

The aerodynamics of avian take-off from direct pressure measurements in Canada geese (*Branta canadensis*)

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Summary

Direct pressure measurements using electronic differential pressure transducers along bird wings provide insight into the aerodynamics of these dynamically varying aerofoils. Acceleration-compensated pressures were measured at five sites distributed proximally to distally from the tertials to the primaries along the wings of Canada geese. During take-off flight, ventral-to-dorsal pressure is maintained at the proximal wing section throughout the wingstroke cycle, whereas pressure sense is reversed at the primaries during upstroke. The distal

sites experience double pressure peaks during the downstroke. These observations suggest that tertials provide weight-support throughout the wingbeat, that the wingtip provides thrust during upstroke and that the kinetic energy of the rapidly flapping wings may be dissipated *via* retarding aerodynamic forces (resulting in aerodynamic work) at the end of downstroke.

Key words: flight, flapping, wing, bird, inertia, power, Canada geese, *Branta canadensis*.

Introduction

Vertebrates power flight with flapping wings of complex and changing geometries. The aerodynamics of such dynamic aerofoils remains obscure. While a fixed-wing view of aerodynamics is likely to be appropriate for gliding and soaring flight, flapping flight involves accelerations, rotations, wing-wing interactions and dynamic changes in both planform and sectional wing shape, with potential for strongly three-dimensional flows. Thus, analogies based on either fixed-wing or propeller aerodynamics are potentially misleading for much of animal flight (Usherwood and Ellington, 2002). Despite aerodynamic inferences drawn from accurate kinematic data (Hedrick et al., 2002) and particle image velocimetry (PIV) of the vortex wake (Spedding et al., 1984, 2003a; Spedding, 1986, 1987), previous experimental studies of vertebrate flight result in, at best, indirect measures of the pressure differentials acting across flapping wings. Here, we introduce a technique to provide direct, dynamic pressure measurements along flapping wings and present results for Canada geese (*Branta canadensis*) in take-off flight.

With the development of more sophisticated techniques in PIV appropriate for bird flight (Rosén, 2003; Spedding et al., 2003a,b), high-resolution (both spatially and temporally) wake dynamics can now be observed, allowing a significant step towards understanding the aerodynamics of avian flight. However, these techniques are currently limited to steady flight of a highly trained bird within a wind tunnel in near darkness and require that images of the wake from several wing beats are pieced together to produce representative wakes for a complete wingstroke cycle at a given flight speed.

In addition, relating flow fields in a wake at some distance downstream from a bird to the pressures experienced by the bird is not trivial. Imaging of the flow immediately around the bird and its wings would help this process, but this has not yet been achieved and is unlikely to be accomplished in the near future.

Sampling of the downwash of a hovering bat by hot-wire anemometry (Norberg et al., 1993) provides an alternative technique for studying the wake of a flapping animal and can be used to derive a value for induced power. However, neither of the techniques for studying the wake of a flying bird (PIV or hot-wire anemometry) is capable of providing direct information on the varying pressures acting along the wing. Assessments of muscle forces during flight have been possible using calibrated strain measurements of the deltopectoral crest of the humerus in the pigeon *Columba livia* (Dial and Biewener, 1993) and magpie *Pica pica* (Dial et al., 1997). However, even without the difficulties inherent in calibration of the strains to provide force data (Tobalske et al., 2003), this technique provides limited information on the aerodynamic forces acting along the wing. This is because the confounding contributions of inertial forces are difficult to identify and remove, and force distributions along a wing cannot be resolved from limited and local bone strain measurements. As an intermediate between studies of flapping-wing aerodynamics focusing on the consequences to the air or consequences to the muscles and bones, we have developed a direct technique for measuring the pressure differentials developed across flapping bird wings.

Materials and methods

Five small, lightweight differential pressure transducers, combined with accelerometers (Fig. 1), were tied between the bases of adjacent flight feathers (two between primaries, two between secondaries and one at the secondary–tertiary boundary) along the wings of three Canada geese [*Branta canadensis* L.; mass, 4.7 ± 0.2 kg (mean \pm s.d. throughout); span 1.58 ± 0.04 m; wing and intervening body area 0.36 ± 0.01 m² (following Pennycuik, 1989)] caught from local pest populations (Massachusetts Division of Fisheries and Wildlife permit 038.02SCB). Acceleration-compensated pressure signals and high-speed video were recorded for the five sites during the first 30 m of take-off flight.

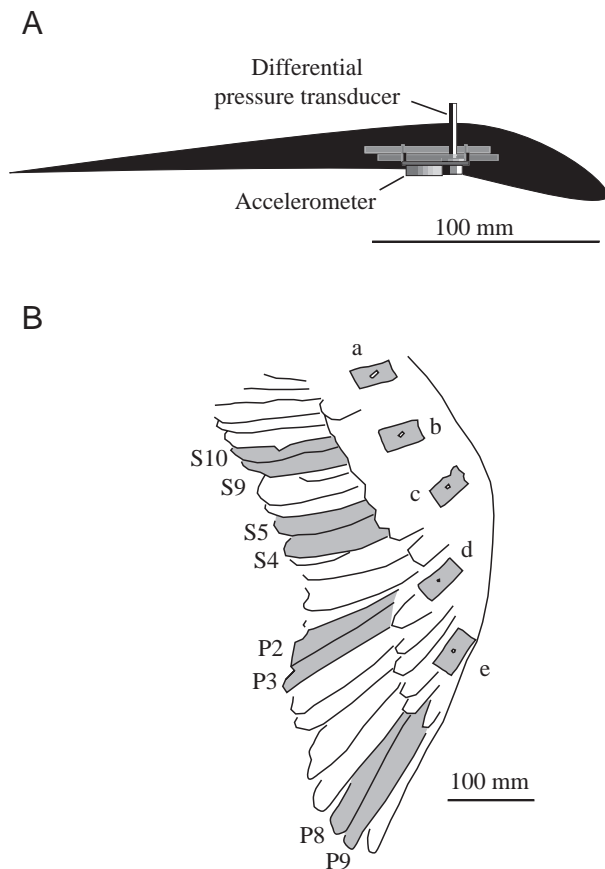


Fig. 1. Positioning of a pressure transducer/accelerometer unit. (A) Position within a wing chord, with dimensions appropriate for the most proximal site, at the secondary–tertiary boundary. Each unit is tied between the bases of two adjacent flight feathers. The dorsal port of the differential pressure transducer projects slightly through the upper surface of the wing; the ventral port is exposed beneath the unit. (B) Positioning of the five units along the right wing. Tabs of sticky tape surrounding the dorsal ports of the pressure transducers (to prevent covering with covert feathers), and the flight feathers between which the units are tied are highlighted in gray (S, secondary; P, primary). The most proximal position (position a) is situated at the secondary–tertiary boundary. Positions b and d have units with pairs of accelerometers; positions a, c and e have single accelerometers.

Acceleration compensation of pressure transducers

Each unit (4.5 g or 7.5 g) consists of a differential pressure transducer (PX74-0.3DV; Omega, Stamford, CT, USA) with a stiff 3.2 mm-diameter nozzle cut to project through the feathers to the upper wing surface when tied between flight feathers (Fig. 1). Each sensor was relatively light compared with the wing (1–2% of wing mass, together totaling 9%), each comparable to the mass of 2–4 primary feathers. While the additional wing mass may have resulted in a slight compensation in kinematics due to increasing the moment of inertia, I {by approximately 12% for the outstretched wing, using the scaling relationship for a single wing $I=0.118[(\text{wing mass}) \times (\text{wing length})^2]^{1.040}$, $r^2=0.997$, from Van den Berg and Rayner, 1995}, we found that the action of the loaded and unloaded wings was similar. Each differential pressure transducer was attached next to either one (sites a, c and e; Fig. 1B) or a pair of (sites b and d; Fig. 1B) single-axis accelerometers (SA20; Sensor One, Sausalito, CA, USA). The response of both accelerometers and pressure transducers to acceleration was determined by steadily (thus avoiding pressure differentials) orientating the units vertically upwards ($+1g$, $+9.81 \text{ m s}^{-2}$), horizontally ($0g$, 0 m s^{-2}) and vertically downwards ($-1g$, -9.81 m s^{-2}). This was done so that the confounding effect of acceleration (because of flapping) on the pressure signal, due to the inertial deflection of the membrane integral to the pressure transducer, could be removed. The units with a pair of accelerometers allow the effects of wing rotation (pronation or supination) and the slight (12.5 mm) separation between pressure transducer and accelerometer to be assessed. The traces for sites b and d in Fig. 2 consist of two lines, one for each accelerometer signal removal. However, the two lines are barely distinguishable, appearing occasionally as a thickening of the trace, showing that the impact of separation between pressure transducer and accelerometer was negligible. Acceleration compensation of the pressure signal was, however, significant. At positions of peak acceleration (around $\pm 75g$ or 750 m s^{-2} , at the beginning/end of downstroke and upstroke at the most distal transducer placement), a false signal of up to $\pm 350 \text{ Pa}$ was removed. While the frequency response of each transducer was high ($>1 \text{ kHz}$), both high-frequency noise and limitations in the kinematic data made high-frequency signals difficult to interpret. As a result, acceleration-compensated pressure signals were low-pass filtered at 25 Hz (2nd order Butterworth), approximately five times that of the wingbeat frequency.

Experimental protocol

The five pressure/accelerometer units were tied in place using 0-silk between flight-feather shafts (a, S17–S18; b, S9–S10; c, S4–S5; d, P2–P3; e, P8–P9; ‘S’ being secondary and ‘P’ being primary) along the right wing of three Canada geese sedated with isoflurane. Blocking of dorsal or ventral ports by displaced covert feathers was prevented with small tabs of elastic adhesive tape (visible in the outline tracings of Figs 1B, 3B). Voltage signals from the five units, consisting of

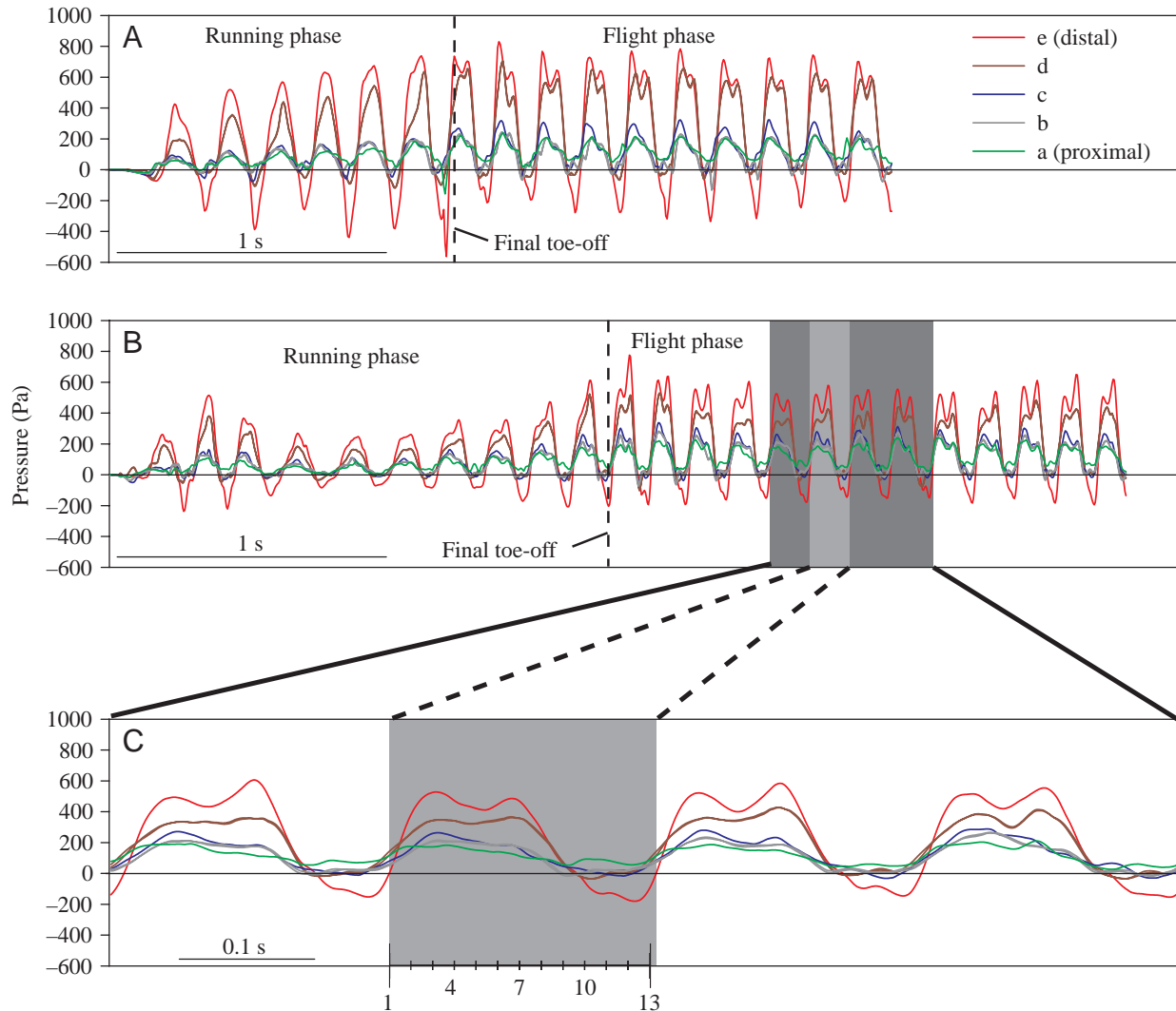


Fig. 2. (A–C) Representative acceleration-compensated pressure traces for five positions (a–e) along the wing during take-off flight. Signals were consistent in general form; A and B show results for the first (4.78 kg, wing loading 127.9 Pa) and the last (4.84 kg, wing loading 138.2 Pa) geese tested, respectively. Traces for positions b and d show two, virtually indistinguishable, lines each, indicating that the displacement between pressure transducer and accelerometer barely affects acceleration-compensation of the pressure signal. Four flaps after lift-off, but well before tension in the tether, are highlighted in B and expanded in C. The single flap highlighted in C relates to the kinematics shown in Fig. 3. Tick-marks indicate the appropriate timing for the 13 ‘snapshot’ images.

12 channels of data (five pressure, seven acceleration), and the bridge supply voltage were transmitted along five 30 m-long, lightweight (9.9 g m^{-1}), shielded cables (NMUF6/30-4046SJ; Cooner Wire, Chatsworth, CA, USA), which were anchored with tape to the back of the goose. A string tether was also connected to the goose, at the right foot, to allow the bird to be controlled at the end of take-off but also permitting a running phase for a few steps prior to flight. Voltage signals (at 5 kHz) were collected and synchronized with $250 \text{ frames s}^{-1}$ video obtained from two cameras (PCI-500 camera; Redlake Inc., San Diego, CA, USA) that provided approximately dorsal and lateral views of the flight, from which accurate timing of wing motions, approximate body speeds, but only qualitative wing and transducer orientations,

were apparent. A total of eight take-off flights (2–3 flights per goose) was recorded.

Results and discussion

All flights recorded from three geese (mean velocity after final toe-off derived from lateral-view kinematics: $8.5 \pm 2 \text{ m s}^{-1}$) show quantitatively and qualitatively consistent results. Two example pressure distributions along the wings of geese in accelerating, take-off flight are shown in Fig. 2. An example of time-varying pressure distribution for a single flap is shown related to kinematics in Fig. 3. Observed pressures range from over four times the mean wing loading ($129 \pm 9 \text{ Pa}$) in the ventral-dorsal sense during downstroke to a dorsal-

ventral pressure with a magnitude close to mean wing loading during the second half of upstroke (Fig. 3). The results provide direct evidence for three interesting phenomena: (1) maintenance of positive (ventral-to-dorsal) pressure at site a (most proximal) throughout the wingstroke cycle; (2) reversal of the pressure sense (indicating a dorsal-to-ventral direction) at site e, the most distal; and (3) double pressure peaks at the distal sites during the downstroke.

Upstroke and 'gaits' in avian flight

Studies by PIV of the wake left behind flying birds have led to the description of two distinct flight 'gaits' (Spedding et al., 1984; Rayner, 1986, 1991, 1995; Spedding, 1986, 1987; Tobalske, 2000): the 'vortex-ring gait', in which the upstroke results in minor aerodynamic forces, and the 'continuous-vortex gait', in which aerodynamic lift is maintained during the upstroke. The concept of 'gaits' in flight is useful in distinguishing between slow, sparrow-like flight and fast, gull-like flight, but the transition between the two gaits as a function of speed, for most birds, is likely to be continuous (e.g. Spedding et al., 2003a), with the aerodynamic role of the upstroke gradually increasing with increasing flight speed. Whether the term 'gait' should be dropped because of this lack of discontinuity with speed

(although 'walking' and 'running' are normally termed gaits even in birds that can show continuous variation in kinematics with speed; Gatesy and Biewener, 1991) and 'flight style' should be adopted, the concept of different flight techniques, largely defined by force production during the upstroke, remains useful. In this context, the results for the goose through upstroke during take-off are interesting. Pressures along the wing divide into three regions: (1) 'positive' (a ventral-dorsal sense) at the wing base; (2) near-zero for the center portion of the wing; and (3) 'negative' (a dorsal-ventral sense) at the wingtip (Fig. 3). The maintenance of ventral-dorsal pressure at the wing base, and the reversal at the wingtip, adds a new flight 'style' to those previously described based on upstroke function; again, however, discontinuity between take-off flight style and other flight styles (whether closer to the 'vortex-ring' or 'continuous-vortex' gaits or styles) should not be inferred.

Wingtip pressure reversal

Circulation (and pressure-sense) reversal at the wingtip during the upstroke has been reasonably argued for take-off flight in the pigeon (Alexander, 1968): wingtip attitudes, and presumed low induced air velocities, are likely to result in the wingtips operating at negative aerodynamic angles of

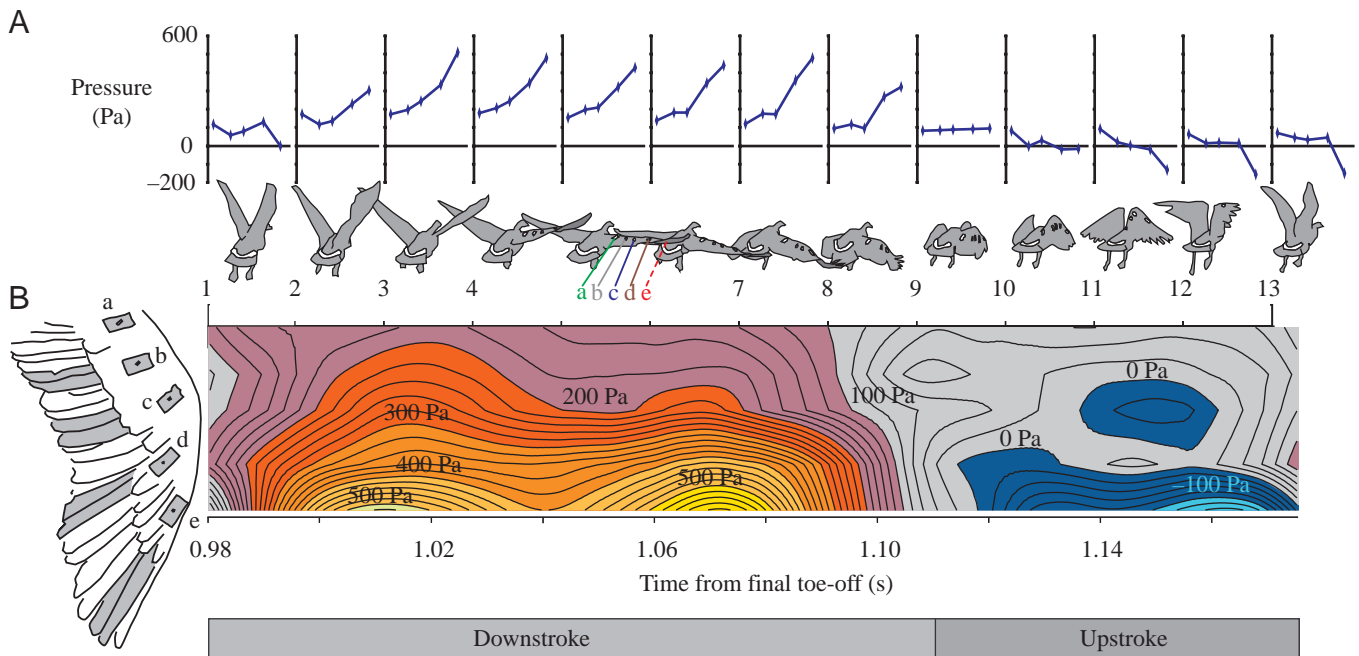


Fig. 3. Pressure distribution related to kinematics for a wing over a single flap during take-off flight, but five flaps after lift-off. The traced outlines and graphs for pressure distribution along the wing (A) show snapshots separated by $4/250$ s. The contour plot (B) shows the pressure distribution through time as it would be mapped to an outstretched wing. Contours are calculated assuming a linear distribution of pressure with spanwise distance between the five measurement sites indicated on the wing image (labeled a–e). Positive pressures indicate a ventral-to-dorsal sense; the wing base maintains a weight-supporting sense throughout the wingstroke cycle. Pressure differentials are greater than mean wing loading (138.2 Pa) for all sites between snapshots 2 and 5 and remain above wing loading for all but site a (base of wing) for most of the downstroke. Wingtips experience the greatest pressure differentials, maximally more than four times the mean wing loading. During upstroke, the distal sites show 'negative' pressures, indicating a dorsal-to-ventral sense. The direction of the resulting forces cannot be determined accurately, but the wingtips are aligned approximately vertically when the negative pressure differential is greatest (the second half of upstroke), suggesting a thrust-orientated force.

incidence. The bending of the primaries (Corning and Biewener, 1998) also suggests that they experience forces orientated upwards and forwards during the upstroke. This phenomenon is difficult to infer, however, for many other cases, both due to the unknown and potentially high local induced velocities and to the relatively low angles at which the air meets the wing (the angles of incidence). Indeed, it is often difficult to determine whether any significant aerodynamic forces are produced during the upstroke or even whether the aerofoil is operating at a positive or negative angle of incidence (see, for instance, the analysis of a hovering bat described by Norberg, 1976).

The orientations of the significant negative pressures observed at the wingtip during upstroke in the flapping Canada goose are impossible to determine precisely from the kinematic data in this study (accurate three-dimensional kinematics are not possible with such unconstrained flight). The pressure does, however, appear to be orientated to provide a predominantly thrust force, as the primaries are approximately vertical during the upstroke (Fig. 3, snapshots 10–12), perhaps with some component acting downwards. Any component against weight-support is presumably detrimental to an animal seeking to gain altitude in take-off flight. The thrust component, however, would be beneficial: the wing in upstroke would act as a conventional propeller, increasing the velocity of the bird, both directly aiding escape and increasing the weight-supporting aerodynamic forces from the inner wing and body. An alternative, although not mutually exclusive, view is that the negative pressures during the upstroke are a physical inevitability related to either kinetic or morphological constraints. Pronation cannot be instantaneous, and negative pressure may be due simply to beginning pronation before the end of upstroke. Alternatively, there may be some morphological constraint prohibiting sufficient supination during the upstroke. Whether the phenomenon should be viewed as a beneficial, thrust-producing action or as an inevitable consequence of using flapping wings in slow flight (and resulting in an ‘undesirable’ downwards force) is impossible to determine at this stage, and the truth may well fall somewhere between these two extremes.

Implications of the double pressure peaks

The timing of the double pressure peaks observed at the distal sites is a consistent phenomenon after lift-off (Fig. 2). The first peak occurs just after downstroke begins. Positive pressure then falls off briefly over mid-downstroke. The second peak occurs near the end of downstroke, possibly associated with a ‘flaring’ of the wing due to supination before the end of downstroke, resulting in an increased angle of incidence. The initial pressure peak may be related either to initiation of the downstroke before the wing is fully pronated or to ‘added mass’ effects associated with rapid wing accelerations. This is followed by a brief drop in pressure when the wing is flapping fastest and presumably operating at some favorable aerodynamic lift-to-drag ratio. The significance of

the second pressure peak is not certain at this stage but may best be described in the context of management of the kinetic energy of the wing. ‘Inertial power’, due to repeated investment into the kinetic energy of flapping wings, need not be metabolically costly, even in the absence of elastic mechanisms, if the energy can be transferred to useful aerodynamic work (Weis-Fogh, 1972; Pennycuik and Lock, 1976; Ellington, 1984; Dudley and DeVries, 1990; Van den Berg and Rayner, 1995; Askew et al., 2001). An appropriate timing of such energy transfer might result in the pressure record indicated here. Towards the end of downstroke, the wings need to be decelerated quickly with minimal metabolic cost, and at the same time a high aerodynamic drag would provide some contribution to weight-support. By using the air to ‘brake’ the wing, a peak in pressure differential is created that may also result in an aerodynamic force useful for weight-support.

Future research with direct pressure measurements

Key future improvements of the technique described here may include: onboard data logging (e.g. Tucker, 1999), thus removing the necessity of trailing signal wires; lighter transducers; flight through a more constrained volume, from which accurate three-dimensional kinematics can be recorded; and improved time-resolution of the pressure signal. Such developments will permit research into the aerodynamics of controlled, steady flight of smaller birds in wind tunnels and near-natural maneuvering, turning, gliding, soaring, hovering, stooping and landing flight in trained or imprinted birds. The current study shows results low-pass filtered at 25 Hz (2 pole digital Butterworth), which limits the temporal resolution: a signal occurring above 20 Hz (or under 0.05 s) is likely to be missed. While this permits variations to be identified throughout a wingbeat cycle lasting approximately 0.2 s, flight at 8.5 m s^{-1} would result in pressure variations for an average chord (0.2 m width) to be neglected for anything less than two chord lengths of travel. As a result, interesting transient effects may be averaged and overlooked. With accurate three-dimensional kinematics and improved, less-filtered pressure signals (the transducers themselves have frequency responses around 1 kHz), transient aerodynamic phenomena, potentially important for slow or unsteady flight, may then be related to details of wing motion.

In conclusion, direct pressure measurements, with appropriate compensation for the sensitivity of pressure transducers to acceleration, allow the aerodynamics of flapping bird wings to be studied without the need for combining data from many wingbeats. Such observations produce direct evidence for both novel aerodynamic features and phenomena previously inferred from kinematics but uncertain due to unknown local induced flow-fields. This technique of direct pressure measurement provides an important link between the properties and consequences of the near-field wake and the physiologically important stresses and strains experienced by muscles and bones developed to generate and transmit the mechanical power necessary for flapping flight.

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