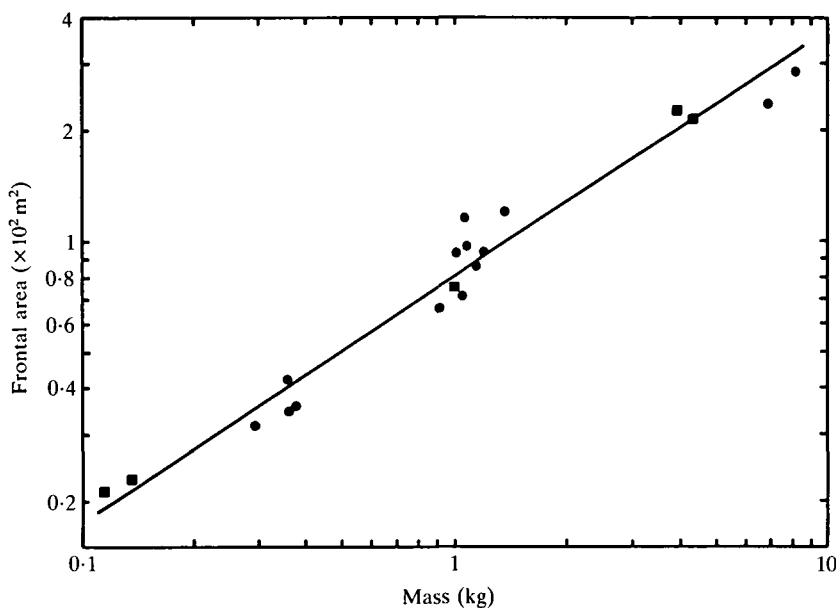


Fig. 2. Double-logarithmic plot of frontal area against mass, from Table 2. Circles, waterfowl; squares, raptors.

combined raptors and waterfowl in the same fitted line, as separate lines for the two sets of points are barely distinguishable. The equation of the combined line is:

$$S_b = (8.13 \times 10^{-3}) m^{0.666}, \quad (6)$$

where mass (m) is in kg and S_b in m^2 . The correlation coefficient is 0.983. Frontal area varies isometrically with mass in this sample.

Drag coefficient

We were not able to obtain drag measurements on the two smallest species in our set at speeds low enough to be used in flight, because of the limitations of the measuring equipment indicated above. Drag coefficients for the other four species are shown in Fig. 3. Our results are consistent with Prior's (1984) finding that drag coefficients vary little with Reynolds number once the Reynolds number exceeds 150 000 or so, but the values of the drag coefficient that we observed are considerably higher than Prior's. At a Reynolds number of 300 000 (at the upper end of his range but in the middle of ours) the bulk of Prior's observations of drag coefficient extended from about 0.16 to 0.24, and were centred at about 0.20, whereas our observations at the same Reynolds number extended from 0.26 for the tundra swan to 0.38 for the mallard.

Boundary layer and contour feathers

On all of our specimens, the boundary layer became thick and turbulent at certain points, and revealed its presence by lifting and agitating the contour feathers. We

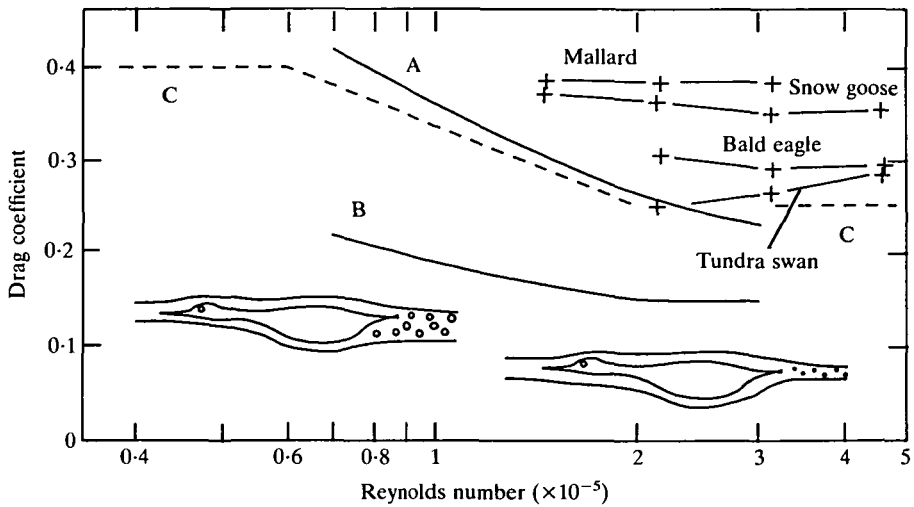


Fig. 3. Crosses: observed drag coefficient plotted against Reynolds number for mallard, snow goose, bald eagle and tundra swan. Solid lines: approximate upper (A) and lower (B) limits of scatter observed by Prior (1984) in drag measurements on waterfowl bodies. Dashed line (C-C): proposed rule for choosing value of C_D for performance estimates. Bottom: contraction of chaotic wake with increasing Reynolds number, reported by Prior (1984), results in less drag, but is caused by *more* extensive turbulence in boundary layer (right).

recorded this on video tape. On the waterfowl specimens, a turbulent wake could be seen streaming from the head along the top of the neck and impinging on the body in the shoulder region. In the case of the mallard and the snow goose, we tried deflecting the neck downwards until this wake passed below the vertical centreline of the body. This reduced the visible disturbance over the back, but made no difference to the drag coefficient. We also noted divergent areas of disturbance on all specimens over the flanks, apparently originating from the support bar. The streamline fairing on our support bar appears to have been less sharp at the trailing edge than Prior's (1984), and it is possible that this caused more extensive separation over the flanks than occurred in his experiments. This might, in turn, have caused an increase in the measured drag.

In initial tests we found that the drag coefficient usually increased as wind speed was increased during a test run, but did not decrease to the original value when the wind speed was reduced through the same series of steps. We attributed this to 'fluffing out' of the feathers, observed at the higher wind speeds. When the wind speed was decreased, the feathers remained fluffed out, so increasing the cross-sectional area, and probably also the thickness of the turbulent boundary layer. To minimize this effect, the measurements used in Fig. 3 were taken during an increasing sequence of wind speed only, and the feathers were smoothed down as much as possible by hand before starting the sequence.

At the end of our measurements on the snow goose, we smoothed down the feathers, then coated the entire surface with a generous application of hair spray, and repeated the drag measurements. At a dynamic pressure of 260 Pa, corresponding to a realistic cruising air speed of 20 m s^{-1} , the effect of this treatment was to reduce the drag coefficient from 0.33 to 0.28, a 15% reduction in drag. It seems possible that the living bird holds its contour feathers in a flattened position when flying, by using its pteromotor muscles. In this case, the body treated with hair spray might give a better approximation to the drag of the living bird than an untreated body.

DISCUSSION

Flow regime and drag coefficient

Following the nomenclature employed by Schmitz (1960), it would appear that all of our specimens exhibited a 'supercritical' flow regime, that is the boundary layer became turbulent near the upstream end of the specimen. A turbulent boundary layer should not be confused with the larger-scale turbulence that forms at the downstream end of the specimen (Fig. 3). The latter is due to separation of the boundary layer from the surface of the specimen, causing a 'dead' area downstream. Such separation occurs more readily at lower Reynolds numbers, where the flow in the boundary layer itself is laminar. As Reynolds number is increased through a 'critical' region, turbulence develops in the boundary layer near the forward end of the specimen and, once initiated, propagates downstream until most of the surface is covered by a thin layer of small-scale turbulence. This 'turbulent boundary layer' follows the converging shape of the downstream end of the specimen more readily than does a laminar boundary layer, hence the width of the chaotic wake contracts and the drag is reduced. Eventually, no further contraction of the wake takes place with further increase of the Reynolds number, and the flow is then said to be 'supercritical'. Prior (1984) considered the flow to be supercritical on his specimens at Reynolds numbers above 200 000, and our observations are consistent with this. The results of Schmitz (1960) would also lead one to expect that reduction of the Reynolds number below the lowest value used by Prior (about 65 000) would lead to a 'subcritical' flow regime, characterized by a laminar boundary layer, a large region of detached flow, and a higher drag coefficient than in the supercritical region. Prior's results explored the transitional region between subcritical and supercritical flow, and the beginning of the supercritical region, but as yet no tests on bird bodies have unequivocally identified the subcritical region. We assume that there is a range of Reynolds numbers below the transition region in which the drag coefficient is relatively constant but has a higher value than in the supercritical region.

The transition to a turbulent boundary layer can also be stimulated by turbulence present in the air stream in the wind tunnel, which may cause supercritical flow to develop around the specimen, at a Reynolds number that would support subcritical flow if the air were perfectly smooth. The more turbulence is present in the wind tunnel, the lower the Reynolds number at which transition to supercritical flow occurs. A difference between the two wind tunnels in this respect could account for

the fact that Prior observed a continuing reduction of drag coefficients even at Reynolds numbers exceeding 150 000, whereas this effect is not discernible in our results. The wind tunnel that we used was said to have a 'turbulence factor' of 1.05, whereas that used by Prior had a 'turbulence intensity' of 1%. It would be beyond the scope of this paper to review the exact meaning of these various measures of turbulence, or to assess the extent to which they can be compared.

Drag coefficient as a function of Reynolds number

We are aware of two effects that could have biased our drag estimates upwards as compared with those of Prior. First, the drag of the horizontal tail rod, which we neglected, could have been more than that of the thin vertical wire which Prior used instead of a horizontal rod to control the pitch attitude of his specimens. Second, the fairings on Prior's support bars appear to have been sharper at the trailing edge than ours. As a result, the area of disturbed airflow over the flanks, caused by the wake of the support bar, may have been more extensive in our experiments than in Prior's. Until the differences between his results and ours can be resolved, we suggest using a compromise estimate for body drag coefficient, between the two sets of results, based on the premise that the drag coefficient of a waterfowl or raptor body is 0.40 at subcritical Reynolds numbers up to 5×10^4 , then decreases through the transition region to a value of 0.25 at a Reynolds number of 200 000. The proposed rule is shown in Fig. 3C. The transitional region may be represented as:

$$C_D = 1.57 - 0.108 \ln(Re) . \quad (7)$$

The above rule is suggested as a fair basis for estimating the body drag coefficient of large birds with well-streamlined bodies. Other birds may have higher drag coefficients, as in the case of a griffon vulture whose drag coefficient was estimated by Pennycuick (1971) to be 0.43. This species is large, but has a long neck that is folded downwards in flight and may account for the high drag. Application of the rule to the subcritical range of Reynolds numbers is somewhat conjectural, and based mainly on a drag coefficient (also 0.43) for a pigeon reported by Pennycuick (1968). Tucker (1973) obtained still higher values for the effective flat-plate area of various species of small and medium-sized birds than would have been predicted on the basis of scaling the pigeon result of Pennycuick (1975). Although Tucker (1973) did not report the drag coefficients as such, they must have been higher than would be estimated here. This may have been due to Tucker's mounting system, in which the body was supported on the end of a cylindrical rod, projecting ventrally from the sternum. As von Mises (1945) points out, the drag of a streamlined body with a cylinder attached is likely to be appreciably greater than the sum of the drag of the cylinder and the body, if each is measured separately. Tucker estimated the drag of the body by subtracting the drag of the cylinder from that of the combination, and thus obtained estimates that were probably too high.

It may be noted that all published measurements of the drag of bird bodies are rather high in comparison with the drag of streamlined bodies with smooth surfaces, as reported in the engineering literature. In view of the drag reduction that resulted

from our application of hair spray to the snow goose (above), it is possible that the reported high values of drag are an artefact, caused by disarray of the feathers on dead bodies. If further observation of living birds confirms this, then our drag coefficient estimates may need to be revised downwards.

Body Reynolds number at V_{mr}

Before the rule illustrated in Fig. 3C can be used to estimate the body drag coefficient, an estimate is needed for Re , that is the Reynolds number of the body when the bird is flying at its maximum range speed (V_{mr}). In geometrically similar birds, V_{mr} should vary with the 1/6 power of the mass, and the body diameter actually does vary with the 1/3 power of the mass (equation 6). Therefore, from equation 3, the Reynolds number should vary with the square root of the mass. The actual slope is probably a little less than this because of allometric effects, but since the range of Reynolds numbers that have to be estimated is quite small (the sloping part of Fig. 3C), it will suffice to assume that, for waterfowl,

$$Re = (1.25 \times 10^5) \sqrt{m}, \quad (8)$$

where m is in kg.

For species that differ greatly in morphology from waterfowl, it is best to estimate the maximum range speed by the method given by Pennycuik (1975), for which the wing span as well as the mass is required, and then to use this estimate to calculate the body Reynolds number. For example, equation 8 will overestimate the Reynolds number for raptors, but nevertheless the required precision is so low that more refined calculations may not be justified.

Application to performance predictions

We now have a basis for estimating the equivalent flat-plate area of a bird on the basis of its mass. First, the body frontal area (S_b) is estimated from equation 6. Then the body Reynolds number (Re) is estimated from equation 8. If the estimated Reynolds number is less than 50 000, the body drag coefficient (C_D) is set to 0.40. If Re is greater than 200 000, C_D is set to 0.25. If Re is between 50 000 and 200 000, C_D is estimated from equation 7. Finally, with estimates for both the frontal area and drag coefficient, the equivalent flat-plate area is estimated from equation 2.

Special thanks are extended to the staff of the Glenn L. Martin Wind Tunnel at the College of Engineering, University of Maryland, and in particular to S. R. Paragiri, J. B. Barlow and W. S. Sekscienski for their expert guidance. We also thank T. Sanderson for advice about test materials, Mark Martell, R. Limpert, W. J. L. Sladen and G. Kearns for providing bird specimens, and L. McAllister, F. P. Ward and W. S. Seegar for practical help. We are most grateful to V. A. Tucker for his helpful comments on a preliminary draft of the manuscript. This project was financed under cooperative agreement No. 14-16-0009-86-965 between the US Fish and Wildlife Service and Sea and Sky Foundation.

REFERENCES

- OBRECHT, H. H., PENNYCUICK, C. J. & FULLER, M. R. (1988). Wind tunnel experiments to assess the effects of back-mounted radio transmitters on bird body drag. *J. exp. Biol.* **135**, 265–273.
- PENNYCUICK, C. J. (1968). A wind-tunnel study of gliding flight in the pigeon *Columba livia*. *J. exp. Biol.* **49**, 509–526.
- PENNYCUICK, C. J. (1971). Control of gliding angle in Ruepell's Griffon Vulture *Gyps rueppellii*. *J. exp. Biol.* **55**, 39–46.
- PENNYCUICK, C. J. (1975). Mechanics of flight. In *Avian Biology*, vol. 5 (ed. D. S. Farner & J. R. King), pp. 1–75. New York: Academic Press.
- PRIOR, N. C. (1984). Flight energetics and migration performance of swans. Ph.D. thesis, University of Bristol.
- RAE, W. H. & POPE, A. (1984). *Low-Speed Wind Tunnel Testing*, 2nd edn. New York: Wiley.
- RAYNER, J. M. V. (1985). Linear relations in biomechanics: the statistics of scaling functions. *J. Zool., Lond. A* **206**, 415–439.
- SCHMITZ, F. W. (1960). *Aerodynamik des Flugmodells*, 4th edn. Duisberg: Carl Lange.
- TUCKER, V. A. (1973). Bird metabolism during flight: evaluation of a theory. *J. exp. Biol.* **58**, 689–709.
- VON MISES, R. (1945). *Theory of Flight*. New York: Dover.