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# Tuning of Strouhal number for high propulsive efficiency accurately predicts how wingbeat frequency and stroke amplitude relate and scale with size and flight speed in birds

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The wing kinematics of birds vary systematically with body size, but we still, after several decades of research, lack a clear mechanistic understanding of the aerodynamic selection pressures that shape them. Swimming and flying animals have recently been shown to cruise at Strouhal numbers ( $St$ ) corresponding to a regime of vortex growth and shedding in which the propulsive efficiency of flapping foils peaks ( $St \approx fA/U$ , where  $f$  is wingbeat frequency,  $U$  is cruising speed and  $A \approx b\sin(\theta/2)$  is stroke amplitude, in which  $b$  is wingspan and  $\theta$  is stroke angle). We show that  $St$  is a simple and accurate predictor of wingbeat frequency in birds. The Strouhal numbers of cruising birds have converged on the lower end of the range  $0.2 < St < 0.4$  associated with high propulsive efficiency. Stroke angle scales as  $\theta \approx 67b^{-0.24}$ , so wingbeat frequency can be predicted as  $f \approx St \cdot U/b\sin(33.5b^{-0.24})$ , with  $St = 0.21$  and  $St = 0.25$  for direct and intermittent fliers, respectively. This simple aerodynamic model predicts wingbeat frequency better than any other relationship proposed to date, explaining 90% of the observed variance in a sample of 60 bird species. Avian wing kinematics therefore appear to have been tuned by natural selection for high aerodynamic efficiency: physical and physiological constraints upon wing kinematics must be reconsidered in this light.

**Keywords:** bird; flight; stroke amplitude; Strouhal number; wingbeat frequency

## 1. INTRODUCTION

The stately sweep of a swan's wings contrasts sharply with a finch's frantic flapping, but despite the obvious systematic scaling of wingbeat frequency ( $f$ ) with body mass ( $m$ ), biologists have yet to determine how functional constraints and selective pressures combine to determine wingbeat frequency. Notional upper and lower limits on wingbeat frequency (Rayner 1988) have been derived theoretically, based on scaling for musculoskeletal strength ( $f \propto m^{-1/3}$ ) and lift generation ( $f \propto m^{-1/6}$ ), respectively. An empirical scaling across species of  $f \propto m^{-0.27}$  has been found for birds, and has been suggested to reflect a compromise between these limits (Rayner 1988). Nevertheless, it seems likely that the exact compromise at which natural selection has arrived will reflect selection for aerodynamic efficiency (Greenewalt 1960), rather than being simply a trade-off between these two constraints about which nothing more can be said.

Given the complexity of current aerodynamic models of avian flight (reviewed in Norberg 1990), it is perhaps unsurprising that previous work has usually attempted to predict wingbeat frequency by scaling against single morphometric variables, such as body mass (Greenewalt 1975; Rayner 1988; Norberg 1990). The most complex predictive equations have been fitted empirically by combining multiple morphometric variables using least-squares regression and a form of dimensional analysis (Pennycuik

1990, 1996, 2001). Whereas the most complex equations predict wingbeat frequency well, within the samples to which they were fitted, they fail to identify the underlying mechanisms that determine wingbeat frequency. Moreover, using wholly empirical relationships to establish the causes of variation in wingbeat frequency obviously risks conflating correlation with causality, and is unlikely to permit useful extrapolation beyond the sample to which the relationship was fitted.

Recent work has shown that animals using oscillatory lift-based propulsion cruise with kinematics configured to operate with a Strouhal number in a range associated with efficient lift and thrust production (Taylor *et al.* 2003; Rohr & Fish 2004). Here, efficiency is assumed to be the ratio of aerodynamic power output to mechanical power input. Strouhal number is estimated as  $St \approx fA/U$ , where  $U$  is cruising speed and  $A$  is the double-amplitude of the wingbeat (stroke amplitude). Stroke amplitude is used as a readily observable proxy for wake height: given that the wake is bounded by vortices shed from the wingtips (Spedding *et al.* 2003), it is reasonable to equate stroke amplitude with vertical wingtip excursion (Taylor *et al.* 2003). A mounting body of theoretical and experimental data indicates that the efficiency of flapping foil propulsion peaks over a narrow range of  $St$  for any given motion, and that the optimum for a particular set of kinematics usually falls in the range  $0.2 < St < 0.4$  (Triantafyllou *et al.* 1991, 1993; Anderson *et al.* 1998; Read *et al.* 2003). These results generally relate to symmetric kinematics generating a net thrust but no net lift, but recent tests with asymmetric kinematics

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also show that the instantaneous force coefficients depend similarly on  $St$  when a net lift is produced (Read *et al.* 2003). The range of  $St$  used by swimming and flying animals coincides with the same range of  $St$  in cruising, which may be indicative of selection for aerodynamic or hydrodynamic efficiency (Taylor *et al.* 2003).

The exact mechanism by which  $St$  controls the efficiency of force production has yet to be fully elucidated, but is generally thought to reflect the role of  $St$  in governing the time-scales of vortex growth and shedding (Triantafyllou *et al.* 1991, 1993; Wang 2000; Lewin & Haj-Hariri 2003). Vortex growth is related to the rate of change in circulation on the airfoil, which in turn depends upon changes in speed or aerodynamic angle of attack. Because  $St$  is inversely related to advance ratio (Ellington 1984), it plays an essential role in controlling the growth in vorticity through the stroke by governing the maximum aerodynamic angle of attack (Wang 2000). If  $St$  is too low then the resulting vorticity will be insufficient to overcome the drag on the wing. Strouhal number also governs the spacing of shed vortices, whether by determining the distance between starting and stopping vortices in a vortex-ring wake (Spedding *et al.* 1984) or by controlling the wavelength of a concertina-like wake (Spedding 1987). Vortex spacing inevitably affects the efficiency of momentum transfer into the wake, and therefore the efficiency of aerodynamic force production.

Given that flying animals cruise within a narrow range of  $St$  (Taylor *et al.* 2003), it should be possible to predict any of the three variables defining  $St$  from knowledge of the other two variables. Specifically, if avian wing kinematics are configured to operate at an aerodynamically efficient Strouhal number, then wingbeat frequency will be predicted as:

$$f \approx St \cdot U/A, \quad (1.1)$$

where  $St$  is a constant expected to fall in the range  $0.2 < St < 0.4$ . The aims of this paper are twofold: first, to use equation (1.1) to derive a reliable predictive equation for wingbeat frequency, involving a minimum of variables and founded upon a mechanism associated with enhancing aerodynamic efficiency; second, to lend further weight to the argument that selection for  $St$  is important in governing flapping frequency in lift-based locomotion.

## 2. METHODS AND ANALYSIS

Out of the three kinematic variables required to estimate  $St$ , stroke amplitude  $A$  (or stroke angle  $\theta$ ) has been measured the least frequently, which accounts for the low sample size available to Taylor *et al.* (2003), who were able to identify only 22 species of bird for which  $f$ ,  $U$  and  $A$  or  $\theta$  had all been measured directly. Stroke angle generally diminishes with increasing size in birds, and we therefore set out to derive a simple predictive relationship for  $\theta$ . We identified 45 species of bird (see electronic Appendix A) for which  $\theta$  had been measured directly. The negative correlation between  $\log_{10}(\theta)$  and  $\log_{10}(b)$  (figure 1) is well modelled by least-squares regression ( $F_{1,43} = 45.2$ ,  $r^2 = 0.51$ ,  $p < 0.0001$ ), as:

$$\log_{10}\theta = 1.83 - 0.24\log_{10}b, \quad (2.1)$$

where  $b$  is in measured in metres and  $\theta$  is in degrees. Stroke angle can therefore be reasonably accurately predicted

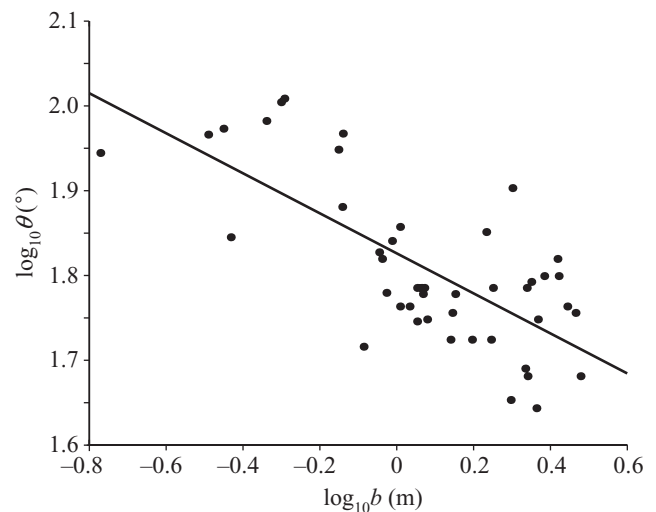


Figure 1. Graph of  $\log_{10}\theta$  (log stroke angle) against  $\log_{10}b$  (log wingspan) for 45 bird species. The equation describing the regression line is  $\log_{10}\theta = 1.83 - 0.24\log_{10}b$  ( $F_{1,43} = 45.2$ ,  $r^2 = 0.51$ ,  $p < 0.0001$ ).

from wingspan across a range of species varying widely in size and morphology, as:

$$\theta = 67b^{-0.24}. \quad (2.2)$$

We used equation (2.2) to predict  $\theta$  for the 60 species of bird for which we could find measurements of  $f$  and  $U$  in cruising flight (see electronic Appendix B). Only 15 of these species were common to the sample used in deriving equations (2.1) and (2.2), but using the identity  $A = b\sin(\theta/2)$  to calculate  $A$  from predicted  $\theta$  (see Taylor *et al.* 2003), we were able to predict  $St$  for all 60 species (figure 2). As in the smaller sub-sample of these data used by Taylor *et al.* (2003), birds using intermittent flight (median  $St = 0.23$ ; interquartile range, 0.22–0.30;  $n = 11$ ) had a significantly higher median  $St$  (Wilcoxon rank sum test,  $p = 0.002$ ) than birds using direct flight (median  $St = 0.20$ ; interquartile range, 0.18–0.23;  $n = 49$ ). This difference is thought to arise because the mean flight speed used in calculating  $St$  underestimates instantaneous flight speed during the flapping phase of intermittent flight, thereby biasing upwards the estimate of  $St$  (Taylor *et al.* 2003). Nevertheless, average  $St$  falls within the range  $0.2 < St < 0.4$  expected for high propulsive efficiency in both cases.

Combining the identity  $A = b\sin(\theta/2)$  with equations (1.1) and (2.2), we derive the following predictive equation for wingbeat frequency in birds (in Hz):

$$f \approx St \cdot U/b\sin(33.5b^{-0.24}), \quad (2.3)$$

where  $St$  is an empirically established constant, expected to fall in the range  $0.2 < St < 0.4$  (equation (2.1)). We used separate estimates of  $St$  for direct and intermittent fliers to account for the discrepancy between average and instantaneous flight speed in the latter, taking mean values of  $St$  for direct and intermittent fliers ( $St = 0.21$  and  $St = 0.25$ , respectively) as our best-fitting estimates of  $St$ .

To test this semi-empirical model of wingbeat frequency, we regressed observed wingbeat frequency against predicted wingbeat frequency (equation (2.3)) for all 60 species (figure 2a). As expected, the regression is highly significant ( $F_{1,58} = 513.3$ ,  $p < 0.0001$ ) and explains an

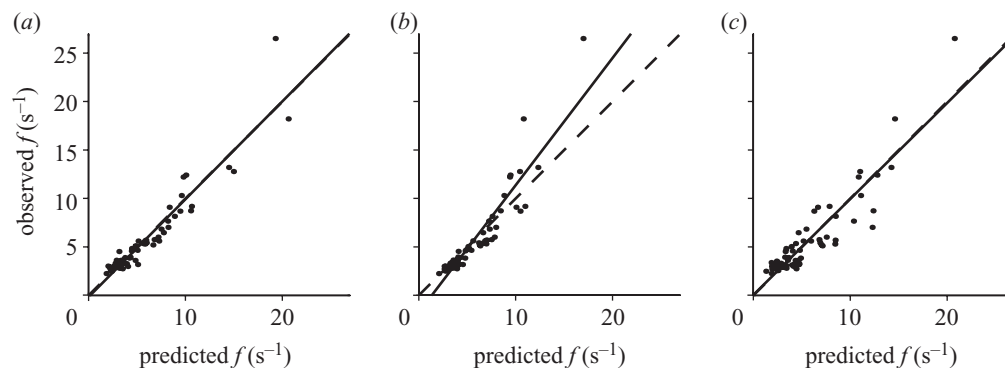


Figure 2. Graphs of observed against predicted wingbeat frequency. Dashed lines denote a perfect fit of predicted and observed frequency. (a) Predicted frequency calculated from the semi-empirical model  $f \approx St \cdot U / b \sin(33.5b^{-0.24})$  derived in this paper (equation (2.3)), where  $St = 0.21$  for direct fliers and  $St = 0.25$  for intermittent fliers. The equation describing the regression line is  $f_{\text{obs}} = -0.17 + 1.01f_{\text{pred}}$  ( $F_{1,58} = 513.3$ ,  $r^2 = 0.90$ ,  $p < 0.0001$ ). (b) Predicted frequency calculated from Pennycuik's predictive equation (Pennycuik 1996, 2001)  $f = m^{3/8}(g/q)^{1/2}b^{-23/24}S^{-1/3}\rho^{-3/8}$ , where  $q = 1$  (equation (2.4)). The regression equation describing the trend-line is  $f_{\text{obs}} = -1.77 + 1.31f_{\text{pred}}$  ( $F_{1,58} = 342.5$ ,  $r^2 = 0.86$ ,  $p < 0.0001$ ). (c) Predicted frequency calculated from the empirical scaling function  $f = -1.21 + 5.74b^{-0.75}$ . The regression equation describing the trend-line is  $f_{\text{obs}} = 0.04 + 0.99f_{\text{pred}}$  ( $F_{1,58} = 283.2$ ,  $r^2 = 0.83$ ,  $p < 0.0001$ ).

impressively high proportion of the total variance ( $r^2 = 0.90$ ). Excluding the data-point for the zebra finch *Taenopygia guttata* (which was confined in a wind tunnel and is a clear outlier) further elevates the proportion of the total variance explained to over 93%. The slope of the regression does not differ significantly from unity (95% confidence interval (CI), 0.92, 1.10), and the intercept does not differ significantly from zero (95% CI, -0.80, 0.46). Both of these features are essential acceptance criteria for any predictive model. Note that our model for wingbeat frequency is a two-variable model, requiring knowledge only of cruising speed and wingspan. Out of the three parameters in equation (2.3), only the parameter  $St$  is fitted to the sample against which our predictive model is tested. The two parameters from equation (2.2) are fitted independently, and our model is therefore in essence a two-variable, one-parameter model.

We tested our model against the best-performing empirical predictive equation in the literature to date (Pennycuik 2001):

$$f = m^{3/8}(g/q)^{1/2}b^{-23/24}S^{-1/3}\rho^{-3/8}, \quad (2.4)$$

where  $m$  is body mass (kg),  $g$  is gravitational acceleration ( $9.81 \text{ ms}^{-2}$ ),  $q$  is 'power fraction',  $S$  is wing area ( $\text{m}^2$ ) and  $\rho$  is air density at sea level ( $1.23 \text{ kg m}^{-3}$ ). The 'power fraction'  $q$  accounts for the increased acceleration experienced by bounding birds when pulling up, and is 1 for birds in level flight. Neglecting the environmental variables  $g$  and  $\rho$ , equation (2.4) is a four-variable model, with variables  $m$ ,  $q$ ,  $b$  and  $S$ . However, since  $q$  is rarely known, we may let  $q = 1$  and thereby treat equation (2.4) as a three-variable model of identical form to an earlier predictive equation by Pennycuik (1996). The model has five fitted exponents, and is therefore in essence a three-variable, five-parameter model.

Pennycuik's equation was originally fitted to a sample of 46 different species (Pennycuik 1990, 1996). To test it against our own model, we regressed observed wingbeat frequency against predicted wingbeat frequency from equation (2.4) for the larger sample of 60 species above (figure 2b). As expected, the regression is highly significant

( $F_{1,58} = 342.5$ ,  $p < 0.0001$ ), and explains a high proportion of the total variance ( $r^2 = 0.86$ ). However, the slope of the regression differs significantly from unity (95% CI, 1.17, 1.46) and the intercept differs significantly from zero (95% CI, -2.69, -0.85), which indicates that Pennycuik's equation fails to explain all of the systematic variation in wingbeat frequency. Moreover, the proportion of the total variance explained is 4% less than that explained by our own model, with greater economy of variables and fewer fitted parameters. Considering the uncertainties in both empirical observations and predictions, it is better to use the simplest theoretical model available (Pennycuik 1995), which in this case is our own.

For comparison, we derived an empirical scaling function of wingbeat frequency with span, which was the single best morphometric predictor of wingbeat frequency out of those we tested ( $m$ ,  $S$  and  $b$ ). Regressing  $\log_{10}f$  against  $\log_{10}b$  ( $F_{1,58} = 250.9$ ,  $r^2 = 0.81$ ,  $p < 0.0001$ ) indicated an empirical scaling of  $f \propto b^{-0.75}$ , so we regressed  $f$  against  $b^{-0.75}$  to derive the function  $f = -1.21 + 5.74b^{-0.75}$ . Regressing observed frequency against the frequency predicted by this scaling ( $F_{1,58} = 283.2$ ,  $r^2 = 0.83$ ,  $p < 0.0001$ ) results in 7% less of the total variance being explained than by our own model (figure 2c). Naturally, the slope and intercept of the regression are not significantly different from unity (95% CI, 0.87, 1.11) and zero (95% CI, -0.78, 0.86), respectively, because the scaling function is a purely empirical one, with its two parameters fitted directly to the dataset in hand. This should be contrasted with our own semi-empirical model, for which only the single parameter  $St$  is fitted to the sample of observed wingbeat frequencies against which the predictions are tested.

### 3. DISCUSSION

#### (a) Predicting wingbeat frequency

The excellent performance of our model in predicting wingbeat frequency ( $r^2 = 0.90$ ,  $n = 60$ ) indicates that we have succeeded in the first of our aims: to derive a reliable predictive equation for wingbeat frequency founded upon a mechanism associated with enhancing aerodynamic efficiency. This in itself represents a substantial advance.



The semi-empirical model that we have derived differs crucially from previous relationships used to predict wingbeat frequency, in that the general form of the equation is derived *a priori*. Moreover, although the parameter  $St$  was determined empirically, the values that it takes ( $St = 0.21$  for direct fliers and  $St = 0.25$  for intermittent fliers) coincide closely with theoretical and experimental measures of  $St$  associated with high propulsive efficiency (Triantafyllou *et al.* 1991, 1993; Anderson *et al.* 1998). This is a necessary, but insufficient, condition for invoking causality: tuning of Strouhal number for high propulsive efficiency predicts, and *may* also explain, wingbeat frequency in cruising birds. These empirical values of  $St$  sit at the lower end of the range  $0.2 < St < 0.4$  expected for high propulsive efficiency, which we predict reflects selection of kinematics configured to make use of the attached flows for which the airfoils of birds appear to be appropriate (Taylor *et al.* 2003). At higher  $St$ , high-lift, high-drag separated flows and leading-edge vortices are essentially unavoidable, even with a conventional round-nosed airfoil. Birds may not need the high lift associated with leading-edge vortex mechanisms in cruising flight, and may be adapted to avoid the high drag associated with separated flows.

Pennycuik's predictive equation performs extremely well in predicting wingbeat frequency for the sample of 46 different species that he used (linear regression of observed on predicted frequency:  $r^2 = 0.97$ ,  $n = 47$  including one pseudoreplicate where the same species was included twice), but explains 11% less of the total variance of the wider sample here ( $r^2 = 0.86$ ,  $n = 60$ ). This is not surprising because empirical multivariate analyses in general decline in predictive ability when applied to samples containing new data. Indeed, the five exponents of Pennycuik's original equation (Pennycuik 1990) had to be modified considerably (Pennycuik 1996), and a further variable added later (Pennycuik 2001) in order to accommodate new data. By contrast, if the relationship derived *a priori* in equation (1.1) correctly encapsulates a causal mechanism behind the selection of wingbeat kinematics in cruising birds, we would expect the parameter  $St$  fitted in equation (2.3) to change little as the sample is expanded. If, as more data are accrued, this turns out not to be the case, then it would be reasonable to reject our model.

Wingbeat frequency scales quite tightly with wingspan, but it is difficult to infer causality from this scaling. This is a fundamental issue with any empirically derived scaling relation. By contrast, as well as being the single best predictor of wingbeat frequency yet proposed, our semi-empirical model is the only successful predictor of wingbeat frequency with a sound mechanistic basis. Other mechanistic models, including tuning for mechanical resonance (Greenewalt 1960), Helmholtz scaling of flight power and speed (Rayner 1988) and constraints upon musculoskeletal strength (Rayner 1988), all fail to predict wingbeat frequency in birds accurately. Our model is both mechanistically plausible and simple to implement, and it succeeds in predicting wingbeat frequency better than any other model proposed to date.

#### (b) *Systematic variation in stroke angle with wingspan*

The highly significant ( $p < 0.0001$ ) negative correlation that we have found between stroke angle and wingspan

does not, to our knowledge, appear to have been discussed in detail elsewhere. This scaling has important consequences for aerodynamic tuning of  $St$ . If stroke angle were scale-invariant, which it is not, then frequency would have to scale as  $f \propto b^{-1/2}$  for  $St$  to remain a constant. This is equivalent to the notional lower limit of  $f \propto m^{-1/6}$  suggested by Rayner (1988) based on scaling for lift generation. This equivalence arises because the argument Rayner (1988) used to arrive at this scaling is based upon maintaining complete kinematic similarity (i.e. keeping stroke angle constant and varying frequency in inverse proportion to flight speed), which is a sufficient condition for  $St$  to be constant across species. The argument that we have made here extends to the more general case in which  $St$  is tuned similarly across species, without complete kinematic similarity necessarily being maintained. In this case, stroke angle must vary systematically with body size in order for  $St$  to remain constant, which is exactly what we find. Thus, the argument made by Taylor *et al.* (2003) that  $St$  should be higher for smaller birds because stroke amplitude scales geometrically with span is flawed; instead, stroke angle appears to scale allometrically with span, thereby opposing the allometry in  $St$  that would result from a geometric scaling of stroke amplitude with span.

Although stroke angle varies significantly with body size, the corresponding logistic regression explains a relatively small proportion of the total variance ( $r^2 = 0.51$ ). The large unexplained component of this variation may arise because the data for stroke angle are themselves noisy: wing flexion makes stroke angle difficult to measure, and birds seem able to adjust stroke angle readily in flight, especially in relation to forward speed. By contrast, tuning for a single optimum value of  $St$  does not predict a single unique scaling of either wingbeat frequency or stroke amplitude alone with body size (Wang 2000): wingbeat frequency and stroke angle are instead expected to covary about their overall scaling functions. In this case, for birds with observed stroke angles higher than predicted by the overall scaling with span (equation (2.2)), we should have observed wingbeat frequencies lower than predicted by our model (equation (2.3)) and *vice versa*. By inspection of the identities  $St = fA/U$  and  $A = b\sin(\theta/2)$ , it is clear that such systematic variation in  $f$  should be linear in the corresponding variation in  $\sin(\theta/2)$ .

To test this prediction, we regressed the residuals from the regression of observed  $f$  on predicted  $f$  (figure 2a) against the residuals from regressing observed  $\sin(\theta/2)$  on predicted  $\sin(\theta/2)$  (equation (2.2)). This could only be done for the subset of 15 species for which we had observations of both wingbeat frequency and stroke angle (figure 3). The resulting regression is significant at  $\alpha = 0.05$  ( $F_{1,13} = 3.73$ , one-tailed  $p = 0.038$ ), given that our prediction is directional (the slope should be negative, which it is), but the proportion of the total variance explained is small ( $r^2 = 0.22$ ), which may again reflect the noise in the underlying data for stroke angle. Nevertheless, the significance, if not the strength, of this effect lends support to the hypothesis that wingbeat frequency and stroke angle covary about their respective scaling functions.

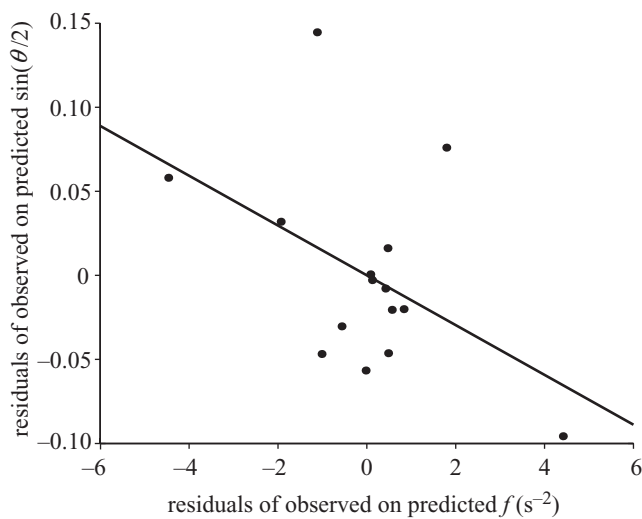


Figure 3. Residuals from regressing observed  $f$  on predicted  $f$  (equation (2.3)), plotted against residuals from regressing observed  $\sin(\theta/2)$  on predicted  $\sin(\theta/2)$  (equation (2.2)) for the subset of 15 species for which we had observations of both  $f$  and  $\theta$ . The slope of the equation describing the regression line is  $-0.015$  and the intercept is zero ( $F_{1,13} = 3.73$ ,  $r^2 = 0.22$ , one-tailed  $p = 0.038$ ).

#### (c) *Are cruising birds tuned to a narrow range of $St$ ?*

The results that we have presented above are consistent with the hypothesis that birds have converged upon a narrow optimum range of  $St$  in cruising flight. The best estimates of  $St$  for the empirical data we have presented fall within the range  $0.2 < St < 0.4$  associated with high propulsive efficiency in theoretical and experimental studies with oscillating foils (Triantafyllou *et al.* 1991, 1993; Anderson *et al.* 1998; Read *et al.* 2003). Moreover, the difference in our estimates of  $St$  between direct and intermittent fliers is in the expected direction, given that the average measures of flight speed that we have used underestimate the instantaneous flight speed during the flapping phase of intermittent flight. This numerical coincidence is not in itself sufficient to conclude a role for natural selection in tuning  $St$ , but two further independent pieces of evidence lend support to the argument that it is so.

First, the semi-empirical relationship that we have established from this assumed mechanism performs better in predicting wingbeat frequency than any empirical relationship (Pennycuik 1990, 1996, 2001) proposed to date. Other models that postulate a mechanism constraining wingbeat frequency (Greenewalt 1960; Rayner 1988) fail to predict wingbeat frequency accurately. Second, the residual variation in our model has a systematic component resulting from covariation in the scatter of wingbeat frequency and stroke angle about their respective scaling relations that is expected given the proposed mechanism. In other words, the scaling of wingbeat frequency and stroke angle with body size constrains  $St$  to a narrow range in the first instance, and residual covariation in the observed values of wingbeat frequency and stroke angle constrains  $St$  still further (see also Taylor *et al.* 2003). The argument that birds have converged upon a single optimum value of  $St$  in cruising flight therefore has a strong internal consistency, and it is this internal consistency that is most convincing.

#### 4. CONCLUSIONS

We have established a simple, but accurate, model for predicting wingbeat frequency in birds, and have presented several independent lines of evidence in support of the underlying mechanism that we have proposed. Cruising birds appear to have converged upon a narrow range of  $St$ , corresponding to a regime in which propulsive efficiency is high. This convergence across a broad size range suggests that optimization of propulsion is substantially independent of Reynolds number within this range. Because  $St \approx fA/U$ , this convergence also implies that the product of wingbeat frequency and amplitude should scale tightly with flight speed. Wingbeat frequency and stroke amplitude must therefore covary, but convergence upon a narrow range of  $St$  does not, in itself, predict a single unique scaling of either wingbeat frequency or stroke amplitude: only of their product. Unless stroke amplitude is observed directly,  $St$  can therefore only be used to predict wingbeat frequency if stroke amplitude scales in some predictable fashion. Our model, containing as its only variables flight speed and wingspan, works only because stroke angle scales predictably with span (equation (2.2)). It is worth noting that this coincidental scaling of stroke angle with span is peculiar to birds. In other taxa, it may be necessary to know stroke amplitude as well as cruising speed to predict stroke frequency.

Convergent tuning of wing kinematics to a narrow range of  $St$  predicts that the product of wingbeat frequency and stroke amplitude should scale as  $fA \propto m^{1/6}$  in opposition to the scaling of flight speed as  $U \propto m^{1/6}$ , but this still begs the question of why natural selection should have configured wing kinematics such that the scaling of wingbeat frequency takes the particular form  $f \propto m^{-0.27}$  across birds as a whole (see Rayner 1988). Why should natural selection have resulted in this particular scaling of wingbeat frequency and corresponding scaling of stroke amplitude, rather than in any other? Stroke amplitude is arguably more strongly constrained than wingbeat frequency in that, for a given stroke angle, stroke amplitude is constrained by geometry to vary directly with span. Nevertheless, variation in stroke angle is sufficient to relax this constraint, and it is not at all clear whether constraints upon stroke amplitude will drive selection of wingbeat frequency, or *vice versa*. The truth is likely to lie between these extremes, with physical and physiological constraints upon wingbeat frequency and stroke amplitude both affecting their optimal scaling within the constraint that  $fA \propto m^{1/6}$ .

Physical and physiological arguments along the lines of those made by Greenewalt (1960) and Rayner (1988) therefore still have a part to play in arriving at an integrated understanding of how wingbeat frequency varies in birds. Strouhal number adds an important aerodynamic dimension that has previously been lacking. Further studies are required to elucidate how physics and physiology interact with selection for aerodynamic efficiency to constrain wingbeat frequency in birds. We have shown that wingbeat frequency and stroke angle must be considered together in order to understand the action of physical and physiological constraints. In so doing, we may finally be able to arrive at a proper mechanistic understanding of how natural selection tunes birds for the astonishing physiological feats of speed and endurance that they are able to achieve.

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