

From: Dominika Phillips <DOMPH@orsted.co.uk>

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To: KJ Johansson <KJ.JOHANSSON@planninginspectorate.gov.uk>; Kay Sully <Kay.Sully@pins.gsi.gov.uk>; Hornsea Project Three <HornseaProjectThree@pins.gsi.gov.uk>

Cc: Andrew Guyton <ANGUY@orsted.co.uk>; Stuart Livesey <STLIV@orsted.co.uk>

Subject: Hornsea Project Three (UK) Ltd response to Deadline 6 (Part 5)

Dear Kay, K-J

Please find attached the 5th instalment of documents.

Best regards,

Dr Dominika Chalder PIEMA

Environment and Consent Manager



Environmental Management UK; Wind Power
5 Howick Place | London | SW1P 1WG



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Appendix 15 to Deadline 6 submission –
Pennycuik 1997

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5 Howick Place,

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ACTUAL AND ‘OPTIMUM’ FLIGHT SPEEDS: FIELD DATA REASSESSED

C. J. PENNYCUICK*

School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

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Summary

Previously published field observations of the air speeds of 36 species of birds, all observed by the same method (ornithodolite), were compared with estimates of the corresponding minimum power speeds, calculated with a default body drag coefficient of 0.1. This value, which was derived from recent wind tunnel studies, represents a downward revision from default values previously used and leads, in turn, to an upward revision of estimated minimum power speeds. The mean observed air speeds are now distributed around the minimum power speed, rather than in between the speeds for minimum power and

maximum range, as they were before. Although the field data do not represent migration, examination of the marginal effects of small changes of speed, on power and lift:drag ratio, indicates that flying at the maximum range speed on migration may not represent an ‘optimal’ or even a practical strategy and that cruising speeds may be limited by the muscle power available or by aerobic capacity. Caution in constructing ‘optimisation’ theories is indicated.

Key words: bird, flight, speed, measured optimum.

Introduction

The mechanical power available from a bird’s flight muscles is limited, and this in turn places both lower and upper limits on the speed at which it can fly horizontally. Similar limits are part of the everyday experience of pilots of both fixed-wing and rotary-wing aircraft. They result from elementary physical principles, which apply to all heavier-than-air flying machines or animals that support their weight aerodynamically. For any such animal or machine, the curve of power *versus* speed for horizontal flight passes through a minimum at an air speed which is commonly called the ‘minimum power speed’ (V_{mp}). There is also a higher air speed, the ‘maximum range speed’ (V_{mr}) at which the ratio of speed to power is a maximum, and therefore so is the (air) distance flown per unit work done. Alerstam and Lindström (1990) and Hedenström and Alerstam (1995a) have considered what choice of air speed would minimise either energy consumption or flight time on a multi-stage migratory flight and claimed that the bird’s choice between various alternative ‘currencies’ could be distinguished by observing actual cruising speeds. Such an approach assumes that the characteristic air speeds V_{mp} and V_{mr} can be accurately calculated for the bird under observation, that there are no unknown implications of flying at one speed rather than another, and that the bird is free to select whatever speed produces optimum results, as defined by the theorist. These are bold assumptions.

One cannot observe directly in the field whether or not a bird

is flying at V_{mp} , at V_{mr} or at some other point on the power curve. The field observer can only measure the bird’s absolute air speed. Calculating an estimate of V_{mp} or V_{mr} , with which to compare the observed air speed, is a separate operation. The estimate is no better than the theory underlying it, or the values measured or assumed for any variables required in the calculation. This paper is a reassessment of previously published field observations by this author of the air speeds at which 36 species of birds were observed flying (Pennycuick, 1982b, 1987, 1990; Pennycuick and de Santo, 1989). These are not speed measurements drawn from anywhere in the literature, but a homogeneous set in which all the field data were obtained by the same method (ornithodolite) and were subject to the same assumptions and sources of error. They are compared with estimates of the minimum power speeds, which were also all obtained in the same way, from Program 1A of Pennycuick (1989). Although estimates of V_{mp} and V_{mr} were published along with the original field data, evidence from recent wind tunnel studies (Pennycuick *et al.* 1996) indicates that these earlier estimates were too low, because the default values used for the body drag coefficient were too high. Upward revision of the calculated speeds calls for a reinterpretation of the speeds at which the birds were observed flying, and this in turn highlights the hazards of extrapolating from a physical theory to predict the speeds at which birds ‘should’ fly in different circumstances.

*e-mail: C.Pennycuick@bristol.ac.uk

Materials and methods

Observed speeds

The ornithodolite, described by Pennycuick (1982a), is an optical instrument which records a series of three-dimensional, timed points along a bird's track. The horizontal and vertical distances between each pair of successive points are calculated, and divided by the time difference to get the average horizontal and vertical ground speeds. The air speed (rather than the ground speed) is required for comparison with calculated speeds, and this has to be obtained from the ground speed by vector subtraction of the wind vector (wind speed and direction). Wind measurement is always a significant source of error in field observations of flight speeds, as the wind cannot be measured at the exact time and place where the bird is flying. It was measured immediately after each observation from an electrical anemometer with speed and direction sensors mounted on a pole near the observing position, with a remote readout on the ornithodolite. The ornithodolite is limited to ranges between approximately 50 and 150 m and, while this severely limits the circumstances in which it can be used, it also ensures that the wind sensor is not far from the bird. Care is still needed to ensure that neither the bird nor the wind sensor is affected by upwind obstructions such as trees or buildings, which would modify the wind. All the species were observed in sustained, level, flapping or flap-gliding flight. Speed observations were excluded if the bird was seen to be searching for food, landing, taking off or performing other transient manoeuvres. Most of the observations were of birds flying between feeding areas and nests or roosts in their breeding or wintering areas, covering distances long enough to allow the bird to settle down in steady flight, i.e. a few hundred metres to a few kilometres. The ornithodolite is not suited to measuring very short flights (tens of metres), and these would be excluded anyway, as being inherently unsteady. At the other extreme, some of the birds were observed moving about in migration staging areas, but were believed to be moving relatively short distances when actually observed, and were not thought to be engaged in non-stop migratory flights of hundreds of kilometres.

Calculated speeds

The minimum power speed V_{mp} was estimated from the formula:

$$V_{mp} = [0.807k^{1/4}(mg)^{1/2}]/[\rho^{1/2}b^{1/2}(S_b C_{Db})^{1/4}], \quad (1)$$

whose derivation was explained by Pennycuick (1975). Estimates are required for each of the seven variables on the right-hand side of equation 1, three of which are morphological, two environmental and two aerodynamic. It is an inherent weakness of field studies that the primary morphological variables, the mass (m) and the wing span (b), have to be estimated from the means of measurements from samples of specimens, in contrast to wind tunnel studies, where these measurements can be determined for the particular individual under observation. The body frontal area

(S_b) is a secondary morphological variable, estimated from the mass (Pennycuick *et al.* 1988). The two environmental variables are the acceleration due to gravity (g), for which the standard value 9.81 m s^{-2} was used, and the air density (ρ), which was recorded together with each speed observation. All observations in this data set were made near sea level, permitting the air density to be set to a constant value of 1.23 kg m^{-3} .

The two aerodynamic variables are the induced power factor (k) and the drag coefficient of the body (C_{Db}). New evidence on likely values for these variables is the reason for this re-evaluation of the field observations. Program 1A, as published by Pennycuick (1989), calculates V_{mp} (amongst other results) for a specified bird, using a fixed default value of $k=1.2$, and a default value for C_{Db} between 0.25 (for large birds) and 0.40 (for small ones). These values were derived from wind tunnel measurements of the drag of frozen bird bodies, from which the wings had been removed, but were recognised as anomalous, being far higher than the values usually associated with streamlined bodies (Pennycuick *et al.* 1988; Tucker, 1990). Recently, wind tunnel observations of a teal (*Anas crecca*) and a thrush nightingale (*Luscinia luscinia*) by Pennycuick *et al.* (1996) revealed a well-defined minimum in the graph of wingbeat frequency *versus* air speed, and evidence was presented that this minimum-frequency speed was identical with the minimum power speed. In both birds, the measured minimum frequency speeds were approximately 50% higher than the V_{mp} estimates from equation 1, using the above default values for k and C_{Db} . The discrepancy could not be resolved by revising the value of k , even far outside the range of values considered possible, but it was resolved by retaining $k=1.2$ and assigning a value near 0.08 to C_{Db} for both birds, i.e. reducing the earlier estimates by a factor between 3 and 5. The provisional recommendation was to use a default value of $C_{Db}=0.1$, recognising that the true value might be as low as 0.05 in birds with well-streamlined bodies, but might also be above 0.1 in species with drag-enhancing characteristics, such as trailing legs or prominent heads.

Results

Revising the value assumed for C_{Db} has no effect on the observed speed (V_{obs}), but alters the estimate of the minimum power speed (V_{mp}), in the sense that a lower body drag estimate leads to a higher estimate for V_{mp} , and hence to a lower estimate for the ratio V_{obs}/V_{mp} . In Table 1, the values of the morphological variables and the observed mean speed (V_{obs}) are listed for each species, together with two estimates for the minimum power speed. V_{mp1} is the estimate obtained by using the 'old' default procedure, which gives a value for C_{Db} in the range 0.25–0.40, depending on the size of the bird, as above. V_{mp2} is a higher value, obtained by using a fixed value of $C_{Db}=0.1$, regardless of the size of the bird. In Fig. 1, the two ratios V_{obs}/V_{mp1} and V_{obs}/V_{mp2} are shown as open and filled circles respectively. The species in both Table 1 and Fig. 1 have been arranged in descending order of the ratio V_{obs}/V_{mp2} .

Table 1. Morphological data and observed and calculated speeds

Species	Body mass (kg)	Wing span (m)	Wing area (m ²)	V _{obs} (m s ⁻¹)	V _{mp1} (m s ⁻¹)	V _{mp2} (m s ⁻¹)
1 <i>Tachycineta bicolor</i>	0.0201	0.320	0.0133	11.3	4.8	6.8
2 <i>Oceanites oceanicus</i>	0.035	0.396	0.0215	10.4	5.2	7.3
3 <i>Stercorarius parasiticus</i>	0.390	1.05	0.117	13.3	7.3	10.1
4 <i>Colaptes auratus</i>	0.132	0.510	0.0478	12.7	7.1	10.1
5 <i>Fratercula arctica</i>	0.398	0.549	0.0369	17.6	10.2	14.0
6 <i>Rissa tridactyla</i>	0.387	0.965	0.101	13.1	7.6	10.5
7 <i>Pachyptila desolata</i>	0.155	0.635	0.0469	11.1	6.7	9.5
8 <i>Uria aalge</i>	0.950	0.707	0.0544	19.1	12.5	16.5
9 <i>Catharacta skua</i>	1.35	1.37	0.214	14.9	10.3	13.3
10 <i>Daption capensis</i>	0.418	0.875	0.0773	12.3	8.3	11.3
11 <i>Alca torda</i>	0.620	0.661	0.0462	16.0	11.0	14.8
12 <i>Fulmarus glacialis</i>	0.815	1.13	0.124	13.0	9.3	12.4
13 <i>Rynchops niger</i>	0.300	0.990	0.0888	9.9	6.9	9.5
14 <i>Falco sparverius</i>	0.090	0.502	0.0344	9.1	6.3	8.9
15 <i>Larus marinus</i>	1.55	1.65	0.285	13.0	9.9	12.7
16 <i>Macronectes giganteus/M. halli</i>	3.24	1.98	0.326	15.2	11.8	14.9
17 <i>Phalacrocorax auritus</i>	1.41	1.16	0.179	14.5	11.3	14.7
18 <i>Sula bassanus</i>	3.01	1.85	0.262	14.9	11.9	15.0
19 <i>Larus atricilla</i>	0.325	1.03	0.106	9.5	6.9	9.6
20 <i>Sterna maxima</i>	0.470	1.15	0.108	10.0	7.5	10.2
21 <i>Diomedea melanophris</i>	3.08	2.19	0.354	13.3	11.1	13.9
22 <i>Eudocimus albus</i>	0.900	0.951	0.160	12.9	10.6	14.0
23 <i>Casmerodius albus</i>	0.874	1.34	0.222	10.6	8.8	11.7
24 <i>Phalacrocorax aristotelis</i>	1.81	1.04	0.158	15.4	13.2	16.9
25 <i>Diomedea exulans</i>	8.55	3.01	0.583	15.0	13.3	16.7
26 <i>Egretta caerulea</i>	0.340	0.980	0.134	8.8	7.2	10.0
27 <i>Fregata magnificens</i>	1.47	2.29	0.408	9.3	8.2	10.6
28 <i>Ajaia ajaja</i>	1.30	1.25	0.226	11.9	10.6	13.8
29 <i>Cathartes aura</i>	1.55	1.75	0.442	10.6	9.6	12.4
30 <i>Larus argentatus</i>	0.950	1.36	0.203	9.9	9.0	11.9
31 <i>Pandion haliaetus</i>	1.49	1.59	0.300	10.6	9.9	12.8
32 <i>Ardea occidentalis</i>	2.50	1.91	0.493	11.0	11.0	13.9
33 <i>Pelecanus occidentalis</i>	3.39	2.26	0.450	10.1	11.2	14.1
34 <i>Ardea herodias</i>	1.92	1.76	0.419	9.4	10.4	13.2
35 <i>Haliaeetus leucocephalus</i>	4.68	2.24	0.756	11.2	12.6	15.8
36 <i>Coragyps atratus</i>	2.08	1.38	0.327	10.8	12.1	15.4

V_{obs}, observed mean speed; V_{mp1}, minimum power speed calculated assuming C_{Db}=0.25–0.40 depending on size of bird; V_{mp2}, minimum power speed calculated assuming C_{Db}=0.1; C_{Db}, drag coefficient of the body.

Points that fall on the solid vertical line in Fig. 1 mean that the observed air speed was equal to the appropriate estimate of V_{mp}; that is V_{mp1} for the open circles, and V_{mp2} for the filled circles. Further to the right are two vertical dashed lines representing speeds of 1.45V_{mp} and 1.70V_{mp}. The calculated maximum range speeds (V_{mr}) from Program 1A of Pennycuick (1989) fall between these dashed lines for all species in the sample.

Effect of revised body drag estimates

Fig. 1 shows that, if the estimate of V_{mp} is based on the 'old' estimates of body drag (open circles), most of the field observations fall between the estimates for V_{mp} and V_{mr}. This unsurprising result was noted in the original papers describing

the field observations and was taken as evidence that the predicted values for V_{mp} and V_{mr} were not seriously in error, even though the drag measurements, on which they were based, were known to be anomalously high. This position became untenable following the wind tunnel observations on the teal and thrush nightingale described by Pennycuick *et al.* (1996), as the calculated minimum power speeds were below the lowest speeds at which either bird would fly. The filled circles in Fig. 1 show the effect of recalculating the minimum power speeds of the birds in the field sample, using a lower value of C_{Db}=0.1. This value is reconcilable with the wind tunnel observations, but may be an underestimate for some species in the sample, which have poorly streamlined bodies. The result of increasing the estimates of V_{mp} and V_{mr} is that

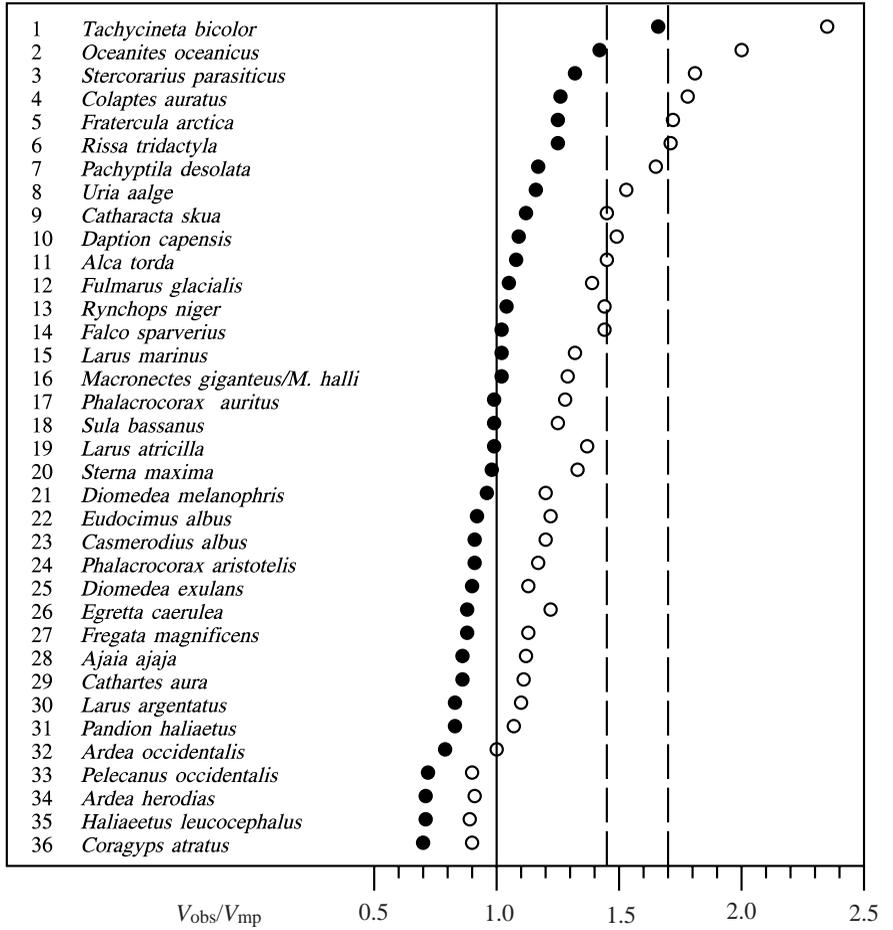


Fig. 1. Ratio of observed air speed V_{obs} to calculated minimum power speed V_{mp} for 36 species, from data in Table 1. Open circles: minimum power speed calculated according to default values of body drag coefficient given in Pennycuick (1989). Filled circles: minimum power speed recalculated according to reduced body drag estimates from Pennycuick *et al.* (1996).

the observed speeds are now centred around the new estimate of V_{mp} , rather than falling between V_{mp} and V_{mr} .

Trend with body mass

Fig. 2 shows that the position of a species in Fig. 1 is correlated with its mass. The smaller species tend to be at the top of the list, that is, with the largest values of the ratio V_{obs}/V_{mp2} , while the larger species are at the bottom. Fig. 3

expresses this in a different way. The ratio V_{obs}/V_{mp2} is well above 1 in the smallest species, but below 1 in some of the larger ones. This ratio can be above 1 for one or both of two different and independent reasons: (1) the bird actually was flying faster than its minimum power speed, and/or (2) the estimate of the minimum power speed is too low. Different reasons may apply to different species, and the differences may be size-related.

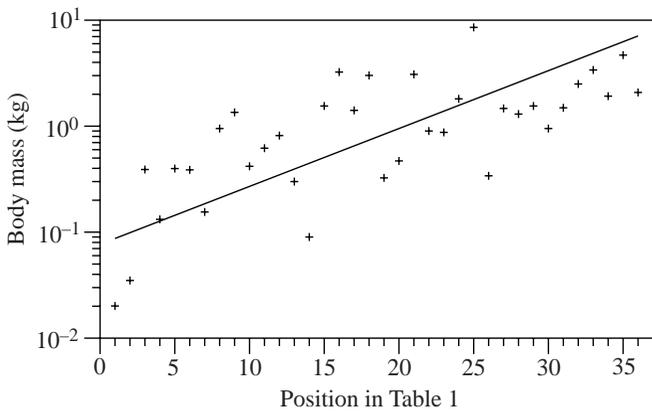


Fig. 2. Linear-logarithmic plot with standard major axis line of body mass *versus* position in Table 1, for the 36 species in the table ($r=0.692$).

Discussion

Species apparently flying faster than V_{mp}

There is a well known scale effect that makes it easier for small than for large species to extract enough power from their

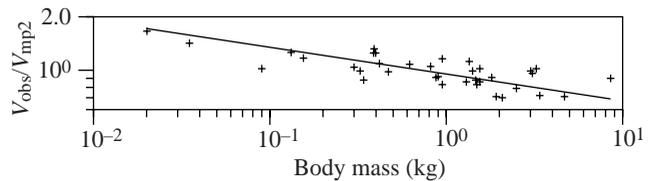


Fig. 3. Double logarithmic plot of the ratio of observed air speed V_{obs} to calculated minimum power speed V_{mp2} (revised drag assumptions), *versus* body mass, for the 36 species in Table 1, with standard major axis line ($r=-0.743$).

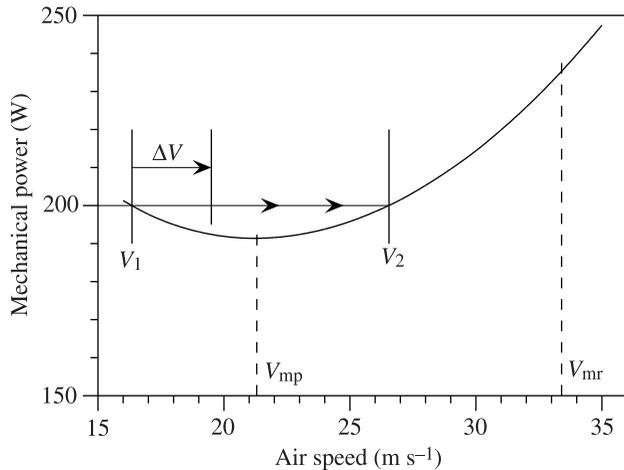


Fig. 4. Curve of mechanical power *versus* air speed at sea level for the whooper swan of Table 2. A steady power output of 200 W from the flight muscles corresponds to a stable equilibrium at speed V_2 or an unstable equilibrium at speed V_1 (see text for explanation). Note that the zeroes are suppressed on both x and y scales.

flight muscles to fly level at any characteristic speed such as V_{mr} or V_{mp} (Pennycuick, 1989). This is no doubt part of the reason for the trends shown in Figs 2 and 3, and for the isolated position of the two smallest species at the top of the table. These are the tree swallow *Tachycineta bicolor* and Wilson's storm petrel *Oceanites oceanicus*, both showing values of V_{obs}/V_{mp2} which suggest that they were flying nearer the maximum range speed rather than the minimum power speed (Fig. 1, filled circles). Under the old assumptions of body drag, the estimates for V_{mr} for these two species would be lower, so that the observed speeds would be much faster than V_{mr} (open circles).

The swallows were passing through a migration staging area, Assateague Island on the east coast of the USA, where they were spending much time feeding, but might also have been moving intermittently further south. The storm petrels were departing from their nesting area on Bird Island, South Georgia, and were believed to be on foraging flights which might take them a few tens or possibly hundreds of kilometres out to sea (Pennycuick, 1982*b*). Either of these situations might give the birds an incentive to maximise their range by flying at or near V_{mr} , but there is no obvious incentive to fly faster than V_{mr} . The observed speeds would be anomalously high under the old estimates of body drag, but intelligible under the new, lower estimates. The next species in order, *Stercorarius parasiticus*, is a chasing predator which may be adapted for high speed in level flight. This is followed by a very heterogeneous set of species, which appeared to be flying near V_{mr} under the old assumptions, but nearer V_{mp} under the new ones.

Species apparently flying slower than V_{mp}

Looking now at the bottom of Table 1, the last four species were apparently flying at only approximately $0.7V_{mp}$ under the new assumptions and $0.9V_{mp}$ under the old ones. This is even

Table 2. Measurements of a female whooper swan (*Cygnus cygnus*), and values assumed for other variables, to calculate the curves of Figs 4 and 5 from Program 1A of Pennycuick (1989)

Empty body mass (kg)	10.0
Fat load (kg)	1.5
Wing span (m)	2.26
Wing area (m ²)	0.589
Aspect ratio	8.67
Profile power ratio	0.969
Induced drag factor	1.2
Body drag coefficient	0.1
Air density (kg m ⁻³)	1.23

The profile power ratio is $8.4/R$, where R is the aspect ratio.

more unlikely than flying faster than V_{mr} , for the reason shown in Fig. 4, which is a calculated curve of power *versus* air speed for a particular whooper swan (*Cygnus cygnus*), calculated using Program 1A of Pennycuick (1989). The values used in the calculation are given in Table 2. If we suppose that the swan's flight muscles can produce 200 W (for example) of mechanical power, then the swan would have sufficient power to fly below V_{mp} , at the speed marked V_1 . Suppose some disturbance, such as a gust, causes it to speed up by a small amount ΔV , while the power output from its muscles remains unchanged. The power required (curve) decreases, so the bird is now exerting more power than is needed to maintain equilibrium at the new speed. It therefore continues to accelerate, until it reaches V_2 , where the power required is the same as at the original speed V_1 . Equilibrium is possible with the same power output (200 W) at either V_1 or V_2 , but the equilibrium at V_2 is stable, whereas that at V_1 is unstable. Steady flight at V_1 is possible, but requires continuous control inputs to overcome the tendency to accelerate. Birds are therefore not expected to fly slower than V_{mp} on foraging or migratory flights. They may do so when searching for, or attempting to catch, slow-moving prey or in other special circumstances such as song flights (Hedenström, 1995; Hedenström and Alerstam, 1995*b*). According to Thomas (1993), spreading the tail lowers V_{mp} , so that the bird is able to fly more slowly without speed instability. Birds seen to be searching for food or making low-speed manoeuvres were excluded from the field data.

Birds that proceed by flap-gliding rather than steady flapping flight are not necessarily subject to speed instability at speeds below V_{mp} . A flap-gliding bird slows down during the gliding phase, possibly to some speed well below V_{mp} . During the flapping phase, it speeds up again, but only until it stops flapping, which it may do before it reaches V_{mp} . In that case, the speed oscillates over a range that never reaches V_{mp} . Birds that normally flap-glide on foraging or positioning flights, such as the American black vulture *Coragyps atratus* (at the bottom of Table 1), may therefore maintain an average speed below V_{mp} . Some other species low down in Table 1, such as the two

large herons, *Ardea occidentalis* and *A. herodias*, normally flap steadily in horizontal flight. In their case, it is unlikely that they would be flying slower than V_{mp} , for the reason given above, and more likely that the estimate of V_{mp} is too high. This would be the case if their body drag coefficients were higher than was assumed when calculating V_{mp} . In fact, the old estimates of C_{Db} , 0.25 or higher, might be correct in the case of large herons, which have long legs that trail behind in flight and also prominent heads that retract upwards and are not fully faired in flight. As the open circles show, the observed speeds were near the old estimates of V_{mp} for these aerodynamically 'dirty' species (Fig. 1).

'Optimum' speed selection – marginal costs and benefits

Whilst it is true that the greatest range (relative to the air) is obtained by flying at the maximum range speed (V_{mr}), it does not necessarily follow that flying at that speed represents an optimal or even a practical strategy for a migrating bird. The upper curve in Fig. 5 is the same curve of mechanical power *versus* air speed as in Fig. 4, and below it is the corresponding curve of effective lift:drag ratio (also from Program 1 of Pennycuick, 1989), which is proportional to the distance flown per unit work done. The flat maximum in the curve of lift:drag ratio indicates that the value of V_{mr} is poorly defined, meaning that, in the vicinity of V_{mr} , substantial changes of speed, either way, make very little difference to the effective lift:drag ratio. Moreover, the exact value of V_{mr} depends on the shape of the upper (power) curve, which is poorly known. A small change in the curvature of this region of the power curve would have a large effect on the value of V_{mr} , but very little effect on the maximum effective lift:drag ratio. In contrast, small changes of speed in the vicinity of V_{mr} require large changes of power, because that part of the power curve bends ever more steeply upwards.

The bird's practical options in the selection of speed depend on the *marginal* changes of lift:drag ratio and power resulting from small changes of speed. By definition, the power required

to fly is least at the minimum power speed (V_{mp}), but since the power curve is almost horizontal in the region of V_{mp} , the power required is almost the same if the bird elects to fly a little faster (or slower) than V_{mp} . For example, the marginal increase in power required to fly at $1.1V_{mp}$, rather than actually at V_{mp} , is only 0.8%. As this represents a 10% increase in speed, the ratio of speed to power increases by 9%, and so also does the effective lift:drag ratio, which determines the range. Further equal increments of speed result in progressively larger increments of power, because the power curve bends upwards. The curve of effective lift:drag ratio, however, bends downwards and peaks at V_{mr} . The marginal gain in range declines, until eventually the curve becomes horizontal at V_{mr} . To get the last 1% to the maximum value of the effective lift:drag ratio, the bird has to accelerate from 30.5 to 33.4 $m\ s^{-1}$, which requires a 7.7% increase of power.

One would expect any bird whose immediate need is to make some progress over the ground to fly somewhat faster than V_{mp} , because this results in a substantial saving of energy and shortening of the journey time at the cost of a very small increase in power. However, the marginal benefit from further increases of speed diminishes to a barely perceptible level long before the mathematical 'optimum' speed (V_{mr}) is reached, while the marginal increase in the power required becomes ever larger. Birds that migrate long distances over hostile terrain have the strongest incentive to fly in whatever manner maximises their range, but even these may not fly actually at V_{mr} . In the example of Fig. 5, the swan needs 7.7% more power to get the last 1% of range, and that translates (roughly) into 7.7% more muscle, which in turn requires an enlarged respiratory and circulatory system with 7.7% greater aerobic capacity. It may be energetically cheaper to fly slower than V_{mr} , at a slightly lower effective lift:drag ratio, because this will permit a substantial reduction in the weight of muscles and supporting systems required, so eliminating the energetic cost of transporting that extra weight and the metabolic cost of maintaining the extra tissues. The reverse might be true if part of the flight muscles can be consumed as supplementary fuel in the course of long flights, as suggested by Pennycuick (1975).

Physiological complications

Sustained cruising flight (other than soaring) requires the bird to have sufficient aerobic capacity to supply the flight muscles with fuel and oxygen, and to remove heat, at a fast enough rate to maintain equilibrium. This is a separate requirement from mechanical muscle power, discussed above. The speeds at which some birds can fly may be limited by aerobic capacity, rather than by muscle power. As an extreme example, there is evidence that some large galliform birds, whose muscle power is sufficient for explosive take-off and rapid acceleration under predator attack, are actually incapable of cruising aerobically at any speed (Pennycuick *et al.* 1994). In terms of added mass or metabolic maintenance costs, little or nothing is known about the implications of providing increased aerobic capacity. This would have to be rectified,

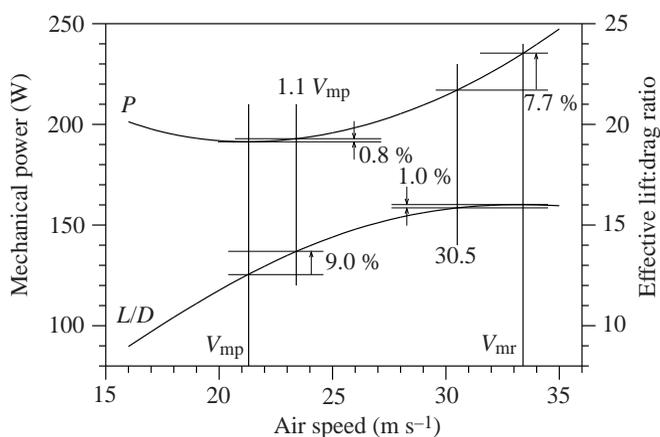


Fig. 5. The same power curve as in Fig. 4 (P), with a corresponding curve of effective lift:drag ratio (L/D), illustrating the marginal effects (given as percentages) of small changes of speed (see text explanation).

before any meaningful theory of 'optimisation', involving these variables, could be formulated.

Response to wind

It has commonly been observed that birds increase their air speeds when flying against a head wind (Alerstam, 1990). This is easily understood if the bird's objective is to make progress relative to the ground rather than the air (Pennycuick, 1975). However, if a bird's objective were simply to remain airborne and making progress over the ground were unimportant, then the selection of air speed would not be affected by wind. For example, a swift flying at night, and unable to feed, might be unconcerned where it is carried by the wind, and in that case it would be free to select an air speed near V_{mp} , where the power is minimal, regardless of the wind strength. The observation that a particular population of migrating or foraging birds increases air speed when flying against a head wind, and slows down with a tail wind, indicates only that position relative to the ground is significant for the birds. It does not indicate anything about the whereabouts of the chosen air speed relative to the power curve.

Conclusion

The power curve for a particular bird, to the extent that it can be reliably calculated, is a convenient summary of the physics of horizontal flight. The two characteristic air speeds V_{mp} and V_{mr} are properties of the power curve that do not in themselves define an 'optimum strategy' for a migrating bird. As noted above, limitations of either muscle power or aerobic capacity may limit the cruising speed to a value below V_{mr} . Such complications would have to be fully understood before it would be possible to build a further layer of theory purporting to predict the speeds at which birds 'should' fly, in order to achieve objectives which may appear more clearly defined from the viewpoint of the theorist than from that of the bird. As to the speeds at which birds actually do fly, the present comparison of air speeds observed in the field with the best currently available estimates of V_{mp} suggests that most of the species in the sample habitually fly at speeds near V_{mp} , at least on short journeys. A longer-range method of speed measurement, such as tracking radar, would be needed to determine whether the same conclusion applies to birds engaged on long, non-stop migratory flights.

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References

- ALERSTAM, T. (1990). *Bird Migration*. Cambridge: Cambridge University Press.
- ALERSTAM, T. AND LINDSTRÖM, Å. (1990). Optimal bird migration: the relative importance of time, energy and safety. In *Bird Migration* (ed. E. Gwinner), pp. 331–351. Heidelberg: Springer.
- HEDENSTRÖM, A. (1995). Song flight performance in the skylark *Alauda arvensis*. *J. avian Biol.* **26**, 337–342.
- HEDENSTRÖM, A. AND ALERSTAM, T. (1995a). Optimal flight speed of birds. *Phil. Trans. R. Soc. Lond. B* **348**, 471–487.
- HEDENSTRÖM, A. AND ALERSTAM, T. (1995b). Skylark optimal flight speeds for flying nowhere and somewhere. *Behav. Ecol.* **7**, 121–126.
- PENNYCUICK, C. J. (1975). Mechanics of flight. In *Avian Biology*, vol. 5 (ed. D. S. Farner and J. R. King), pp. 1–75. New York: Academic Press.
- PENNYCUICK, C. J. (1982a). The ornithodolite: an instrument for collecting large samples of bird speed measurements. *Phil. Trans. R. Soc. B* **300**, 61–73.
- PENNYCUICK, C. J. (1982b). The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. *Phil. Trans. R. Soc. Lond. B* **300**, 75–106.
- PENNYCUICK, C. J. (1987). Flight of auks (Alcidae) and other northern seabirds compared with southern procellariiformes: ornithodolite observations. *J. exp. Biol.* **128**, 335–347.
- PENNYCUICK, C. J. (1989). *Bird Flight Performance. A Practical Calculation Manual*. Oxford: Oxford University Press.
- PENNYCUICK, C. J. (1990). Predicting wingbeat frequency and wavelength of birds. *J. exp. Biol.* **150**, 171–185.
- PENNYCUICK, C. J. AND DE SANTO, T. (1989). Flight speeds and energy requirements for white ibises on foraging flights. *Auk* **106**, 141–144.
- PENNYCUICK, C. J., FULLER, M. R., OAR, J. J. AND KIRKPATRICK, S. J. (1994). Falcon *versus* grouse: flight adaptations of a predator and its prey. *J. avian Biol.* **25**, 39–49.
- PENNYCUICK, C. J., KLAASSEN, M., KVIST, A. AND LINDSTRÖM, Å. (1996). Wingbeat frequency and the body drag anomaly: wind tunnel observations on a thrush nightingale (*Luscinia luscinia*) and a teal (*Anas crecca*). *J. exp. Biol.* **199**, 2757–2765.
- PENNYCUICK, C. J., OBRECHT, H. H. AND FULLER, M. R. (1988). Empirical estimates of body drag of large waterfowl and raptors. *J. exp. Biol.* **135**, 253–264.
- THOMAS, A. L. R. (1993). On the aerodynamics of birds' tails. *Phil. Trans. R. Soc. Lond. B* **340**, 361–380.
- TUCKER, V. A. (1990). Body drag, feather drag and interference drag of the mounting strut in a peregrine falcon, *Falco peregrinus*. *J. exp. Biol.* **149**, 449–468.