Uncertainty Calculations for Theoretical Flight Power Curves

G. R. Spedding* and C. J. Pennycuick†

Department of Aerospace and Mechanical Engineering, University of Southern California, Los Angeles, CA 90089-1191, U.S.A. and †School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, U.K.

The comparison of theoretical and experimental estimates of the mechanical power requirement for flight is currently impossible owing to the absence of complete experimental data based on *mechanical* power, as opposed to measurements of metabolic rates. Nevertheless, comparisons of measured and predicted characteristic speeds, and inferred power curves are frequently made, despite the total absence of uncertainty estimates of the theoretically predicted quantities. Here the method for correct calculation of uncertainty estimates in mechanical power models is outlined in detail, and analytical and numerical results are derived for realistic examples. The sensitivity of the calculated variations in power requirement varies greatly among the independent variables, and the practical and theoretical consequences of this variation are discussed. Pending the arrival of appropriate experimental measurements, it is now possible, in principle, to make quantitative comparisons with theoretical predictions.

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1. Introduction

1.1. MECHANICAL OR AERODYNAMIC POWER CURVES

Flight is locomotion in a fluid (air), whose density is so low compared with that of the flying body that hydrostatic forces can be neglected. In that case, the entire weight of the bird has to be supported by accelerating air downwards, which in turn requires work to be done on the air at some minimum rate (the induced power). At the same time, additional work has to be done against the aerodynamic drag forces caused by the bird's forward motion through the air (parasite power), and by the relative motion between its wings and the air (profile power).

An accurate and complete calculation of the forces exerted by a sufficiently realistic, flapping, wing–body system on the surrounding air (and hence the drag forces on the bird from the air), by direct numerical solution of the Navier–Stokes

equations, lies well beyond the reach of current computer capacity, and in practice, some kind of more simple physical model must be solved instead. The basic approaches were reviewed in Spedding (1992), and papers by Hall & Hall (1996) and Hall *et al.* (1998) represent recent examples of elegant, state-of-the-art calculations with potential application to practical problems (e.g. Spedding & Lissaman, 1998).

The more sophisticated models usually concentrate on the accurate estimation of the induced power component, but without exception, simplifying assumptions limit the range of flight regimes that can be covered, and the additional problems of estimating viscous losses at the appropriate Reynolds numbers ($Re \equiv Uc/v$ for a wing chord, $c = 10$ cm and flight speed, $U = 10$ m s^{-1}, with v the kinematic viscosity of air, is approximately 7×10^4) remain particularly vexing. In the spectrum of flight models, ranging

from simple and easy to use, to complex and unwieldy, practical applications have tended towards the former, in part because the frequently small-to-negligible practical benefits of incremental improvements in the accuracy of computing one particular component do not justify the extra cost incurred (as measured in dollars, CPU or program debugging time, backpack weight, number of field measurements, etc.).

The purpose of this paper is primarily to draw attention to the principles and benefits of including appropriate error analysis in *any* flight model prediction and calculation. The example analysis will be performed on the model outlined in Pennycuick (1989), because it is simple. The same reason makes it the most widely applied model in practical ornithology, and ensures the broadest practical application of the results herein. This focus is for clarity of exposition and directness of practical application, and it would be very gratifying to see a more widespread application of these types of calculation to other models, which, incidentally, might also usefully be compared on this basis.

Back at the bird, the total rate at which work has to be done, that is the power required from the muscles, depends on the forward speed, and on whether the bird is climbing or descending, accelerating or decelerating. These latter complications are avoided by restricting attention to the special case of level flight at a constant true air speed, V. For that special case, the Pennycuick (1989) model calculation of the power required by a particular bird to fly at a particular speed requires estimates for the values of eight input variables, falling into three categories:

1. *Morphological variables*: these must be measured on the particular bird, using specified procedures. They are the total mass, m, the wing span, b, the wing area, S, and the body cross-sectional area, S_b.
2. *Aerodynamic variables*: outside of controlled laboratory experiments, typically involving wind tunnels, these usually cannot be measured for the individual bird, so their values are calculated from general relationships established by such experiments. These include the constants, k, the induced power factor, C_{Db}, the body drag coefficient,

and X_1 (or equivalently, C_2), a multiplying constant for the profile power factor. This is assigned a constant value internally, since there is currently little rational basis for making any particular modification to the constant itself, short of modifying the formulation of the entire calculation, which is explained further in Section 3.3. It is notable that each of these constants corresponds to a component of the aerodynamic power calculation, and reflects a significant degree of uncertainty in the calculation of all three components of the aerodynamic power.
3. *Environmental variables*: These are the acceleration due to gravity, g, and the air density, ρ. They are frequently assigned constant values, although g can vary by 0.8% across the globe, and ρ can vary substantially, by 20% or more, in flights involving significant, but normal, changes in altitude.

Once the bird, and the air through which it flies, have been defined by assigning values to the above variables, Program 1A in Pennycuick (1989) sets the true air speed, V, successively to a series of different values, and estimates the mechanical power required to fly at each speed. It follows from the underlying mechanics (this is equally true for birds, planes, helicopters, and gliders, where the rate of loss of potential energy substitutes for power) that the resulting form of $P(V)$—the power curve—is U-shaped, whose minimum value defines a characteristic speed, the minimum power speed, V_{mp}, where the total combined aerodynamic power requirement (mechanical work done per unit time) is at its minimum value.

1.2. METABOLIC POWER CURVES

The metabolic power curve represents the rate at which the animal consumes fuel energy, but it is not a simple transform of the physical power curve outlined in the previous section. Part of the fuel energy consumed by a flying bird is converted into mechanical work, and this component can be derived from the physical power curve, if a value is known or assumed for the efficiency with which the muscles convert fuel energy into work. In sustained, aerobic flight, the muscles that ventilate the lungs also consume fuel energy,

as does the heart. These secondary demands for fuel energy are presumably related in some way to the primary mechanical power output of the flight muscles, but there is unfortunately no physiological theory from which their magnitude can be calculated. In addition, it is usually assumed that basal metabolism is an additional overhead, which can be simply added to any other demands for fuel energy. Basal metabolism is measured by definition in the inactive animal, and there is currently no theory that determines whether it continues when the animal is active, and if so, at what rate.

1.3. EXPERIMENTAL TESTING OF PREDICTED POWER CURVES

1.3.1. *Comparing Metabolic Power Curves*

Many investigators have measured variables that can be used as indicators of the rate of fuel consumption (the metabolic power) in flying animals, usually the rate of oxygen consumption, the rate of carbon dioxide production, or the rate of mass loss. Certain authors, notably Rothe *et al.* (1987), have made such measurements over a range of air speeds, on birds flying at a steady speed in a wind tunnel. There has been much discussion as to whether such measurements do or do not confirm the shape of predicted power curves, but insufficient attention has been paid to the nature of the curves being compared, or to the formal basis of the comparison. Such a comparison requires estimates of uncertainty for both the predicted power and the experimental measurements, and it also obviously requires that like be compared with like, i.e. that the predicted and observed values either both refer to physical, or both to metabolic power. The uncertainty of predicted powers can be calculated only if the predictions come from a formal theory. As noted above, this condition is satisfied for the physical, but not for the metabolic power curve. There is as yet no formal or quantitative theory for deriving the metabolic power curve from the physical curve, and therefore it is not practical to use measurements of the rate of fuel energy consumption to verify a predicted power curve of either type. For this reason, the numerous measurements of metabolic power in the physiological literature cannot be used for this purpose.

1.3.2. *Direct Comparison of Physical Power Curves*

It *is* feasible to calculate uncertainties for the physical power curve, and this paper sets out a method for doing it. Experimental values are then required for physical, not metabolic power. Measuring the physical power depends on purely mechanical measurements, and has so far been attempted twice on birds flying in a wind tunnel (Biewener *et al.*, 1992; Dial *et al.*, 1997). The method used in both cases was to bond a strain gauge to the dorsal surface of the bird's humerus, at the proximal end, and calibrate it so as to determine the force which the pectoralis muscle applied to the bone. The amplitude of the displacement of the muscle attachment was then estimated from video, so giving an estimate of the work done during shortening. The power was obtained by multiplying this cycle work by the wingbeat frequency. Such a measurement could be compared directly with the predicted power, if all the measurements needed for the prediction were also recorded. Unfortunately, the necessary measurements were not recorded in these two experiments, but it is anticipated that this will be done in future wind tunnel experiments, and also that less intrusive methods for measuring the cycle work will be developed.

1.3.3. *Testing Predictions Through Observations of the Flight Speed, V*

The accuracy of the flight power model can also be tested indirectly, by comparing predicted and observed values of the characteristic minimum power speed. For example, it is possible to measure V_{mp} in a bird trained to fly in a wind tunnel. If there is indeed a flight speed at which the observed metabolic power consumption is lowest, and it is close ("close" can be defined quite precisely using the methods outlined below) to that predicted by the mechanical power curve, then the calculation method and the values assumed for the constants in Section 1.1 (the *aerodynamic variables*) are supported. Note that a minimum metabolic power speed need not *necessarily* accord with V_{mp}, because variations in the energy conversion efficiency may skew the estimate in either direction (increasing, or decreasing V). However, significant variations in

muscle efficiency so close to the presumed design point of the flight system are perhaps unlikely. Alternatively, the speeds at which wild birds are observed to fly in the field can be compared with calculated values of V_{mp} for each species. If the birds are, in fact, flying at V_{mp}, then this also constitutes a broad test of the underlying model predictions. We should note here that the assumptions about the desirability, and/or feasibility of flying at and maintaining a true air speed of V_{mp} may well be more suspect, and less general, than frequently assumed in the literature.

1.4. OBJECTIVES

The objectives of this paper are thus three-fold: (i) to give an explicit but general method for the calculation of uncertainties in functions of multiple variables in terms that can readily be applied to quantitative and theoretical biology; (ii) to present a detailed application of such methods to the particular case of the mechanical flight power curve, in anticipation of future comparisons with appropriate experimental results; and (iii) to analyse the implications of the numerical results for the theoretical power curve calculation.

2. Methods for Estimating Uncertainties

2.1. DEFINITIONS

The formal treatment of uncertainty analysis in experimental measurements with multiple variables appears to have been introduced by Kline & McClintock (1953). Recent summaries can be found in various textbooks, e.g. Beckwith et al. (1993); and Figliola & Beasley (1995). The following presentation is thus not entirely new, but it is a unique collection and selection of the most important methods required to perform the uncertainty analysis in the subsequent sections. It is both a little more selective, and a little more complete, than a standard treatment; the goal is to show all necessary derivations so that no mystery remains, and all of these methods can be put to practical use.

The following definitions are elementary and not unusual, but in this context it is essential that they be clearly stated for a precise technical discussion of the more applied, ensuing calculations.

Let x be a real-valued physical quantity. It is never possible to know x exactly, only to make some estimate that attempts to minimize the error, E, defined by

$$E = x - x_i, \qquad (1)$$

where x_i is an observation or measurement. Since x is unknown, then, without exception, so is E. When multiple observations are made, then x_i can be replaced by a mean value, $\bar{x}$, and the average error is now

$$E = x - \bar{x} \qquad (2)$$

and is still unknown. Errors can be of two kinds: systematic and random. The former lead to bias in estimates of x, and can in principle be corrected. The remaining random errors can be estimated, and the numerical estimate of their *likely* magnitude is the *uncertainty* in the measurement, Δx. When a normal distribution about x is expected, a reasonable measure of Δx is the standard deviation, σ, whose value can be calculated from the usual statistics. For single measurements in otherwise ideal conditions, Δx is not likely to be less than 1/2 of the instrument resolution. This marks the lower bound of the possible values for Δx. Higher values will accrue in non-ideal circumstances, and numerical estimates should reflect this. Given a realistic estimate of Δx, it is now possible to compare two such numbers according to whether their values are within their respective uncertainty ranges. In other words, one simply determines the truth or falsehood of the proposition: $x_i \pm \Delta x_i = x_j \pm \Delta x_j$. Without uncertainty estimates, Δx_i, Δx_j, it is not possible to determine the truth or falsehood of $x_i = x_j$.

2.2. PROPAGATION OF UNCERTAINTIES

If y is a real, continuous function of n independent variables,

$$y = f(x_1, x_2, \ldots, x_n),$$

then given small increments, $\Delta x_1, \Delta x_2, \ldots, \Delta x_n$, Δy, the change in value of y, is

$$\Delta y = f(x_1 + \Delta x_1, x_2 + \Delta x_2, \ldots, x_n + \Delta x_n)$$

$$- f(x_1, x_2, \ldots, x_n) = \Delta f. \qquad (3)$$

Equation (3) can be approximated by retaining the linear, first-order terms of a Taylor series expansion about $x_1, x_2, \ldots, x_n$,

$$\Delta f = \frac{\partial f}{\partial x_1} \Delta x_1 + \frac{\partial f}{\partial x_2} \Delta x_2 + \cdots + \frac{\partial f}{\partial x_n} \Delta x_n$$

$$+ \varepsilon_1 \Delta x_1 + \varepsilon_2 \Delta x_2 + \cdots + \varepsilon_n \Delta x_n, \quad (4)$$

where the ε's are small coefficients for higher-order terms. $\varepsilon_{1,2,\ldots,n} \to 0$ as $\Delta x_{1,2,\ldots,n} \to 0$, and the total differential, Δf, can be written as

$$\Delta f = \frac{\partial f}{\partial x_1} \Delta x_1 + \frac{\partial f}{\partial x_2} \Delta x_2 + \cdots + \frac{\partial f}{\partial x_n} \Delta x_n. \quad (5)$$

Recalling the original motivation for this exercise, we now have an expression for the change in value of a function given small changes in the values of its independent variables. In the case of experimental uncertainty analysis, the Δ's represent uncertainties in the estimates of physical quantities, and can be of any sign, provided systematic biases have been removed or compensated for. In any single instance, there is thus no expectation of a particular sign for a particular component, and a positive quantity can be assured by taking the square of eqn (5). For convenience, consider an example with just two variables, $\Delta x_1, \Delta x_2$, where

$$(\Delta f)^2 = \left(\frac{\partial f}{\partial x_1} \Delta x_1 + \frac{\partial f}{\partial x_2} \Delta x_2 \right)^2, \quad (6)$$

which can be expanded as

$$(\Delta f)^2 = \left(\frac{\partial f}{\partial x_1} \Delta x_1 \right)^2 + 2 \frac{\partial f}{\partial x_1} \Delta x_1 \frac{\partial f}{\partial x_2} \Delta x_2$$

$$+ \left(\frac{\partial f}{\partial x_2} \Delta x_2 \right)^2.$$

Now, provided Δx_1 and Δx_2 are uncorrelated, then the middle term will, on average, be zero, so the *most likely* value of the uncertainty, $\overline{\Delta f}$, is

$$\overline{\Delta f} = \left\{ \overline{\left(\frac{\partial f}{\partial x_1} \Delta x_1 \right)^2} + \overline{\left(\frac{\partial f}{\partial x_2} \Delta x_2 \right)^2} \right\}^{1/2}. \quad (7)$$

3. Uncertainty Estimates for Power Curve Components

The total mechanical power, P, required for flight is calculated as,

$$P = P_i + P_{par} + P_{pro}, \quad (8)$$

where P_i is the induced power required to support the weight, P_{par} is the parasite power required to overcome viscous drag on the body and P_{pro} is the profile power required to overcome viscous drag on the wing surface. It is convenient to consider each of these terms separately, and then combine the results.

3.1. INDUCED POWER

The induced power can be written as

$$P_i = \frac{kW^2}{2\rho V S_d}, \quad (9)$$

where k is the aerofoil efficiency factor, $W = mg$ is the body weight, ρ is the air density and V is the flight speed. S_d is the actuator disc area,

$$S_d = \frac{\pi b^2}{4}$$

and so in terms of the independent variables,

$$P_i = \frac{2kW^2}{\rho V \pi b^2}. \quad (10)$$

The underlying rationale is that the power is first calculated for an actuator disc of diameter b, producing a force equal to W. This is regarded as a minimum or ideal estimate for P_i. It is then multiplied by the induced power factor, k, whose default value is 1.2, to account for the departure of the effect of the real flapping wings from the ideal actuator disc. It may eventually be possible to replace this simple scenario with a more elaborate and/or realistic calculation, based on the structure of the vortex wake (e.g. Spedding, 1987a), but insufficiently general information about birds' vortex wakes is available at present for this to be attempted with great confidence.

We wish to know ΔP_i, given uncertainties in each of the variables in eqn (10). For small

deviations, the total differential of eqn (10), following eqn (5), is

$$\Delta P_i = \frac{\partial P_i}{\partial k} \Delta k + \frac{\partial P_i}{\partial W} \Delta W + \frac{\partial P_i}{\partial \rho} \Delta \rho$$

$$+ \frac{\partial P_i}{\partial V} \Delta V + \frac{\partial P_i}{\partial b} \Delta b. \tag{11}$$

The partial derivatives of P_i can be evaluated and so eqn (11) becomes

$$\Delta P_i = \frac{2W^2}{\rho V \pi b^2} \Delta k + \frac{4kW}{\rho V \pi b^2} \Delta W - \frac{2kW^2}{\rho^2 V \pi b^2} \Delta \rho$$

$$- \frac{2kW^2}{\rho V^2 \pi b^2} \Delta V - \frac{kW^2}{\rho V \pi b^3} \Delta b. \tag{12}$$

A less cumbersome expression can frequently be found by writing the relative uncertainty, which here is

$$\frac{\Delta P_i}{P_i} = \frac{\Delta k}{k} + \frac{2\Delta W}{W} - \frac{\Delta \rho}{\rho} - \frac{\Delta V}{V} - \frac{2\Delta b}{b}. \tag{13}$$

Note that, for now, the signed terms in eqn (13) are retained [rather than taking sums of squares as in eqn (7)] because the remaining components of P in eqn (8) also involve some of the same primitive variables.

3.2. PARASITE POWER

The parasite power is

$$P_{par} = \tfrac{1}{2}\rho V^3 S_b C_{db}, \tag{14}$$

where S_b is the equivalent body frontal area, and C_{db} is the body drag coefficient. Proceeding as for P_i, the relative uncertainty is

$$\frac{\Delta P_{par}}{P_{par}} = \frac{\Delta \rho}{\rho} + \frac{3\Delta V}{V} + \frac{\Delta S_b}{S_b} + \frac{\Delta C_{db}}{C_{db}}. \tag{15}$$

3.3. PROFILE POWER

The profile power is not a simple quantity to calculate because it depends sensitively on details of flow separation on the wing, which at these Reynolds numbers, are to all intents and purposes, unknown. It can rather be roughly

estimated as the product of some multiplying factor times the absolute minimum power,

$$P_{pro} = X_1 P_{am}. \tag{16}$$

P_{am} can be found from the minimum of $P_i + P_{par}$ vs. V. If

$$P_i + P_{par} = P_{i+par} = \frac{kW^2}{2\rho V S_d} + \frac{1}{2}\rho V^3 S_b C_{db} \tag{17}$$

then the condition

$$\frac{\partial P_{i+par}}{\partial V} = 0$$

is met at the characteristic flight speed, V_{mp},

$$V_{mp} = \left(\frac{kW^2}{3\rho^2 S_b S_d C_{db}}\right)^{1/4}. \tag{18}$$

Substitution of this expression for V_{mp} back into eqn (17) gives

$$P_{am} = C_1 \frac{k^{3/4} W^{3/2} S_b^{1/4} C_{db}^{1/4}}{\rho^{1/2} S_d^{3/4}}, \tag{19}$$

where $C_1 = (2/3)3^{1/4} \cong 0.877$. X_1 is the profile power ratio, which was assigned a fixed default value of 1.2 in the original Version 1.0 programs of Pennycuick (1989), but which now (Version 1.1 onwards) has a default value

$$X_1 = C_2 \frac{S}{b^2}, \tag{20}$$

where S is the wing area, and $C_2 = 8.4$. The effect of this is to make the default value of X_1 proportional to the wing area, with the same value as before for a bird of aspect ratio 7. Profile power has never been directly measured in a flying bird, nor is there any valid analytical basis for calculating it, as the underlying physical principles are poorly understood. The principle that P_{pro} can be considered independent of speed, and proportional to P_{am} is more than a guess, however, and comes from an early analysis of wind tunnel results by Pennycuick (1968, 1969). It remains the best available approximation for speeds near and

somewhat above the minimum power speed, but not for very low or very high speeds.

Substituting eqns (19) and (20) into eqn (15), and expressing the result in primitive variables,

$$P_{pro} = C_1 C_2 \frac{k^{3/4} W^{3/2} S_b^{1/4} C_{db}^{1/4} S}{(\pi/4)^{3/4} \rho^{1/2} b^{7/2}}. \qquad (21)$$

Note that while P_{pro} is not a function of V, it is a strong function of the wingspan, b. The relative uncertainty in ΔP_{pro} is

$$\frac{\Delta P_{pro}}{P_{pro}} = \frac{3}{4}\frac{\Delta k}{k} + \frac{3}{2}\frac{\Delta W}{W} + \frac{1}{4}\frac{\Delta S_b}{S_b} + \frac{\Delta S}{S}$$

$$- \frac{1}{2}\frac{\Delta\rho}{\rho} - \frac{7}{2}\frac{\Delta b}{b}. \qquad (22)$$

4. Calculation of ΔP

4.1. QUICK ESTIMATES

The total uncertainty in predicted mechanical power, from eqn (8) is

$$\Delta P = \Delta P_i + \Delta P_{par} + \Delta P_{pro}. \qquad (23)$$

Let us suppose that in the neighbourhood of V_{mp}, $P_i \cong P_{par}$, in which case $P_{am} \cong 2P_i \cong 2P_{par}$. If, in eqn (16), $X_1 \cong 1$, then

$$P_{pro} \cong 2P_i - 2P_{par} \qquad (24)$$

and the relative contributions of the relative uncertainties in the power components are

$$\frac{\Delta P}{P} \cong \frac{\Delta P_i}{P_i} + \frac{\Delta P_{par}}{P_{par}} + 2\frac{\Delta P_{pro}}{P_{pro}}. \qquad (25)$$

The ratios chosen here are for convenience only, and do not have to be exactly correct. They are in fact demonstrably incorrect for the numerical example given later, based on data in Table 1, but we shall see that the predictions emerge relatively unscathed. This simplification allows the comparative importance of contributions to the total uncertainty from all the independent variables to be assessed by direct inspection of the sums of the terms of each variable uncertainty in eqns (13), (15) and (22). There are eight independent

TABLE 1
Analytical estimates for the relative contributions to the total uncertainty in calculation of mechanical power. The relative contribution to each power component from each independent variable can be compared in columns 2–4. The contribution to the total is calculated from taking the modulus of the sum of columns 2, 3 and 2 times column 4 [as indicated in eqn (25)]. The actual contribution to the most likely uncertainty will depend on the square of each individual term, and is given in the rightmost column 6

Δ	ΔP_i	ΔP_{par}	ΔP_{pro}	ΔP	$(\Delta P)^2$
$\Delta b/b$	-2		$7/2$	5	25
$\Delta W/W$	2		$3/2$	5	25
$\Delta k/k$	1		$3/4$	$2\frac{1}{2}$	$6\frac{1}{4}$
$\Delta V/V$	-1	3		2	4
$\Delta S/S$			1	2	4
$\Delta S_b/S_b$		1	$1/4$	$1\frac{1}{2}$	$2\frac{1}{4}$
$\Delta C_{db}/C_{db}$		1	$1/4$	$1\frac{1}{2}$	$2\frac{1}{4}$
$\Delta\rho/\rho$	-1	1	$-1/2$	1	1

variables, whose relative contributions to the total uncertainty are given in Table 1. Note that the contributions from individual terms are summed as signed quantities. Over all the i-variables in the left column of Table 1, the most likely value for the uncertainty in any of the power calculations (components in columns 2–4, or the total in column 5) can be written

$$\overline{\frac{\Delta P_n}{P_n}} = \left\{ \sum_{i=1}^{8} (C_i \Delta_i)^2 \right\}^{1/2}, \qquad (26)$$

where P_n denotes either P_i, P_{par}, P_{pro} or P, and the C_i coefficients are given for the i-th variable in Table 1. The accuracy of these estimates depends almost entirely on the validity of the assumptions behind the approximate equation (25), and a 20% margin of error is not unreasonable.

Table 1 shows immediately that certain variables contribute much more than others to the total variation in mechanical power. The likely relative magnitudes can be seen in the rightmost column. From the practical point of view it is obvious that considerable care ought to be taken in making measurements of the wingspan, b, and

the body weight, W, either in the field, or in the laboratory. The same remark applies also to using values quoted in the literature, or to using mean values from a variable population applied to one single event or individual.

The sensitivity of P, as measured by ΔP, to small variations in b and W is also of extreme importance to the individual doing the flying (here one should consider the ratio of sums in ΔP, column 5, rather than their squares in column 6). One can further note that the contribution of ΔV is by no means negligible. Crude estimates of V derived by dividing long distances over long times in winds of uncertain direction and magnitude can be expected to generate differences in subsequent calculations of P that are comparable in magnitude to the total probable range of P in common use by the individual bird, bat or insect.

4.2. COMPUTATION OF $\Delta P(V)$

Numerical calculation of $\Delta P(V)$ can be performed directly on eqn (23), without resorting to the assumptions behind eqn (25). Here, the dependent variable is P, the mechanical power transmitted by the muscles to the wings. V is used as the ordinate for plotting both the predicted power and the uncertainty. The remaining independent, primitive variables (b, m, g, k, S, S_b, C_{db}, ρ) make up the same list as discussed in the previous section, with m and g being treated separately.

Equations (10), (14) and (21) are differentiated with respect to each variable, as before, only V, as the control parameter, is not included, and the values of the partial differentials in each variable (when used) are now calculated at each speed, for each component of power. Up to three partial differentials are then added together, to give the partial differential of the total power with respect to that variable. Thus, for input variable x_i,

$$\frac{\partial P}{\partial x_i} = \frac{\partial P_i}{\partial x_i} + \frac{\partial P_{par}}{\partial x_i} + \frac{\partial P_{pro}}{\partial x_i}. \tag{27}$$

The partial differentials are given for reference in Appendix A. After adding all (signed) contributions from each of the power components to each of the independent variables, the most likely

value for the total uncertainty is found by

$$\overline{\Delta P} = \left\{ \sum_{i=1}^{8} \left(\frac{\partial P}{\partial x_i} \Delta x_i \right)^2 \right\}^{1/2} \tag{28}$$

as indicated in eqn (7).

5. Uncertainty Bands in Calculated Power Curves

5.1. SOURCES OF UNCERTAINTY

Most input variables can be directly measured, but values have to be assumed for some of them. The precision (a measure of the variation in repeated measurements; when the bias is zero, then the precision is a reasonable measure of the uncertainty) with which variables such as wing span, wing area and body mass can be measured depends on the circumstances. For an individual bird flying in a wind tunnel, it is possible to monitor these variables to a precision better than $\pm 1\%$. At the other extreme, when air speed measurements are made in the field, on wild birds that cannot be individually measured, the observer has to be content with mean values, measured on samples of specimens that have been caught. In this case, the uncertainty is much higher, and can be estimated from the standard deviation of the sample. Typical values might be $\pm 3\%$ for $\Delta b/b$, $\pm 10\%$ for $\Delta m/m$ and $\pm 6\%$ for $\Delta S/S$. Dimorphic species, in which the sexes cannot be distinguished in the field, will have higher standard deviations. Body drag coefficients can also now be measured in individual wind tunnel birds, and estimates for birds observed in the field have improved as a result of wind tunnel experiments (Pennycuick *et al.*, 1996). It may eventually be possible to estimate values for the induced power factor, k, from studies of the vortex wakes of wind tunnel birds. Spedding (1987b), for example, inferred a value of close to 1.0 from the wake spacing in a gliding kestrel. However, for the most part, a value has to be assumed in both wind tunnel and field situations, with no objective way to determine the uncertainty.

5.2. THE TEAL EXAMPLE FOR WIND TUNNEL AND FIELD STUDIES

Table 2 shows measured and assumed values for the eight variables required for a power curve

TABLE 2

Input data for a teal (Anas crecca) *observed in wind tunnel experiments by Pennycuick* et al. (1996). *Δ here is the relative uncertainty, given by the standard deviation of the estimate divided by the estimate itself*

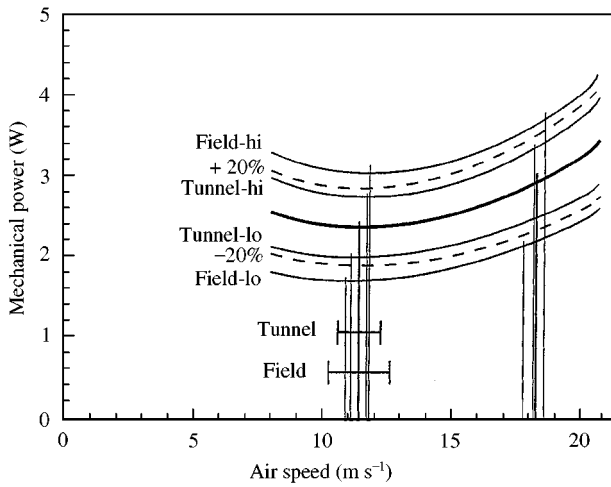| Variable	Symbol	Estimate	Units	$\Delta_{windtunnel}$	Δ_{field}
Body mass	m	0.235	kg	0.01	0.10
Wing span	b	0.582	m	0.01	0.05
Induced power factor	k	1.2		0.2	0.2
Gravitational acceleration	g	9.81	m s^{-2}	0.005	0.005
Air density (sea level)	ρ	1.23	kg m^{-3}	0.005	0.01
Body frontal area	S_b	0.0031	m^2	0.05	0.2
Body drag coeffcient	C_{db}	0.10		0.2	0.2
Wing area	S	0.0458	m^2	0.05	0.2

FIG. 1. Heavy curve: power curve $P(V)$ for the teal, calculated from data in Table 2. Dashed curves: $P \pm 20\%$. Thin curves: $P \pm \Delta P$, where ΔP is calculated from the uncertainty values in Table 2. There are two pairs of curves, for wind tunnel and field conditions. Horizontal bars: uncertainty limits for the minimum power speed V_{mp}, also for wind tunnel and field conditions.

calculation, for an individual teal (*Anas crecca*), which was used in wind tunnel experiments. Each variable is accompanied by two uncertainty estimates.

The column headed "$\Delta_{wind\,tunnel}$" represents the precision with which variables could be measured on the individual bird in laboratory settings, while the column headed "Δ_{field}" contains (mostly higher) values that would apply if measurements were being made on a population of wild teal, which could not be individually caught and measured.

Figure 1 shows a power curve [$P(V)$] calculated from these values, with two sets of

boundary curves representing $P \pm \Delta P$, where ΔP is the uncertainty from eqn (28) for the wind tunnel and field uncertainty values.

5.3. EFFECT OF INDIVIDUAL INPUT VARIABLES

Each of the eight panels of Fig. 2 shows the same power curve for the teal as Fig. 1, with curves above and below representing $P \pm \Delta P$ at each speed. In each panel, the curves of $P \pm \Delta P$ have been calculated by setting the uncertainties of seven out of the eight input variables to zero, with the uncertainty of the remaining variable set to 10% of its value. On each graph the magnitude of $\Delta P/P$ at the minimum power speed (V_{mp}) is shown.

As previously found in the analytical results of Table 1, the magnitude of ΔP is much higher for some input variables than for others, and the ratio of their numerical values is quite consistent with the predictions of Table 1. A 10% uncertainty in the wing span, b, results in over 24% uncertainty in P at the minimum power speed, whereas a similar proportional uncertainty in the body frontal area, S_b, or the body drag coefficient, C_{Db}, results in only 2.6% uncertainty in P. Generalizing over the range of V, the uncertainty of P is far more sensitive to that of b than to any other input variable, including the wing area S. The implication for the practical ornithologist is that it is essential to obtain the most accurate possible estimate of the wing span of any bird for which power curves are to be calculated, but less important to get an accurate wing area. If necessary, the wing area can be estimated from the wing span, using a value for the aspect ratio, obtained from
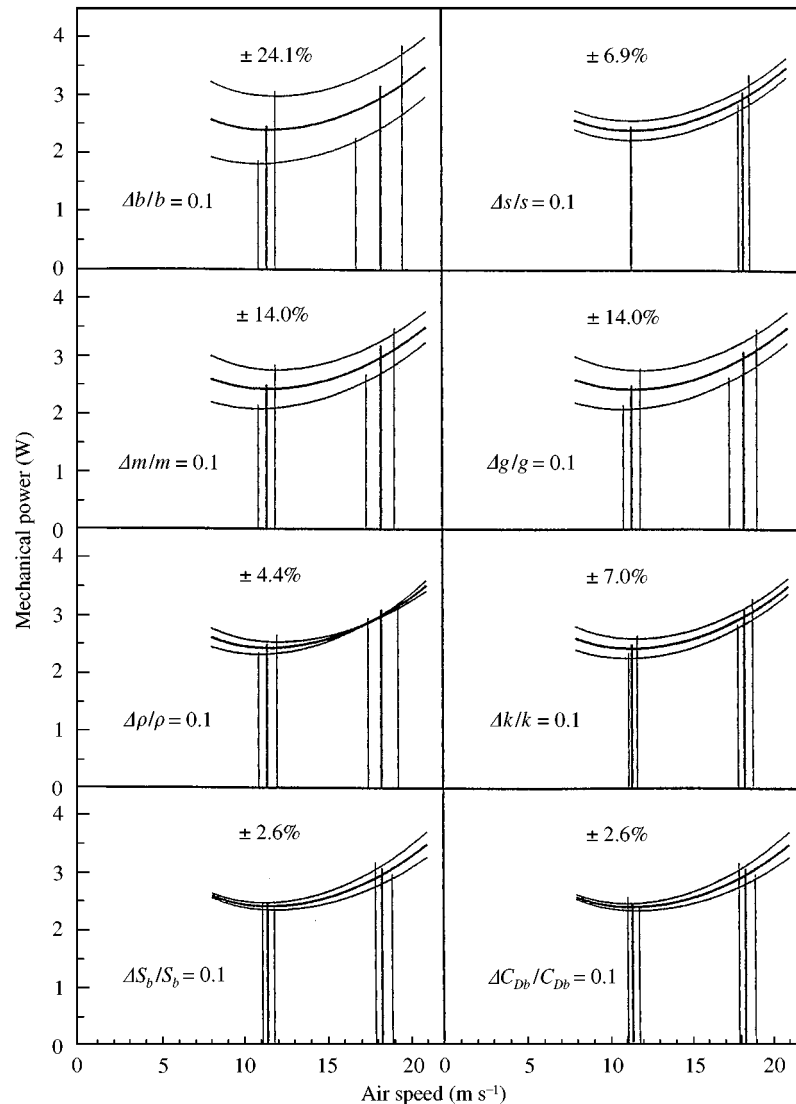
FIG. 2. The same power curve $P(V)$ as in Fig. 1, with uncertainty curves $P \pm \Delta P$ calculated on the basis that one input variable (identified in each panel) has 10% uncertainty, while the other seven have zero uncertainty. The percentage uncertainty of P is shown for the minimum power speed in each panel.

a sample of birds of the same species. Figure 2 also shows that a fixed proportional uncertainty of some variables (wing span, mass, gravity, air density and induced power factor) has more effect on the uncertainty of P at low than at high speeds, whereas for others (body frontal area and the body drag coefficient) the reverse is the case. There is one particular speed at which any uncertainty in the air density has no effect at all on the uncertainty of the power.

5.4. LIMITATIONS

Although the uncertainty bands in Figs 1 and 2 give clear apparent limits to the range of likely

values of $P(V)$, their calculation shares the same assumptions, and hence limitations, as those of the formulation of the flight power components themselves. For example, on a very basic level, departures from ideal actuator discs are subsumed into the constant coefficient, k, whose value is given a fairly large relative uncertainty of 0.2. However, the degree of departure from model conditions is quite likely to be a function of V, and so an improvement would be to find a reasonable expression for $k(V)$. The effect of this, and other more sophisticated modifications to the theory (for example, deriving from improved models of the geometry of the wake vortices), are

not necessarily correctly contained within the given uncertainty bands.

6. Characteristic Speeds

Each of the curves in Figs 1 and 2 is marked with the minimum power speed, V_{mp}, and the maximum range speed, V_{mr}, at which the ratio of speed to power passes through a maximum. These speeds are shifted by uncertainties in individual variables, not always in the same direction (Fig. 2). V_{mp} is easier to calculate than V_{mr}, and is useful for normalizing the speeds of a particular bird. It can be measured in wind tunnel birds by observing wingbeat frequency (Pennycuick *et al.*, 1996).

V_{mp} from eqn (18) can be written as

$$V_{mp} = \left(\frac{k(mg)^2}{3\rho^2 S_b S_d C_{db}} \right)^{1/4}. \qquad (29)$$

The relative uncertainty $\Delta V_{mp}/V_{mp}$ is

$$\frac{\Delta V_{mp}}{V_{mp}} = -\frac{1}{2}\frac{\Delta m}{m} - \frac{1}{2}\frac{\Delta g}{g} - \frac{3}{4}\frac{\Delta k}{k} - \frac{3}{2}\frac{\Delta \rho}{\rho}$$
$$- \frac{3}{2}\frac{\Delta b}{b} - \frac{5}{4}\frac{\Delta S_b}{S_b} - \frac{5}{4}\frac{\Delta C_{db}}{C_{db}}. \qquad (30)$$

Following eqn (7), the most likely value for ΔV_{mp} is

$$\overline{\Delta}_{mp} = V_{mp} \left\{ \left(\frac{1}{2}\frac{\overline{\Delta m}}{m} \right)^2 + \left(\frac{1}{2}\frac{\overline{\Delta g}}{g} \right)^2 \right.$$
$$+ \left(\frac{3}{4}\frac{\overline{\Delta k}}{k} \right)^2 + \left(\frac{3}{2}\frac{\overline{\Delta \rho}}{\rho} \right)^2$$
$$\left. + \left(\frac{3}{2}\frac{\overline{\Delta b}}{b} \right)^2 + \left(\frac{5}{4}\frac{\overline{\Delta S_b}}{S_b} \right)^2 + \left(\frac{5}{4}\frac{\overline{\Delta C_{db}}}{C_{db}} \right)^2 \right\}^{1/2}.$$
$$(31)$$

Using the uncertainty values listed in Table 2 for most likely estimates of "field" and "wind tunnel" conditions yields two pairs of upper and lower limits for V_{mp}, which are marked as horizontal bars in Fig. 1. These can be used to determine whether an experimental result differs significantly from the predicted V_{mp}.

7. Summary and Conclusions

This paper began by outlining a procedure for performing an uncertainty analysis for a general problem involving a function of several variables. Many problems of biological interest can be broken down this way, even, for example, a simple calculation of velocity = distance/time. A slightly more complicated example of generating uncertainty measures for the flight power curve was then examined, and the sensitivity of the calculation to small variations in its component variables was examined. It was immediately clear that the relative sensitivity of the total result varied greatly (the change in mechanical power was 6 times more sensitive to changes in wingspan, b, than to changes in wing area, S, for example), with evident practical consequences.

Calculations and discussion of the flight power usually occurs within the context of the flight power curve, where V is set as an independent variable, and $P(V)$ is generated over some useful range of V. Here, the uncertainty values can also be computed as a function of V, and so variations in $P(V)$ due to a specified variation in one or more of the other variables can be drawn as bands that enclose the central, most-likely line corresponding to the original prediction. Now we have arrived at the point promised in the introduction, with theoretical power curves, complete with uncertainty estimates. When suitable experimental measurements allow estimates of the mechanical power, complete with their own uncertainty estimates, of course, it will then be possible, for the first time, to make a direct comparison between the two.

In the meantime, indirect checks can be made by comparing predictions of characteristic speeds, such as V_{mp}, and explicit formulae are given for this also, together with numerical examples.

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APPENDIX A

A Complete Calculation of the Partial Derivatives for Mechanical Flight Power Calculations

For completeness, and possibly handy reference, the partial differentials for each independent, primitive variable in each power component are presented, collected as complete expressions for the total differential for each power component. It is understood that each calculation is, by itself, rather elementary, but since the practice seems rarely actually practiced, it is felt that demonstrating its simplicity by detailing each step might encourage broader usage in similar, or even completely different, investigations.

A.1. TOTAL DIFFERENTIALS OF P_i, P_{par} AND P_{pro}

A.1.1. *Induced Power*

The equation for P_i is repeated from eqn (10)

$$P_i = \frac{2k(mg)^2}{\rho V \pi b^2}. \tag{A.1}$$

Following the form of eqn (5), the total differential with respect to all variables other than V is

$$\Delta P_i = \frac{\partial P_i}{\partial k} \Delta k + \frac{\partial P_i}{\partial m} \Delta m + \frac{\partial P_i}{\partial g} \Delta g$$

$$+ \frac{\partial P_i}{\partial \rho} \Delta \rho + \frac{\partial P_i}{\partial b} \Delta b. \tag{A.2}$$

Equation (A.2) evaluates to

$$\Delta P_i = \frac{2(mg)^2}{\rho V \pi b^2} \Delta k + \frac{4kmg^2}{\rho V \pi b^2} \Delta m + \frac{4km^2 g}{\rho V \pi b^2} \Delta g$$

$$- \frac{2k(mg)^2}{\rho^2 V \pi b^2} \Delta \rho - \frac{4k(mg)^2}{\rho V \pi b^3} \Delta b. \tag{A.3}$$

A.1.2. *Parasite Power*

The equation for P_{par} is repeated from eqn (14),

$$P_{par} = \tfrac{1}{2} \rho V^3 S_b C_{db}, \tag{A.4}$$

whose total differential (again, omitting V) is

$$\Delta P_{par} = \frac{\partial P_{par}}{\partial \rho} \Delta \rho + \frac{\partial P_{par}}{\partial S_b} \Delta S_b + \frac{\partial P_{par}}{\partial C_{db}} \Delta C_{db}. \tag{A.5}$$

The result is

$$\Delta P_{par} = \tfrac{1}{2} V^3 S_b C_{db} \Delta \rho + \tfrac{1}{2} \rho V^3 C_{db} \Delta S_b$$

$$+ \tfrac{1}{2} \rho V^3 S_b \Delta C_{db}. \tag{A.6}$$

A.1.3. *Profile Power*

The equation for P_{pro} is repeated from eqn (21),

$$P_{pro} = C_1 C_2 \frac{k^{3/4}(mg)^{3/2}S_b^{1/4}C_{db}^{1/4}S}{(\pi/4)^{3/4}\rho^{1/2}b^{7/2}} \quad (A.7)$$

and the total differential is

$$\Delta P_{pro} = \frac{\partial P_{pro}}{\partial k}\,\Delta k + \frac{\partial P_{pro}}{\partial m}\Delta m + \frac{\partial P_{pro}}{\partial g}\,\Delta g$$
$$+ \frac{\partial P_{pro}}{\partial S_b}\,\Delta S_b + \frac{\partial P_{pro}}{\partial C_{db}}\,\Delta C_{db}$$
$$+ \frac{\partial P_{pro}}{\partial S}\,\Delta S + \frac{\partial P_{pro}}{\partial \rho}\,\Delta \rho + \frac{\partial P_{pro}}{\partial b}\Delta b, \quad (A.8)$$

which evaluates to

$$\Delta P_{pro} = \frac{3}{4}C_1 C_2 \frac{(mg)^{3/2}S_b^{1/4}C_{db}^{1/4}S}{(\pi/4)^{3/4}k^{1/4}\rho^{1/2}b^{7/2}}\Delta k$$
$$+ \frac{3}{2}C_1 C_2 \frac{k^{3/4}m^{1/2}g^{3/2}S_b^{1/4}C_{db}^{1/4}S}{(\pi/4)^{3/4}\rho^{1/2}b^{7/2}}\,\Delta m$$
$$+ \frac{3}{2}C_1 C_2 \frac{k^{3/4}m^{3/2}g^{1/2}S_b^{1/4}C_{db}^{1/4}S}{(\pi/4)^{3/4}\rho^{1/2}b^{7/2}}\,\Delta g$$

$$+ \frac{1}{4}C_1 C_2 \frac{k^{3/4}(mg)^{3/2}C_{db}^{1/4}S}{(\pi/4)^{3/4}S_b^{3/4}\rho^{1/2}b^{7/2}}\,\Delta S_b$$
$$+ \frac{1}{4}C_1 C_2 \frac{k^{3/4}(mg)^{3/2}S_b^{1/4}S}{(\pi/4)^{3/4}C_{db}^{3/4}\rho^{1/2}b^{7/2}}\,\Delta C_{db}$$
$$+ C_1 C_2 \frac{k^{3/4}(mg)^{3/2}S_b^{1/4}C_{db}^{1/4}}{(\pi/4)^{3/4}\rho^{1/2}b^{7/2}}\,\Delta S$$
$$- \frac{1}{2}C_1 C_2 \frac{k^{3/4}(mg)^{3/2}S_b^{1/4}C_{db}^{1/4}S}{(\pi/4)^{3/4}\rho^{3/2}b^{7/2}}\,\Delta \rho$$
$$- \frac{7}{2}C_1 C_2 \frac{k^{3/4}(mg)^{3/2}S_b^{1/4}C_{db}^{1/4}S}{(\pi/4)^{3/4}\rho^{1/2}b^{9/2}}\,\Delta b. \quad (A.9)$$

At this point, the comparatively simple form of eqn (22) can probably be appreciated. In fact, as a practical matter, it is usually more convenient to take the individual relative contributions, as given for example in eqn (22), and then multiply them by the power component. Thus, the last term in eqn (A.9) can be written, and calculated, as the right-hand side of

$$\frac{7}{2}C_1 C_2 \frac{k^{3/4}(mg)^{3/2}S_b^{1/4}C_{db}^{1/4}S}{(\pi/4)^{3/4}\rho^{1/2}b^{9/2}}\,\Delta b = P_{pro}\frac{7}{2}\frac{\Delta b}{b}.$$
$$(A.10)$$