# Simulating Avian Wingbeats AND WAKES 

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# Abstract 

Simulating Avian Wingbeats and Wakes

Ben Parslew • The University of Manchester • Doctor of Philosophy • 05/01/2012

Analytical models of avian flight have previously been used to predict mechanical and metabolic power consumption during cruise. These models are limited, in that they neglect details of wing kinematics, and model power by assuming a fixed or rotary wing (actuator disk) weight support mechanism. Theoretical methods that incorporate wing kinematics potentially offer more accurate predictions of power consumption by calculating instantaneous aerodynamic loads on the wing. However, the success of these models inherently depends on the availability and accuracy of experimental kinematic data. The predictive simulation approach offers an alternative strategy, whereby kinematics are neither neglected nor measured experimentally, but calculated as part of the solution procedure.

This thesis describes the development of a predictive tool for simulating avian wingbeat kinematics and wakes. The tool is designed in a modular format, in order to be extensible for future research in the biomechanics community. The primary simulation module is an inverse dynamic avian wing model that predicts aerodynamic forces and mechanical power consumption for given wing kinematics. The model is constructed from previous experimental studies of avian wing biomechanics. Wing motion is defined through joint kinematic time histories, and aerodynamic forces are predicted using blade element momentum theory. Mechanical power consumption at the shoulder joint is derived from both aerodynamic and inertial torque components associated with the shoulder joint rotation rate.

An optimisation module is developed to determine wing kinematics that generate aerodynamic loads for propulsion and weight support in given flight conditions, while minimising mechanical power consumption. For minimum power cruise, optimisation reveals numerous local minima solutions that exhibit large variations in wing kinematics. Validation of the model against wind tunnel data shows that optimised solutions capture qualitative trends in wing kinematics with varying cruise speed. Sensitivity analyses show that the model outputs are most affected by the defined maximum lift coefficient and wing length, whereby perturbations in these parameters lead to significant changes in the predicted amount of upstroke wing retraction.

Optimised solutions for allometrically scaled bird models show only small differences in predicted advance ratio, which is consistent with field study observations. Accelerating and climbing flight solutions also show similar qualitative trends in wing kinematics to experimental measurements, including a reduction in stroke plane inclination for increasing acceleration or climb angle. The model predicts that both climb angle and climb speed should be greater for birds with more available instantaneous mechanical power.

Simulations of the wake using a discrete vortex model capture fundamental features of the wake geometry that have been observed experimentally. Reconstruction of the velocity field shows that this method overpredicts induced velocity in retracting-wing wakes, and should therefore only be applied to extended-wing phases of an avian wingbeat.

## DECLARATION

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## Nomenclature

| $a$ | Acceleration |
| :---: | :---: |
| AR | Advance ratio |
| c | Wing chord length |
| $c_{l}$ | 2D section lift coefficient |
| $c_{455}$ | 2D section lift coefficient at $45^{\circ}$ angle of attack |
| $c_{d}$ | 2D section drag coefficient |
| $c_{d_{0}}$ | 2D section drag coefficient at $0^{\circ}$ angle of attack |
| $c_{d_{90}}$ | 2D section drag coefficient at $90^{\circ}$ angle of attack |
| $C_{D}$ | Drag coefficient |
| $C_{D_{b}}$ | Body drag coefficient |
| $C_{F_{x}}$ | Axial force coefficient |
| $C_{F_{y}}$ | Lateral force coefficient |
| $C_{F_{z}}$ | Normal force coefficient |
| $C_{L}$ | Lift coefficient |
| $C_{P}$ | Mechanical power coefficient |
| $C_{T_{\phi}}$ | Torque coefficient |
| $d$ | 2D section drag per unit span |
| D | Drag |
| $e$ | Wing extension parameter |
| E | Wing extension amplitude |
| $f$ | Wingbeat frequency |
| $f_{w}$ | Vortex point release rate |
| F | Force |
| $g$ | Acceleration due to gravity |
| $h$ | Hand to wing length ratio |
| $I_{x x}$ | Wing moment of inertia |
| $J$ | Number of control points on wing |
| $J_{a}$ | Number of control points on arm |
| K | Number of wake control points on wing |
| $l$ | 2D section lift per unit span; wing length |
| $L$ | Lift |
| $L^{\prime}$ | Lift per unit span |
| $m$ | Body mass |


| $m_{w}$ | Wing mass |
| :---: | :---: |
| $n_{w}$ | Number of wake control points per wing |
| $N_{j}$ | Number of spanwise elements |
| $N_{t}$ | Number of timepoints |
| $P$ | Power |
| PL | Power loading |
| p | Control point position vector |
| P | General position vector |
| $q$ | General variable |
| r | Distance from wing root |
| $r_{c}$ | Viscous vortex core radius |
| R | Rotation matrix |
| $R_{g}$ | Wing radius of gyration |
| $s$ | Blade element reference area |
| $S$ | Wing reference area |
| $S_{b}$ | Body reference area |
| $t$ | Time |
| $T$ | Wingbeat time period; torque |
| $T_{d}$ | Downstroke fraction |
| $T_{w}$ | Vortex point release time period |
| V | Velocity |
| $V_{f}$ | Root-flapping wing velocity |
| $V_{w}$ | Root-flapping wing local wind velocity |
| $V_{\text {ref }}$ | Reference velocity |
| $V_{\infty}$ | Freestream velocity |
| $w$ | Distance from the shoulder to wrist |
| W | Velocity downstream of actuator disk |
| WL | Wing loading |
| $\mathrm{x}_{0}$ | Vortex point position vector |
| $\alpha$ | Angle of attack |
| $\alpha_{0}$ | Zero-lift angle of attack |
| $\beta$ | Descent angle |
| $\gamma$ | Stroke-plane angle |
| $\Gamma$ | Bound circulation |
| $\zeta$ | Extension parameter phase lag |
| $\theta$ | Shoulder pronation angle |
| $\Theta$ | Shoulder pronation amplitude |


| $\Theta_{0}$ | Shoulder pronation angle offset |
| :--- | :--- |
| $\xi$ | Pronation angle phase lag |
| $\rho$ | Local air density |
| $\sigma$ | Hand circumduction angle |
| $\phi$ | Shoulder elevation angle |
| $\Phi$ | Shoulder elevation amplitude |
| $\Phi_{0}$ | Shoulder elevation angle offset |
| $\Phi^{\prime}$ | Upper bound shoulder elevation amplitude |
| $\psi$ | Angle between freestream velocity vector and actuator disk normal |
| $\omega$ | Wingbeat frequency in radians; vorticity |
| $\omega_{k}$ | Wing angular velocity about the $k$ th axis |

## Subscripts

| $a$ | Aerodynamic force/torque |
| :--- | :--- |
| $B$ | Blade element |
| $c p$ | Control point |
| $E$ | Earth axes |
| $i$ | Induced velocity |
| $j$ | Blade element index |
| $k$ | Point vortex index |
| $m$ | Shoulder rotation; muscle |
| $m c$ | Minimum cost of transport |
| $m p$ | Minimum power |
| $n$ | Timestep index |
| $r$ | Wing retraction |
| $R$ | Retracted wing property |
| $x$ | $x$-direction |
| $y$ | $y$-direction |
| $z$ | $z$-direction |
| 0 | Freestream wind axes |
| $l$ | Stoke-plane axes |
| 2 | Elevation-depression axes |
| 3 | Wing axes |
| 4 | Blade element axes |
| 5 | Local wind axes |
| $\infty$ | Freestream |

## Superscripts

* Fully-extended wing property; optimal value Upper bound; per unit span


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## Chapter 1. Introduction

Flapping wings have evolved as the only propulsion mechanism for powered flight in nature. Developing an understanding of the physics of organic flapping wings assists in forming hypotheses on flight evolution (e.g. [1],[2]) and various ecological phenomena, such as migration (Figure 1) [3]. In addition, animal flight research provides insight for the design of flapping wing air vehicles [4],[5] and for graphical reconstruction of insects, birds, bats and pterosaurs in computer animation [6],[7]. The present work will contribute to these fields through the development of theoretical models of bird flight, which are transferable to studies on other flapping wing animals.


Figure 1. Barnacle geese (Brantaleucopsis) taking off for migration. The wing posture is observable at various stages throughout the wingbeat cycle, including the fully extended mid-downstroke and retracted upstroke.

Original theories on the aerodynamics of avian flight were formed from simple observations of birds in their natural environments [8],[9]. This form of empirical study was refined by using controlled laboratory conditions to analyse the kinematics of birds flying between perches (e.g. [10],[11]). The degrees of freedom in flight experiments were further restricted by employing wind tunnels as a test environment (e.g. [12],[13]). This approach effectively synthesized rectilinear flight conditions, for which mathematical models were developed for predicting aerodynamic forces and mechanical power consumption.

Early mathematical models of bird flight applied theories for fixed or rotary wing aerodynamics taken from aerospace literature (reviewed by Rayner [9]). The success of these models was based on formulating simple analytical expressions that described flight performance for different scale birds at different cruise speeds. More advanced models aimed to increase the accuracy of predictions of aerodynamic force and power by modelling the dynamics of flapping wings (e.g.
[13],[14]). These methods require inputs of wing kinematic data, and are therefore limited by the availability of experimental data. This highlights scope for developing a theoretical model that can be used to predict avian wing kinematics. The inspiration for this proposal comes from the use of predictive simulation in studies of terrestrial locomotion, whereby kinematics are predicted through mathematical optimisation of dynamic models.

An additional experimental method commonly employed in animal flight research is the visualisation and analysis of flowfields during flight in wind tunnels ${ }^{1}$; aerodynamic forces are inferred through quantitative analysis of the wake velocity and vorticity fields [15]. By incorporating established methods of simulating fluid motion the predictive simulation approach can also be used to predict wake geometries to assist in the design of such experiments. Thus, the contribution of the present work will be to complement existing theoretical and experimental techniques for avian flight research by simulating kinematics, energetics and wake geometries.

### 1.1. SCOPE

In accordance with the majority of previous experimental and theoretical research on avian flight, the present work will be limited to modelling rectilinear flight conditions. This will include hovering, horizontal or climbing flight at constant speed, and horizontal accelerating flight. The work will not include an analysis of stability and control aspects of flapping flight [18].

### 1.2. AIM

Develop a scalable theoretical tool that extends the capabilities of animal flight research methods.

### 1.3. OBJECTIVES

- Introduce fundamental topics in the field of flapping-wing flight and overview the proposed strategy for constructing a predictive simulation tool (chapter 2);
- Critically assess previous predictive simulation methods for flapping-wing flight and identify a strategy for constructing a theoretical model (chapter 3);
- Formulate extensible mathematical tools for simulating avian wing kinematics and wakes (chapter 4);

[^0]- Confirm the approach is robust by demonstrating the numerical accuracy, stability and convergence (chapter 4);
- Validate simulated kinematics against experimental data from biomechanics literature (chapter 5);
- Discuss the implications of the research findings to the fields of avian flight performance and flight evolution (chapter 6);
- Provide logical routes for extending the model capabilities to test other existing hypotheses on flight performance and evolution (chapter 7).


## Chapter 2. Background Theory

This chapter will describe some common physical concepts related to studies of flapping flight, starting with a simple discussion of how the flapping motion of wings can be used to generate a net aerodynamic force for powered flight. A collection of fundamental topics and terminology will be introduced to clarify the discussions made in the remaining chapters.

### 2.1. FLAPPING WING PROPULSION \& WEIGHT SUPPORT

Figure 2a shows a pitching-plunging wing in a uniform flow. The wing flapping velocity (Figure $2 b$ ) arises due to the plunging motion of the wing relative to the surrounding fluid. The local wind velocity is equal to the vector sum of the freestream and wing flapping velocities ${ }^{2}$. The aerodynamic force on the wing can be decomposed into components of drag and lift, which are defined as forces acting parallel and perpendicular to the local wind velocity vector, respectively. The angle of attack is defined as the angle between the local wind velocity vector and the wing zero-lift line; the angle of attack is zero when the wing generates no lift.

[^1]

Figure 2. (a) Example 2D kinematics of a pitching-plunging wing in a freestream flow. (b) Local wind velocity diagram showing the orientation of local lift and drag forces and the angle of attack. (c) Aerodynamic forces acting on a plunging wing during both downstroke and upstroke, illustrating the Knoller-Betz mode of thrust generation. (d) Aerodynamic forces acting on a plunging wing with a constant pitch angle, generating both thrust and weight support.

A wing can generate a net aerodynamic force in a direction opposite to the freestream velocity vector (termed "thrust" in the present work for horizontal flight ${ }^{3}$ ) by reciprocating in a direction perpendicular to the freestream velocity vector. This phenomenon is known as the Knoller-Betz effect, and in its simplest form can be observed for a wing plunging at a constant speed with no pitching motion (Figure 2c). The thrust provides propulsion for horizontal flight. By using a

[^2]constant wing pitch angle a mean aerodynamic force can be generated that is not aligned with the freestream velocity, which can provide both thrust and weight support in horizontal flight (Figure $2 d)$. Other wing kinematics can be used to vary the magnitude and orientation of the mean aerodynamic force, which also affects the amount of mechanical power consumed by the wing actuation system. The prediction of aerodynamic force and mechanical power consumption is fundamental to the present work for simulating wing kinematics, and will be discussed in detail throughout the remaining chapters.

### 2.2. AERODYNAMIC FORCE COEFFICIENTS

Lift and drag coefficients are dimensionless quantities commonly used in aerodynamic analysis. These coefficients can be used to compare the aerodynamic properties of wings of different scale. For a body moving in a fluid lift and drag coefficients are commonly expressed in the following form:

$$
\begin{align*}
& C_{L}=\frac{L}{\frac{1}{2} \rho\|\mathbf{V}\|^{2} S},  \tag{1}\\
& C_{D}=\frac{D}{\frac{1}{2} \rho\|\mathbf{V}\|^{2} S}, \tag{2}
\end{align*}
$$

where $L$ and $D$ are the lift and drag, respectively, $\rho$ is the local air density, $\|\mathbf{V}\|$ is the local wind velocity magnitude and $S$ is a reference area. Similarly, for a 2D model of a flow over a wing such as those shown in Figure 2 the 2D section lift and drag per unit span are given as
$c_{l}=\frac{l}{\frac{1}{2} \rho\|\mathbf{V}\|^{2} c}$,
$c_{d}=\frac{d}{\frac{1}{2} \rho\|\mathbf{V}\|^{2} c}$,
where $c$ is the wing chord length, and $l$ and $d$ are the 2D section lift and drag per unit span, respectively. For a given geometry under steady flow conditions the lift and drag coefficients depend only on the flow Reynolds number ${ }^{4}$ and Mach number ${ }^{5}$, and the angle of attack.

[^3]
### 2.3. FLIGHT PERFORMANCE

In the context of flying organisms the term flight performance generally relates to the amount of energy consumed in powered flight [13] ${ }^{6}$. This may be based purely on the consumption of mechanical energy to overcome aerodynamic and/or inertial loads, or it may go further to consider flight metabolism.

A central focus of flight performance studies has been the analysis of the power curve [23], which gives the relationship between power consumption and flight speed. Power curves provide a rapid means of identifying characteristic flight speeds: Figure 3 depicts a synthesised power curve, and highlights the minimum power speed, $V_{m p}$ (also known as the maximum endurance speed), and the minimum cost of transport speed, $V_{m c}$ (also known as the maximum range speed). This provides insight into the self-selected flight speeds used by birds, which can be applied to studies on bird migration, for example.


Figure 3. Illustration of the variation of power consumption with cruise speed for typical powered flight. The minimum power cruise speed, $V_{m p}$, and minimum cost of transport cruise speed, $V_{m c}$ are highlighted as characteristic speeds.

Power curves have been predicted for avian flight using various theoretical models [9]. The net aerodynamic power is usually derived from separate models that calculate the wing profile power, the body parasite power, and the induced power, which are each illustrated on the power curve (e.g. [23]). The present work will not separate the mechanical power into these components, and will also include inertial effects. Therefore, the power curves predicted will illustrate total mechanical power consumption (chapter 5).

[^4]
### 2.4. GAIT

A hypothesis that emerged from studies on flight mechanics and performance is that the kinematics of flying organisms may be described using gaits. This section will overview the use of this term in other works, and explain why the topic of gaits is not included in the remaining chapters.

In terrestrial locomotion a gait is generally used to describe a style or pattern of locomotion that is characteristic over a range of speeds [24]. This term was adopted in studies of flight to distinguish between different wing kinematics [25]. However, it has been used predominantly to describe the geometry of the wake shed by flying organisms, following the observation that different wake geometries reflect different wing dynamics (e.g [25],[26]). Central to these discussions is the idea that in some flight conditions negligible aerodynamic lift is generated on the upstroke, in which case the upstroke can be regarded as being aerodynamically inactive, or passive [27].

Initially it was believed that birds may exhibit two distinct wake geometries (or gaits), one in which the upstroke is passive (the "vortex ring gait"), and one in which the upstroke is active (the "continuous vortex gait") [25],[26],[28]. More recent experimental studies have concluded that alternative wake geometries also exist and therefore this gait classification system may not be accurate [29],[30]. This is perhaps why gaits have been less commonly referred to in recent experimental studies of bird flight (e.g. [31],[32]). It is plausible that future studies may devise an alternative gait classification for avian flight, but this will not be addressed in the present work. To avoid confusion with the hypothesis presented above the term gaits will be avoided here, and instead the term kinematic modes will be used to distinguish between cases with significant differences in kinematics. The contribution of the present work will be to provide the capability to predict, rather than categorise these modes.

### 2.5. MATHEMATICAL OPTIMISATION OF DYNAMIC MODELS

Optimisation is commonly used in an engineering context to make improvements to existing designs by adjusting parameters such as geometry or material properties. Optimisation can be applied to a dynamic system, whereby the motion is optimised to yield a favourable outcome, or meet some form of optimisation criteria. This approach is used by the biomechanics community in studies of terrestrial locomotion (reviewed by Xiang et. al [33]). For example, the kinematics of a theoretical model of a human may be optimised to reduce metabolic energy consumption in walking. The philosophy behind this approach is that given a suitable theoretical model and optimisation criteria the optimised kinematics should represent those used by real animals. The present work will apply this philosophy to the aerial locomotion of birds.

Mathematically, the optimisation problem is formulated in two parts: the dynamic model, and the optimiser. The dynamic model includes a mathematical description of the physics that govern the system being studied. The optimisation variables are independent variables within the dynamic model. In the present work this will include parameters that define the kinematics of the model; it may also include geometric parameters, as will be discussed in section 3.5. Optimisation constraints are used to define certain criteria that the dynamic model must adhere to. These may be limits on the optimisation variables that constrain the kinematics to within a certain range. Or they may be limits on other variables, such as forces and torques in the dynamic model. The cost function is an output from the dynamic model that is used to quantify the success or failure of a given set of values of the optimisation variables. For animal locomotion a number of different cost functions have been used [24],[33], including the amount of mechanical or metabolic energy consumed, and the peak torques applied at the joints.

The second part of the model, the optimiser, is used to drive the dynamic model by inputting values for the optimisation variables, and then adjusting them according to the cost function. This process aims to minimise the cost function, which can lead to the identification of local minima in the optimisation space, or the global minimum (Figure 4); both local and global minima are regarded as solutions to the optimisation procedure. While the dynamic model and optimiser are required to exchange information, chapter 3 will describe how these processes can be formulated as being separate and distinct to create a more robust simulation environment.


Figure 4. Illustration of how an optimisation cost function might vary with a single optimisation variable. This particular example has two local minima and a global minimum.

It is important to note that mathematical optimisation applies equally to both forward and inverse dynamics models. At the simplest level, forward dynamics models calculate the kinematics of a body due to the applied forces and torques; the optimisation variables for forward dynamics models describe the time histories of forces and torques applied to the model. Inverse dynamics models calculate the forces and torques for defined kinematics, and the optimisation variables describe the kinematic time histories.

Both forward and inverse dynamics models have been used in studies of terrestrial locomotion (e.g. forward dynamics: [34]; inverse dynamics: [35]). However, an advantage of the inverse model for aerial locomotion is that it can be tested without invoking an optimiser, using existing experimental data for input kinematics, which greatly simplifies the model development process. While some experimental data is available for forces applied by avian muscles [36], it is far less abundant, and has only be obtained for some specific flight muscles. It would therefore be difficult to define force time histories explicitly to test a forward dynamics model without an optimiser. For these reasons an inverse dynamics model is considered a more practical option for the present work.

## Chapter 3. Literature Review

This chapter will critically review previous applications of predictive simulation to flapping flight. Predictive methods are defined here as those where the main outputs are kinematic variables ${ }^{7}$. The review will consider a subset of literature in order to focus on works that are relevant to the proposed research strategies of the present work. Aerodynamic models employed in these works will be introduced in this chapter, and a more detailed discussion of aerodynamic methods for analysing fixed, rotary and flapping wings will be given in section 4.2.5.

A previous article upon which the present work is based will not be reviewed, but will be referred to throughout the remaining chapters [37]. Studies that use predictive methods to optimise flapping wing geometries will be excluded (e.g. [38]), although these serve as a useful reference due to similarities in the numerical methods employed. Reviews of models for aerodynamics of flapping wings, and for avian flight performance can be found elsewhere, and so are not repeated here [9],[39]. As the current work aims to complement existing experimental data, the reader is also referred to previous reviews of experimental techniques used in research on animal flight aerodynamics [15]-[17].

### 3.1. SCALING LAWS FOR KINEMATICS

Scaling laws are used to predict variations in avian wing and body geometric properties with overall body mass. These laws tend to be derived empirically, using least squares analysis of experimental data. Based on simple physical arguments some scaling relationships can be derived theoretically, including those that predict the variation in certain kinematics variables with scale. A detailed summary of these was given by Norberg [40], and examples include the variation of minimum power cruise speed and wingbeat frequency with bird body mass.

The strength of these models is that they can be used to provide rapid estimates of certain kinematic parameters. The obvious limitation is that experimental data are required to determine the constants of proportionality, without which the equations are unusable. Despite this, scaling laws can still be regarded as a form of predictive tool as they can be used to extrapolate kinematic data to a much broader range of scales than have been measured experimentally. The main caveat with these models is that they capture general trends in kinematic parameters with scale, but offer

[^5]little insight into variations in kinematic parameters for different species of the same scale. Furthermore, it is unlikely that such a rudimentary approach could be extended to predict more detailed aspects of wing kinematics.

### 3.2. 2D BLADE-ELEMENT MODEL OF HOVER

Hovering flight is conceptually the simplest flight condition for analysing flapping and rotary wing systems because the freestream velocity is zero. A model posed by Wang [41] analyses this flight condition for flapping flight by comparing the efficiency of different wing kinematics. The aim of the study is to identify wing kinematics that yield minimal power consumption in generating aerodynamic loads. The model is described as using simple wing kinematics whereby the motion is defined by four parameters. The motivation for this was to be able to visualise the parameters space using a series of isosurfaces of calculated efficiency. However, is it believed that this aim should be secondary to constructing a model that offers sufficient flexibility to capture accurately the underlying physics.

In Wang's model the wing is represented as a pitching-plunging aerofoil. Therefore, the model does not capture the variation in flapping velocity along the wing length that is seen in flying organisms. In keeping with the low order approach a simplified aerodynamic model is used to calculate lift and drag coefficients as trigonometric functions of angles of attack. Aerodynamic efficiency is defined as the reciprocal of the average power consumed in overcoming aerodynamic loads. However, the induced velocity is not included in the model and so the local wind velocity and power consumption will be underpredicted. Furthermore, due to the lack of induced velocity the model will not reflect the increase in aerodynamic efficiency that can be achieved by using large amplitude wingbeats to reduce effective disk loading [19].

The variations in efficiency with kinematic variables follow the same qualitative trends for Reynolds numbers ranging from $10^{2}$ to $10^{6}$. Unsurprisingly, the most efficient solutions found are those that represent a steady translating wing at constant angle of attack that yields the best lift to drag ratio. Other "near-optimal" motions are found that are asymmetric, whereby the downstroke and upstroke have different angles of attack and different inclinations with respect to gravity. By identifying a range of high efficiency solutions this approach highlights that different kinematic modes are physically plausible in hovering flight.

### 3.3. CFD-BASED MODEL OF 2D AEROFOIL IN AXIAL FLIGHT

The use of flapping wings as a propulsion system for micro air vehicles has renewed the interest in researching unsteady flows over aerofoils. A number of theoretical and experimental studies have demonstrated that plunging aerofoils can achieve maximum propulsive efficiency at certain Strouhal numbers (e.g. [42],[43]), where the efficiency is defined as the ratio of mean thrust generated to mean aerodynamic power. The propulsive efficiency is also influenced by the pitching motion of the aerofoil, and hence Strouhal number alone is insufficient for predicting efficiency of aerofoils that pitch and plunge [43]. This conclusion is particularly important for analysing the flight of birds, which tend to pronate and supinate their wings in typical cruising flight conditions [44].

A series of numerical studies performed by Tuncer and Kaya has contributed significantly to this field by showing how the combination of pitching and plunging motion affects propulsive efficiency and peak thrust (Figure 5) [45],[46]. A multi-objective gradient-based method is used to predict wing motions that have maximum thrust, maximum propulsive efficiency, or combined high thrust and efficiency. A computational fluid dynamics (CFD) numerical method is used to calculate aerodynamic loads. These methods will be discussed further in section 4.2.5, but for now it is sufficient to highlight that they are regarded as high order, computationally expensive methods. Because of this the optimisation routine takes up to 100 h of wall clock time (10-16 Pentium 4, 2.4 GHz processors running in parallel), which is presumably what limits the scope of the study: only a single flight condition is considered, using a fixed value for the reduced flapping frequency. Also, the sensitivity of the solutions is not considered with respect to the choice of numerical solution parameters, such as the numerical grid density.


Figure 5. The flowfield downstream of a pitching-plunging aerofoil [46]. Laminar flow simulations achieved using time dependent numerical solutions of the Navier-Stokes equations.

One of the key conclusions drawn from these studies is that maximum propulsive efficiency can be achieved using sinusoidal variations in aerofoil plunge displacement and pitch angle, with a pitch angle phase lag of $90^{\circ}$. However, no discussion is made of whether such a high order aerodynamic model is needed to reach this conclusion.

### 3.4. EXPERIMENTAL \& NUMERICAL MODELS OF 3D WING KINEMATICS IN HOVER

A logical extension to the analysis of flapping aerofoils is to incorporate 3D wing kinematics. A wing that rotates around a joint at the wing root is a closer physical representation of flapping-wing organisms. Hovering flight can still be regarded as the simplest flight condition for analysis of rootflapping wings. However, unlike in Wang's hovering model [41], the instantaneous local wind velocity now varies along the wing.

A number of experimental studies have examined how kinematics of wing models can be adjusted to increase mean aerodynamic forces in hover. An early example of this approach is presented by Sane and Dickinson [47], who measure instantaneous aerodynamic loads on a flapping model of a hoverfly wing. The model is actuated so that the wing kinematics are representative of those used by real hoverflies. Instantaneous forces were measured using force transducers located at the wing root, and inertial effects were subtracted to yield the instantaneous aerodynamic forces on the wing. The results are presented as maps of force coefficients for ranges of wing kinematics. While the model does not directly predict kinematics the main findings are based on kinematics, and hence this study is applicable to this review.

In deriving aerodynamic force coefficients Sane and Dickinson base the reference velocity on the wing flapping velocity alone, without including the effects of induced velocity; this discrepancy will lead to an overprediction of the mean force coefficients, but this will be cancelled out in the data presented for mean lift to drag ratio. A potentially useful metric that is presented is the ratio of mean aerodynamic forces to mean power consumption. This ratio is the reciprocal of the power loading, used for analysing performance of rotary wing vehicles [19] (section 4.2.8). Sane and Dickinson calculate the aerodynamic power as the product of the instantaneous load on the wing and the "instantaneous wing velocity", however it is not clear which velocity this term refers to and is therefore difficult to assess the validity of these results.

Khan and Agrawal [48] also measure the aerodynamic loads on flapping wings, but with proposed application to micro air vehicles. In addition to the experimental measurements a theoretical model of the wing and thorax dynamics is also included. A blade element model is used to predict
instantaneous aerodynamic load distribution along the wing. Aerodynamic forces that arise from flapping the wings are assumed to be directed normal to the wing surface, however no theoretical or experimental evidence is provided to justify this. Coefficients required to close the system of equations that described the aerodynamic forces are derived by calibrating the wing kinematics predicted from the theoretical model against those measured experimentally. This approach makes it difficult to determine the accuracy of the theoretical models, and whether or not the equations for added mass and rotational lift are significant.

Arguably the main contribution by Khan and Agrawal's theoretical model is the use of numerical optimisation to predict wing kinematics that maximise the mean lift and mean lift-to-drag ratio. Unfortunately, the optimised solutions are only presented for a single case study for which fundamental physical parameters, such as the thorax spring stiffness values, are given defined values without any reasoning.

The hovering flight studies by Khan and Agrawal [48] and by Sane and Dickinson [47] both illustrate the general trends in mean force coefficients and lift to drag ratios with different wing kinematics. However, neither of these studies considers the constraint that the mean aerodynamic load must support the overall system weight. Therefore, neither identify the wing kinematics that are plausible for hovering flight of a specific flying organism or micro air vehicle. The converse can be said of an advanced theoretical model derived by Berman and Wang [49], which predicts wing kinematics for three types of insects in hover. The model is described as being phenomenological, in that it aims to capture certain kinematic phenomena that have been observed experimentally, such as the figure-of-eight path of a wingtip.

Berman and Wang formulate an inverse dynamic model of an insect wing that predicts aerodynamic forces and torque, and mechanical power consumption for given input wing kinematics. A blade-element model is used to calculate aerodynamic loads and numerical optimisation is used to determine wing kinematics that incur the minimum average mechanical power while providing a mean aerodynamic force to support the insect weight.

The optimised kinematics show strong qualitative similarities to those measured experimentally for three different insects. However, the model always tends to overpredict wingbeat amplitude, and constraints are imposed to avoid solutions with unrealistically large amplitudes. It is likely that in the model these large amplitude, low frequency kinematics are optimal as they reduce power consumption by reducing inertial loads when compared to low amplitude, high frequency kinematics. Added mass and rotational lift effects are also included in the aerodynamic model, though as with the model from Khan and Agrawal [48] their relative contributions to the total
aerodynamic force are not discussed. As with Wang's 2D model [41] no induced velocity is included and so disk loading effects are not captured.

The aerodynamic model used by Berman and Wang can be regarded as a low order model, which allows optimisation to be performed with less computation time than Kaya and Tuncer's CFDbased models (e.g. [45],[46]), even though the wing kinematics are described using more parameters. The choice of aerodynamic model and the method of parameterising wing kinematics both strongly influence the computation time needed for optimisation.

Berman and Wang parameterise the insect wing geometry so that it can be readily adapted to represent different species. The scalability of the model is demonstrated as some wing kinematic parameters can be constrained in order to isolate specific physical phenomena of interest. These two features provide scope for applying the model in future studies for different species, and using more detailed kinematics. Extending the capability to model flight conditions other than hover would also be beneficial to the others researching insect flight.

### 3.5. FLAPPING-WING VEHICLE MODEL FOR CRUISE AT VARYING SPEEDS

de Margerie et al. [50] and Doncieux \& Hamdaoui [51] apply predictive simulation to flappingwing air vehicles (Figure 6). A hybrid forward-inverse dynamics model is used in which wing kinematics are defined, while the motion of the vehicle is solved as a model output. The model uses an evolutionary algorithm to adjust the amplitudes and phases of sinusoidal wing joint trajectories. Optimal solutions are defined as those that propel the vehicle along a horizontal flight path at a given speed using minimum mechanical power.
de Margerie et al. aim to use the philosophy of biomimicry to develop a design that exhibits some of the capabilities of flying organisms. The dynamic model is assigned with baseline values of wing geometric parameters and mass that are based loosely on those of a real bird. In addition to the wing and tail kinematics, the wing area and aspect ratio are also included as free variables to be optimised. Some other parameters, such as the body mass, are fixed with no justification for the choice of values used.


Figure 6. Flapping-wing air vehicle design based on the geometry of a bird [51]. The shoulder joint can elevate and depress the wing and also rotate the wing about its major axis. The wrist joint rotate the out wing panel about its major axis and also sweep the outer panel to reduced the exposed surface area, and also pronate-supinate.
de Margerie et al. use a form of blade element theory to calculate aerodynamic loads on the wings and tail. Lift and drag coefficient variation with angle of attack is defined using data collected from wind tunnel testing of a specific aerofoil which is claimed to be representative of avian wing aerofoils. In the post-stall region, where experimental data was not available, the lift coefficient is assumed to fall at an increasing rate with increasing angle of attack, though this is uncharacteristic of avian wing aerofoils [52]. No discussion is made on the aerodynamic properties of the tail, which would be expected to differ from those of the wing due to the low aspect ratio and swept geometry.

The optimisation objective function combines two separate objectives of maximising the distance travelled in a given flight time, and minimising the mean power consumed. The evolutionary algorithm identifies numerous 'optimal' solution that are compromises between these two objectives. An insightful feature of the work is that all of these solutions, rather than just a single optimum, are presented as part of the results. This leads to a key finding, which is that different solutions have large variations in wing kinematics, showing that there is some flexibility in the choice of kinematic mode used by the vehicle. If one kinematic mode incurs a penalty that is not included in the model, such as excessive joint torques, the results provide scope for identifying alternative modes.

The results presented by de Margerie et al. and Doncieux \& Hamdaoui are given for a range of cruise speeds. The predicted mechanical power follows the typical U-shaped curve, with minimum power occurring at a cruise speed of $12 \mathrm{~ms}^{-1}$. The trends in wing kinematic variables with cruise speed are qualitatively similar to the those predicted in previous simulations of avian flight [37]. Unfortunately, de Margerie et al. and Doncieux \& Hamdaoui make no comparison between the predicted kinematics and those from other theoretical models, or from experimental measurements.

Several of the solutions presented by de Margerie et al. use a wing aspect ratio that is equal to the defined upper bound value. This is because the aerodynamic model captures the reduction in induced drag that would be expected with higher aspect ratio wings, which in turn reduces mechanical power. However, the model does not take into account the greater structural mass that would be needed to support greater bending moments that would be applied to higher aspect ratio wings. Similarly, the wing mass remains fixed, even though the wing area is a free variable. Therefore, the model does not accurately capture changes in inertial loads and mechanical power that would occur for changes in wing geometry. For these reasons the incorporation of geometric parameters as free optimisation variables is believed to detract slightly from the main findings of the work.

### 3.6. AVIAN FLIGHT MODEL FOR CURVILINEAR TRAJECTORIES

Predictive simulation has been used extensively by the computer graphics community in order to recreate realistic character motion using physics-based animations. In this field, special attention is given to both character geometry and kinematics. This is apparent not only in simulations of human terrestrial locomotion, but also those of swimming and flying animals. As a goal in computer graphics is to increase believability in animations, it is unsurprising than physics-based animations of bird flight have focussed heavily on detailed reconstruction of avian anatomy. This is most evident in the work of Wu and Popović [6] who simulate birds using a highly detailed representation of avian geometry and kinematics (Figure 7).


Figure 7. (a) Model of the avian wings, body and tail, including individual primary and secondary feathers [6]; joint degrees of freedom are based on those of real birds. (b) Predicted kinematics of a raven taking off, showing a retracting wing up stroke, and the bending of feathers on the downstroke.

Wu and Popović use numerical optimisation to predict wing and tail kinematics that will propel a bird along a user-defined flight trajectory. Other objectives are defined, including the use of
minimal torque at the wing joints and the avoidance of high rotation rates of the body. Optimised solutions are obtained according to the weighted sum of these different objectives. It is therefore difficult to isolate the importance of any one objective, especially as no physically reasoning is given for the choice of objective weighting.

The model used by Wu and Popović captures some of the key features of avian wing kinematics, such as the synchronous retraction of wing skeletal segments that will be discussed in detail in section 4.2.3. However, despite aiming to avoid unnecessary complexity the model also includes the dynamics of individual feathers. While this may add to the aesthetics of the animation, it is unlikely that these effects would increase the accuracy of the predicted kinematics.

The blade element method of simulating aerodynamic forces is clearly central to the formulation of Wu and Popović's physics-based model. Rather than deriving force coefficients on blade elements, they are calculated for each individual feather. This method overcomplicates the solution procedure and offers no obvious advantage in terms of accuracy or numerical stability. More important is the choice of model of lift and drag coefficient variation with angle of attack, which is stated as being based partly on experimental data taken from wind tunnel tests of birds wings. However, for high angles of attack the lift coefficient is assumed to plateau, and even has a significant value at $90^{\circ}$ angle of attack where it would be expected to be negligible. This discrepancy will lead to overprediction of lift for given wing kinematics.

Wu and Popović demonstrate that their model can be used to simulate wing kinematics of different scale birds and for different trajectories. However, in each case a specific set of parameters is used in obtaining optimised kinematics. These parameters include joint torque coefficients and values for peak lift and drag coefficients, none of which are readily available data for birds. This strongly limits the scalability of this approach if a wide range of species were to be simulated. As the objective function weighting values also vary for each case it seems likely that some tuning of these parameters is required in order to generate plausible kinematics. Therefore, the model cannot be regarded as being robust because a high level of user intervention is required in its operation.

### 3.7. LITERATURE REVIEW SUMMARY

The findings from the literature review are summarised as follows:

- Scaling laws are limited by the need for experimental data to calibrate the models of kinematic variables;
- For predictive simulation the aerodynamic model and method of kinematic parameterisation should be selected strategically, balancing accuracy, computational cost and extensibility of the model;
- Scalable models can be used to simulate different species, providing more scope for validation with existing experimental data;
- A robust model should simulate different species and flight conditions without requiring adjustments to the numerical scheme, which extends its applicability as a research tool;
- Mathematical optimisation can be used to identify not only the optimal solution, but also a range of near-optimal solutions to explore alternative kinematic modes that may be used by real animals.


## Chapter 4. Method

This chapter overviews the conceptual and technical approaches used in developing a predictive simulation framework for avian flight. Three simulation modules and their mutual interaction will be described as part of the modelling philosophy (section 4.1). Following this, details of the individual modules will be provided with justifications for the modelling decisions.

Section 4.2 will describe the construction of the inverse dynamics model that serves as the basis for the simulation framework. This will include an overview of biomechanics literature on avian wings, as well as mathematical descriptions of the dynamic model developed for the present study. Fundamental aspects of the model, such as the method of predicting aerodynamic loads, will be given special attention and examples of the model output will be provided.

Section 4.3 will describe the optimisation module, which can be used to control the inputs to the inverse dynamic model in order to function as a predictive simulation tool. Constraints to the optimisation process will be defined from physical arguments, and will also be used to maintain numerical stability.

Finally, a method of simulating the wake shed from a flapping wing will be presented, based on techniques developed for the simulation of wakes from rotary wings (section 4.4). This module accepts inputs of user defined wing kinematics, and can also be with predicted kinematics from the other two simulation modules.

### 4.1. MODELLING PHILOSOPHY

Based on the success of previous flight simulation tools, a modular approach to simulation offers some distinct advantages in achieving the aim of the present work. One example of modular simulation is a previously developed flight energetics program that has been used to predict the performance of different species of birds under various flight conditions [3]. The underlying modules for this program have been refined to accommodate new scientific evidence, providing extensibility to the overall program. Another collection of theoretical tools includes methods for simulating aerodynamic, structural and control aspects of flapping wing flight for unmanned air vehicle (UAV) design [53]. These tools can be used independently or collectively, and provide the capability to test new theoretical models at varying stages of development.

The process of optimisation of a dynamic model also lends itself to modular design as the method of optimisation and the dynamic model are largely separable in terms of their functionality ${ }^{8}$. In the present work the optimiser and dynamic models are considered as two distinct modules that can exchange information (Figure 8). The dynamic model is optimised to make predictive simulations of kinematics. The dynamic model can also be used independently with user-defined wing kinematics to predict force, torque and power time histories, for example. Defining these two modules as distinct and separable not only increases the functionality of the simulation framework as a whole, but also streamlines the development process as changes to the dynamic model can be tested without implementing the optimisation module.

Results from the dynamic model can also be passed to a third module that simulates the unsteady wake shed from a bird's wing (Figure 8). Visualisation of the wake geometry will provide data to compliment experimental data on avian flowfields [15]-[17]. The wake simulation module is again designed to be independent, in that it may also be implemented without the other modules. For example, a wake could be simulated using experimental data for aerodynamic loads on the wing (e.g. [54]).

[^6]

Figure 8. Modular simulation tools. The simulation modules are designed to function independently, or collectively. *The joint trajectories can be inputted directly (e.g. from experiment), or a method of parameterising the trajectories can be used to predict the wing kinematics using the optimisation module.

As well as having a modular design the simulation framework will also incorporate a balanced level of complexity in each of the modules. Chapter 3 discussed how some predictive simulation approaches are impeded by the complexity of the dynamic model; high order aerodynamic methods require lengthy solution times for optimisation, while complex representations of wing geometry can lead to non-robust models. Furthermore, it is difficult to determine the root cause of inaccuracies in these models, due to their inherent complexity. Other methods that use a consistently low order approach have had success in predicting flapping wing kinematics of insects and birds [37],[49].

The philosophy of balanced modular design will be maintained throughout this chapter. The resulting simulation framework will be shown to be both scalable and robust, in being capable of simulating a range of different scale birds in various flight conditions (sections 5.2-5.5). Extensibility of the simulation framework will be demonstrated by altering the dynamic model to incorporate alternative wing aerodynamic properties and by testing an alternative set of wing kinematic parameters (section 5.2.7).

### 4.2. INVERSE DYNAMIC MODEL

This section will describe the development of an inverse dynamic bird model, extending the detail presented in a previous study using a similar approach [37]. The model will be demonstrated by predicting mechanical loads, torque and power consumption for a wing with pre-defined kinematics.

### 4.2.1. Avian Flight Apparatus

This study aims to develop a tool for simulating symmetric rectilinear flight, rather than manoeuvring flight of birds. The generation of a net aerodynamic load for propulsion and weight support can be regarded as the main role of the flight apparatus in this flight condition. Birds generate these aerodynamic loads primarily using their wings, though some other aspects of their physiology may contribute. As a relatively bluff body the main influence of the body on the aerodynamics is to generate drag, which has a significant impact when modelling mechanical power consumption (e.g. [13],[55]).

Several recent studies have considered the role of birds' tails in generating lift (e.g. [56],[57]) and reducing drag [58]. As a highly swept, low aspect ratio surface the tail would be expected to have a significantly lower lift curve slope than the wings. Also, the surface area of tails is much smaller than that of wings, and the local wind velocity at the wings will be much greater for typical kinematics in powered flight. This suggests that the wings generate significantly more aerodynamic load that the tail. It seems more likely that the main role of the tail is for stability and control [18],[59], though it may assist in increasing drag for rapid deceleration in perched landings. It is also recognised that the tail may reduce mechanical power consumption in low speed flight [38].

To construct a tractable model that captures the most fundamental aspect of avian flight dynamics necessary for simulating rectilinear flight, the present work includes a model of the wing dynamics, and also a model of the drag acting on the body ${ }^{9}$. The dynamic model will be used to predict aerodynamic forces needed for propulsion and weight support, and the power consumed in doing so. In this sense, the dynamic model has some similarities with previous models of flight performance [13],[55] although it will also incorporate the effects of wing inertia on mechanical power consumption.

[^7]Following previous predictive simulation studies the present work will use a jointed, sevensegment bird model [37]. Due to strong similarities in avian wing geometry between different species this approach is representative of most flying birds [40]. The segment model is shown in Figure 9 in comparison to the skeleton of the Rock Pigeon, Columbia livia. The present work draws largely on the wealth of experimental data for the pigeon, and will use a model of the pigeon as a case study for presenting the results of the inverse dynamic model.

One of the segments is used to represent the body, and three are used for each wing. As the model will be applied in rectilinear flight conditions only it will be assumed that the kinematics of the wings are symmetrical. Therefore, the wing kinematic and dynamic models formulated in sections 4.2.3 and 4.2.4 for a single wing will be assumed applicable to both wings.

The proximal arm segment represents the humerus of the real avian skeleton. This segment is connected to the body by the shoulder joint and to the forearm segment by the elbow joint. The wrist joint connects the forearm and hand, and will be discussed further in section 4.2.3. The hand is modelled as a single segment, though it is appreciated that the real avian hand also has moveable digits. Even though their movement is severely restricted, it is likely that small extensions and retractions of the digits affect aerodynamic loads near the wing tip [60]. This functionality will be implicitly modelled with the aggregate wing retraction motion that will be described in section 4.2.3.


Figure 9. Multi-segment avian model shown in comparison to parts of a Rock Pigeon skeleton [61]. Each arm is modelled as three segments, and the body is represented as a single segment.

### 4.2.2. Bird Dynamics

Before constructing a dynamic model it is first necessary to define the reference systems that will be used throughout this work. These systems are defined so as to model symmetric rectilinear flight of a bird in any direction with respect to the Earth. The axis systems used to define the motion of the bird are shown in Figure 10a.

If modelled as a point mass, the velocity of the bird relative to the Earth is given by the freestream velocity vector, $\mathbf{V}_{\infty}$.


Figure 10. (a) Earth and freestream wind axis systems shown assuming freestream velocity vector is parallel to $x_{E}-z_{E}$ plane. (b) Gravitational and averaged aerodynamic loads acting on the bird in Earth axes. Forces acting on the bird in the Earth reference frame for three rectilinear flight conditions that will be considered in the present study: (c) horizontal cruise, (d) horizontal acceleration and (e) climbing flight. Bird shown for reference in arbitrary orientation.

The Earth axes are oriented such that the axis $z_{E}$ opposes the gravity vector, $\mathbf{g}$. The Earth $x_{E}$ axis points in any arbitrary direction perpendicular to the $z_{E}$ axis, and the $y_{E}$ axis is oriented perpendicular to the $x_{E}$ and $z_{E}$ axes to form a right-handed set. The Earth axes remain fixed with respect to the Earth at any arbitrary location.

A freestream wind axis system $\left(x_{0}, y_{0}, z_{0}\right)$ is defined that translates with the movement of the bird with respect to the Earth. This system is used primarily for describing net aerodynamic loads on the bird. The origin of the freestream wind axes lies at any arbitrary location with respect to the bird. A positive rotation of the Earth axes about $y_{E}$ by the descent angle, $\beta$, yields axes that are aligned with the freestream wind axes. Therefore, positive descent angles are defined when the bird translates with a velocity relative to the Earth that has a positive component in the $-z_{E}$ direction.

Throughout this work, forces and velocities described as acting "horizontally", "laterally" and "vertically" will be defined as acting parallel to, and in the same direction as the positive $x_{E}, y_{E}$ and $z_{E}$ directions, respectively. While "thrust" is defined here as the horizontal component of aerodynamic force generated by the wings, "weight support" is the vertical component. "Axial" and "normal" forces and velocities are defined as acting parallel to, and in the same direction as the positive $x_{0}$ and $z_{0}$ directions. The average axial and normal aerodynamic loads generated by the wings, and the drag on the body are shown in Figure 10 as $\bar{F}_{x_{0}}, \bar{F}_{z_{0}}$ and $D_{0}$, respectively.

The equations of motion that describe the general case of rectilinear flight in any direction are given as follows:
$\bar{F}_{x_{0}}+m g \sin \beta-D_{0}=m a_{x_{0}} ;$
and
$\bar{F}_{z_{0}}-m g \cos \beta=0$,
where $a_{x_{0}}$ is the acceleration of the bird in the $x_{0}$ direction. The three specific cases of rectilinear flight that will be referred to in chapter 5 are horizontal cruise ( $\beta=0 ; a_{x_{0}}=0$ ), horizontal acceleration ( $\left.\beta=0 ; a_{x_{0}} \neq 0\right)$ and climbing ( $\beta \neq 0 ; a_{x_{0}}=0$ ), and are illustrated in Figure 10c-e. Using small angle approximations climbing and descending at shallow angles is equivalent to accelerating and decelerating: if $\beta$ is small, equations [5] and [6] can be written as

$$
\begin{equation*}
\bar{F}_{x_{0}}-D_{0}=m\left(a_{x_{0}}-g \beta\right) ; \tag{7}
\end{equation*}
$$

and

$$
\begin{equation*}
\bar{F}_{z_{0}}=m g, \tag{8}
\end{equation*}
$$

respectively. These equations would be the same for horizontal flight with an acceleration of $\left(a_{x_{0}}-g \beta\right)$.

The equations of motion are fundamental to the present model, just as the generation of thrust and weight support are central to previous flight performance models [13],[23]. If the model were to be used in flight dynamics analysis of avian stability, an equation for the pitching motion of the bird would also be necessary. Preliminary analyses found that including pitching motion in the present model yielded no significant changes in the predictions of wing kinematics or power consumption that is the major contribution of this work. However, modelling pitching motion did introduce some uncertainty in terms of requiring estimates for the inertial properties of the bird body. For these reasons the pitching motion will not be included here.

The body drag is approximated using the standard aerodynamic model:

$$
\begin{equation*}
D_{0}=\frac{1}{2} \rho\left\|\mathbf{V}_{\infty}\right\|^{2} S_{b} C_{D_{b}} \tag{9}
\end{equation*}
$$

where $\rho$ is the local air density, $S_{b}$ is the body reference area and $C_{D_{b}}$ is the body drag coefficient. The body drag coefficient will vary according to the body orientation with respect to the freestream wind. However, no experimental data could be found to quantify this, therefore the body drag coefficient will be assumed to be constant. This assumption may not be appropriate for models aiming to capture the dynamics of braking manoeuvres where the angle of attack and thus the drag coefficient would be greater than in cruise.

Wind tunnel testing of real and modelled avian bodies have measured drag coefficients up to around 0.4 , though Pennycuick's flight performance models suggest a default value of 0.1 is appropriate for most birds [62]. Previous simulations found that the choice of body drag coefficient had little influence on the prediction of wing kinematics, and so an average value of 0.25 will be used here [37]. The body reference area, $S_{b}$, will be taken as the body frontal area. For models of the pigeon the body frontal area, outstretched wing reference area, $S^{*}$, and unretracted wing length, $l^{*}$, will be obtained using previous experimental data [12],[13]. For allometrically scaled models (section 5.3) these variables will be derived from allometric scaling laws [63]; scaling laws will also be used to define the wing mass, $m_{w}$, and outstretched wing radius of gyration $R_{g}^{*}$ [64].

Having formulated a general dynamic model of the bird, the following sections will explain how the inverse dynamic model of the wing will be constructed. This will be used to predict the mean aerodynamic loads in equations [5] and [6], and also the mechanical power consumption.

### 4.2.3. Wing Kinematics

The predictive simulation technique in the present work is similar in principle to previous methods used for simulating insects in hovering flight [49]. However, unlike insects birds wings are
comprised of a number of skeletal segments, allowing them to fold and retract. This fundamental difference in wing biomechanics requires additional degrees of freedom to be included in a mathematical model of the wing kinematics. Previous predictive simulations using the present approach overviewed the degrees of freedom of real avian wings [37]. A convenient way to summarise these is to consider first the aggregate motion of the wing caused by rotation about the shoulder joint, and then to include the process of wing retraction.

## Shoulder rotation

Avian biomechanics literature suggests that as the shoulder of most modern birds is a hemi-sellar (half saddle) joint it is capable of three degrees of freedom and can be modelled a ball and socket joint [65]. These degrees of freedom are represented as three rotations in Euclidean space, and define the commonly used terms of stroke-plane angle ( $\gamma$; Figure 11a), wing elevation- depression ( $+\phi$ and $-\phi$, respectively; Figure 11b), and wing pronation-supination ( $+\theta$ and $-\theta$, respectively; Figure 11c). Examples of wing kinematics for rotation about the shoulder joint during a single wingbeat are shown in Figure 11d-f. The wingbeat phase is defined as the ratio of the time at any point during the wingbeat to the wingbeat time period $\left(=\frac{t}{T}\right)$. The time and phase are zero at the beginning of the downstroke, when the elevation angle is at its maximum value.
a. Stroke-plane

b. Elevation-depression

c. Pronation-supination

d. Elevation-depression only (side view along $y_{0}$ )

e. Elevation-depression, non-zero stroke plane (side view along $y_{0}$ )

f. Elevation-depression, non-zero stroke plane, pronation-supination (side view along $y_{0}$ )


Figure 11. (a) Wing depicted elevating-depressing with the stroke plane inclined by an angle $-\gamma$ with respect to the freestream wind axes when placed at the shoulder joint. (b) Wing rotated by the elevation angle, $\phi$, with zero stroke plane and pronation-supination angles. (c) Wing supination ( $-\theta$ ) shown with zero stroke plane and elevation. (d)-(f) Example wing kinematic time histories over a single wingbeat.

Stroke plane axes $\left(x_{1}, y_{1}, z_{1}\right)$, wing elevation axes $\left(x_{2}, y_{2}, z_{2}\right)$ and wing axes $\left(x_{3}, y_{3}, z_{3}\right)$ are all right handed systems with origins positioned at the shoulder joint. The $y_{1}, y_{2}$ and $y_{3}$ axes are defined as being normal to, and pointing away from, the assumed plane of symmetry of the bird when the elevation-depression angle is zero ${ }^{10}$. The $x_{1}, x_{2}$ and $x_{3}$ axes are defined as being aligned

[^8]with the $x_{0}$ axis during horizontal flight when the stroke-plane, elevation-depression and pronationsupination angles are zero. If the wing is assumed to be a plane the stroke plane $x_{1}$ and $y_{1}$ axes remain coplanar with the wing when the shoulder is rotated by the stroke plane angle, and the elevation-depression and pronation-supination angles are zero; the elevation $x_{2}$ and $y_{2}$ axes remain coplanar with the wing when the shoulder is rotated by the stroke-plane and elevation-depression angles, and the pronation-supination angle is zero; the wing $x_{3}$ and $y_{3}$ axes remain coplanar with the wing when the shoulder is rotated by all three angles.

To perform a coordinate transformation of the freestream velocity vector in the freestream axes, $\mathbf{V}_{\infty}$, to the freestream velocity vector in wing axes, $\mathbf{V}_{\infty_{3}}$, the following alias rotation matrices can be used:

$$
\begin{equation*}
\mathbf{V}_{\infty_{3}}=\mathbf{R}_{\theta} \mathbf{R}_{\phi} \mathbf{R}_{\gamma} \mathbf{V}_{\infty} \tag{10}
\end{equation*}
$$

where $\mathbf{R}_{\theta}, \mathbf{R}_{\phi}$ and $\mathbf{R}_{\gamma}$ are the alias rotation matrices corresponding to the three degrees of freedom of the shoulder:
$\mathbf{R}_{\gamma}=\left[\begin{array}{ccc}\cos \gamma & 0 & -\sin \gamma \\ 0 & 1 & 0 \\ \sin \gamma & 0 & \cos \gamma\end{array}\right] ;$
$\mathbf{R}_{\phi}=\left[\begin{array}{ccc}1 & 0 & 0 \\ 0 & \cos \phi & \sin \phi \\ 0 & -\sin \phi & \cos \phi\end{array}\right] ;$
$\mathbf{R}_{\theta}=\left[\begin{array}{ccc}\cos \theta & 0 & -\sin \theta \\ 0 & 1 & 0 \\ \sin \theta & 0 & \cos \theta\end{array}\right]$.
These rotation matrices can also be used to define the position of any point on the wing in the freestream axes following rotation of the shoulder ${ }^{11}$. A point on the wing is defined in the freestream axes by the position vector, $\mathbf{P}$, when the stroke plane, elevation-depression, and pronation supination angles are zero. The position of this point when the shoulder rotation angles are non-zero is given as

$$
\begin{equation*}
\mathbf{P}_{0}=\mathbf{R}_{\gamma} \mathbf{R}_{\phi} \mathbf{R}_{\theta} \mathbf{P} ; \tag{14}
\end{equation*}
$$

this approach will be used in section 4.2.6 to determine the position and velocity of the aerodynamic control points on the wing.

[^9]
## Wing retraction and extension

A well known feature of avian wings is that the movement of each skeletal segment is not completely independent. Due to skeletal and muscular mechanisms rotation about the elbow and wrist is coupled, and the wing appears to possess a form of mechanical automation when retracting and extending [66]. This process has been described in detail from a biomechanical perspective through surgical examination and observation in flight [66],[67], and is illustrated in Figure 12.
a. Partially retracted wings


c. Stages of wing retraction

Unretracted/ fully extended ( $\mathrm{e}=1$ )
(side view along $\mathrm{y}_{0}$ )

(top view along $-z_{0}$ )

d. Elevation-depression with upstroke retraction
(side view along yo)


Figure 12. (a) Illustration of a bird with partially retracted wings. (b) Hand circumduction angle, $\sigma$, measured between the $x_{3}$ and $x_{4}$ axes. (c) The stages of retraction of the wing from being unretracted (fully extended, $e=1$ ), to partially retracted $(0<e<1)$, to fully retracted $(e=0)$. (d) Example wing kinematic time history over a single wingbeat with full retraction at the mid-upstroke.

As the wing retracts the skeletal segments of the upperarm and forearm rotate about the shoulder and elbow, respectively; the axes of rotation remain aligned with the $z_{3}$ axis, which is perpendicular to the arm wing if it is assumed to be planar. The rotation of the hand about the wrist is more complex, and has been the subject of much discussion in literature [66]-[68]. While quantitative data for avian wrist kinematics are not available, it is recognised that the axis of rotation of the wrist does not remain aligned with the $z_{3}$ axis. Rather, the wrist undergoes combined processes of retraction and circumduction ${ }^{12}$ (Figure 12b) [67]. Circumduction of the hand wing will influence the aerodynamic loads on the wing, which will be discussed further in section 4.2.6.

Wing retraction reduces the wing length, which in turn reduces the flapping velocity distribution along the wing for given kinematics. Wing retraction also reduces wing wetted area. These two factors reduce the aerodynamic load on the wing for given kinematics. As such, both were included in a previous study based on the model presented here, which found that wing retraction was beneficial for reducing aerodynamic power consumption [37]. To capture these phenomena wing retraction is modelled as an aggregate process that reduces wing length and area. This is expressed mathematically by a wing extension parameter, $e$, that defines the length of the retracted wing, $l$, as a fraction of the unretracted wing length, $l^{*}$ :

$$
\begin{equation*}
l=e l^{*}, \tag{15}
\end{equation*}
$$

where $l$ and $l^{*}$ are both measured from the shoulder joint to the wing tip in the $y_{3}$ direction. This approach will be used in section 4.2.6 to define the position of aerodynamic control points as the wing retracts. A similar model is used to define the area of the retracted wing, $S$, as a fraction of the area of the unretracted wing, $S^{*}$ :
$S=e S^{*}$.

An additional factor that will be included in the present work is the effect of wing retraction on the wing moment of inertia. Experimental investigations have been performed that measured the wing mass and moment of inertia for several species [64],[69]. These studies provide data for the moment of inertia of an unretracted wing about an axis around which the wing elevates and depresses. It is reasonable to assume that the centre of mass of the wing lies close to the $y_{2}$ axis, as this is where the majority of the skeletal and muscle structures are located [70]. For simplicity, the wing can then be modelled using a point mass located on the $y_{2}$ axis. Literature data for wing moments of inertia are used to define the principal components of the moment of inertia tensor that

[^10]are associated with wing rotation about the $x_{2}$ and $z_{2}$ axes, $I_{x x}$ and $I_{z z}$, respectively; $I_{y y}$ is equal to zero. These components are given as
\[

$$
\begin{equation*}
I_{x x}=I_{z z}=m_{w} R_{g}^{2}, \tag{17}
\end{equation*}
$$

\]

where $R_{g}$ is the wing radius of gyration about the $x_{2}$ or $z_{2}$ axis. Retraction of the wings causes a reduction in the moment of inertia and radius of gyration. This is modelled in the present work by assuming the following linear relationship:
$R_{g}=e R_{g}^{*}$,
where $R_{g}^{*}$, is the radius of gyration of the unretracted wing about the $x_{2}$ axis.

It is recognised that for real birds the radius of gyration may not be directly proportional to wing length, and also that the moment of inertia tensor consists of other components. However this approach is believed to be a suitable first order approximation to demonstrate the underlying effects of wing retraction on wing inertial properties.

### 4.2.4. Wing Dynamics

The main flight muscles of birds (M. pectoralis and M. supracoracoideus) serve predominantly to actuate rotation of the wing around the shoulder joint for elevation and depression [71]. This would indicate that the torque at the shoulder joint is significantly larger than at the other wing joints. Because of this, previous predictive simulations were able to reduce the equations of motion describing the wing dynamics to an equation for the shoulder torque, although this only included aerodynamic loads and not inertial loads [37]. Several other works have mentioned that inertial loads may also be significant (e.g. [64]). The present work will include both inertial and aerodynamic effects in the dynamic model (Figure 13), and their relative contribution will be discussed in section 4.2.9.


Figure 13. Modular inverse dynamic model. Joint kinematics are input directly, or are obtained from the optimiser, in which case the mean aerodynamic force and mechanical power are passed from this model to the optimiser.

The Euler equations describing the wing motion in the (rotating) elevation-depression axes $\left(x_{2} y_{2} z_{2}\right)$ are
${ }_{m} T_{x_{2}}+{ }_{a} T_{x_{2}}=I_{x x} \dot{\omega}_{x_{2}}+I_{z z} \omega_{y_{2}} \omega_{z_{2}}$,
${ }_{m} T_{y_{2}}+{ }_{a} T_{y_{2}}=0$,
${ }_{m} T_{z_{2}}+{ }_{a} T_{z_{2}}=I_{z z} \dot{\omega}_{z_{2}}-I_{x x} \omega_{x_{2}} \omega_{y_{2}}$.
where ${ }_{m} T_{k_{2}}$ and ${ }_{a} T_{k_{2}}(k=x, y, z)$ are the torque applied by the flight muscle and the aerodynamic torque, respectively, and $\omega_{k_{2}}$ is the angular velocity of the wing about the $k_{2}$ axis. In the present work the parameterised wing kinematics that will be described in section 4.3 .2 will utilise a fixed stroke plane, and thus $\omega_{z_{2}}$ and $\dot{\omega}_{z_{2}}$ are zero. In typical wing kinematics in cruising flight conditions the angular velocity term, $\omega_{y_{2}}$, is small as only limited pronation-supination is used; for this reason the inertial term, $I_{x x} \omega_{x_{2}} \omega_{y_{2}}$, in equation [21] is negligibly small in comparison to the aerodynamic torque, and will be omitted here. The torque due to gravity, and torque due to acceleration of the bird are 1-2 orders of magnitude smaller than the peak aerodynamic torques, and are therefore neglected from the present work.

The model does not include any form of restoring torque on the wing. This means that torque from the muscles is required to accelerate and decelerate the wing with no kinetic energy recovery. While there is some experimental evidence of a spring-type structure within birds' skeletons, this has not been proven to function as a mechanism for storing mechanical energy [72]. The elasticity of muscle tissue may also offer some method of storing and recovering energy, though limited quantitative data of mechanical properties on this is available for birds [36],[71]. It is therefore
believed that including a restoring torque would introduce unnecessary uncertainty into the model. For similar reasons, the resistance to motion due to internal friction in the wings is also omitted.

As the present work assumes a fixed stroke plane, $\omega_{z_{2}}=0$, and as the angular velocity term, $\omega_{y_{2}}$, is small in cruise the mechanical power at the shoulder joint due to rotation about the elevationdepression axes is modelled in the present work as
${ }_{m} P_{x_{2}}=\omega_{x_{2}}\left(I_{x x} \dot{\omega}_{x_{2}}-{ }_{a} T_{x_{2}}\right)=\dot{\phi}\left(I_{x x} \ddot{\phi}{ }_{a} T_{x_{2}}\right)$.
It should be noted that the mechanical power can be both positive and negative. As no method of energy recovery is included in the present model, both positive and negative power values contribute to the instantaneous power consumption, and the total power consumption due to rotation of the wing about the shoulder joint is given as

$$
\begin{equation*}
{ }_{m} P=\left\|_{m} P_{x_{2}}\right\| . \tag{23}
\end{equation*}
$$

This highlights that the model cannot be used to represent flapping wing systems that extract kinetic energy from the freestream wind.

Mechanical power would also be required to overcome aerodynamic and inertial torques at the other wing joints. The fact that the majority of the wing mass is distributed along the upper arm means that inertial torque at other joints will be minimal and can be ignored. Aerodynamic torques around the wrist tend to be much smaller than those at the shoulder due to the shorter moment arm between the wrist joint and the loads applied to the hand wing. However, the power consumed due to rotation of the wrist joint will still be accounted for, by modelling the power associated with wing retraction.

Based on the wing retraction model presented in the previous section, a simplified model of the dynamics of wing retraction is formulated by representing the wing as a point mass. Using this approach an equation of retraction motion in the $y_{2}$ direction is given as

$$
\begin{equation*}
{ }_{m} F+{ }_{a} F_{y_{2}}=m_{w} \ddot{y}_{2}, \tag{24}
\end{equation*}
$$

where ${ }_{m} F$ is the force applied to the wing by the muscles and ${ }_{a} F_{y_{2}}$ is the aerodynamic load, which will be derived in section 4.2.6. For similar reasons to those given for the shoulder torque model, no restoring force or internal resistance will be included. The instantaneous mechanical power consumption at the shoulder due to wing retraction is then given as

$$
\begin{equation*}
{ }_{r} P=\left\|_{m} F \dot{y}_{2}\right\|=\left\|\left(m_{w} \ddot{y}_{2}-{ }_{a} F\right) \dot{y}_{2}\right\| . \tag{25}
\end{equation*}
$$

Thus, the total instantaneous mechanical power consumption is given as the sum of the power consumed due to wing rotation and retraction:
$P={ }_{m} P+{ }_{r} P$.
In order to close the system of equations describing the wing dynamics, the aerodynamic forces and torque on the wing must be derived. The aerodynamic model will be described in the following section as a separate, and distinct process, which is largely independent of the modelling decisions used up until now in constructing the inverse dynamic model.

### 4.2.5. Aerodynamic Modelling

This section will begin by overviewing a range of commonly used methods of predicting aerodynamic forces and torques to identify one that is best suited to the present modelling approach. Following this, details will be given of the how this method can be implemented in the inverse dynamic model.

## Choice of aerodynamic model

One of the major concerns when formulating a predictive simulation method is balancing the accuracy of the dynamic model with the computational cost incurred in obtaining a solution. In predictive simulations of aerial locomotion this is particularly apparent when selecting a model to predict aerodynamic loads. A vast spectrum of aerodynamic models exists, and these have been applied to fixed, rotary and flapping wings. Some of these models require a high level of userintervention which makes them impractical when using mathematical optimisation.

The first methods to be considered are those that resolve the flow around a body by obtaining numerical solutions to the equations that govern fluid motion ${ }^{13}$. This class of methods can be subdivided into two groups based on the specification of the flow field. Eulerian methods, such as those that solve the Navier-Stokes or Euler equations, calculate the flow properties at discrete positions and times in the flow field using a computational grid or mesh. Lagrangian methods, such as smoothed-particle hydrodynamics or vortex methods, are grid-free methods that track the flow properties on a set of particles.

Both Eulerian and Lagrangian methods are generally regarded as being computationally expensive in comparison to other aerodynamic methods. In the context of modelling flapping wing

[^11]aerodynamics, a grid-based method would have to adapt the grid throughout the solution to account for changes in wing orientation, which would incur additional computational cost. Iterative numerical schemes are commonly employed in grid-based solvers, and these generally require some level of user-intervention to maintain numerical stability and achieve a converged solution. The solutions from both Eulerian and Lagrangian approaches tend to be sensitive to the surface geometry, and therefore require detailed information to reconstruct the geometries of real wings which limits the extent to which a generic, scalable model can be formulated. For these reasons, aerodynamic methods that resolve the flow field are not believed to be practicable in the current simulation framework.

An alternative class of numerical method for modelling aerodynamics are known as panel methods. These are derived from the potential flow equations, which describe inviscid, irrotational flow of fluid. The crucial factor in these methods is that rather than resolving the flow properties across a domain, they can predict aerodynamic loads from analysis of fluidic singularities modelled on the body surface only; this approach is therefore accepted to a computationally economical method of aerodynamic analysis [73].

As well as being used extensively for fixed and rotary wing analysis, panel methods have also been applied to the analysis of flapping wings [39],[74]. One of the problems recognised when using panel methods is that an estimate of the wake shape must be made, which for flapping wings may change throughout the wingbeat. Wake geometry can either be prescribed based on experimental evidence, or solved explicitly, which incurs significant computational cost [19].

Another important issue with panel methods is that they are generally applicable to attached flows only [73]. This means that under certain flow conditions a panel method would not capture the effects of stall that would be seen on a real wing under the same conditions, and would therefore tend to overpredict lift and underpredict drag. Therefore, the possible benefits of panel methods over flow domain solutions in terms of reduced computational cost are perhaps outweighed by their limited applicability to attached flows only.

Lifting-line theories developed for analysis of fixed wing aircraft have been adapted to predict aerodynamic loads and power consumption on flapping wings. Lifting-line methods calculate circulation distribution along the wing, and determine lift from the two dimensional KuttaJoukowski theorem [73]. A previous review demonstrated that the approximation of low amplitude wing kinematics limits the applicability of these methods for modelling flapping flight of organisms [39].

Blade-element theory (BET) is often regarded as one of the most rudimentary methods of aerodynamic analysis. This method is commonly used as a tool for preliminary design of rotary wing vehicles, offering robust predictions of aerodynamic forces and torques with low computational cost [19]. A blade-element aerodynamic model has been used in predictive simulation of insects in hovering flight, and the resulting kinematics correlate strongly to experimental data [49].

Unlike lifting line models, BET alone does not include a representation of the induced velocity. To account for this, blade-element theory is often coupled with a momentum theory model that predicts the induced velocity for given net aerodynamic loads [19]. The combined blade-elementmomentum theory (BEMT) has already been used for predictive simulation of birds in forward flight [37]. This approach was found to be sufficiently accurate to capture experimental trends in kinematics of real birds. The same method could be applied over a range of flight conditions with modest computational resources due to the rapid solution times. Moreover, no adjustments would be required to the model between simulating different flight conditions. BEMT therefore stands as a robust tool that is sufficiently accurate for predictive simulation of bird flight.

## Blade element momentum theory

BET models a wing as a series of quasi-2D aerofoils [19]. The aerodynamic loads and moments are calculated at an aerodynamic control point on each individual aerofoil, or element, based on the aerofoil aerodynamic properties and its orientation to the local wind velocity vector. The properties required to calculate aerodynamic loads in this approach are the 2 D lift and drag coefficients of the aerofoils. These are generally defined empirically from experimental measurements, or using a theoretical model such as thin aerofoil theory [19].

## a. Blade element wing representation

b. Blade element local axes


Figure 14. (a) Illustration and blade element representation of the wing in freestream axes, depicted with the blade element zero lift lines parallel to the $x_{0}$ axis. Skeletal segments are shown for reference. (b) Local wind velocity for a blade element, comprised of components of freestream velocity, induced velocity and wing flapping velocity. Derivation of local blade angle of attack neglects the effective induced camber that arises due angular velocity of pronationsupination.

An example of a blade element representation of an avian wing is shown in Figure 14a. The wing planform geometry was constructed from that of a pigeon wing used in previous predictive simulations [37],[70] ${ }^{14}$. Local blade element axes are defined with the origins at the aerodynamic control points and the axes of the $j$ th blade element are given the notation $x_{4}^{(j)}, y_{4}^{(j)}, z_{4}^{(j)}$. The $x_{4}^{(j)}$ axes are aligned with the blade zero-lift lines, the $y_{4}^{(j)}$ axes are parallel to the $y_{3}$ axis when the wing is unretracted, and the $z_{4}^{(j)}$ axes are oriented to form right handed sets. Figure 14 b illustrates the local axes for the $j$ th blade element.

The orientation of the blade element lift and drag vectors is shown in Figure 14b. The local wind velocity is comprised of three components: the freestream velocity, the wing flapping velocity and the induced velocity. The exact method of determining the induced velocity from momentum theory will be detailed in section 4.2.6.

[^12]Central to the formulation of the blade element method is the choice of functions to represent the element lift and drag coefficient variation with angle of attack. Experimental data for aerodynamic properties of avian wings offer some useful guidelines for this aspect of the model. Results from wind tunnel tests have shown that avian wings tend not to exhibit strong stall characteristics at flow Reynolds numbers similar to those of real birds in typical flight conditions ( $\sim 10^{3}-10^{5}$ ) [52]. More recently, results from experimental studies using revolving birds wings supported this conclusion, and went further to show a smooth variation in aerodynamic force coefficients for an angle of attack range from $-20^{\circ}$ to $120^{\circ}$ [75],[76].

Smooth trends in force coefficients were also seen in studies on rotating insect wing models [76],[77]. These data were later used as the basis for trigonometric models for lift and drag coefficients in predictive simulations of insects [49]. Trigonometric models were also used in previous versions of the current model for simulating avian flight [37]; at the time this was intended to be a simple extrapolation of a standard post-stall aerofoil model to the pre-stall region [19], however the experimental evidence suggests that this is an accurate representation of the actual pre-stall aerodynamic properties. A similar approach will be used in the present work, whereby the lift and drag coefficients are given as

$$
\begin{align*}
& c_{l}=A \sin 2\left(\alpha-\alpha_{0}\right)  \tag{27}\\
& c_{d}=B+C \cos 2\left(\alpha-\alpha_{0}\right) \tag{28}
\end{align*}
$$

where $A, B$ and $C$ are parameters defining the maximum and minimum force coefficients and $\alpha_{0}$ is the angle of attack at which zero lift is generated. Throughout the present work only uncambered wings will be considered and therefore $\alpha_{0}$ is zero. The maximum section lift coefficient in this model occurs when the angle of attack is $45^{\circ}$, and so is also referred to as $c_{l_{45}}$; the section drag coefficient at $0^{\circ}$ angle of attack is referred to as $c_{d_{0}}(=B+C)$, and at $90^{\circ}$ is referred to as $c_{d_{90}}$ $(=B-C) ;$ these represent the minimum and maximum section drag coefficients, respectively.

Previous predictive simulations found that the maximum section lift coefficient was the dominant parameter in predicting aerodynamic loads [37]. The choice of maximum lift coefficient has also been the source of some debate in previous theoretical models of bird flight (e.g. [40]), and therefore warrants careful consideration here. Previously, this value was based on measurements of revolving pigeon wing experiments at Reynolds numbers similar to those encountered by real pigeons [75]. Similar maximum steady lift coefficients of around 1.6 were measured for revolving quail wings and model insect wings [76],[77]. Therefore, a value of 1.6 will be used in the present work, which is recognised as being representative of a wide range of species, and is therefore appropriate for the current scalable modelling approach. Experimental studies have also shown that
there is little variation in this value with changes in Reynolds number [75], so the section lift coefficient is modelled here as a function of the angle of attack only (equation [27]).

It should be noted that force coefficients from revolving wing experiments tend not to include the induced velocity as part of the reference speed. As the induced flow effects are likely to be significant when compared to the wing rotational speed, the force coefficients will be over predicted. However the predicted values for $c_{l_{45}}$ are still plausible as similar values have been obtained using wind tunnel tests of avian wing models with high-lift devices at similar Reynolds numbers [78]. Therefore, the same value will be used in the present model, but the effect of using different values for $c_{l_{45}}$ will also be examined in terms of the dynamic model sensitivity (section 4.2.10), and the predictive simulation accuracy (section 4.3.5).

Revolving wing experiments estimate maximum drag coefficients of less than 3, though substantial variation exists between different wing models [76]. A conservative approach used in previous simulations [37] will be adopted here, that assumes values of $B=1.135$ and $C=-1.05$ that are deemed appropriate for an arbitrary aerofoil [19]; this yields a value for $c_{d_{90}}$ of around 2.2. The effects of using different values will be examined in section 4.2.10.

The instantaneous blade element lift and drag acting on the $j$ th $\left(j=1,2,3 \ldots N_{j}\right)$ control point are given as
$l^{(j)}=\frac{1}{2} \rho\left\|\mathbf{V}_{4}^{(j)}\right\|^{2} s^{(j)} c_{l}^{(j)}$,
$d^{(j)}=\frac{1}{2} \rho\left\|\mathbf{V}_{4}^{(j)}\right\|^{2} s^{(j)} c_{d}^{(j)}$,
where $\rho$ is the local air density, $\mathbf{V}_{4}^{(j)}$ is the control point local wind velocity (see section 4.2.6 for derivation), $s^{(j)}$ is reference area of the $j$ th blade element, and $c_{l}^{(j)}$ and $c_{d}^{(j)}$ are the lift and drag coefficients of the $j$ th blade element, respectively.

If the local angle of attack is calculated at the 3/4-chord point the model implicitly accounts for effective camber [19] or rotational lift [49]. However, preliminary tests found that under typical cruising flight conditions the aerodynamic force and mechanical power consumption are insensitive to the chordwise location at which the angle is derived for an element, suggesting that rotational lift effects are negligible. For simplicity, the present work will calculate the angle of attack at the location of the aerodynamic control point, and in doing so will neglect rotational lift.

The equations for blade element lift and drag can also be used to formulate the local blade torque around the $y_{2}$ axis, but this requires knowledge of the moment arm between each blade element
control point and centre of rotation. While experimental measurements of the centre of pressure variation with angle of attack have been made for insects [79], such data for bird wings are not available. For this reason the aerodynamic torque around the $y_{2}$ axis will be derived assuming the aerodynamic control points are fixed on the $1 / 4$-chord line, which is the theoretical location of the centre of pressure of thin, symmetric aerofoils [20]. For any chordwise location of the centre of pressure the torque around the $y_{2}$ axis is found to be significantly smaller than aerodynamic and inertial torque components about the $x_{2}$ axis for all flight conditions.

The blade element theory can also accommodate models of unsteady aerodynamics. An example is the added mass model that captures the loads that arise due to of acceleration of the fluid surrounding the wing. Equations for the added mass aerodynamic loads are generally defined in the local aerofoil axis system (e.g. [49]). The section lift and drag on a blade element in equations [29] and [30] are defined in the blade local wind axes $\left(x_{5}^{(j)}, y_{5}^{(j)}, z_{5}^{(j)}\right)$, and therefore added mass forces cannot be summed directly with these forces.

The blade element aerodynamic force vector on the $j$ th control point is given as

$$
{ }_{B} \mathbf{F}_{5}^{(j)}=\left[\begin{array}{c}
d^{(j)}  \tag{31}\\
0 \\
-l^{(j)}
\end{array}\right] .
$$

A coordinate transformation is used to obtain the blade element forces in the blade local axes $x_{4}^{(j)} y_{4}^{(j)} z_{4}^{(j)}$ :
${ }_{B} \mathbf{F}_{4}^{(j)}=\mathbf{R}_{\alpha}^{(j)} \mathbf{F}_{5}^{(j)}$,
where $\mathbf{R}_{\alpha}^{(j)}$ is a rotation matrix:

$$
\mathbf{R}_{\alpha}^{(j)}=\left[\begin{array}{ccc}
\cos \alpha^{(j)} & 0 & \sin \alpha^{(j)}  \tag{33}\\
0 & 1 & 0 \\
-\sin \alpha^{(j)} & 0 & \cos \alpha^{(j)}
\end{array}\right] .
$$

The added mass effects are now included following the method used in by Berman \& Wang [49], giving the total aerodynamic load in the in the blade local $x_{4}$ and $z_{4}$ axes as

$$
\begin{align*}
& F_{x_{4}}^{(j)}=_{B} F_{x_{4}}^{(j)}-\frac{1}{4} \rho \pi^{(j)} s^{(j)} V_{z_{4}}^{(j)} \dot{\alpha}^{(j)},  \tag{34}\\
& F_{\left.z_{4}\right)}^{(j)}{ }_{B} F_{z_{4}}^{(j)}+\frac{1}{4} \rho \pi^{(j)} s^{(j)} \dot{V}_{z_{4}}^{(j)}, \tag{35}
\end{align*}
$$

where $c^{(j)}$ is the chord length of the $j$ th blade element. Equations [34] and [35] are based on the assumption that the wing thickness to chord ratio is small. Without making this assumption and assuming a typical thickness to chord ratio for an avian wing of $10 \%$ [80], no significant change in aerodynamic loads occurs.

It is possible to incorporate additional unsteady aerodynamic models such as dynamic stall behaviour into the current blade element approach. However, the possible benefits that these models offer in terms of accuracy are believed to be outweighed by the level of experimental validation required in their implementation. Other unsteady models that incorporate the influence of the unsteady wake on aerodynamic loads tend to be limited to low amplitude flapping flight only, and are therefore not applicable in the present context [19].

### 4.2.6. Finding Local Blade Wind Velocity Vector

The previous section presented the method of determining the aerodynamic loads on a blade element for known local wind velocity. This section will overview the exact procedure for calculating the local wind velocity for each blade element under any flight condition. A description will then be given of how these results are used to predict net aerodynamic loads and shoulder torque, which are required for closure of the rectilinear flight model (equations [5] and [6]) and the mechanical power model (equations [22]-).

Figure 15 depicts the location of a set of $J$ aerodynamic control points on the wing, where there are $J_{a}$ control points on the arm wing and the remainder on the hand wing. For a fully-extended wing with no shoulder rotation the position of a control point in the freestream axes is given as

$$
{ }_{E} \mathbf{p}_{0}^{(j)}=\left[\begin{array}{l}
p_{x_{0}}^{(j)}  \tag{36}\\
p_{y_{0}}^{(j)} \\
p_{z_{0}}^{(j)}
\end{array}\right] .
$$

When the wings retract all aerodynamic control points are assumed to translate in the $-y_{3}$ direction (equal to the $-y_{0}$ direction when the shoulder rotation angles are zero; Figure 15). Following equation [15] that defined the retracted wing length, the displacement of a control point in the $y_{3}$ direction is expressed as a fraction of its displacement when the wing is fully extended. Control points on the hand wing also rotate about the wrist joint, as shown in Figure 15b.


Figure 15. (a) Blade element representation of the wing in freestream axes, depicted with the blade element zero lift lines parallel to the $x_{0}$ axis. (b) Blade element transformation when the wing is partially retracted; blade element width (spanwise) reduces when the wings retract, and elements on the hand wing rotate by the hand circumduction angle, $\sigma$.

The position vector for the $j$ th control point on the retracted wings is then given as

$$
{ }_{R} \mathbf{p}_{0}^{(j)}=\left\{\begin{array}{cc}
{\left[\begin{array}{c}
p_{x_{0}}^{(j)} \\
e p_{y_{0}}^{(j)} \\
p_{z_{0}}^{(j)}
\end{array}\right]} & j \leq J_{a}  \tag{37}\\
{\left[\begin{array}{c}
p_{x_{0}}^{(j)} \\
e\left(p_{y_{0}}^{(j)}-w_{y_{0}}\right) \cos \sigma+e w_{y_{0}} \\
e\left(p_{y_{0}}^{(j)}-w_{y_{0}}\right) \sin \sigma
\end{array}\right]} & j>J_{a}
\end{array}\right.
$$

where $w_{y_{0}}$ is the distance from the shoulder to the wrist joint of the outstretched wing in the $y_{0}$ direction. Note that for reasons given above the position of the control points in the $x_{0}$ axis is fixed at the $1 / 4$-chord location, and is unaffected by wing retraction.

The control point locations of the retracted wing are then rotated by the shoulder rotation angles using the method described in section 4.2.3. The $j$ th control point position vector in the freestream axes is given as
$\mathbf{p}_{0}^{(j)}=\mathbf{R}_{\gamma} \mathbf{R}_{\phi} \mathbf{R}_{\theta R} \mathbf{p}_{0}^{(j)}$.

By evaluating equation [38] at times $t$ and $t+\Delta t$ (where $\Delta t$ is a small time increment) the velocity of the control point can be evaluated numerically using a finite difference approximation. In the present work the time derivate of a variable, $q$, is approximated using a first order central differencing scheme:

$$
\begin{equation*}
q^{\prime}(t) \approx \frac{q(t+\Delta t)-q(t-\Delta t)}{2 \Delta t} \tag{39}
\end{equation*}
$$

However when applying this method over a time period, $T$, for the cases of $t=0$ and $t=T$ forward and backward differencing methods must also be used:

$$
\begin{align*}
& q^{\prime}(0) \approx \frac{q(\Delta t)-q(0)}{\Delta t},  \tag{40}\\
& q^{\prime}(T) \approx \frac{q(T)-q(T-\Delta t)}{\Delta t} . \tag{41}
\end{align*}
$$

Applying equations [39]-[41] to elements of the $j$ th control point position vector, $\mathbf{p}_{0}^{(j)}$, yields the flapping velocity vector of the $j$ th control point in freestream axes, ${ }_{c p} \mathbf{V}_{0}^{(j)}$. The flapping velocity vector is then summed with the freestream wind velocity to yield the combined wind velocity at the control point in the freestream axes:
$\mathbf{V}_{0}^{(j)}={ }_{c p} \mathbf{V}_{0}^{(j)}+\mathbf{V}_{\infty}$.
This velocity vector does not include the effects of induced velocity. Following convention the induced velocity, ${ }_{i} \mathbf{V}_{1}$, will be derived in the stroke-plane axes (section 4.2.7), and thus the velocity in the stroke plane axes is given as

$$
\begin{equation*}
\mathbf{V}_{1}^{(j)}=\mathbf{R}_{\gamma} \mathbf{V}_{0}^{(j)}+{ }_{i} \mathbf{V}_{1}, \tag{43}
\end{equation*}
$$

noting that the induced velocity is assumed to be equal for all control points.
The local wind velocity at the $j$ th control point in the blade element axes is then given as

$$
\begin{equation*}
\mathbf{V}_{4}^{(j)}=\mathbf{R}_{\sigma}^{(j)} \mathbf{R}_{\theta} \mathbf{R}_{\phi} \mathbf{V}_{1}^{(j)}, \tag{44}
\end{equation*}
$$

where

$$
\mathbf{R}_{\sigma}^{(j)}=\left\{\begin{array}{cc}
{\left[\begin{array}{lll}
1 & 0 & 0 \\
0 & 1 & 0 \\
0 & 0 & 1
\end{array}\right]} & j \leq J_{a}  \tag{45}\\
{\left[\begin{array}{ccc}
1 & 0 & 0 \\
0 & \cos \sigma & \sin \sigma \\
0 & -\sin \sigma & \cos \sigma
\end{array}\right]} & j>J_{a} .
\end{array}\right.
$$

The angle of attack at the $j$ th control point is given as
$\alpha^{(j)}=\operatorname{atan} 2\left(\frac{-V_{t^{(j)}}^{(j)}}{V_{x 4}^{(j)}}\right)$.
The local blade lift and drag coefficients can then be calculated from equations [27] and [28]. These can be inserted into equations [29] and [30] along with the local wind velocity from equation [44] to find the local blade lift and drag in local wind axes. Equations [31]-[35] are then used to give the aerodynamic loads in the blade local axes, $\mathbf{F}_{4}^{(j)}$, which includes added mass effects. The loads in the elevation-depression axes are given as

$$
\begin{equation*}
\mathbf{F}_{2}^{(j)}=\mathbf{R}_{\theta}^{\mathrm{T}} \mathbf{R}_{\sigma}^{(j) \mathrm{T}} \mathbf{F}_{4}^{(j)} \tag{47}
\end{equation*}
$$

Thus, the instantaneous aerodynamic torque on the wing is given in elevation depression axes as

$$
\begin{equation*}
{ }_{a} \mathbf{T}_{2}=\sum_{j=1}^{J_{a}}\left(\mathbf{p}_{0}^{(j)} \times \mathbf{F}_{2}^{(j)}\right), \tag{48}
\end{equation*}
$$

which is used in equations [22]- to find the mechanical power consumption. The instantaneous aerodynamic load on the wing in the freestream axes is given as

$$
\begin{equation*}
\mathbf{F}_{0}=\mathbf{R}_{\gamma}^{\mathrm{T}} \mathbf{R}_{\phi}^{\mathrm{T}} \sum_{j=1}^{J_{a}} \mathbf{F}_{2}^{(j)} \tag{49}
\end{equation*}
$$

The time-averaged aerodynamic load in the freestream axis, $\overline{\mathbf{F}}_{0}$, and mechanical power consumption, $P$, are obtained using numerical integration. In the present work the time-average of a variable, $q$, is approximated using a trapezoidal integration scheme. If instantaneous values of $q$ are obtained at $N_{t}$ evenly spaced timepoints, the time-averaged value is given as

$$
\begin{equation*}
\bar{q}=\sum_{n=1}^{N_{t}-1}\left(t_{n+1}-t_{n}\right) \frac{q\left(t_{n}\right)+q\left(t_{n+1}\right)}{2} . \tag{50}
\end{equation*}
$$

The mean force components, $\bar{F}_{x_{0}}$ and $\bar{F}_{z_{0}}$, computed using equation [50] can be used in equations [5] and [6] that describe the overall bird dynamics.

### 4.2.7. Modified Momentum Theory

The momentum theory models a helicopter rotor or flapping wing as an actuator disk of infinitesimal thickness, over which a pressure difference exists. The aerodynamic force exerted by the actuator disk on the surrounding fluid is equal to the force generated by the rotor or wings, and increases the kinetic energy of the slipstream (Figure 16) [19].
a. Rotary and flapping wing flows
b. Momentum theory flow model


Figure 16. (a) Flow models for rotary and flapping wing systems. (b) Momentum theory model, where the actuator disk is located at the rotor disk plane when modelling a rotary wing, or the stroke plane for a flapping wing system.

The mass flow rate through the disk is given as
$\dot{m}=\rho A_{d} U$,
where $A_{d}$ is the actuator disk reference area and $U$ is the net velocity through the disk. The disk reference area for a flapping wing system is defined as the area swept by the wings during a wingbeat. The net velocity through the disk is given by
$U=\sqrt{\left(\left\|\mathbf{V}_{\infty}\right\| \cos \psi+{ }_{i} V_{x_{1}}\right)^{2}+\left(-\left\|\mathbf{V}_{\infty}\right\| \sin \psi+{ }_{i} V_{z_{1}}\right)^{2}}$,
where $\psi$ is the angle between the freestream wind vector and the normal to the disk, and ${ }_{i} V_{x_{1}}$ and ${ }_{i} V_{z_{1}}$ are the induced velocity components perpendicular and parrallel to the disk, respectively (Figure 16).

Conservation of momentum perpendicular to the disk gives the disk normal force as
$\bar{F}_{x_{1}}=\dot{m}\left(W_{x_{1}}+\left\|V_{\infty}\right\| \cos \psi\right)-\dot{m}\left\|V_{\infty}\right\| \cos \psi=\dot{m} W_{x_{1}}$,
where $W_{x_{1}}$ is the perpendicular velocity immediately downstream of the disk.

Considering conservation of energy perpendicular to the disk, the aerodynamic power consumption in this direction is given as
$P_{x_{1}}=\bar{F}_{x_{1}}\left({ }_{i} V_{x_{1}}+\left\|\mathbf{V}_{\infty}\right\| \cos \psi\right)=\frac{1}{2}\left(W_{x_{1}}+\left\|\mathbf{V}_{\infty}\right\| \cos \psi\right)^{2}-\frac{1}{2} \dot{m}\left(\left\|\mathbf{V}_{\infty}\right\| \cos \psi\right)^{2}$
$=\frac{1}{2} \dot{m}\left(W_{x_{1}}^{2}+2 W_{x_{1}}\left\|\mathbf{V}_{\infty}\right\| \cos \psi\right)$.

Substituting equation [53] into equation [54] and simplifying gives
${ }_{i} V_{x_{1}}=\frac{1}{2} W_{x_{1}}$.

Substituting equations [51], [52] and [55] into equation [53] gives the perpendicular induced velocity as
$V_{x_{1}}=\frac{\bar{F}_{x_{1}}}{2 \rho A \sqrt{\left(\left\|\mathbf{V}_{\infty}\right\| \cos \psi+{ }_{i} V_{x_{1}}\right)^{2}+\left(-\left\|\mathbf{V}_{\infty}\right\| \sin \psi+{ }_{i} V_{z_{1}}\right)^{2}}}$,

It is important to note that in equation [56] the perpendicular induced velocity term appears on both sides of the equation, and therefore must be obtained iteratively. Equation [56] is equivalent to the induced velocity used in the analysis of the forward flight of helicopters, with the addition of the parallel induced velocity term [19]. To derive this parallel term, a similar approach to the above can be repeated, considering components parallel to the actuator disk. Applying conservation of momentum parallel to the disk gives the disk parallel force as

$$
\begin{equation*}
\bar{F}_{z_{1}}=\dot{m}\left(W_{z_{1}}-\left\|\mathbf{V}_{\infty}\right\| \sin \psi\right)-\dot{m}\left(-\left\|\mathbf{V}_{\infty}\right\| \sin \psi\right)=\dot{m} W_{z_{1}}, \tag{57}
\end{equation*}
$$

where $W_{z_{1}}$ is the parallel velocity immediately downstream of the disk.

Considering conservation of energy parallel to the disk, the aerodynamic power consumption in this direction is given as
$P_{z_{1}}=\bar{F}_{z_{1}}\left(V_{z_{1}}-\left\|\mathbf{V}_{\infty}\right\| \sin \psi\right)=\frac{1}{2} \dot{m}\left(W_{z_{1}}-\left\|\mathbf{V}_{\infty}\right\| \sin \psi\right)^{2}-\frac{1}{2} \dot{m}\left(-\left\|\mathbf{V}_{\infty}\right\| \sin \psi\right)^{2}$
$=\frac{1}{2} \dot{m}\left(W_{z_{1}}^{2}+2 W_{z_{1}}\left\|\mathbf{V}_{\infty}\right\| \sin \psi\right)$.

Substituting equation [57] into equation [58] and simplifying gives

$$
\begin{equation*}
{ }_{i} V_{z_{1}}=\frac{1}{2} W_{z_{1}} . \tag{59}
\end{equation*}
$$

Finally, substituting [51], [52] and [59] into equation [57] gives the parallel induced velocity as

$$
\begin{equation*}
{ }_{i} V_{z_{1}}=\frac{\bar{F}_{z_{2}}}{2 \rho A \sqrt{\left(\left\|\mathbf{V}_{\infty}\right\| \cos \psi+{ }_{i} V_{x_{1}}\right)^{2}+\left(-\left\|\mathbf{V}_{\infty}\right\| \sin \psi+{ }_{i} V_{z_{1}}\right)^{2}}}, \tag{60}
\end{equation*}
$$

which is similar to equation [56], and must also be solved iteratively. This method of predicting both parallel and perpendicular components distinguishes the model from the actuator disk theory for rotary wings, which only consider flow normal to the disk.

An important point to note from the equations for the induced velocity is that these components can be solved iteratively, providing that the parallel and perpendicular disk loads are known. However, these loads are themselves dependent upon on the induced velocity. Therefore, it is necessary to perform two iterative procedures, one to predict the induced velocity components in equations [56] and [60] using momentum theory, and another that derives the net parallel and perpendicular loads using blade element theory. This is illustrated in Figure 17.
a.

b.


Figure 17. (a) Inner and outer loop iterations for blade element momentum theory. The mean aerodynamic force is calculated using the blade element theory for a given initial guess value for the induced velocity. The momentum theory is then used $t$ update the induced velocity based on the mean force. (b) Example results for the net induced velocity taken from the outer iteration loop of a model of hovering flight of the pigeon.

Example results for the outer iteration loop are shown in Figure 17b, which shows 20 iterations of the vertical induced velocity for a hovering model of the pigeon. The iteration of induced velocity is found to be a robust numerical procedure that converges rapidly and is independent of the choice of the initial guess value.

### 4.2.8. Dimensional Analysis \& Performance Metrics

Force, torque and power coefficients can be defined to compare predictions from the dynamic model for different scales and flight conditions. The approach used here is inspired largely by the
standard methods employed in the analysis of rotary wing vehicles [19]. The axial, lateral and normal force coefficients are defined as
$C_{F_{x}}=\frac{F_{x_{0}}}{\frac{1}{2} \rho V_{r e f}^{2} S}$,
$C_{F_{y}}=\frac{F_{y_{0}}}{\frac{1}{2} \rho V_{r e f}^{2} S}$,
$C_{F_{z}}=\frac{F_{z_{0}}}{\frac{1}{2} \rho V_{r e f}^{2} S}$,
where $V_{\text {ref }}$ is the maximum wing tip speed during a wingbeat.

Unlike the aerodynamic force, the torque vector tends to be dominated by a single component for typical flight conditions. Therefore, a single shoulder torque coefficient is defined as
$C_{T_{\phi}}=\frac{{ }_{m} T_{x_{2}}}{\frac{1}{2} \rho V_{\text {ref }}^{2} S l^{*}}$.

The mechanical power coefficient is defined as

$$
\begin{equation*}
C_{P}=\frac{P}{\frac{1}{2} \rho V_{r e f}^{3} S} . \tag{65}
\end{equation*}
$$

The advance ratio is a scaling parameter used to characterise the operating conditions of rotary wing vehicles [81]. A similar approach can be used for flapping wing systems, by defining the advance ratio as the ratio of freestream velocity magnitude to the maximum wingtip speed:
$A R=\frac{\left\|\mathbf{V}_{\infty}\right\|}{V_{\text {ref }}}$.
The significance of the advance ratio will be made evident in section 5.3, when comparing the cruising kinematics of birds of varying scale.

Two performance metrics will be used to compare simulated birds of varying scale in section 5.3.3: the wing loading, WL, and power loading, PL. The wing loading is used to analyse performance of fixed wing aircraft and is the ratio of weight to wing area:

$$
\begin{equation*}
W L=\frac{m g}{2 S} ; \tag{67}
\end{equation*}
$$

The power loading is the ratio of force generated to power consumed, and is mainly used for rotary wing aircraft:

$$
\begin{equation*}
P L=\frac{\left\|\mathbf{F}_{0}\right\|}{P} \tag{68}
\end{equation*}
$$

### 4.2.9. Example Force Time Histories

Having formulated a closed set of equations for the inverse dynamic model it is now useful to demonstrate the model output for typical wing kinematics. Hovering flight will be used as a test case as it represents the simplest flight conditions from an aerodynamic perspective as the freestream velocity is zero. Using wing kinematics that will be predicted in section 5.2 for a model of the pigeon, examples of the shoulder torque coefficient and mechanical power coefficient are shown in Figure 18. The results from the dynamic wing model are shown in comparison to those predicted by models that include aerodynamic effects only, and inertial effects only.

The shoulder torque coefficient reaches a large negative peak at the beginning of the downstroke (phase=0), and a large positive peak at the beginning of the upstroke (phase=0.5; Figure 18d). At the beginning of each half-stroke significant torque is required to overcome inertial effects as this is where the wing angular acceleration is greatest. At the mid-downstroke (phase=0.25) and midupstroke (phase $=0.75$ ) the instantaneous torque due to inertial effects is zero as the wing is not accelerating. However, around this time the flapping velocity peaks, which yields significant aerodynamic torque. The shoulder torque coefficient variation in not symmetric about 0.5 phase due to added mass effects.

The mechanical power coefficient shows two distinct peaks during each half-stroke (Figure 18e), which have been observed in other flapping wing simulations that include both aerodynamic and inertial loads [49]. For the complete dynamic model at the first peak in power (phase $\approx 0.13$ ) both inertial and aerodynamic torques are negative. At the second peak in power (phase $\approx 0.38$ ) the inertial torque is positive as the wing is now decelerating, while the aerodynamic torque is still negative. As these two torque components are summed in deriving the mechanical power (equations [22]-), the power consumed near the beginning of the downstroke is greater than that consumed near the end, which explains the differences in size of the two peaks; the same process occurs on the upstroke. It is important to note that the mechanical power predicted using the total (aerodynamic + inertial) torque is not equal to the sum of the powers predicted using only aerodynamic, and only inertial torques, as implied by other works [64].

In hovering flight the inertial torques are of similar magnitude to the aerodynamic torque. In forward flight the aerodynamic torque becomes the more significant component, and so the first peak in power on each half-stroke becomes more pronounced.
a. Hovering kinematics (side view along $y_{0}$ )


b. Hovering kinematics (top view along $-z_{0}$ )


Figure 18. (a),(b) Example kinematics for hovering flight of a model of the pigeon. Time histories joint angles (c), shoulder torque coefficient (d) and mechanical power coefficient (e) for the complete dynamic model, a model with aerodynamic forces only, and a model with inertial forces only.

Another key output to be demonstrated is the predicted instantaneous aerodynamic force. Force coefficients predicted using the blade-element model presented in section 4.2.5 are shown in Figure 19. Blade-element models that omit the added mass effects and the induced velocity effects are also shown for comparison.

Axial and normal aerodynamic forces and force coefficients reach their peak values at the middownstroke (phase $\approx 0.25$ ) and mid-upstroke (phase $\approx 0.75$ ), when the wing flapping velocity is greatest (Figure 19a,c). The negative axial force generated on the downstroke is cancelled out by the positive force on the upstroke, leading to zero net axial force over the wingbeat, as required for hovering flight conditions (Figure 19a). The net lateral force coefficient is non-zero, but the lateral load would be cancelled out by an equal and opposite load from the other wing (Figure 19b). The net normal force coefficient is required as the normal force provides weight support in hovering flight (Figure 19c).


Figure 19. Time histories of axial (a), lateral (b) and normal (c) aerodynamic force coefficients, and shoulder torque coefficient (c) and mechanical power coefficient (d) for hovering flight of a model of the pigeon. Models without added mass effects and induced velocity effects are shown for reference.

Previous predictive simulations of insects hovering included added mass effects, but no induced velocity [49]. In the present work the added mass model only contributes significantly to the lateral force coefficient (Figure 19b). However, the induced velocity is seen to play a much bigger role, as it influences the prediction of normal force coefficient in hovering flight (Figure 19c). For fixed kinematics without induced velocity the mean normal force coefficient is greater. It can also be shown that using alternative kinematics with no induced velocity the same weight support can be achieved but using less mechanical power. The same observation was made with typical cruising flight kinematics (predicted in section 5.1). The added mass effects contribute more than the induced velocity effects to the peak shoulder torque coefficient (Figure 19d). However, neither of these make a significant difference to the mechanical power coefficient (Figure 19d).

Further insight into the model functionality can be gained by considering the variation in aerodynamic properties at different locations on the wing. The local section lift coefficient, $c_{l}$, is shown in Figure 20 for a hovering flight simulation with control points positioned at varying spanwise locations. Control points located from half way along the wing to the wing tip reach the maximum local lift coefficient of 1.6 , and retain high lift coefficients for the majority of the downstroke and upstroke. As the local wind velocity increases towards to wingtips due to the increase in wing flapping velocity, the majority of the aerodynamic load is generated in this region.


Figure 20. Time history of section lift coefficients for hovering flight of a model of the pigeon for blade elements positioned at three locations on the wing: the wingtip (i), $1 / 2$ of the wing length from the root (ii) and $1 / 4$ of the wing length from the root (iii).

If the induced velocity model were removed all blade elements would generate the same local lift coefficients in hover (Figure 20). However in the present model control points closer to the shoulder joint have lower local lift coefficients. This is mainly due to the induced velocity, which significantly reduces the local angle of attack for elements with low flapping velocities. The result of this is that not all blade elements can achieve the same angle of attack, and therefore cannot achieve the same local lift and drag coefficients.

A constant angle of attack can be achieved on a flapping wing using a distributed twist along the wing. For idealised conditions of axial flight, which represents hovering and high advance ratio forward flight, this twist distribution can be approximated analytically (see Appendix). Whether real birds are capable of actively achieving this kind of distributed twist is unknown. It is plausible that passive dynamic effects, such as feather bending under aerodynamic loads, may assist in doing so. However these properties are regarded as being highly species specific, and not applicable at this stage of the construction of a generic simulation model. It is more useful to recognise that the proposed model may unpredicted the aerodynamic loads on the wing in the region close to the shoulder joint for given wing kinematics. This will be discussed further in section 5.2.6.

### 4.2.10. Convergence \& Sensitivity Screening Analysis

The predicted mean aerodynamic loads and mechanical power consumption depend on the spatial distribution of control points along the wing and the temporal resolution of the dynamic model. To assess the convergence properties of the model the net aerodynamic load and mechanical power can be calculated under given flight conditions for increasing numbers of spanwise elements and solution timepoints. Figure 21 shows these data using optimised kinematics for a model of the pigeon in minimum power cruising flight that will be simulated in section 5.1.


Figure 21. Numerical convergence of the axial force (a), normal force (b) and mechanical power (c) with varying numbers of spanwise blade elements and numbers of solution timesteps; results are shown as percentage changes from the baseline values that were obtained using a model from a previous predictive simulation [37] i.e. using 2 spanwise elements and 100 timesteps.

When increasing the number of spanwise elements from 2, as used in a previous predictive simulation model [37], to 4, a significant drop of around $40 \%$ is seen in axial force (Figure 21a); normal force and mechanical power reduce by around $5 \%$. The numerical method converges towards a solution for aerodynamic load and power for both increasing numbers of timesteps and increasing numbers of spanwise elements. As with many numerical methods the exact convergence criteria must be selected somewhat arbitrarily, as the exact solution is unknown. Here, the numerical convergence is defined when a further doubling of number of elements or timepoints yields less than a $1 \%$ change in the solution. Therefore, based on the results in Figure 21, 32 spanwise elements and 400 timesteps will be used throughout this work.

Having defined the numerical parameters for the inverse dynamic model, a sensitivity analysis can now be performed on the model input physical parameters. This will provide insight into which input parameters are most influential for predicting aerodynamic force and mechanical power. Using the inverse dynamics model with defined wing kinematics rather than with the optimisation module allows an initial sensitivity screening analysis to be performed [82]. This allows the solution sensitivity to be disassociated from numerical uncertainties associated with optimisation, such as optimisation tolerances. The sensitivity analysis is purely aimed at assessing the influence of uncertainty in theoretical model parameters. Therefore, it does not take into consideration the coupling between physical parameters, such as the implicit change in wing mass that is likely to occur with changes in wing length.

A standard one-at-a-time (OAT) sensitivity analysis was performed for a model based on the pigeon, by incrementing input parameters from their baseline values (Table 1) [82]. Net aerodynamic force and mechanical power consumption were calculated for each set of input parameters, again using kinematics for minimum power cruising flight of the pigeon (Figure 22).

| Wing Length | Wing Mass | Wing radius <br> of gyration <br> $R_{g}\left(10^{-3} \mathrm{~m}\right)$ | Hand:wing length <br> ratio | Max. wrist <br> Circumduction |
| :---: | :---: | :---: | :---: | :---: |
| $l^{*}(\mathrm{~m})$ | $m_{w}\left(10^{-3} \mathrm{~kg}\right)$ | 96.9 | $h$ | $\left(^{\circ}\right)$ |
| 0.32 | 25.8 | 0.74 | 90 |  |
| Control point <br> chord-fraction | Section max. <br> lift coefficient | Section zero-lift <br> drag coefficient | Section max. <br> drag coefficient | $c_{d_{90}}$ |

Table 1. Input physical parameters of the baseline pigeon model taken from previous experimental studies where available [12],[13] and remainder obtained from allometric scaling laws [64].


Figure 22. Sensitivity screening analysis, showing the variation in net aerodynamic force on the wings and mechanical power consumption with changes in nine input parameters. Force and power are shown as percentages of the baseline values from Table 1.

The parameters that have the greatest influence on both the aerodynamic force and the power consumption are the wing length (Figure 22a) and maximum lift coefficient (Figure 22g). These will be termed the screened sensitivity parameters. The radius of gyration only influences the mechanical power consumption, and not the aerodynamic force. The reason that the aerodynamic force is sensitive to changes in the wing length is because increasing the wing length increases the wing flapping velocity and local wind velocity at the control points. As the blade element loads are
proportional to the square of the local wind flapping velocity (equations [29] and [30]), this causes a significant increase in axial and normal loads, which in turn increase torque and mechanical power consumption.

The results in Figure 22 allow quantification of the solution accuracy for given potential errors in the individual model input parameters. By varying more than one impact parameter at the same time, it can be shown that the solution accuracy is affected even more so for combined changes of input parameters. Using a two-at-a-time sensitivity analysis on the same model it is found that combined changes in wing length and maximum lift coefficient have the greatest influence on predicted aerodynamic loads and power consumption.

### 4.3. OPTIMISATION

This section will describe the optimisation module depicted in Figure 8 that is used with the inverse dynamics module to make predictive simulations of avian kinematics. As mentioned previously, the optimisation module will be largely independent of the input parameters to the inverse dynamics module. This allows optimised kinematics to be predicted using different input parameters, such as different bird geometries or flight conditions, without changing the optimisation module. However, the mathematical properties of the inverse dynamics model are taken into account when selecting a method of optimisation.

### 4.3.1. Cost Function

As described in chapter 2 mathematical optimisation generally involves the definition of the optimisation variables, constraints and a cost function. In the present simulation framework the cost function is used to assess the penalty associated with using given kinematics to achieve powered flight under given conditions.

Some of the fundamental models of terrestrial locomotion (e.g. [83]) defined optimum walking techniques as those that required the lowest mechanical energy consumption. More recently predictive simulation of multi-segment models have shown that minimising mechanical energy can lead to accurate predictions of body segment kinematics that closely resemble those measured experimentally ([35] and references therein). A similar approach was applied in two previous predictive simulations of flapping flight, which also captured experimental trends in kinematics for different species [49] and flight conditions [37].

It is recognised that cost functions based on metabolic power consumption have also been widely used in terrestrial locomotion simulations (e.g. [84]). Measurements of metabolic power
consumption in avian flight could potentially be used to validate a predictive model using this as an optimisation cost function [23]. However, muscle models that predict metabolic power typically require input parameters of muscle physical properties, as well as some representation of the muscle dynamics. These additional uncertainties limit the applicability of metabolic power models to the present simulation framework, and therefore mechanical power is regarded as being a more robust and generic cost function. For this reason the optimisation module will be used to minimise the time averaged mechanical power consumption at the shoulder joint, as detailed in section 4.2.4.

### 4.3.2. Optimisation Variables \& Wingbeat Parameterisation

The optimisation variables are a set of parameters that define the bird kinematics. In the general case this includes variables defining the kinematics of the wing with respect to the body and variables defining the descent angle, cruise speed and axial acceleration. It is also possible to predefine any of these kinematic variables prior to optimisation, in which case they are no longer included as optimisation variables. Throughout this work the descent angle and axial acceleration will be predefined. Cases where the cruise speed is also predefined will be stated clearly.

In the present work the kinematics of the wing are assumed to be periodic over the wingbeat time period, $T$. One caveat of previous simulations using the present model was that the wingbeat frequency, $f\left(=\frac{1}{T}\right)$, had to be predefined. The present work will overcome this shortcoming by including wingbeat frequency as an optimisation variable. Over the wingbeat time period the wing kinematics are governed by time histories (or trajectories) of the shoulder joint angles and the wing extension parameter defined in section 4.2.3. It is necessary to parameterise the time histories to yield a finite set of kinematic variables for optimisation. This should be done strategically as the number of optimisation variables greatly influences the computational cost of the optimisation problem.

Drawing on the success of previous models this work aims to find a compromise between two different approaches to wing kinematic parameterisation [37],[48]. The first approach is based on parsimony, which aims to capture the underlying physics of flapping flight using the simplest model possible [41]. The second approach is phenomenology, in which the model complexity reflects the desire to capture experimentally observed phenomena [49]. An intermediate approach was used in a previous application of the present model, whereby avian flight was simulated using only four wing kinematic variables [37]; the results captured trends observed experimentally for variations in kinematics with cruise speed. This method defined sinusoidal trajectories for wing elevation angle, $\phi$, wing pronation angle, $\boldsymbol{\theta}$, and wing extension parameter, $e$, giving a wing that has an implicitly cyclic motion, or that is stationary. By applying appropriate constraints to the
amplitudes sinusoidal motions prevent prediction of excessive force, torque and power in the dynamic model ${ }^{15}$. A similar approach will be applied in the present work, with the following mathematical definitions for elevation and pronation amplitude:

$$
\begin{align*}
& \phi=\Phi \cos (\omega t)+\Phi_{0},  \tag{69}\\
& \theta=\Theta \cos (\omega t+\xi)+\Theta_{0}, \tag{70}
\end{align*}
$$

where $\Phi$ and $\Theta$ are the amplitudes of elevation and pronation angle, $\Phi_{0}$ and $\Theta_{0}$ are the elevation and pronation angle offsets, respectively, $\xi$ is the pronation phase lag, and $\omega(=2 \pi f)$ is the wingbeat frequency in radians. A pronation phase lag of $\xi=0.25$ ensures that the maximum pronation angle is concurrent with the maximum wing flapping velocity at the mid-downstroke, allowing maximum aerodynamic force to be generated [37]. By setting angle offsets to zero the wings elevate and depress by equal amounts, and pronate and supinate by equal amounts. This simplification reduces the subspace of possible solutions to the optimisation problem, but still allows predictions to be made for hovering and forward flight conditions. Such a range of flight conditions can only be achieved by varying the stroke-plane angle, $\gamma$, which for simplicity is assumed to remain constant throughout the wingbeat.

A similar rationale used to define elevation and pronation angle trajectories is applied to the wing extension parameter:
$e=\frac{1}{2}(1-E) \cos (\omega t+\zeta)+\frac{1}{2}(1+E)$,
where $E$ is the extension amplitude, defined as the ratio of wing length on the mid-upstroke, to the maximum wing length, and $\zeta$ is the extension ratio phase lag. An extension ratio phase lag of $\zeta=0.25$ ensures that at the mid-downstroke the wing is always fully extended, again allowing maximum aerodynamic force to be generated, while maximum wing retraction occurs at the midupstroke.

For the present work the parameterisation described above will be used as a baseline model for predictive simulations of varying scale birds in varying flight conditions; an example of typical joint trajectories for minimum power cruising flight of the pigeon model are shown in Figure 23a.

[^13]

Figure 23. (a) Example time histories for joint angles and wing extension parameter for typical cruising flight conditions. (b) Phase transformation to generate non-sinusoidal trajectories. (c) Example elevation time histories for varying phase transformations. (d)-(f) Example kinematics for cruising flight of a model of the pigeon for varying values of $T_{d} ; T_{d}=0.5$ represents sinusoidal joint trajectories.

One special case will be considered in section 4.2.7, where non-sinusoidal elevation angle, pronation angle and extension parameter trajectories will be used. This will be done using a simple phase transformation function described by Wu \& Popovic [6]. This transforms the phase using the downstroke ratio, $T_{d}$, that defines the ratio of the downstroke time period to the total wingbeat time period. The resulting joint angle trajectories are still given by equations [69]-[71] but using the transformed phase (Figure 23b). This model is valid in the range $0.3 \leq T_{d} \leq 0.7$ and if $T_{d}=0.5$ the time histories revert to being sinusoidal. Examples of elevation angle time histories are shown in Figure 23c and example cruising flight kinematics are shown in Figure 23d-f for various values of $T_{d}$.

### 4.3.3. Optimisation Constraints

The main constraint necessary for simulating rectilinear flight is that the mean aerodynamic loads on the wing are equal to the sum of the inertial load, body drag, and gravitational load, as given by equations [5] and [6]. As mentioned in the previous section, the cruise speed will also be constrained in some cases. In addition, the wing kinematic variables given in section 4.3 .2 can also be constrained to fixed values, or fixed ranges of values.

In most predictive simulation methods optimisation variables are constrained by upper and lower bounds. These bounds prevent physically unrealistic solutions being obtained. In the present work the optimisation bounds will be defined for each flight condition in chapter 5 . Bounds on the wing kinematics could potentially be based on the ranges of motion of real bird wings. However, experimental data on avian joint ranges of motion is not readily available in biomechanics literature. Chapter 5 will demonstrate that in most cases the optimised kinematic variables do not reach the upper or lower bounds proposed in Table 2. However, one exception for cruising flight is the wing elevation amplitude, which at some cruise speeds does reach its upper bound. In the present work a baseline value of $75^{\circ}$ is used for maximum elevation amplitude as this is the maximum value recorded experimentally [13], including surveys of field study observations. Section 5.2.1 will demonstrate the effects of varying this upper bound on optimised kinematics in cruising flight. In addition, section 5.5 will show a special case of descending flight with a relaxed constraint of the lower bound on the stroke plane angle.

|  | Optimisation variables | Constraints |  |
| :---: | :---: | :---: | :---: |
| Flight kinematics |  | Forces |  |
|  | Cruise Speed $\quad\left\\|\mathbf{V}_{\infty}\right\\|$ | Axial force | $F_{x_{0}}=m a_{x_{0}}-m g \sin \beta+D_{0}$ |
|  |  | Normal force | $F_{z_{0}}=m g \cos \beta$ |
| Wing kinematics |  | Kinematic bounds |  |
|  | Frequency $f$ |  | $0<f<50 \mathrm{~Hz}$ |
|  | Elevation amplitude $\Phi$ |  | $0<\Phi<75^{\circ}$ |
|  | Pronation amplitude $\Theta$ |  | $0<\Theta<90^{\circ}$ |
|  | Stroke plane angle $\gamma$ |  | $-90^{\circ}<\gamma<0^{\circ}$ |
|  | Extension amplitude $E$ |  | $0<E<1$ |
|  | Downstroke ratio $T_{d}$ |  | $0.5<T_{d}<0.7$ |

Table 2. Baseline optimisation variables and constraints. The specific sets of variables and constraints used for each flight condition are given in chapter 5 .

Applying fixed value constraints to optimisation variables can also serve as a useful method of investigating the properties of the dynamic model. It is possible to constrain some of the kinematics variables to fixed values, and observe the effects of varying the remaining variables. As an example, a rudimentary hovering simulation was performed on a hummingbird dynamic model using data from literature to define mass and geometric parameters and also constrain all wing kinematics variables apart from the pronation amplitude [85]. Figure 24 shows the variation in mean vertical aerodynamic force with pronation amplitude. Two different values of pronation amplitude yield a mean vertical force that is equal to the weight of the modelled bird. The greater of these two values, $\Theta \approx 70^{\circ}$, requires less mechanical power, and can therefore be regarded as the global minimum to the optimisation problem.


Figure 24. Mean vertical aerodynamic force generated by a modelled pair of hummingbird wings, for varying pronation amplitude. The grey line indicates the vertical force that is equal to the weight of the hummingbird from which the kinematic and wing geometric data were taken [85]

Perhaps the most important point to draw from this preliminary analysis is that even with a heavily constrained system, more than one solution to the optimisation problem is identified. With more kinematic variables it follows that more solutions are likely to exist, and therefore the optimiser must be capable of resolving these various local minima to identify the global solution.

### 4.3.4. Optimisation Method

The choice of numerical method for optimisation is influenced by the properties of the dynamic model. If the dynamic model yields a solution space with basins of attraction, gradient-based methods of optimisation may not identify the global minimum. Conversely, it is likely to be computationally inefficient to apply a global optimisation method to a problem with only a single basin of attraction.

Previous predictive simulations found that the various local minimum could be resolved by using gradient based methods with numerous starting points for the optimisation variables [35],[37]. A similar approach is adopted here, whereby a mesh of initial starting points is defined using evenly spaced values of each optimisation variable between their upper and lower bound values. For all
simulation results that will be presented in chapter 5 it was found that using four evenly spaced starting points for each optimisation variable local minima were adequately resolved. Increasing the number of starting points, or using additional random starting points did not identify any unique solutions. While this approach is appropriate with the current number of optimisation variables, it is recognised that global optimisation methods may be more computationally efficient if more optimisation variables are included.

### 4.3.5. Sensitivity Analysis of Optimised Kinematics

The sensitivity screening analysis of the inverse dynamic model in section 4.2.10 showed that predicted aerodynamic force and mechanical power consumption were most sensitive to the defined wing length and the defined $c_{l_{45}}$. It is reasonable to assume that when the optimisation module is used the optimised kinematics will also be most sensitive to these screened input parameters. A second sensitivity analysis is conducted here to quantify the changes in optimised kinematics for changes in screened model input parameters.

It is important to note that this analysis does not indicate which parameters will be predicted with the greatest accuracy in the present work, as this depends on the specific values chosen for the model input parameters. It does, however, give some indication of how accurately an input parameter needs to be defined in order to achieve a desired level of accuracy in the model output. Therefore, if the model input parameters are defined from experimental data with known errors, this analysis give the corresponding error magnitudes of predicted kinematic parameters.

Minimum power cruising flight was chosen as a characteristic flight condition under which to perform the analysis. For $0.5-1 \%$ increments in screened model parameters it was found that resulting changes in predicted kinematics of the pigeon model were of a similar magnitude to the changes that would be associated with reducing optimisation tolerances. To minimise the influence of optimisation tolerances the model parameters were incremented over a larger range than used in the preliminary sensitivity screening (Figure 25). All predicted kinematics are taken from the globally optimum solution for minimum power cruising flight that will be discussed further in section 5.1.


Figure 25. Variation in optimised kinematics and power consumption with changes model input wing length (a) and $c_{l_{45}}$ (b); solutions obtained for minimum cruising flight of the pigeon model.

An increase in wing length creates wings with larger aerodynamic surface area that can utilise lower flapping velocities and therefore less power to achieve a given aerodynamic load (Figure $25 a$ ). For the same reason increasing $c_{l_{45}}$ also reduces the mechanical power consumption; for the trigonometric aerodynamic model used increasing $c_{l_{45}}$ increases the magnitude of lift to drag ratio for all angles of attack (Figure 25b).

Of the predicted kinematic parameters, wing extension amplitude tends to be the most sensitive to changes in model input parameters. This indicates that accurate prediction of wing extension amplitude for a given species would require the most accurate measurements of wing geometry and aerodynamic properties. Conversely, prediction of wingbeat frequency is likely to be more robust, in that is not as strongly affected by changes in input parameters.

Overall the results are consistent with the sensitivity screening analysis done prior to optimisation. However, this analysis goes further to show that predicted kinematic parameters tend to show greater sensitivity to reductions, rather than increases of the screened sensitivity parameters. Therefore, if there is some uncertainty in a model input parameter, overprediction, rather than underprediction of the parameter is a more conservative approach.

### 4.4. WAKE SIMULATION

The final module to be described is used to simulate and visualise the wake shed from the wings of a bird. The main aim is to generate accurate representations of wakes and flow fields using different forms of visualisation in order to complement existing experimental data. This module will be designed to function using aerodynamic data from optimised wing kinematics, or using data from the inverse dynamic model with user-defined wing kinematics. The method used will be based on well established theoretical models, and will be capable of simulating and visualising the wakes from fixed, flapping or rotary wings.

### 4.4.1. Discrete Vortex Method

The present wake simulation model is inspired largely by methods developed for simulating the wake of helicopter rotors [86]. These so-called free-wake methods are used to predict the evolution of the wake geometry over time ${ }^{16}$. Free wake models have been extended to analyse phenomena such as flight in ground effect [87], which is also important in modelling the flight performance of some birds.

The particular free wake model to be used is known as the vortex point or vortex blob method. This belongs to the class of methods known as vortex methods, which were mentioned in section 4.2.5. These methods have been described in detail in previous works [86]-[88], and so only a brief summary of the vortex point implementation will be given here.

The essence of most vortex models of fluid flow is that vorticity is assumed to be concentrated on discrete line vortices. This assumption is justifiable for many practical situations, whereby viscous flow effects tend to be confined to much smaller regions than those that can be described using potential (inviscid, irrotational) flow methods. A Lagrangian approach can be used to describe the motion of the line vortices. Assuming that the flow is inviscid and irrotational the line vortices move as material lines, and the motion of any point on a line vortex (defined as a vortex point or vortex blob) is given by the following equation [87]:
$\frac{d \mathbf{x}_{0}}{d t}=\mathbf{V}_{0}$,
where $\mathbf{x}_{0}$ is the position vector of the point, and $\mathbf{V}_{0}$ is the local fluid velocity at that position. The main challenge in solving equation [72] is in calculating the fluid velocity vector, which is comprised of the freestream wind velocity and also the mutually induced velocity from the vortex wake.

The solution process is initialised by defining a series of $K$ wake control points along the wing (Figure 26). These points define the spanwise locations at which vortex points will be released. At each wake control point the local wing lift per unit span, $L^{\prime}$, is derived using a finite difference approximation of the lift distribution obtained from the blade element method (section 4.2.5). By applying the Kutta-Joukowski theorem the circulation around the wing at the $k$ th control point is given as:

[^14]\[

$$
\begin{equation*}
\Gamma^{(k)}=\frac{L^{\prime(k)}}{\rho\left\|\mathbf{V}_{\infty}\right\|} \tag{73}
\end{equation*}
$$

\]

The wake region is modelled as a series of trailing vortex filaments (Figure 26). The strength of a vortex point on the filament is defined in the same manner as in the standard vortex lattice method, by subtracting the strength the two neighbouring vortex filaments at the instant the vortex point is released from the wing. Vortex points released from the most inboard or outboard wing control points are assigned strengths based on the circulation of the most inboard or outboard filaments, respectively. This differs slightly from similar models used for modelling the wakes from fixed wing aircraft, where the lift and circulation are generally assumed to be non-zero in the region between the two wings. However, for flapping-wing flight this makes little difference to the simulated wakes, the geometry of which is dominated by higher vortex point strengths in the outboard wake regions.


Figure 26. Model of trailing vortex lines shed from the wing, The strengths assigned to vortex points released from the wing are calculated from the instantaneous strengths of neighbouring vortex lines.

Each vortex point induces a velocity on every other point based on its assigned strength, and also its location. The second stage of the solution is to derive these induced velocity values by applying the Biot-Savart law repeatedly between each pair of vortex points. The induced velocity at a point, $\mathbf{x}_{0}$, from the $k$ th vortex point is given as

$$
\begin{equation*}
{ }_{V I} \mathbf{V}^{(k)}=\frac{\Gamma^{(k)} \hat{\mathbf{d}}^{(k)} \times\left(\mathbf{x}_{0}-\mathbf{x}_{0}^{(k)}\right)}{4 \pi\left\|\left(\mathbf{x}_{0}-\mathbf{x}_{0}^{(k)}\right)^{3}\right\|} f\left(h, r_{c}\right), \tag{74}
\end{equation*}
$$

where $\Gamma^{(k)}$ and $\mathbf{x}_{0}^{(k)}$ are the strength and location of the $k$ th vortex point, respectively, $\hat{\mathbf{d}}_{0}^{(k)}$ is the unit direction vector of the vortex filament at the $k$ th vortex point location, $h$ is the perpendicular distance from $\mathbf{x}_{0}$ to $\hat{\mathbf{d}}_{0}^{(k)}$, and $r_{c}$ is the radius of the viscous vortex core. The function, $f\left(h, r_{c}\right)$ which is multiplied by the right hand side of equation [74] is a model of the vortex core, which is required to prevent numerical singularities occurring when two vortex points occupy the same location. The core model essentially captures the effects of viscosity by enforcing that the induced tangential velocity reduces to zero at the centre of the vortex. A variety of different vortex core models exist, but for simplicity a standard model used in previous rotor wake simulations is applied here [86],[87]. This models the function from equation [74] as

$$
\begin{equation*}
f\left(h, r_{c}\right)=\frac{h^{2}}{\sqrt{r_{c}^{4}+h^{4}}} . \tag{75}
\end{equation*}
$$

The influence of the core model is dependent upon the value chosen for the core $r_{c}$, which defines the distance from the centre of a vortex point to the radial location with maximum tangential velocity. Typical values for $r_{c}$ used for rotary wing analyses are around half of the mean wing chord [87]. Section 4.4.2 will show that the predicted wake geometries are insensitive to the choice of value for $r_{c}$. Preliminary tests using a Lamb-Oseen core model applied in other rotor wake simulations [87] also found little change to the overall wake geometry for varying core radius.

The total induced velocity at a point in the flowfield is given as the sum of the induced velocity contributions from all vortex points. Thus the velocity of each vortex point can be derived by summing the total induced velocity and the freestream velocity. This is the first step of a time marching process, and the positions of all vortex points can then be updated by numerically integrating the velocity over a small time step, $\Delta t$. Using a simple Euler integration scheme the updated position vector of any vortex point is given as
$\mathbf{x}_{0}(t+\Delta t)=\mathbf{x}_{0}(t)+\mathbf{V}_{0}(t) \Delta t$.
Providing that a suitably small simulation time step was used, this integration scheme was found to be numerically stable. Equations [74]-[76] are applied repeatedly for the first set of vortex points released from the wake control points.

Vortex points are released from each of the wake control points at a rate of $f_{w} \mathrm{~Hz}$. After a time period of $T_{w}\left(=\frac{1}{f_{w}}\right)$ new vortex points are released. The same procedure of defining vortex point strengths and calculating induced velocities is still applied, however equation [74] is now valid for a total of $2 K$ vortex points. This process is repeated over the total desired simulation time period, with new sets of vortex points released from the wake control points after every period, $T_{w}$.

### 4.4.2. Numerical Stability \& Convergence

The wake simulation method presented in the previous section includes four numerical parameters that influence the predicted wake geometry: the number of wake control points along the wing, $n_{w}$, the rate at which Lagrangian markers are released from these points, $f_{w}$, the size of the time step, $\Delta t$, and the radius of the viscous vortex core, $r_{c}$. To assess the convergence properties of the numerical method wakes were simulated for variations in each of these parameters across a range of values. The time dependant marker release locations and wing aerodynamic loads were derived from wing motions optimised for minimum power cruising flight of the pigeon, that will be presented in section 5.1.

To quantify the predicted wake geometry the root mean square of all of the marker locations from a single wingbeat was calculated, similar to the approach used for rotor wake analysis [86]; the results are shown for all variations in numerical parameters in Figure 27. It was found that after simulating for three wingbeat time periods the RMS wake geometry converged to within $1 \%$ of that calculated from the previous time period. Therefore, RMS wake geometry data was assumed to be converged when captured over three wingbeat time periods.


Figure 27. Numerical convergence of the RMS wake geometry simulated from the predicted wing kinematics for minimum power cruise of the model of a pigeon. Wake geometries simulated for varying numbers of timesteps per wingbeat, vortex point release rates, numbers of control points per wing, and viscous vortex core radii.

Using 8 wake control points on each wing yielded a detailed representation of the wake that captured flow features observed experimentally (Figure $27 \mathrm{~g}-\mathrm{i}$ ); these results will be shown in section 5.6.1. With 8 control points the RMS geometry converges for increasing numbers of wake simulation timesteps and increasing marker release rate. Wakes will be simulated using 400 simulation timesteps per wingbeat and a release rate of 20 markers per wingbeat; further increase in either of these parameters yielded less than a $1 \%$ change in the RMS wake geometry.

A significant conclusion from these data is that the radius of vortex core does not strongly affect the RMS wake geometry. With no viscous core model some (but not all) simulations developed numerical instabilities (Figure 27d). This was due to as an overprediction of induced velocity between a single pair of markers as they came into close proximity. For this and other flight conditions tested the simulations were found to be numerically stable providing that the viscous vortex core radius was at least a quarter of the mean wing chord.

### 4.4.3. Visualisation

A rudimentary form of wake visualisation is simply to plot the Lagrangian markers used in the vortex point simulation (Figure 28a). If only the tip vortices are simulated this approach has proven sufficient in illustrating the wake geometry, particularly when the vortex filaments are plotted by connecting points vortices released from the same wing control point [86]. When more than one vortex filament is modelled the value of this approach as a visualisation tool depends largely on the complexity of the wake. A more intuitive method of visualisation uses additional information of connectivity between markers released at the adjacent wing control points to plot a wake surface rather than a series of filaments. By interpolating between control points a smooth surface can be plotted that portrays the complex 3D wake geometries in a more intelligible format than simple plotting of the filaments (Figure 28b). Alternatively the markers released from a single control point can be interpolated to generate wake streamlines (Figure 28c).
a. Lagrangian markers
b. Wake surface

c. Wake streamlines


Figure 28. Simulated wake of a pigeon in gliding flight. (a) Lagrangian markers used in the vortex point method, with point vortices released from the same spanwise location connected by straight line segments. (b) Wake surface and (c) streamline visualisations obtained from cubic interpolation of lagrangian markers.

Using a vortex point simulation is also possible to reconstruct the velocity and vorticity field data. One approach to doing this would be to release Lagrangian markers throughout the flowfield during the simulation. The motion of the markers could then be found by deriving their induced velocity as done for the vortex points. A more flexible approach is to derive the induced velocities at an array of control points, that are fixed with respect to the freestream axes. This can be done after the wake simulation has completed, and can be limited to specific regions of interest in the flowfield, and at specific times over the solution period. In the present work the latter approach will be used to determine velocity components, $V_{y_{0}}$ and $V_{z_{0}}$, in planes parallel to the $y_{0}-z_{0}$ plane. The vorticity in these planes is then given as

$$
\begin{equation*}
\omega\left(y_{0}, z_{0}\right)=\frac{\partial_{V I} V_{z_{0}}}{\partial y_{0}}-\frac{\partial_{V I} V_{y_{0}}}{\partial z_{0}} . \tag{77}
\end{equation*}
$$

The vorticity will be calculated using a first order central differencing approximation for the spatial derivate of induced velocity, just as done for the temporal variable derivate in equation [39]. Examples of the velocity and vorticity fields, along with other wake visualisation techniques described above, will be given in section 5.6.

## Chapter 5. Results

The inverse dynamic model and optimisation routine described in chapter 4 can be used to simulate wing kinematics of a bird in various flight conditions. This chapter will present and discuss the predicted kinematics, along with details of aerodynamic force, torques and mechanical power consumption. Kinematic data will be validated through comparison with experimental measurements taken from biomechanics literature.

The first case presented is the characteristic flight condition of minimum power cruise, using the dynamic model of a pigeon. The optimised solutions are compared between local minima and the global solution. Other flight conditions will also be analysed using the pigeon model, including horizontal cruise at varying speeds, horizontal acceleration, and constant speed climbing and descending flight. In addition, results will be presented for different dynamic models to simulate the flight of birds of varying scale. The chapter will conclude by demonstrating some applications of the wake visualisation model in different flight conditions.

### 5.1. MINIMUM POWER CRUISING FLIGHT

Minimum power cruising flight serves as a useful reference point for assessing avian flight performance, as it represents a self-selected flight condition at which real birds could be expected to operate. To analyse the numerical accuracy and stability of the theoretical model, optimisation of an inverse dynamic model of a pigeon will be used to simulate wing kinematics in minimum power cruise according to the parameters defined in Table 3; as the cruise speed is unknown prior to optimisation, it will also be used as a free optimisation variable. Similar results to those shown in this section are also found using different scale dynamic models and alternative flight conditions, such as flight at the minimum cost of transport speed.

| Flight condition <br> Minimum power <br> horizontal cruise Mechanical power, C | Optimisation variables | Constraints |
| :--- | :---: | :---: | :---: |
|  | Frequency, $f$ | $0<f<50 \mathrm{~Hz}$ |
|  | Elevation amplitude, $\Phi$ | $0<\Phi<75^{\circ}$ |
|  | Pronation amplitude, $\Theta$ | $0<\Theta<90^{\circ}$ |
| Stroke plane angle, $\gamma$ | $-90^{\circ}<\gamma<0^{\circ}$ |  |
|  | Extension amplitude, $E$ | $0<E<1$ |
|  | Cruise speed, $V_{\infty}$ | $\bar{F}_{x}=D_{0}$ |
|  |  | $\bar{F}_{z}=m g$ |

Table 3. Optimisation parameters used for simulating minimum power cruising flight. All constraints are subject to optimisation tolerance of $\pm 10^{-5}$.

### 5.1.1. Kinematics of Local Minima

Optimisation revealed numerous local minima for minimum power cruising flight. Each local minimum corresponds to a set of wing kinematics and a cruise speed that satisfy the optimisation constraints. The local minima tend to be clustered in small groups (Figure 29), also referred to as solution families in other predictive simulation studies [35]. Each family lies within a basin of attraction in the solution space, and captures a certain flight style or mode of flight. Differences between solutions in one family are due to the numerical tolerances of the optimisation function and constraints.


Figure 29. Illustration of basins of attraction, optimisation solutions and solution families. Families of solutions are clustered within basins of attraction and arise due to numerical tolerances in the optimisation algorithm.

Insight into the functionality of the theoretical model and the underlying physical principles can be gained by analysing the kinematics predicted for various predicted modes of flight, rather than focussing purely on the global minimum solution. Kinematic data for three flight modes are shown in Table 4 and are illustrated in Figure 30. These solutions represent three distinct modes of flight, each with significant differences in optimised kinematic variables. The stiff-wing mode and the retract-twist mode are examples of local minima that use $35 \%$ and $13 \%$ more mechanical power than the minimum power mode, respectively. Other local minimum solutions were identified that used more than four times the minimum mechanical power, however these will not be considered further.

| Mech. Power, P (W) | Cruise Speed, $V_{\infty}\left(\mathrm{ms}^{-1}\right)$ | $\begin{aligned} & \text { Frequency, } f \\ & (\mathrm{~Hz} .) \end{aligned}$ | Elevation Amp., $\Phi$ (deg.) | Pronation Amp., $\Theta$ (deg.) | Stroke Plane Angle, $\gamma$ (deg.) | Extension Amp., E |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Minimum power mode |  |  |  |  |  |  |
| 20.7 | 12.1 | 9.15 | 55.0 | 17.2 | -15.5 | 0.37 |
| Stiff-wing mode |  |  |  |  |  |  |
| 27.9 | 13.4 | 13.6 | 32.7 | 11.7 | -12.9 | 0.93 |
| Retract-twist mode |  |  |  |  |  |  |
| 23.4 | 11.8 | 11.1 | 46.4 | 28.1 | -25.2 | 0.1 |

Table 4. Solutions from optimisation of the model of the pigeon for minimum power cruising flight, showing the minimum power mode (global solution) and the stiff-wing and retract-twist modes (examples of local minima).

The minimum power mode (Figure 30a,d) uses a cruise speed and stroke plane inclination close to the mean values of all the local minima identified. This solution also uses intermediate pronation amplitude and extension amplitude, along with a lower frequency and greater elevation amplitude than most other local minima. The stiff-wing mode (Figure 30b,e) uses an almost fully-extended wing upstroke and is similar to the flight mechanism used by hummingbirds in fast forward flight [85].

The use of a retracted upstroke reduces power consumption. Some solutions even use a fully retracted upstroke, whereby the wing length is modelled as reducing to zero at the mid-upstroke. The retract-twist mode (Figure 30c,f) is an example of a retracted upstroke mode in which wing retraction is concurrent with significant supination. This mode is similar to the commonly named "tip-reversal" stroke that has been observed in low speed flight and take-off of several species [89][90].

Overall, a wide range of kinematics satisfy the optimisation constraints, showing that several alternative flight modes can provide the fundamental functions of weight support and thrust. It is likely that an even wider range of kinematics could be expected to satisfy the constraints if nonsinusoidal joint trajectories were considered. An implication of this in a biological context is that there may have been some flexibility in the evolution of kinematics needed for flapping flight. For example, even though birds with non-retracting wings consume excess mechanical power, they could still generate sufficient weight support and thrust for cruising flight. This emphasizes the limitations of determining flight capability of extinct birds through comparison of their likely kinematics with those of modern birds. It is plausible that extinct birds were capable of using very different kinematics, which may have consumed more mechanical power, but still achieved powered flight.
a. Minimum power mode (side view along $y_{0}$ )

b. Stiff-wing mode (side view along $y_{0}$ )

c. Retract-twist mode (side view along $y_{o}$ )

d. Minimum power mode (top view along $-z_{0}$ )

e. Stiff-wing mode (top view along $-z_{0}$ )

f. Retract-twist mode (top view along $-z_{0}$ )


Figure 30. Optimised wingbeat kinematics for minimum power cruising flight of the pigeon model. (a),(d) Minimum power mode (global solution). (b),(e) Stiff-wing and (c),(f) retract-twist modes (examples of local minima).

### 5.1.2. Upstroke Function in Minimum Power Cruise

Both experimental and theoretical studies have attempted to resolve instantaneous aerodynamic forces on the wing throughout the wingbeat (e.g. [13],[91]). One of the main motivations for doing this is to understand better the function of the upstroke, and how the role of the upstroke in flapping wing flight may change according to flight conditions. In addition, it is also useful for determining factors such as the peak loads and torques that the wing structure has evolved to withstand, as well as the rate of energy expenditure. In the present work these data are derived implicitly within the dynamic model.

Force, torque and mechanical power time histories for the three flight modes discussed in the previous section are shown in Figure 31. When considering the variation of force coefficients over a wingbeat (Figure 31a-c) it is unsurprising that the normal force coefficient, $C_{F_{z}}$, has the largest mean and peak values, as this component provides weight support, which is greater than the axial component needed to overcome body drag at typical minimum power cruise speeds. The axial force coefficient is greatest for all three modes just after the mid-downstroke (phase $\approx 0.3$ ); this is when the majority of the thrust is generated to overcome body drag. The stiff-wing mode also generates a positive axial force coefficient at the mid-upstroke (phase $=0.75$ ), but this is counteracted by the generation of negative axial force coefficients near the start (phase $\approx 0.05$ ) and end (phase $\approx 0.95$ ) of the stroke.

The lateral force coefficient reaches a peak value of approximately three times that of the axial force coefficient for all kinematic modes shown. Lateral force serves no obvious aerodynamic function in cruising flight conditions as it would be cancelled by the opposing force from the other wing. Therefore, the contribution to mechanical power from lateral loads can be regarded as nonuseful power.


Figure 31. Time histories of axial (a), lateral (b) and normal (c) aerodynamic force coefficients, shoulder torque coefficient (d) and mechanical power coefficient (e). Optimised solutions shown for three predicted kinematics modes of cruising flight of a model of the pigeon.

The stiff-wing mode is unique in generating negative normal force during the wing upstroke, which is detrimental to the goal of providing weight support (Figure 31c). To counteract this, additional normal force is generated on the downstroke.

As discussed in section 4.2.9, at the beginning and end of each half-stroke the wing acceleration, and thus the inertial torque, reaches its peak value. This is most noticeable in the case of the stiffwing mode as the moment of inertia is higher than in the other two modes. Retracted-wing modes inherently reduce aerodynamic and inertial loading by reducing the wing surface area and moment of inertia. This leads to the minimum power mode and retract-twist mode having lower torque coefficient magnitudes than the stiff-wing mode throughout most of the wingbeat (Figure 31d).

For all three modes the peak mechanical power coefficient arises near the mid-downstroke (phase $\approx$ 0.25 ) as the aerodynamic torque at the shoulder and elevation angular rate both reach their maximum values (Figure 31e); the inertial torque is zero at the mid-downstroke. The mechanical power coefficient of the stiff-wing mode is significantly larger than the other two modes during the upstroke due to the greater torque, but similar elevation angular rates. The force, torque and power coefficients of the minimum power and retract-twist modes are significantly smaller during the upstroke than during the downstroke. These modes can therefore be regarded as using the passive upstroke referred to in section 2.4.

### 5.2. VARYING CRUISE SPEED

Section 2.4 discussed how previous studies have examined how avian wing kinematics change according to flight conditions. Specifically, wind tunnel studies have recorded the changes in wing
kinematics with cruise speed, and these data have been used as inputs for models of avian flight performance (e.g. [13]). This section will investigate whether the predictive simulation approach could provide complementary data to these models by simulating wing kinematics over a range of cruise speeds. The pigeon model will again be used as a test case.

While the results in section 5.1 included cruise speed as a free optimisation variable, this section will use a range of fixed values of cruise speed. It is arguably simpler to optimise for fixed cruise speeds, as removing speed as an optimisation variable reduces the size of the solution space. The parameters used in optimisation for varying speed cruise are shown in Table 5.

| Flight condition | Cost function | Optimisation variables |
| :---: | :---: | :---: |
| Horizontal cruise at <br> varying speed | Mechanical power, P | Frequency, $f$ |
|  | Elevation amplitude, $\Phi$ | $0<f<50 \mathrm{~Hz}$ |
|  | Pronation amplitude, $\Theta$ | $0<\Phi<75^{\circ}$ |
|  | Stroke plane angle, $\gamma$ | $0<\Theta<90^{\circ}$ |
|  | Extension amplitude, $E$ | $-90^{\circ}<\gamma<0^{\circ}$ |
|  | Downstroke ratio, $T_{d} *$ | $0<E<1$ |
|  |  | $0.3<T_{d}<0.7$ |
|  | $\bar{F}_{x}=D_{0}$ |  |
|  |  | $\bar{F}_{z}=m g$ |

Table 5. Optimisation parameters used for simulating cruising flight at varying speed. All constraints are subject to optimisation tolerance of $\pm 10^{-5}$. *The downstroke ratio will only be included as a free optimisation variable in section 5.2.7.

### 5.2.1. Wing Elevation Amplitude Upper Bound

In predicting minimum power flight in section 5.1 none of the optimisation variables reached their defined upper or lower bounds. However, when optimising with a fixed cruise speed, at some speeds the wing elevation amplitude and wing extension amplitude did reach their upper bounds. The peak extension amplitude is well defined as being the maximum wing length of the outstretched wing, and so is this can be regarded as a legitimate result. However, the same cannot be said for the peak wing elevation amplitude.

Section 4.3.3 explained how the upper bound on elevation amplitude has been estimated from the maximum values recorded experimentally. To analyse the implications of this assumption, optimisation over a range of fixed cruise speeds was repeated using smaller and larger upper bounds on elevation amplitude than that of the baseline case (Table 6).

In hovering and forward flight up to around $8 \mathrm{~ms}^{-1}$ the optimised global solution always uses the maximum allowed elevation amplitude. With a larger elevation amplitude the effective disk loading is reduced, and so less power is required to overcome the additional drag from induced velocity. To generate the correct net aerodynamic force for weight support with greater elevation amplitudes the wingbeat frequency is reduced to maintain the same wing flapping velocity. This also tends to reduce mechanical power consumption by reducing the inertial component of torque on the shoulder. At cruise speeds greater than around $20 \mathrm{~ms}^{-1}$ the predicted elevation amplitude also tends to reach the defined upper bound value. This is coupled with a high wingbeat frequencies, as large wing flapping velocities are required to generate increased aerodynamic force to balance the body drag.

In the absence of any upper bounds the wing elevation amplitude tends to increase indefinitely in hover and low speed flight. This is accompanied by a decrease in wingbeat frequency, which tends to zero. The result is effectively a rotary wing mode, whereby the wing rotates around and around the shoulder joint, similar to a helicopter blade. This mode is obviously not plausible for birds as the shoulder joint has a limited range of motion, but it does offer some insight into the underlying physical processes: by maximising elevation amplitude the disk loading and induced power loading are minimised, while minimising frequency reduces inertial torque and associated mechanical power consumption.

At cruise speeds of around $12 \mathrm{~ms}^{-1}$ the minimum power mode has an elevation amplitude less than the defined upper bound. The choice of upper bound value makes no significant difference to the predicted kinematics around this speed. Small differences between kinematic variables at $12 \mathrm{~ms}^{-1}$ in Table 6 can be attributed to numerical artefacts within the optimisation algorithm, as varying the upper bound value requires the initial guess values to be adjusted accordingly.

| Upper Bound Elevation Amp., $\Phi^{\prime}$ (deg.) | Mech. Power, P (W) | Frequency, $f$ <br> (Hz.) | Elevation Amp., $\Phi$ (deg.) | Pronation Amp., $\Theta$ (deg.) | Stroke Plane Angle, $\gamma$ (deg.) | Extension Amp., E |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $0 \mathrm{~ms}^{-1}$ |  |  |  |  |  |  |
| 65.0 | 33.8 | 10.3 | 65.0 | 53.3 | -89.8 | 1.0 |
| 75.0 | 30.5 | 9.0 | 75.0 | 55.3 | -89.6 | 1.0 |
| 85.0 | 27.9 | 8.0 | 85.0 | 56.2 | -89.6 | 1.0 |
| $12 \mathrm{~ms}^{-1}$ |  |  |  |  |  |  |
| 65.0 | 20.7 | 9.2 | 55.0 | 17.6 | -15.8 | 0.38 |
| 75.0 | 20.7 | 9.0 | 56.8 | 18.8 | -16.9 | 0.34 |
| 85.0 | 20.7 | 9.2 | 54.7 | 17.0 | -15.3 | 0.40 |
| $24 \mathrm{~ms}^{-1}$ |  |  |  |  |  |  |
| 65.0 | 41.5 | 10.0 | 65.0 | 11.3 | -2.3 | 0 |
| 75.0 | 40.8 | 8.9 | 74.0 | 13.1 | -4.0 | 0 |
| 85.0 | 40.7 | 8.2 | 80.7 | 13.1 | -4.4 | 0 |

Table 6. Predicted mechanical power consumption and wing kinematics for varying cruise speed, using different upper bounds for the wing elevation amplitude, $\Phi^{\prime}$.

The reason why the elevation amplitude does not tend to the upper bound value at around $12 \mathrm{~ms}^{-1}$ cruise relates to the orientation of the aerodynamic force vector on the wing, $\mathbf{F}_{0}$. By reducing the elevation amplitude a greater component of the aerodynamic force on the downstroke is vectored vertically to provide weight support. This is illustrated for axial flight in Figure 32 where two wingbeats are compared that have the same flapping velocity, but different elevation amplitudes and frequencies. The high amplitude, low frequency mode vectors more of the aerodynamic force laterally, so the $F_{y_{0}}$ component is greater than in the low amplitude, high frequency mode. As discussed in section 4.2.9 the power required for generating this lateral force is essentially nonuseful. The low amplitude, high frequency mode can generate more weight support during the downstroke by vectoring more of the aerodynamic force vertically, increasing $F_{z_{0}}$. Therefore, to generate the equivalent weight support with this mode the flapping velocity can be reduced, which decreases the mechanical power consumption.
a. High amplitude, low frequency
(front view along $-x_{0}$ )
b. High amplitude, low frequency (side view along $y_{o}$ )

d. Low amplitude, high frequency (side view along $y_{o}$ )


Figure 32. Aerodynamic force vectoring in axial flight for wingbeats with high amplitude and low frequency (a),(b), and low amplitude and high frequency (c),(d). For both cases the wing flapping velocity and angle of attack are assumed to be equal in the postures depicted, so that the magnitudes of the aerodynamic force, $\mathbf{F}_{0}$, are equal.

The key point to note from this section is that at minimum power cruise speeds the predicted kinematics and power are largely independent of the bounds on the solution variables; the same result can be shown for the minimum cost of transport cruise speed. Therefore, in typical cruising conditions the model is not impeded by the lack of experimental data on avian joint ranges of motion.

### 5.2.2. Envelopes of Local Minima

Section 5.1 demonstrated the importance of considering not only the global minimum solution identified through optimisation, but also other local minima in the solution space. In some instances, local minima may prove to be numerical artefacts that are somewhat nonphysical, such as the rotary wing mode described in the previous section. Others actually give some insight into alternative, plausible modes of flapping wing flight. To identify such modes, a strategy of identifying an envelope of local minima is adopted (Figure 33). This includes all solutions whose mechanical power consumption exceeds that of the global minimum by a defined amount.


Figure 33. Illustration of how the envelopes of local minimum are used to encapsulate a range of solutions that lie within a defined range of cost function (mechanical power).

Using the pigeon model for a solution envelope of $5 \%$ surplus power over the minimum power it was found that the largest variations in predicted kinematics occurred at cruise speeds of $10-14 \mathrm{~ms}^{-1}$ (Figure 34). If envelopes were increased further the local minima discussed in section 5.1 would also be included in the envelopes. With envelopes of 1,3 and $5 \%$ mechanical power, around the minimum power speed of $12.1 \mathrm{~ms}^{-1}$ local minima are found that show variations in all kinematic variables. These results go further than those in section 5.1 by showing that various kinematic modes exists for a broad range of cruise speeds. This is consistent with the findings from similar studies that optimised kinematics of a jointed-wing air vehicle [50].


Figure 34. Predicted kinematics over a range of cruise speeds, highlighting the global minimum power solution for each speed. The range of local minima are also shown in the shaded power envelopes, defined by the percentage power over the minimum power solution for each speed.

Of all kinematic variables the extension amplitude shows the greatest variation, ranging from around 0.05 to 0.75 within a $5 \%$ envelope of mechanical power. This suggests that changes in the extension amplitude have less effect than changes in other kinematic variables on the predicted
mechanical power. The physical implications of this result will be considered further in section 5.2.8.

Within the envelopes of local minima similar ranges of predicted frequency and elevation amplitude are seen (Figure 34a,b). For some local minima it is found that the frequency is higher than that used in global minimum solution, while the elevation amplitude is lower. For other minima, the opposite case is found. The reason for this is that the aerodynamic load is derived from the flapping velocity, which is proportional to both frequency and elevation amplitude. So a fixed aerodynamic load can be maintained using a fixed flapping velocity, regardless of the values of elevation amplitude and frequency. However, as explained previously the mechanical power does depend on the elevation amplitude and frequency. This explains why many local minima are identified with the same flapping velocity, but different amounts of power consumption.

When examining the effects of varying cruise speed it is important to consider that birds are likely to have evolved optimal performance in specific flight conditions. For example, migratory birds may have evolved specifically to reduce their minimum cost of transport. If the biomechanical structure has evolved to function primarily at a given speed, it follows that an optimal set of wing kinematics would also be expected for the given structure and flight condition. This may even limit the range of kinematic modes that a particular bird can undertake. The reason why this argument is pertinent to the present study is that if the kinematics are limited by evolutionary constraints, Figure 34 shows that there is still potential to vary cruise speed by using non-optimal kinematics, without suffering a substantial increase in energy consumption.

### 5.2.3. Experimental Validation of Wing Tip \& Wrist Trajectories

In the previous sections the optimised wing kinematics have been discussed in terms of the numerical solution procedure and the underlying physical process included in the theoretical model. To establish whether these kinematics are representative of real birds it is important to compare the predictions with experimental data. This section will use wingtip and wrist trajectory data collected during previous wind tunnel tests as a means of qualitatively validating the predictions from the present theoretical model.

A number of wind tunnel tests have been performed using different species, however, there is great inconsistency in the choice of kinematic variables recorded. Furthermore, insufficient data is sometimes given to determine the exact wing kinematics. For example, some studies (e.g. [92]) only record the wingtip vertical excursion, without isolating the individual contributions from wing elevation and stroke plane inclination.

An exemplary case is that of the pigeon, which has been analyzed in wind tunnel tests from at least two independent studies [13],[89]. The kinematic data recorded in these studies is comparable to some of the founding works on avian flight analysis [10],[11], and sufficient detail is presented to allow direct comparison with the results from the present work. Furthermore, wingtip and wrist trajectories are documented, providing an in depth representation of the wing kinematics [89].

Several accounts have been made of real pigeons exhibiting a figure-of-eight wingtip paths in low speed flight (e.g. [11],[89]). Previous predictive simulations that the current work was derived from did not capture this effect, and the tips were seen to follow a shallow arc [37]. However in the revised model presented here, at $6 \mathrm{~ms}^{-1}$ cruise a figure-of-eight wingtip path is predicted (Figure 35a). The reason for this is that a figure-of-eight path is generated for kinematic modes that incorporate significant wing retraction and wing pronation, which was not the case for the previous model. It should be noted that at lower cruise speeds, the present model also reverts back to an extended wing mode with a shallow arc tip path. Therefore, the fact that a figure-of-eight path is predicted at $6 \mathrm{~ms}^{-1}$ may be somewhat coincidental, and should not be regarded as conclusive evidence of similarity between experimental and simulated kinematics.

Perhaps a more robust point of comparison is the orientation of the stroke plane, which follows the same trend with cruise speed for simulated and experimental data (Figure 35). As the cruise speed increases the stroke plane tilts so that a greater component of the aerodynamic force generated by the wings is vectored axially in order to overcome body drag. In the following section this will be shown to be true across a broad range of cruise speeds, and has also been observed in other species (e.g. [89],[92]).

When viewed laterally the tip paths at 12 and $18 \mathrm{~ms}^{-1}$ cruise are approximately elliptical (Figure $35 \mathrm{~b}, \mathrm{c})$. This is because when the wings retract with little pronation, rotation of the wrist joint causes the tips to translate in the $-x_{0}$ direction (downstream); if viewed from above translation in the $-y_{0}$ direction would also be seen for the left wing. The fact that the paths followed by the wrist and the tip are of opposite sense is due to geometry and the rates of retraction of the different skeletal segments. In the present model as the forearm is modelled as being longer than the upper arm, wing retraction causes the wrist to translate in the $-x_{0}$ direction, opposite to the motion of the wing tip.


Figure 35. Comparison of simulated and experimental measurements of the wing tip (filled circles) and wrist (open circles) trajectories for cruising flight of the pigeon. The tip path is the path of 8th primary, the orientation of which was defined for the simulated model using illustrations of outstreched wing feather geometries [70]; the angle between the feather major axis and the $x_{3}$ axis is assumed to be proportional to the wing extension parameter. Visualisations of simulated kinematics are constructued under the assumption that the body maintains a fixed orientation with respect to the stroke plane.

### 5.2.4. Predicted Mechanical Power Consumption

The predicted mechanical power consumption follows the characteristic U -shaped curve described in chapter 2 (Figure 36). The minimum power cruise speed is $12.1 \mathrm{~ms}^{-1}$ and the minimum cost of transport cruise speed is around $16 \mathrm{~ms}^{-1}$. One of the early blade-element momentum theory models of pigeon flight performance predicts a minimum mechanical power cruise speed of around $8 \mathrm{~ms}^{-1}$, and a minimum cost of transport cruise speed of $16 \mathrm{~ms}^{-1}$ [13]. A more recent application of the vortex wake models [14],[25],[93] that uses measured wing kinematics [89] predicts a minimum power cruise speed for the pigeon of around $12 \mathrm{~ms}^{-1}$, and a minimum cost of transport cruise speed of slightly higher than this [23]. While comparison with other theoretical models does not validate the predicted mechanical power, it does add some credibility to the predictive simulation approach.


Figure 36. Predicted mechanical power consumption for a model of the pigeon at varying cruise speeds.
Despite the similarities in trends in mechanical power between different theoretical models, the present work predicts significantly greater power consumption at all cruise speeds. For example, the minimum mechanical power is predicted to be around 20W (Figure 36a), compared to previously predicted values of less than 10W [13],[23]. The main reason for this relates to differences in the aerodynamic models used. For instance, a vortex model of flight performance used a value of $c_{d_{0}}=0.02$, more than four times lower than the value used here [23]; a previous blade-element model defined $c_{d_{0}}$ as a function of lift coefficient, with a minimum value of 0.01 . However, as mentioned in section 4.2.9 the present model may underpredict aerodynamic loads for given wing kinematics as no twist distribution is included. Section 5.2 .6 will discuss how this factor leads to an overprediction of flapping velocity, which will lead to an overprediction of power consumption.

Another reason for the differences in power prediction is that the present work also includes inertial loads, which tends to increase net mechanical power. This model is somewhat conservative in assuming that no methods of energy storage exist, giving perhaps a pessimistic view of the capability of the wing. These factors suggest that the results presented here may represent an
upper-bound to amount of mechanical power consumed. It is therefore unsurprising that the predicted power exceeds the metabolic power measured for pigeons in wind tunnel tests (plotted in [94], based on experimental studies in [95]).

A final point to consider with regards to energetics is that in the present model power consumption is predicted for a series of distinct kinematic modes, but no indication is given of the energy required to change between these modes. For example, from 5 to $6 \mathrm{~ms}^{-1}$ cruise the minimum power frequency increases from around 8 to 9.5 Hz . This change in kinematics would consume mechanical energy due to the required acceleration of the wing. This phenomenon of consuming energy when transitioning between different kinematic modes is observed in terrestrial locomotion and is likely to occur in flight as well [96].

### 5.2.5. Changes in Kinematics with Varying Cruise Speed

To make quantitative comparisons between simulated and experimental data the predicted wing kinematics are shown in Figure 37 alongside two independent sets of kinematic data for the pigeon recorded during wind tunnels tests [13],[89]. While the mechanical power varies smoothly with changes in cruise speed the predicted kinematics show some abrupt changes. Similar changes were also observed in previous results from the present model [37]. From a numerical perspective, these changes illustrate the presence of local minima in the solution space. A change in cruise speed alters optimisation constraints and also the shape of the basins of attraction in the solution space. This can lead to a flight mode that was previously identified as a local minimum, becoming the global optimum. Alternatively, it can identify a completely new optimum flight mode, that is, a set of kinematic variables that did not satisfy the optimisation constraints at other cruise speeds


Figure 37. Predicted kinematics for a model of the pigeon over a range of cruise speeds shown in comparison to experimental data recorded during wind tunnel tests [13],[89]. Corrections made to experimental data to allow for orientation of the camera [13].

The experimental data presented in Figure 37 show kinematic variables changing in a continuous fashion from around $6-20 \mathrm{~ms}^{-1}$, and one additional recorded flight mode at $0 \mathrm{~ms}^{-1}$. No data is provided in the intermediate range of cruise speeds, so it cannot be concluded whether or not there is a sudden change in kinematics. Real birds may be capable of abruptly changing their wing kinematics with cruise speed, but doing so would require additional energy consumption and might incur some other penalty such as excessive joint torques.

Of all the predicted kinematic variables, the stroke plane shows the closest agreement with the experimental data (Figure 37d). The fact that the two experimental data sets for this variable show some differences may be the result of experimental errors, or may be due to the fact that the pigeons used had slightly different masses and wing geometries.

For all optimised models in the present work, predictions of the stroke plane tend to be the most robust, in that they are largely unaffected by changes in the numerical parameters in the dynamic model, or tolerances in the optimisation scheme. The opposite can be said of the extension amplitude, which has already been shown to be sensitive to the model physical parameters (section 4.3.5) and varies widely between different local minima of similar power consumption (section 5.2.2). This may explain the substantial differences between predicted and measured values of extension amplitude (Figure 37e).

The wingbeat frequency and elevation amplitude are overpredicted for all cruise speeds (Figure 37a,b). As mentioned previously, when examining local minima the frequency and elevation amplitude are in some ways interchangeable as both are used primarily as a means of controlling
the wing flapping velocity. Therefore, the overprediction of these two variables may be more accurately recognised as an overprediction of wing flapping velocity. This will be discussed further in the following sections.

### 5.2.6. Overprediction of Flapping Velocity

Over the range of cruise speeds tested almost all local minima predict a wingbeat frequency that is higher than that measured experimentally. If the frequency is constrained to be equal to that measured experimentally at a given cruise speed, no solutions can be found that satisfy the optimisation constraints. In previous work predictive simulations using a pigeon model the frequency was fixed at the highest frequency that has been recorded experimentally for the pigeon, and the elevation amplitude was again overpredicted; using lower frequencies and elevation amplitudes yielded no valid solutions [37].

When the frequency and elevation amplitude are limited, or more specifically when the flapping velocity is limited to equivalent values measured experimentally, the model generates insufficient net vertical force for weight support. One of the reasons for this may be that the current wing model undepredicts lift for given kinematics. Another reason may be that additional sources of lift generation, such as the body and tail, make a significant contribution to the net lift of the bird. A third possibility is that the real birds may use non-sinusoidal joint trajectories to yield, for example, greater instantaneous flapping velocity during the downstroke for a given wingbeat frequency and elevation amplitude; this may allow more lift to be generated for a lower mean flapping velocity.

Considering underprediction of lift on the wing first, if the average lift generated by the inverse dynamic model is lower than that generated by a real wing for the same kinematics, it follows that the wing lift coefficient is also underpredicted. From a blade-element level, this may imply that the modelled local element lift coefficient, $c_{l}$, underpredicts the local lift coefficients for real avian aerofoils. However, as the lift coefficient variation with angle of attack was derived from several independent experimental studies this is not believed to be the case. It is more likely that the wing lift coefficient is underpredicted because each blade element has a different angle of attack at a given time and the angle of attack varies throughout the wingbeat (section 4.2.9).

Lift generated by the wing may also be underpredicted by the exclusion of rotational lift or of some unsteady aerodynamic mechanisms in the dynamic model. While this study did not aim specifically to test these longstanding hypotheses, it is important to recognise that they do provide possible explanations for the overprediction of flapping velocity. The modular design of the present model means that additional aerodynamic phenomena could readily be incorporated, and proposals regarding the importance of unsteady aerodynamics could be examined. For example, a dynamic
stall model could be included in the blade-element model to test whether it is pertinent to the generation of lift on flapping wings, as suggested elsewhere [77]. While this is somewhat outside the scope of the present work, the current simulation framework does accommodate such an approach.

Having proposed that the overprediction of elevation amplitude and frequency may be due to an underprediction in blade-element lift, or due to the constraint on joint trajectories, these hypotheses will be tested in the following section.

### 5.2.7. Testing Hypotheses on Overprediction of Flapping Velocity

The sensitivity analysis determined that the choice of $c_{l_{45}}$ was one of the most influential parameters on the optimised kinematics. By increasing $c_{l_{45}}$ the lift coefficient magnitudes increase for all angles of attack, resulting in more lift being generated for a given flapping velocity. This simple modification to the blade-element model can be used to investigate whether increasing the lift reduces the flapping velocity.

Optimised kinematics for wings with varying defined values of $c_{l_{45}}$ follow similar trends, but wings with higher lift coefficients are found to use lower flapping velocities. This is seen as a reduction in optimised frequency and elevation amplitude across a range of cruise speeds (Figure 38a,b); in low speed cruise the optimised elevation amplitude again reverts to the upper bound value (section 5.2.1), but the flapping velocity is still reduced by reducing the frequency alone.


Figure 38. Predicted kinematics for a model of the pigeon at varying cruise speeds with varying values of defined maximum section lift coefficient.

An increase in $c_{l_{45}}$ also reduces the mechanical power consumption (Figure 39). The main reason for this is that the increase in $c_{l_{45}}$ causes an effective increase in the wing lift to drag ratio which reduces power consumption from aerodynamic loads. In addition, lower frequency wingbeats have reduced mechanical power consumption from inertial loads.


Figure 39. Predicted mechanical power consumption for a model of the pigeon at varying cruise speeds with varying values of defined maximum section lift coefficient.

It should be stressed that this discussion does not aim to resolve or add to the historical debate over the selection of a suitable lift coefficient for modelling avian flight performance. Rather, it serves as a parsimonious analysis of the effects of increased lift on the predicted flapping velocity in the present model. The results in Figure 38 provide evidence to support the hypothesis that the underprediction of frequency and elevation amplitude is due to the underprediction of lift.

The second proposal to be tested is that using non-sinusoidal joint trajectories may reduce the predicted frequency and elevation amplitude by increasing instantaneous flapping velocity and lift generated on the downstroke. Section 4.3.2 detailed a simple method for varying the ratio of time spent on the downstroke to time spent on the upstroke during a wingbeat. By including the downstroke ratio, $T_{d}$, as a free optimisation variable, the optimised kinematics can again be obtained for a range of cruise speed. However, the inclusion of this additional kinematic variable does not significantly influence the predicted mean flapping velocity. Moreover, the predicted power consumption is only reduced by approximately $2 \%$ around the minimum power cruise speed.

Despite the limited influence that the downstroke ratio has on the predicted flapping velocity and power consumption, it is interesting to note that the predicted ratios capture the trends observed experimentally with changes in cruise speed (Figure 40). Around the minimum power cruise speed the optimised trajectories have a downstroke ratio greater than 0.5 , indicating a rapid upstroke mode. At higher speeds a rapid downstroke mode is used, as the downstroke ratio reduces to less than 0.5 , and continues to reduce with increasing cruise speed.


Figure 40. Predicted downstroke fraction for a model of the pigeon at varying cruise speeds shown in comparison to experimental data.

### 5.2.8. Predicted Extension Amplitude

In hover and low speed flight the optimal wing kinematics always use maximum elevation amplitude and no upstroke retraction (Figure 38f). This mode is representative of the flight of the hummingbird in both hovering and forward flight, though other birds use some degree of wing retraction on the upstroke at all cruise speeds [85]. At the highest cruise speeds tested the solution always tends to a fully-retracted upstroke mode.

To measure the benefits of wing retraction in the present model optimised kinematics were obtained while constraining the extension amplitude to the two extreme cases of complete extension ( $E=1$ ) and complete retraction ( $E=0$ ) during the upstroke (Figure 41). In hover, an extended wing mode uses around $25 \%$ less power than a fully retracted mode. Conversely, in forward flight the fully extended mode uses around $13 \%$ more power at the minimum power cruise, and ever more at high cruise speeds. Around the minimum power cruise speed, optimised solutions with unconstrained wing retraction use a partially retracted mode (Figure 41), but this only offers a small reduction in power consumption of less than $2 \%$ compared to a fully retracted wing mode.


Figure 41. Predicted mechanical power consumption for a model of the pigeon at varying cruise speeds with constrained wing upstroke extension amplitudes; unconstrained extension amplitude solution from Figure 36 is shown for reference.

The convergence of the three sets of data at intermediate cruise speeds provides evidence to support the results in section 5.2.2: around the minimum power cruise speed solutions with widely varying amounts of wing retraction consume similar amounts of power. These results also suggest that there is little advantage of having a wing that partially retracts, though for most birds partial retraction is the predominant mode at all cruise speeds [85].

The benefits of partial retraction may become more apparent if the wing retraction dynamics are modelled more accurately; there may be additional costs or advantages to different amounts of wing retraction that have not been captured in the present model. However, the salient point from these results is that for birds that hover there is a clear advantage in having wings that have evolved to remain fully extended. Similarly, for forward flight retractable wings offer a clear advantage in terms of mechanical energy saving.

### 5.2.9. Variation of Upstroke Function with Cruise Speed

Section 5.1.2 showed that minimum power kinematics use a passive upstroke that generates only a small amount of load, torque and mechanical power compared to the downstroke. When optimising wing kinematics of the pigeon model at fixed cruise speeds this passive upstroke mode is only predicted above a certain threshold speed of around $5 \mathrm{~ms}^{-1}$ (Figure 42). At lower speeds the maximum and mean force, torque and power are significant on both the upstroke and downstroke.

Previous predictive simulations demonstrated that the force coefficient time histories can be loosely grouped into two modes that can also be applied here [37]. In the first mode, which occurs in hover and low speed flight up to $5 \mathrm{~ms}^{-1}$, normal force needed for weight support is generated during both up and downstroke (Figure 42c). In this mode negative axial force is generated on the downstroke, and greater net positive force is generated on the upstroke, which yields a positive axial force to overcome the body drag.


Figure 42. Time histories of axial (a), lateral (b) and normal (c) aerodynamic force coefficients, shoulder torque coefficient (d) and mechanical power coefficient (e). Optimised solutions shown for optimised kinematics for a model of the pigeon at varying cruise speeds.

In the second mode, which occurs at higher cruise speeds, the axial and normal forces are generated predominantly on the downstroke. Negligible load on the downstroke is mostly a consequence of wing retraction, which reduces both aerodynamic and inertial loads.

The present work does not aim to resolve the debate over the function of the avian upstroke, but provides a platform on which the various hypotheses can be tested. However, by examining the force time histories a subtle contribution to this debate can be made. It has been observed that not only lift, but all three orthogonal aerodynamic force components become negligible during the upstroke under certain flight conditions. This suggests that former descriptions of the upstroke as being "passive" or "aerodynamically inactive" are somewhat misrepresentative, as they tend to be based purely on the absence of lift generation [27]. A distinction should therefore be made between whether a wing is aerodynamically inactive in generating insignificant aerodynamic load, or whether it is simply non-lifting.

Previous use of upstroke lift generation as a gait metric is believed to be related to the readiness with which it could be inferred from wake visualisation techniques. However, 3D PIV data can be used to determine force components along all three axes [97]. Therefore, there is potential to construct a more representative means of describing wing aerodynamic function according to instantaneous force rather than instantaneous lift, using existing 3D PIV data from birds.

### 5.3. VARYING SCALE

Chapter 3 discussed how scaling laws have been used to predict the variation in avian kinematics with scale. This section will present an alternative approach for making such predictions, without a
priori knowledge of typical kinematics. The only inputs required are allometric scaling laws that were introduced in section 4.2.2, used to define the wing length, reference area, mass and radius of gyration, and also the body reference area. Scaling effects are not incorporated into the aerodynamic model, but will be discussed in section 5.3.2. The parameters used in optimisation for minimum power and minimum cost of transport cruise are summarised in Table 7.

| Flight condition | Cost function | Optimisation variables | Constraints |
| :---: | :---: | :---: | :---: |
| Minimum power <br> or minimum cost of <br> transport cruise | Mechanical power, $P$ | Frequency,, | $0<f<50 \mathrm{~Hz}$ |
|  | Elest of transport, $\frac{P}{\left\\|\mathbf{V}_{\infty}\right\\|}$ | Elevation amplitude, $\Phi$ | $0<\Phi<75^{\circ}$ |
|  | Pronation amplitude, $\Theta$ | $0<\Theta<90^{\circ}$ |  |
|  | Stroke plane angle, $\gamma$ | $-90^{\circ}<\gamma<0^{\circ}$ |  |
|  | Extension amplitude, $E$ | $0<E<1$ |  |
|  | Cruise speed, $V_{\infty} *$ | $\bar{F}_{x}=D_{0}$ |  |
|  |  | $\bar{F}_{z}=m g$ |  |

Table 7. Optimisation parameters used for simulating minimum power and minimum cost of transport cruising flight of varying scale birds. All constraints are subject to optimisation tolerance of $\pm 10^{-5}$. $*$ Cruise speed is included as a free optimisation variable in sections 5.3.1 and 5.3.2 only.

### 5.3.1. Allometrically Scaled Models of Minimum Power Cruise

Minimum power cruising flight is used as a test condition to conduct a preliminary investigation of the effects of scale on kinematics. Wing kinematics were simulated for allometrically scaled birds of $0.1,0.4$ and 1 kg mass (Table 4). As expected, the mechanical power consumption increases with bird mass. The predicted minimum power cruise speed and minimum cost of transport cruise speed also increase with mass, which correlates to predictions from previous theoretical models, as well as to field study data [55]. The variation in mechanical power with mass will be discussed further in section 5.3.3. With regards to the predicted wing kinematics, the only significant change with bird mass is the predicted wingbeat frequency, $f$, which reduces with increasing mass.

| Mass | Min. Mech. <br> Power <br> $\mathrm{P}(\mathrm{W})$ | Min. Power <br> Cruise Speed <br> $\mathrm{V}_{\infty}\left(\mathrm{ms}^{-1}\right)$ | Frequency <br> $f(\mathrm{~Hz})$. | Elevation Amp. <br> $\Phi($ deg. $)$ | Pronation Amp. <br> $\Theta($ deg. $)$ | Stroke Plane <br> Angle <br> $\gamma($ deg. $)$ | Extension <br> Amp. <br> E |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0.1 | 3.7 | 8.8 | 11.6 | 49.0 | 18.0 | -15.5 | 0.51 |
| 0.4 | 16.8 | 10.3 | 7.7 | 49.3 | 18.1 | -15.5 | 0.48 |
| 1.0 | 46.0 | 11.5 | 5.7 | 51.3 | 18.1 | -15.6 | 0.37 |

Table 8. Predicted mechanical power consumption and kinematics for bird models of different scale. Bird models are allomterically scaled based on their respective masses of $0.1,0.4$ and 1 kg .

To illustrate the changes in kinematics with scale, both the wing and the body movement are visualised over one wingbeat for the three different scale birds in Figure 43. While the resemblance between the visualisations is in part due to the use of a generic wing model, it is also clear that there is some similarity between the kinematics of the three birds. True kinematic similarity cannot be predicted by the current approach, as the bird models are scaled allometrically, not geometrically. However there is still some value in determining whether any form of similarity exists between the predicted kinematics of allometrically scaled models, particularly as this relates to recent proposals made from field study observations [98],[99]. One approach to doing so would be to compare, for example, the wing tip paths of visualisations in Figure 43; kinematic similarity could be proven by showing geometric similarity between wingtip paths. A less cumbersome approach is used in the following section where the numerical values for predicted kinematic variables are compared for different scales, and validated against experimental results from literature.


Figure 43. Spatial variation in wing and body position of birds of different scale shown over a single wingbeat in minimum power cruising flight. Bird models are allomterically scaled based on their respective masses of $0.1,0.4$ and 1 kg.

### 5.3.2. Variation of Kinematics with Scale in Cruising Flight

Previous studies that surveyed the kinematics of birds in cruising flight found that the ratio of wing flapping velocity to cruise speed is similar for different species [98],[99]. This ratio is the inverse of the advance ratio, which was introduced in section 4.2.8. As a non-dimensional quantity, the
advance ratio captures the similarity in kinematics between birds, independent of their scale. In addition to the advance ratio, this section will consider the three kinematic variables from which it is derived: cruise speed, frequency and elevation amplitude.

Literature surveys of kinematic data for birds in cruising flight include mean values from wind tunnel tests, and also from field study observations [98],[99]. Wind tunnel tests have some limitations in that the cruise speed is imposed, rather than self selected. Field study observations are advantageous in this respect, however the motivation behind the self-selected speed may vary, whether it is to minimise power, minimise cost of transport, or meet another criterion. In addition, in field study observations the speed may be varying and as a result the wing kinematics may be transitioning between different modes. The present work will utilise both wind tunnel and field observation data for validation, while considering the limitations mentioned above.

Figure 44 shows the predicted kinematic data for varying scales compared to wind tunnel data. The range of scales was defined so as to capture the range of bird masses that have been measured in wind tunnel tests and field study observations. Of all kinematic parameters measured in the wind tunnel tests, the wingbeat frequency shows the smallest amount of variation with cruise speed (Figure 44b). The predicted and measured wingbeat frequency both show a clear reduction with increasing bird mass. The elevation amplitude is also predicted to reduce with increasing mass, but at a much slower rate.

Cruise speed is predicted to increase with bird mass (Figure 44a). Experimental measurements of cruise speed are also plotted for reference; while the range of speeds used in wind tunnel tests is largely defined by the experimenter, it does give some indication of the speeds that a bird is capable of flying at. However, the spread in the experimental cruise speed data is the main contributor to the spread in advance ratio data in Figure 44d. Simulations predict little variation in advance ratio with changes in bird mass, but wind tunnel data are too scattered to validate this. The advance ratio is underpredicted for all bird masses due to the overprediction of flapping velocity discussed in section 5.2.6. If the present model was adapted to include additional methods of lift generation lower local wind velocities would be needed, and the predicted frequency, elevation amplitude and cruise speed would reduce.

As mentioned previously, the value of $c_{l_{45}}$ is the dominant factor in the aerodynamic model. Section 4.2.5 discussed how this value shows little variation over a range of Reynolds numbers that are representative of flows for typical cruising conditions of birds. For the largest scales tested here the maximum lift coefficient would be expected to increase slightly with increasing Reynolds number [100]. Thus, based on Reynolds number effects, the frequency, elevation amplitude and
cruise speed would all be expected to be lower than the values predicted here for the largest scale birds.


Figure 44. Simulated minimum power and minimum cost of transport kinematics for allometrically scaled bird models compared to kinematic data for different species measured in variable speed wind tunnels test [13],[28],[30],[89],[92],[101],[102]. All $y$-axis scales are shown over two orders of magnitude. Advance ratios are derived for experimental data using allometric scaling of the of the flapping velocity using the equation given in [99]. Note: elevation amplitude (c) was only recorded as an angle for wind tunnel tests of the pigeon.

To focus more on self-selected kinematics, Figure 45 compares predicted kinematics to data obtained predominantly from field study observations [98],[99]. The predicted minimum power and minimum cost of transport cruise speeds capture the trends in experimental data, showing that heavier birds cruise at higher speeds (Figure 45a). As with Figure 44b, the experimental data for frequency again follow a decreasing trend with increasing mass, however the data are now much more scattered (Figure 45b). This illustrates that while frequency shows limited change with cruise speed for one particular species, the interspecies variations at the self-selected cruise speed are much more pronounced. The wingbeat frequency is overpredicted in the majority of cases shown in Figure 45 b when using allometrically scaled models, similar to the results seen for the pigeon model (Figure 36) that was based on species specific geometric and mass parameters.

Elevation amplitude is predicted to decrease slightly with increasing mass (Figure 45c). However, this change is relatively subtle, showing less than a $30 \%$ reduction for a reduction of four orders of magnitude in body mass. Experimental measurements show a steeper reduction in elevation
amplitude, though measurement errors may have been made, such as those that were corrected for in section 5.2.5 (Figure 37). The overprediction of elevation amplitude and frequency can again be explained by the underprediction of lift for given kinematics.


Figure 45. Simulated minimum power and minimum cost of transport kinematics for allometrically scaled bird models compared to kinematic data for different species measured in field study tests and also mean data collected during wind tunnel tests [98],[99].

The key point to draw from this analysis is that the predicted advance ratio shows little variation between birds of different scale. This confirms what has been concluded by other works, which based their analysis on the field data presented here [98],[99]. However, while previous works explained this phenomenon as a method of tuning the vortex shedding frequency, the present work demonstrates the independency of advance ratio with respect to scale without the consideration of such unsteady fluidic phenomena. Even if the added mass and induced velocity effects are removed from the current model, similar trends in advance ratio with scale are found. This means that the similarity in kinematics between birds of different scale can be predicted using a dynamic model that captures only quasi-steady aerodynamic loads and inertial loads.

### 5.3.3. Varying Cruise Speed for Different Scales

In the previous section the concept of kinematic similarity was considered at certain cruise speeds that are deemed to be self-selected to minimise power or cost of transport. In some instances birds may be required to cruise at different speeds, or even hover. To extend the analysis of kinematic variations with scale, this section will examine combined effects of scaling and varying cruise speed; the cruise speed is no longer used as an optimisation variable but is defined explicitly.

Wing kinematics of the three bird models from section 5.3.1 were optimised in hover and cruising flight over a range of speeds. The predicted wing kinematics are shown in Figure 46, compared to their corresponding advance ratios. From hover, an increase in cruise speed increases the advance ratio. The advance ratio increases up to a threshold of around 1 for all scale bird models, at which the wing tip speed at the mid-downstroke is approximately equal to the freestream velocity and the angle of attack is around $45^{\circ}$. This corresponds to the maximum section lift coefficient, highlighting that the wing is required to generate a large amount of aerodynamic load, which is needed to balance the significant body drag.


Figure 46. Predicted wing kinematics at varying advance ratios for models of varying scale.

At a given advance ratio, heavier birds use a lower wingbeat frequency, while the differences in other kinematics parameters is smaller (Figure 46a-e). This is the first evidence to suggest that there may be some similarity in kinematics for birds of different scales away from the minimum power or minimum cost of transport cruise speeds.

The discontinuity in data between advance ratios of around 0.35 corresponds to the abrupt change in elevation amplitude that was seen in the pigeon model in Figure 37; simulating over a finer range of cruise speeds does not remove this discontinuity.

As expected, birds of greater mass were found to consume more mechanical power in cruising flight. However, as heavier birds have more available mechanical power [40], it is more insightful to compare power consumption relative to scale. As mentioned in section 4.2 .8 the power loading, given by the ratio of net aerodynamic force generated to mechanical power consumed, can be used as a measure of efficiency for comparing birds of different scales (Figure 47).

For the range of scales shown in Figure 47a the maximum power loading occurs at similar advance ratios. Over a wider range of scales it can be shown that the advance ratio for maximum power loading actually increases with bird mass, just as the advance ratios for minimum power and minimum cost do (Figure 44, Figure 45). The cruise speed for maximum power loading also increases with mass. This speed may serve as a useful metric for future avian flight performance studies, alongside the minimum power and minimum cost of transport speeds.


Figure 47. (a) Predicted power loading for birds of different scale at varying advance ratios. (b) Predicted maximum power loading for birds of different scale shown for respective wing loading.

The maximum power loading reduces as the bird mass increases. The reason for this is that with increasing scale, power consumption due to aerodynamic loads increases more quickly than mass (first noted in [103]). This is due to the fact that heavier birds have greater wing loading, so to maintain sufficient aerodynamic load for weight support and thrust they are subject to greater local wind velocities. This is achieved through travelling at a higher cruise speed with a higher wing flapping velocity, which increases the mechanical power consumption and causes the reduction in power loading seen in Figure 47b.

### 5.4. ACCELERATING FLIGHT

Until now, kinematics have only been predicted for cruising flight conditions, where the net aerodynamic and gravitational forces are in equilibrium. This approach is somewhat restricted, in that it only captures wing kinematics that might be observed during wind tunnel tests, or in some specific cases of non-accelerating free flight such as migration. To extend the model to non-
cruising flight conditions a first step is to analyse the effects of acceleration and deceleration in horizontal flight. The optimisation parameters to be used in this section are shown in Table 9.

| Flight condition | Cost function | Optimisation variables |
| :---: | :---: | :---: |
| Horizontal acceleration | Mechanical power, $P$ | Frequency,, |
|  | Elevation amplitude, $\Phi$ | $0<f<50 \mathrm{~Hz}$ |
|  | Pronation amplitude, $\Theta$ | $0<\Phi<75^{\circ}$ |
|  | Stroke plane angle, $\gamma$ | $0<\Theta<90^{\circ}$ |
|  | Extension amplitude, $E$ | $-90^{\circ}<\gamma<0^{\circ}$ |
|  |  | $0<E<1$ |
|  | $\bar{F}_{x}=D_{0}+m a_{x}$ |  |
|  | $\bar{F}_{z}=m g$ |  |

Table 9. Optimisation parameters used for simulating minimum power accelerating flight. All constraints are subject to optimisation tolerance of $\pm 10^{-5}$.

### 5.4.1. Simulating Wing Kinematics During Acceleration

A typical range of acceleration values for birds at a given flight speed can be determined from previous experiments. For the pigeon, acceleration values ranging from around -0.5 g to +0.5 g have been observed at speeds of around $14 \mathrm{~ms}^{-1}$ [89].

Simulated wing kinematics of the pigeon model show an increase in stroke plane angle with increasing acceleration at constant speed (Figure 48). Increasing the stroke plane generates greater axial force needed for acceleration by vectoring the aerodynamic force on the wings. This process also reduces weight support, and so it is used in conjunction with an increase in upstroke retraction to counteract this.

Interestingly, with an acceleration of -0.5 g (Figure 48a) the model predicts a non-flapping kinematic mode, which uses stroke plane inclination and a fixed elevation angle to generate a constant negative aerodynamic force. This could be regarded as a braking mode of flight when used at high speed. It is also representative of gliding flight, though is not at the optimum lift to drag ratio. It should be noted that in wind tunnel tests at similar flight conditions the pigeon did maintain a flapping wing mode along with an inclined stroke plane, similar to that predicted to occur at 0.25 g (Figure 48 b ). It is likely that for real birds a non-flapping flight mode would still consume mechanical energy through isometric contraction of muscles. Inclusion of this process within the present model may provide better insight into the most energy efficient methods of decelerating. As mentioned in section 4.2.1 the tail is also likely to be used for increasing aerodynamic load for braking.

b. Acceleration $=-0.25 \mathrm{~g}$ (side view along $y_{0}$ )

c. Acceleration $=0\left(\right.$ side view along $\left.y_{0}\right)$

d. Acceleration $=0.25 \mathrm{~g}$ (side view along $y_{0}$ )

e. Acceleration $=0.5 \mathrm{~g}$ (side view along $y_{0}$ )


Figure 48. Optimised wingbeat kinematics for minimum power flight of the pigeon model at $12 \mathrm{~ms}^{-1}$ with varying degrees of acceleration.

Simulation of acceleration in low speed flight provides insight into the physics of takeoff and landing. Figure 49 shows the predicted kinematics for the same range of accelerations used in Figure 48 , but at a lower speed of $4 \mathrm{~ms}^{-1}$. As with the high speed case an increase in acceleration at low speeds is also characterised by an increase in stroke plane angle. In contrast to the high speed results, wing retraction at low speed is favoured for deceleration, but not for acceleration. For deceleration a large negative stroke plane angle is used to increase drag on the downstroke and provide negative axial force. An extended wing upstroke would generate drag in the opposite direction, having the adverse effect of reducing the net axial force, and so a retracted wing upstroke is used for deceleration.
a. Acceleration $=-0.5 \mathrm{~g}$ (side view along $y_{0}$ )




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b. Acceleration $=-0.25 \mathrm{~g}$ (side view along $\left.y_{0}\right)$

c. Acceleration $=0\left(\right.$ side view along $\left.y_{0}\right)$

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d. Acceleration $=0.25 \mathrm{~g}$ (side view along $y_{0}$ )

e. Acceleration $=0.5 \mathrm{~g}$ (side view along $y_{0}$ )


Figure 49. Optimised wingbeat kinematics for minimum power flight of the pigeon model at $4 \mathrm{~ms}^{-1}$ with varying degrees of acceleration.

### 5.4.2. Accelerating Flight for a Range of Speeds

The above analysis can be extended by simulating a range of plausible speeds and accelerations for the pigeon model. In accelerating flight the U-shaped power curve is seen to flatten, and above acceleration values of around 0.3 g the lowest power solution is at a speed of $0 \mathrm{~ms}^{-1}$, i.e acceleration from rest (Figure 510). Unsurprisingly, at most speeds an increase in acceleration leads to an increase in mechanical power consumption. At speeds of less than around $1 \mathrm{~ms}^{-1}$, deceleration is predicted to require more power than acceleration. The reason for this is that at low speeds the stroke plane inclination reaches the defined lower bound of $-90^{\circ}$ (Figure 51d), but a lower power mode can be found if this bound is reduced further. The bound used here was defined to provide numerical stability and limit the solutions to those deemed physically plausible. It is conceivable that a stroke plane less than $-90^{\circ}$ may be an optimal solution, but it is more likely that the tail may be used to increase drag, and that the body drag coefficient would increase due to being at a high
angle of attack (section 4.2.2). Alternative wing kinematics may also be employed for heavy deceleration, that are not captured with the current wingbeat parameterisation.


Figure 50. Predicted mechanical power consumption for a model of the pigeon at varying speeds with varying degrees of acceleration.

At higher speeds acceleration of -0.5 g is achieved using no mechanical power through non-flapping modes, where the frequency reduces to 0 (Figure 51a). With increasing speed the non-flapping mode reduces the wing elevation angle (equal to the elevation amplitude in Figure 51b), and increases stroke plane angle. Due to the mathematical implementation of the pronation time history, the pronation angle is zero for any non-flapping modes. The wing extension is also fixed for a non flapping mode, and is given as the extension amplitude in Figure 51e. This variation in kinematics for non-flapping modes is used in order to provide the necessary axial and normal loads, but the minimisation of power no longer serves an optimisation goal as no mechanical power is consumed in these modes. No alternative non-flapping modes were identified that satisfied the optimisation constraints.


Figure 51. Predicted kinematics at varying speeds for a model of the pigeon, with varying degrees of accceleration.

As the mechanical power consumption increases with acceleration, it is reasonable to expect a highly manoeuvrable bird to have greater instantaneous power availability than a less agile bird of equivalent scale. In addition, large acceleration tends to involve high wing flapping velocities for a given speed, so more manoeuvrable birds are likely to be able to fly at lower advance ratios. For real birds there will be limitations to both wingbeat frequency and mechanical power, largely governed by limitations on flight muscles [104].

A more general finding from the results in this section is that over a plausible range of acceleration, the pigeon model exhibits distinctive changes in kinematics that could potentially be observed without requiring measurement apparatus. This suggests that in field study observations wing kinematics may serve as useful visual cues for identifying whether a bird is accelerating, decelerating or cruising.

### 5.5. CLIMBING \& DESCENDING FLIGHT

Climbing and descending can be used to achieve several different goals in flight, including avoiding obstacles, reaching a perch, and changing altitude during migration. This section predicts generic climbing and descending at a constant speed that captures the fundamental changes in kinematics associated with non-horizontal flight. Section 5.5 .1 will simulate climb and descent over a wide range of angles that have been observed in recent experimental studies [105]. Section 5.5.2 will consider the special case of climb and descent at small angles with varying speeds that was introduced in section 4.2.2. Where only climbing is considered in section 5.2.2, the term "climb angle" ( $=-\beta$ ) will be used for clarity.

For comparison with previous sections of the current work and with recent experimental data, climbing and descending is considered here for the pigeon model only, but can be equally well tested with any scale bird model. The optimisation parameters used in simulating climbing and descending flight are shown in Table 10.

| Flight condition <br> Climbing flight at <br> constant speed Mechanical power, $P$ | Optimisation variables | Constraints |
| :---: | :---: | :---: |
|  | Frequency, $f$ | $0<f<50 \mathrm{~Hz}$ |
|  | Elevation amplitude, $\Phi$ | $0<\Phi<75^{\circ}$ |
|  | Pronation amplitude, $\Theta$ | $0<\Theta<90^{\circ}$ |
|  | Stroke plane angle, $\gamma$ | $-180^{\circ}<\gamma<0^{\circ}$ |
|  | Extension amplitude, $E$ | $0<E<1$ |
|  |  | $\bar{F}_{x}=D_{0}-m g \sin \beta$ |
|  | $\bar{F}_{z}=m g \cos \beta$ |  |

Table 10. Optimisation parameters used for simulating minimum power climbing and descending flight. All constraints are subject to optimisation tolerance of $\pm 10^{-5}$.

### 5.5.1. Varying Climb Angle

The range of angles at which a bird can climb and descend is likely to depend on the availability of mechanical power, and the maximum aerodynamic load that a particular species can generate. Recent experiments recorded pigeons using flight paths inclined from $-60^{\circ}$ to $60^{\circ}$ with respect to the horizontal [105]. In an attempt to model this behaviour, optimised solutions were obtained for constant speed flight over the same range of angles. It is recognised that in the experiments birds tended to change speed during flight, but to isolate the effects of descent angle from those of acceleration (modelled in section 5.4) a constant speed will be used for simulation. It should be noted, however, that the current model is capable of capturing combined effects of descending/climbing and accelerating/decelerating (equations [5] and [6]).

For flight at $4 \mathrm{~ms}^{-1}$ the optimised wing kinematics predict little change in elevation and pronation amplitude with varying descent angle (Figure 52). Furthermore, for all climb angles the wing is fully outstretched. Similar kinematics are observed over a range of speeds from $0-6 \mathrm{~ms}^{-1}$, which will be considered in more detail in the following section.


Figure 52. Optimised wingbeat kinematics for minimum power flight of the pigeon model at $4 \mathrm{~ms}^{-1}$ with varying angles of descent.

An interesting point from Figure 52 is that the stroke plane orientation with respect to the Earth axes does not appear to change significantly with changes in descent angle. The same result was also seen for lower speeds. The reason for this is that when the speed is low the gravitational force is much greater than the body drag, so a large component of the aerodynamic force vector must be oriented vertically for weight support, regardless of the climb angle. As the main local wind velocity component is the wing flapping velocity, to vector the lift vertically the stroke plane remains orientated close to the horizontal plane.

Experimental studies of birds in climbing and descending flight measured the stroke plane angle for various climb angles [105]. Both simulated and experimental data show that at steep angles of climb and descent the stroke plane becomes more inclined with respect to gravity (Figure 53a). For steep angles the body drag vector is aligned more closely with the gravity vector than in horizontal flight (Figure 53b). This means that the mean aerodynamic force from the wing, $\mathbf{F}_{\mathbf{0}}$, must be inclined closer to the vertical in steep climb and descent, which is achieved through rotating the stroke plane closer to the horizontal plane.


Figure 53. (a) Predicted stroke plane angle with respect to gravity for a model of the pigeon at $4 \mathrm{~ms}^{-1}$ speed with varying angles of descent. (b) Illustration of how the mean aerodynamic force vector on the wings, $\mathbf{F}_{\mathbf{0}}$, has a greater vertical component when climbing or descending than in horizontal flight.

### 5.5.2. Varying Speed \& Climb Angle

As mentioned in the previous section, experimental studies have revealed that birds change their speed while climbing in free-flight [105]. To better understand this behaviour, this section will consider the coupled effects of varying speed and climb angle. As mentioned in section 4.2.2 climbing and descending at shallow angles is equivalent to accelerating and decelerating in horizontal flight. This is reflected by the similarity in the kinematics predicted for $+/-15^{\circ}$ descent (Figure 54) and those predicted for acceleration at $-/+0.25 \mathrm{~g}$ (Figure 51). For example, at a given speed both climb and acceleration are predicted to use greater wingbeat frequency and elevation
amplitude than in horizontal cruise. This is done in order to increase aerodynamic force by increasing the wing flapping velocity.


Figure 54. Predicted kinematics at varying speeds for a model of the pigeon with varying degrees of descent.

Unsurprisingly, more mechanical power is required in climbing flight than in horizontal flight at the same speed, and less is required in descending flight (Figure 55). Interestingly, for descent angles less than $-15^{\circ}$ (i.e. climb angles greater than $15^{\circ}$ ) the power required to fly at any speed is greater than the power required to hover. This highlights that climb data could potentially be used to predict which birds have sufficient power to hover, based on observations of their maximum climb angles achieved during experiments.


Figure 55. Predicted mechanical power consumption for a model of the pigeon at varying speeds with varying angles of descent.

The minimum power speed reduces as the descent angle reduces. Therefore, to climb with the minumum power, birds would be expected to climb at speeds less than their the minimum power speed for horizontal flight. However, a more suitable metric for assessing climbing performance is the amount of energy used to climb to a given altitude, essentially the cost of vertical transport. By
simulating climbing flight over a broader range of climb angles, and with varying speed, the climb angle can be predicted that gives minimum cost of vertical transport.

Figure 56a shows the power variation for different climb angles, compared to the vertical climb velocity. The minimum cost of vertical transport for a given climb angle is given as the shallowest tangent to the curve for that climb angle that passes through the origin. This minimum cost reduces with increasing climb angle. Therefore, to obtain the lowest possible cost of vertical transport, a climb angle of $90^{\circ}$ (vertical climb) should be used, and a speed of approximately $13 \mathrm{~ms}^{-1}$. It may seem counterintuitive that vertical climbing should save energy for a required increase in altitude. As mentioned previously, vertical climb requires extra mechanical power as drag and weight vectors align, meaning that greater net aerodynamic force must be generated by the wing. This highlights one performance limitation, in that to climb vertically a stronger wing structure would be required to withstand these loads. However the main point to note is that even though this mode uses less energy for a given change of altitude, it also requires more mechanical power. Therefore, the ability to save energy by climbing vertically would also be limited by the maximum continuous mechanical power availability (which is limited by maximum rate of oxygen absorption [104]).

As exact details of mechanical power availability for real birds are not available, a range of available mechanical power can be used to assess changes in climbing flight performance. Figure 56b-d illustrates the optimum climb conditions based on minimising the cost of vertical transport subject to the defined limits on mechanical power. With an increase in mechanical power availability the minimum cost of vertical transport reduces, but this occurs at a diminishing rate (Figure 56b). The optimum climb angle increases with greater mechanical power availability (Figure 56c), while the optimum speeds reduces (Figure 56d).


Figure 56. (a) Predicted mechanical power consumption with varying vertical speed for varying angles of climb (- $\beta$ ). (b) Minimum cost of vertical transport, for varying amounts of available mechanical power. (c) Optimum climb angle and (d) optimum climb speed that yield lowest cost of vertical transport for varying amounts of available mechanical power. (b)-(d) obtained from linear interpolation of data presented in (a).

The main implication of the results in this section is that climbing performance and optimal kinematics are strongly influenced by the availability of mechanical power. It is important to stress that the amount of mechanical power available for short bursts would be expected to be larger than the amount required for sustained periods. For this reason, for short bursts of climbing flight birds are more likely to fly vertically to reduce energy consumption than in longer commutes, such as climbing to high altitude for migration. It should also be considered that to achieve the defined optimal climbing flight conditions the availability of additional mechanical power and the generation of greater aerodynamic loads could be expected to incur some penalty, such as additional mass for structural support and flight muscle.

### 5.6. WAKE VISUALISATION

The wake simulation method was designed to serve as a standalone module that functions with any arbitrary set of wing dynamics, whether they are optimised for a particular flight condition or defined explicitly. This section of the work will visualise the wakes both from optimised solutions for horizontal cruise of the pigeon model, and also for the defined case of gliding flight.

### 5.6.1. Visualising Wake Geometries

The wake simulated for the optimised minimum power cruising flight mode of the pigeon is shown in Figure 57. The Lagrangian markers used in the wake simulation track the overall undulating motion from the flapping wings. The wake downwash effect can also be seen, particularly by comparing markers released at the bottom of successive downstrokes, which increase in displacement in the $-z_{0}$ direction as they advect downstream (Figure 57a). The regions where the vortex filaments converge laterally show where the wings retract during the upstroke (Figure 57b).
a. Simulated wake (side view along $y_{0}$ )

b. Simulated wake (top view along $-z_{0}$ )


Figure 57. Lagrangian markers for simulated wake of the pigeon model over three wingbeats. Wingbeat kinematics and circulation distribution determined from optimised solutions for minimum power cruising flight ( $12 \mathrm{~ms}^{-1}$ ).

The wake surface depicts more clearly the 3D structure of the wake (Figure 58a,c,e,g). Around the inboard section of the wing the wake surface remains relatively planar, while at the outboard section the surface edges rollup, particularly at the mid-downstroke. When viewed from in the $+x_{0}$ direction the left sheet rolls clockwise while the right sheet rolls anticlockwise (Figure 58g). This rolling motion is a result of the mutually induced velocity between vortex points, which is greatest in the outboard wing wake where the vortex strengths are highest.

The streamlines for minimum power cruising flight of the pigeon model show not only the rolling of the wake near the wingtips, but also slight rotation of the opposite sense in the inboard section of the wake (Figure 58b,d,f,h). This arises as the lift decreases towards the wing root due to the reduction in wing flapping velocity. Subsequently, the strengths of vortex points released from the most inboard control points tend to have the opposite sign to those released from the outboard points on the same wing. This modelled process is representative of the underlying physics of wake, and there is some evidence to suggest that for real birds vorticity in the inboard region is of opposite sign to that in the outboard region [106],[31]. However, it should also be noted that in the
inboard region the wake geometry will be influenced by the body and tail, which is not captured in the present work.

The wake simulated at $5 \mathrm{~ms}^{-1}$ cruising flight using the optimised kinematics is much more complex (Figure 59). Advection of vortex points is slow with respect to the flapping velocity. This causes some regions of the wake shed during the downstroke to intersect with regions shed during the upstroke. As a result there are many instances where vortex points come into close proximity, leading to an overprediction of induced velocity and subsequent numerical instability. Therefore, wake simulation in low advance ratio flight is less robust than in minimum power cruising flight, and is more sensitive to the choice of viscous vortex core model. For cruise at $16 \mathrm{~ms}^{-1}$ speeds (Figure 60) the wake geometry is similar to that predicted for minimum power cruise (Figure 58). More rapid spiralling of the streamlines is seen at $16 \mathrm{~ms}^{-1}$ than at $12 \mathrm{~ms}^{-1}$ as the strengths of the vortex points are greater, particularly for those shed from the wingtips.


Figure 58. Wake surfaces ( $\mathrm{a}, \mathrm{c}, \mathrm{e}, \mathrm{g}$ ) and streamlines ( $\mathrm{b}, \mathrm{d}, \mathrm{f}, \mathrm{h}$ ) for simulated pigeon model. Wingbeat kinematics and circulation distribution determined from optimised solutions for minimum power cruising flight ( $12 \mathrm{~ms}^{-1}$ ).


Figure 59. Wake surfaces (a,c,e,g) and streamlines (b,d,f,h) for simulated pigeon model. Wingbeat kinematics and circulation distribution determined from optimised solutions at $5 \mathrm{~ms}^{-1}$ cruise.


Figure 60. Wake surfaces (a,ce,, g ) and streamlines (b,d,f,h) for simulated pigeon model. Wingbeat kinematics and circulation distribution determined from optimised solutions at $16 \mathrm{~ms}^{-1}$ cruise.

### 5.6.2. Velocity \& Vorticity Field Data

Whether plotted as Lagrangian markers, wake surfaces or streamlines the simulated vortex points capture and portray some of the fundamental aspects of the wake physics. However, commonly used experimental methods used in avian flight analysis resolve the velocity and vorticity fields throughout the wake region and for some distance upstream of the bird. It therefore follows that the current wake simulation method could better complement existing experimental techniques by reconstructing the wake velocity and vorticity fields.

The simulated wake for a fixed (non-flapping) wing is the simplest test case that can be used to validate the reconstruction of the flowfield. This kinematic mode is representative of gliding flight and has been analysed extensively for birds using fixed wing theories of aerodynamics (e.g. [12]), as well as using experimental studies (e.g. [107],[108]). Two non-flapping cases are defined here, with the wing orientation fixed to yield the best lift to drag ratio (Figure 61a,b), and also the maximum lift coefficient (Figure 61c,d). In this mode the velocity field depicts two circulating regions of flow, each centred downstream of a wingtip (Figure 61a,c). The viscous vortex core model reduces the induced velocity towards the centre of these circulating regions. These regions correspond to the regions of high vorticity in Figure 61b,d. As expected, simulations at the maximum lift coefficient yield greater velocity and vorticity magnitudes than at the maximum lift to drag ratio, as the increased lift distribution leads to greater vortex point strengths

With constant freestream wind velocity and wing orientation the lift predicted by the aerodynamic model tends to decrease from the inboard to outboard blade elements. This is because the chord length and element areas reduce towards the wing tips. For a single gliding wing based on the pigeon wing geometry the maximum blade element circulation actually occurs at the most inboard section. Most of the vorticity in the downstream wake of the inboard sections is cancelled by that of the opposite wing. However, vortex points shed from inboard elements still induce a large vertical component of velocity, which contributes to the downwash along the bird line of symmetry (Figure $61 \mathrm{a}, \mathrm{c})$. It should be noted that for a real wing the lift distribution decreases towards the wingtips even if the chord length is constant due to tip loss effects, but this is not captured by the present model. However, this effect is only apparent in non-flapping wing modes, because in powered flight the induced velocity is much smaller than the wing flapping velocity.


Figure 61. Velocity ( $\mathrm{a}, \mathrm{c}$ ) and vorticity ( $\mathrm{b}, \mathrm{d}$ ) field data for the pigeon model in the $y_{0}-z_{0}$ plane (perpendicular to the freestream wind direction), viewed from in front of the bird in the $-x_{0}$ direction. Field data was reconstructed from wakes simulated using circulation distribution from non-flapping modes defined to yield $c_{l}=0.6(\mathrm{a}, \mathrm{b})$ and $c_{l}=1.6$ ( $\mathrm{c}, \mathrm{d}$ ). Note that the vorticity contours fluctuate slightly due to numerical interpolation of velocity field data.

Experimental data taken from gliding studies of real birds also shows the rolling up of wingtip vortices [107],[108]. While quantitative data such as the induced velocity magnitudes is clearly species specific, all experimental studies capture similar qualitative results, including the influence of the body and tail on the wake downstream of the inboard wing region. The aerodynamics of a specific body and tail geometry could be accounted for using a panel method [39]. However, this goes beyond the scope of the present work that aims to capture the fundamental wake geometry, which is largely governed by the wake shed from the wings.

To extend this analysis to flapping-wing modes a stiff-wing mode like that presented in section 5.1.1 is a useful test case as it removes the uncertainty with modelling retracting wing wakes that will be discussed further in the following section. The wake simulated from the stiff-wing mode is found to be numerically stable for all cruise speeds, including the characteristic minimum power
cruise speed of $12 \mathrm{~ms}^{-1}$. At this speed the velocity field at the mid-downstroke shows some resemblance to that of the previous gliding flight mode, with two pronounced circulating flow regions near the wing tips (Figure 62a).

At the mid-upstroke the stiff-wing wake still shows similar recirculating regions to those at the mid-downstroke, despite the fact that the instantaneous lift on the wing is negative. The reason for this is that the velocity field reconstruction calculates the induced velocity from all shed point vortices, and therefore captures some history of the wake. In this particular case the high strengths of vortex points released during the downstroke still dominate the induced velocity field at the midupstroke. This can also be seen in the vorticity field contours which are greatest close to the wingtips, but also appear to be somewhat stretched along the wing path due to the influence of point vortices shed earlier in the wingbeat.


Figure 62. Velocity ( $\mathrm{a}, \mathrm{c}$ ) and vorticity ( $\mathrm{b}, \mathrm{d}$ ) field data for the pigeon model in the $y_{0}-z_{0}$ plane (perpendicular to the freestream wind direction), viewed from in front of the bird in the $-x_{0}$ direction. Field data reconstructed from wakes simulated using kinematics and circulation distribution from optimised solutions for the stiff-wing mode (section 5.1.1). Note that the vorticity contours fluctuate slightly due to numerical interpolation of velocity field data.

The velocity induced by vortex points was overpredicted when the wings retracted. This effect was not sufficient enough to influence the overall wake geometries portrayed in section 5.6.1, but did lead to some anomalies in the reconstructed wake field data during the upstroke (Figure 63c,d). As the wing retracts the release locations of the vortex points are forced into close proximity. Even with a viscous vortex core model, when all vortex points are released in a small region the cumulative effect is the overprediction of induced velocity.


Figure 63. Velocity ( $\mathrm{a}, \mathrm{c}$ ) and vorticity ( $\mathrm{b}, \mathrm{d}$ ) field data for the pigeon model in the $y_{0}-z_{0}$ plane (perpendicular to the freestream wind direction), viewed from in front of the bird in the $-x_{0}$ direction. Field data was reconstructed from wakes simulated using kinematics and circulation distribution from optimised solutions for minmum power cruising flight. Note that the vorticity contours fluctuate slightly due to numerical interpolation of velocity field data.

The strengths of the vortex points released during the mid-upstroke are much smaller than those released throughout the downstroke. This means that the overpredicted induced velocity at the midupstroke does not to influence the results at other phases of the wingbeat; the predicted velocity and vorticity fields during the mid-downstroke are still plausible (Figure 63a-b), with similar magnitudes to those seen in the stiff-wing mode (Figure 62a-b). Therefore, the method can be regarded as being robust, whereby anomalous predictions of induced velocity tend not to propagate
to other phases. However, a more conservative approach would be to only apply this method in a piecewise fashion, whereby point vortices are only released when the wing is full extended.

## Chapter 6. Conclusions

This chapter summarises the major findings from the present work and discusses the main implications of the results. For clarity the conclusions are presented as a series of statements, each with a discussion to highlight the supporting evidence:

## Not all unsteady aerodynamic mechanisms are fundamental to the generation of aerodynamic loads in biological flapping wing flight.

Chapter 4 demonstrated that the added mass contribution to aerodynamic loads was small in comparison to the quasi-steady aerodynamic loads. Therefore, the commonly cited argument that unsteady aerodynamics are fundamental for modelling avian flight should be revised to include the specific mechanisms that generate significant aerodynamic force when compared to quasi-steady aerodynamic force.

Input values of wing geometric data are more important than maximum aerodynamic force coefficients for making accurate predictions of aerodynamic force and mechanical power consumption in forward flight.

In the present work aerodynamic loads are proportional to the square of the local wind velocity magnitude. For given joint kinematics longer wings have greater wing flapping velocity, which augments local wind velocity, aerodynamic force, and mechanical power in forward flight. However, aerodynamic loads only vary linearly with maximum aerodynamic force coefficients. As a result, the predicted aerodynamic loads were shown to be more sensitive to the input wing length than the maximum lift and drag coefficients.

Historically, quasi-steady aerodynamic models have placed strong emphasis on defining values for peak aerodynamic force coefficients. However the implication of this work is that even though the wing length can be determined using low order techniques, the accuracy of measurements is more important than that of measurements of wing aerodynamic data. While some previous attempts have been made to lay out formal procedures for measuring wing geometry [3], experimental errors in such measurements are rarely published. Furthermore, statistical variation in wing length for a given species is not taken into consideration in theoretical models of avian flight.

## Assessment of extant species' wing kinematics has limited use in predicting potential flight capabilities of extinct species, because a wide variety of alternative wing kinematics can be used in flight.

Optimisation of the dynamic model identified numerous local minima, especially around the minimum power and minimum cost of transport cruise speeds. For example, while minimum power solutions tend to use partial upstroke wing retraction, other fully extended wing modes also exist. These modes consume more mechanical power, but satisfy the constraints of generating aerodynamic force that balances the required thrust and weight support. They therefore represent alternative wingbeat kinematics that can be used to achieve the same fundamental goals in cruising flight.

Comparing the kinematics used by modern birds with the apparent kinematic function of fossilised wings only provides insight into whether these species had similar kinematics. However, it does not indicate whether extinct species could have achieved flight using alternative kinematics, such as the fully-extended wing modes identified in this work.

## Wing retraction serves as an energy saving mechanism in forward flight.

It is commonly cited that wing retraction reduces exposed wing surface area, which in turn reduces aerodynamic loads for given local wind velocity. This process can be regarded as a means of creating disparity in force generation between the upstroke and downstroke in order to provide a net aerodynamic force for weight support [109]. However, some birds can maintain forward flight with virtually no wing retraction [85].

The simulations presented here showed that at low advance ratios an extended wing upstroke requires less mechanical power than a retracted wing upstroke; at high advance ratios the converse case is true. Therefore, wing retraction is more accurately recognised as a method of saving energy in high advance ratio flight than as a means of providing weight support. This is achieved by reducing both aerodynamic and inertial loads during the upstroke.

It is likely that bird wing retraction mechanisms have evolved to suit their most common flight style. As a result, birds that usually cruise will always utilise a wing retraction mechanism, while those that usually hover will use an extended upstroke at all cruise speeds.

In forward flight intermediate values of wing elevation amplitude are used as a compromise between reducing inertial loads and disk loading, and vectoring aerodynamic force for weight support.

In hover the wing elevation amplitude is maximised to reduce inertial loads and reduce disk loading. While this goal is also present in forward flight, reducing elevation amplitude can assist in providing weight support. This is achieved by using smaller elevation amplitudes to vector a greater a component of lift from the lateral to the vertical direction. Therefore, optimal solutions in forward flight use intermediate values of wing elevation to balance these two opposing constraints.

Analyses of wing aerodynamic function should incorporate axial, normal, and lateral aerodynamic force components over each half-stroke.

Previous experimental studies have described the upstroke as being "passive" or "aerodynamically inactive" due to the absence of lift. In the present work, time histories of aerodynamic force coefficients revealed that axial, normal and lateral force components on a single wing during the upstroke all became negligible under certain flight conditions. As lift and drag both contribute to these three force components, the analysis of lift alone is not representative of the aerodynamic force on the wing. A more accurate description of the upstroke aerodynamic function should be based on instantaneous aerodynamic force, rather than instantaneous lift.

Birds of all scales cruise at similar advance ratios, which can be modelled by quasi-steady aerodynamic and inertial loads alone.

In minimum power and minimum cost of transport cruise, optimisation results for allometrically scaled birds models showed similar ratios of cruise speed to maximum wing tip speed. As the models were not scaled geometrically, this result does not confirm exact kinematic similarity. However, it does support observations made from field study data on the constancy of wing tip speed to cruise speed ratio. While these observations had previously been explained by a desire to maintain a fixed Strouhal number, this work predicts this phenomenon without considering unsteady aerodynamic effects.

Wing kinematics predicted using the current method serve as an accurate visual cue for determining whether birds are accelerating or cruising during field study observations.

At a given cruise speed pronounced changes in wing kinematics were predicted for acceleration magnitudes equal to those observed experimentally. While changes were observed in all kinematic parameters, variations in wingbeat frequency and amplitude would arguably be the easiest to recognise by simple observation of real birds, without requiring any experimental apparatus. For
this reason, acceleration can be readily distinguished from cruising flight during field study observations.

## To reach a given altitude vertical climbing flight uses the least amount of mechanical energy, but the maximum climb angle is limited by the availability of mechanical power.

The minimum cost of vertical transport reduces with increasing climb angle. Therefore, to reduce energy consumption in climb, birds would be expected to always climb as steeply as possible. However, flight at steeper climb angles also incurs greater mechanical power consumption. Therefore, the climb angle selected by a particular bird will reflect biomechanical limitations on the available mechanical power.

If a bird is capable of generating greater mechanical power for short periods than for sustained flight, it is likely that it will use a steep climb angle for short commutes and a shallower angle when climbing to fly at high altitude.

The vortex point method with a viscous vortex core model is a robust and versatile tool for visualising wake geometries for extended-wing flapping and gliding flight.

For wake simulations in cruising flight the vortex point model was found to be numerically convergent when increasing the number of solution timesteps, number of vortex points per wing, and vortex point release rate. Induced velocities for vortex points in close proximity were overpredicted in some instances where no dissipative effects were modelled, and so a viscous vortex core model was found to be necessary for numerical stability.

Predictions of wake geometries capture key features that have been observed experimentally for fixed and flapping wings, such as vortex rollup downstream of the wingtips. The model overpredicts induced velocity when vortex points are released from a retracted wing and should only be applied to extended wing phases of an avian wingbeat.

## Chapter 7. Future Work

The simulation framework presented was designed to be used alongside existing theoretical and experimental studies of avian flight performance. This chapter identifies three logical extensions to the framework that would broaden the model capabilities in-line with other current areas of research interest:

## Predict wingbeat kinematics of other flapping-wing animals.

Wing kinematics were predicted for birds with different wing geometries. This provides scope for using wing geometric data from fossil records to simulate extinct species, such as Archaeopteryx, to complement studies on flight evolution (e.g. [1],[2]). Furthermore, the modelled wing geometry and degrees of freedom could be adapted using biomechanics literature to simulate other animals, including insects, bats and pterosaurs.

## Investigate flight stability and control using a fully dynamic bird model.

In the present work the dynamic model defines the acceleration of the bird based on the mean aerodynamic forces generated during a wingbeat. A fully dynamic model could be formulated where the acceleration is calculated from instantaneous forces and torques. This would provide a tool for investigating avian flight stability and control. The key value of this would be to extend previous theoretical studies of animal flight dynamics in cruise [18],[59] to other conditions, such as take-off and landing, which have been the subject of recent experimental investigations [110].

## Optimise model physical parameters.

Variables used to describe the physical properties of the bird in the inverse dynamic model could also be included as free optimisation variables. This would provide a means of identifying optimal 'designs' of birds for given flight conditions. For example, the optimal wing scale could be determined that minimises power consumption for a bird of predefined body mass. This would be similar to previous approaches used in optimising the design of flapping air vehicles [50],[51]. However, rather than serving as a design tool this approach would provide insight into why the process of evolution favours certain relationships between physical parameters in successive generations of birds.

## APPENDIX

Axial flight is defined as when the wing flapping velocity vector is perpendicular to the freestream velocity vector. For a 3D wing model the wing flapping velocity magnitude varies along the wing length (Figure 64a). Neglecting the induced velocity, the local wind velocity is given as the vector sum of the freestream and wing flapping velocity (Figure 64b).


Figure 64. (a) Wing flapping velocity distribution on a wing rotating about an axis parallel to the freestream velocity vector. (b) Local wind velocity, $V_{w}$, on a 2 D aerofoil section of the wing depicted in (a), comprised of the freestream velocity, $V_{\infty}$, and wing flapping velocity, $V_{f}$, which varies as a function of distance from the wing

For a non-retracting wing, the wing flapping velocity at a distance, $r$, from the wing root is given as
$V_{f}=\dot{\phi} r$
where $\dot{\phi}$ is the angular velocity around the wing root. The instantaneous angle of attack is given as

$$
\begin{equation*}
\alpha(r, t)=\operatorname{atan}\left(\frac{V_{f}}{V_{\infty}}\right)-\theta=\operatorname{atan}\left(\frac{\dot{\phi} r}{V_{\infty}}\right)-\theta . \tag{79}
\end{equation*}
$$

where $\theta$ is the twist angle, and the ratio $\frac{\phi r}{V_{\infty}}$ is the inverse of the advance ratio. To maintain a constant angle of attack, $\alpha^{\prime}$, over a half-stroke, the twist angle at a distance $r$ from the wing root is given as

$$
\begin{equation*}
\theta(r, t)=\operatorname{atan} \frac{\dot{\phi} r}{V_{\infty}}-\alpha^{\prime} \tag{80}
\end{equation*}
$$

By assuming a sinusoidal variation in rotation angle around the wing root the twist distribution along the wing from equation [80] that yields constant angle of attack over a half-stroke is given as

$$
\begin{equation*}
\theta(r, t)=\operatorname{atan}\left(\frac{\Phi \omega r \sin (\omega t)}{V_{\infty}}\right)-\alpha^{\prime} . \tag{81}
\end{equation*}
$$

where $\Phi$ is the rotation angle amplitude. Figure 65 shows example twist angle trajectories that maintain constant angle of attack at three spanwise locations along the wing. Three different advance ratios are shown for reference, but typical bird cruising kinematics are at an advance ratio of around $0.5-1$. As the advance ratio increases the twist angles tend towards varying sinusoidally with time.


Figure 65. Time histories of wing twist angles that yield constant angle of attack at three locations on the wing: the wing tip (i), $2 / 3$ of the wing length from the root (ii) and $1 / 3$ of the wing length from the root (iii). (a)-(c) Fixed angle of attack of zero, and (d)-(f) for fixed angle of attack of $12^{\circ}$. Results shown for three advance ratios.

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[^0]:    ${ }^{1}$ An overview of flow visualisation methods of aerodynamic analysis is given by Spedding \& Hedenström [15], and Bomphrey [16] reviews the findings from such experiments. Taylor et al. [17] present a collection of recent applications of these techniques for animal flight research.

[^1]:    ${ }^{2}$ The velocity induced by the wing on the surrounding fluid will be smaller than the other components in forward flight, and so is neglected for this part of the discussion, however it will be included in the dynamic model (section 4.2).

[^2]:    ${ }^{3}$ The definition of thrust used here differs from that used in rotary wing aerodynamics, where it is defined as acting normal to the rotor disk [19], and also from that used in fixed wing aerodynamics, where it is defined as acting in the opposite direction to the freestream velocity vector (section 4.2.2) [20].

[^3]:    ${ }^{4}$ The Reynolds number is the dimensionless ratio of inertia to viscous forces in a flow [20]
    ${ }^{5}$ The Mach number is the ratio of the flow velocity to the local speed of sound [20]; for animal flight the Mach number is low enough that the effects of flow compressibility can be disregarded, and force coefficients for a given geometry are dependent on angle of attack and Reynolds number only [21]

[^4]:    ${ }^{6}$ Other uses of the term include the a description of an animal's ability to utilise different flight conditions, such as hover (e.g. [22]), but for the present work this is regarded more as a flight capability

[^5]:    ${ }^{7}$ These methods may implicitly derive other physical variables such as power consumption, however the kinematic outputs are the main points of discussion.

[^6]:    ${ }^{8}$ The exact method of optimisation used does reflect the characteristics of the system dynamics, which will be discussed further in section 4.3.

[^7]:    ${ }^{9}$ Even though the dynamics of the tail will not be included in the inverse dynamic model, the overall simulation framework is not restricted to this assumption, and future revisions could incorporate this.

[^8]:    ${ }^{10}$ The $y_{3}$ axis is sometimes referred to as the "wing axis" [64]

[^9]:    ${ }^{11}$ This process is equivalent to using alibi rotation matrices to rotate the position vector of any point on the wing

[^10]:    ${ }^{12}$ Circumduction of the hand wing is equivalent to a rotation of the hand about the $x_{3}$ axis in the present work, although a technical definition such as this is not usually given in biomechanics literature.

[^11]:    ${ }^{13}$ The term "Computational Fluid Dynamics" (CFD) is sometimes used to reference these methods, however this is believed to be misleading because other CFD methods exist that predict aerodynamic loads without resolving the flow around the body [73].

[^12]:    ${ }^{14}$ The model allows for any wing planform geometry to be used, however the specific values chosen for the wing length and wing reference area were found to have a more significant affect than the wing planform on the predicted aerodynamic forces and power consumption .

[^13]:    ${ }^{15}$ An alternative approach used in some predictive simulations is to define explicitly the maximum joint torques based on biomechanical limitations, however these data are not readily available for birds.

[^14]:    ${ }^{16}$ Free-wake methods used in the analysis of helicopter aerodynamics are distinct from other methods of the same name that have been used to simulate bird wakes, which require apriori knowledge of the wake geometry [23].

