FLEXIBLE AND COUPLED STRUCTURAL SYSTEMS DURING AVIAN WING MORPHING

by

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Zoology)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

April 2022

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Abstract

Birds are incredibly successful animals that can be found on every continent on this planet across a large range of habitats and atmospheric conditions. This success can be attributed, in part, to wing morphing, passive or active changes in wing shape, during flight to enable good flight performance during changing environmental conditions or behavioural needs. The morphing wings that facilitate this adaptive flight ability is a structural system with a variety of flexible biological components. It is currently unknown how the structure of one of these components, the flight feathers, and their interaction with neighbouring feathers and active musculoskeletal components can affect aerodynamic performance. First, we used geometric morphometrics on feather specimens from multiple species to quantify shape variation and then used a computational aerodynamic toolkit to evaluate the aerodynamic performance of each feather shape. We found that the lift slope explained more feather shape variation than the feather's location on the wing, the feather type, or phylogenetic relatedness. Second, we did dynamic mechanical analysis testing on a feather in the distal wing (P9) near the leading edge and a feather in the proximal wing (P1) near the wrist joint in an extended and folded wing with and without neighbouring feathers present. We found that wing folding slightly decreases featheranchoring tissue stiffness, but this is overcome by an increase in stiffness in the proximal wing via feather-feather interaction. Damping was consistently high within a wing and independent of wing shape. Finally, we used computational fluid-structure interaction simulations to evaluate the effect of varying stiffness during wing morphing on aerostructural responses and flight performance. We found that aerodynamic performance can be improved by the synchronization between structural deformations and flow vortices, and that as a bird folds its wings for higher speed glides, the increase in stiffness through feather-feather interaction resulted in greater lift

iii

production. Taken together, we propose that the avian wing structural system allows for the coupling of passive flight feathers to a simple active musculoskeletal system for aerostructural flow control and performance enhancement over a large range of flight speeds.

Lay Summary

A bird's ability to change wing shape during flight allows them to adapt their flying to different conditions such as gliding at different speeds. The wing is made up of musculoskeletal components to actively actuate this wing morphing and passive, but highly flexible, feather components coupled the skeletal movements. We make use of experimental and computational methods to understand how feather structures alone or feathers interacting with one another to change wing flexibility can affect flight performance. We find that coupling passive elements to active morphing components allows for the enhancement of performance over a large range of gliding speeds.

Preface

This work was conducted with the approval of the University of British Columbia (UBC)'s Animal Care Committee (certificate #: A15-0116, A19-0113-A007) in the laboratory of Douglas L. Altshuler (DLA) at the UBC Point Grey campus. Chapters 1 to 5 are original and were written by me, Jasmin C.M. Wong (JCMW). Chapter 2-4 are unpublished, and I was the lead investigator, responsible for the majority of conception and experimental design, data collection, and analysis. DLA provided feedback and direction during experiment troubleshooting and data analysis for all data chapters. Chapter 2 was done in collaboration with Vikram B. Baliga (VBB) who taught me geometric morphometrics and phylogenetic Bayesian statistics methods, and Christina Harvey (CH) who provided feedback on my usage of the XFLR5 toolkit. Chapter 3 was done with the help of Po-Yan Cheng (PC) who helped develop the anaesthetic and health monitoring techniques used during surgeries, Robert E. Shadwick (RES) who advised on dynamic mechanical analyses techniques, and VBB who oversaw the statistical methods. Chapter 4 was done in collaboration with Rajeev K. Jaiman (RKJ) and Vaibhav Joshi (VB) who developed the in-house fluid-structure interaction solver and helped me create a wing model and understand the problem set-up files, Shayan Heydari (SH) for advice during troubleshooting, and VB for assistance in the motion capture of a pigeon wing shape. Chapter 4 was also made possible by the UBC Advance Research Computing Sockeye and its support staff.

Table of Contents

Abstractiii		
Lay Summaryv		
Prefacevi		
Table of Contents vii		
List of Tables xi		
List of Figures xii		
List of Supplemental Material xiv		
List of Symbolsxv		
Acknowledgements xvii		
Dedication xviii		
Chapter 1: Introduction 1		
1.1 Form and Flight1		
1.1.1 Avian Flight 5		
1.1.2 Wing Morphing15		
1.2 Flexible Materials		
1.2.1 Mechanical Properties of the Wing		
1.3 Fluid-Structure Interactions		
1.3.1 Structural Dynamics in Nature		
1.3.2 Aeroelastic Tuning		
1.4 Objectives		

feather shape among species		
2.1 Synopsis		
2.1.1 Objectives		
2.2 Methods		
2.2.1 Collection of Feathers		
2.2.2 Image Processing		
2.2.3 Geometric Morphometrics		
2.2.4 Aerodynamic Modelling		
2.2.5 Statistical Analysis		
2.3 Results		
2.3.1 Feathers vary mostly in aspect ratio and curvature with feather type groupings		
along the PC1 axis		
2.3.2 Aerodynamic performance $\left(\frac{\partial C_L}{\partial \alpha}\right)$ accounts most of the shape variation along PC1		
2.4 Discussion		
Chapter 3: Wing morphing makes use of different available mechanisms to locally modify		
mechanical and structural properties		
3.1 Synopsis		
3.1.1 Objectives		
3.2 Methods		
3.2.1 Animal Subjects		
3.2.2 In Situ Set-Up		

Chapter 2: Aerodynamic performance covaries strongly with the largest axis of variation in

	3.2.3	Force-Displacement Measurements	
	3.2.4	Statistical Analysis	
	3.3 I	Results	69
	3.3.1	Feathers are anchored against cyclic loads in a non-linear, and largel	y elastic
	fashic	on	69
	3.3.2	Stiffness decreases with wing folding due to increasing tissue compl	iance and
	increa	uses near joints due to increasing feather-feather interaction.	
	3.3.3	Work absorption is greater in the distal portion of the wing but incre-	ases in work
	absor	ption in the proximal wing due to feather-feather interaction during wi	ng folding
	result	in uniform damping over the entire wing	
	3.4 I	Discussion	
(Chapter 4:	Wing stiffness modulates aerodynamic performance according to wing	g posture
ť	hrough ch	anges in aeroelastic response	
	4.1 \$	Synopsis	
	4.1.1	Objectives	
	4.2 N	Methods	
	4.2.1	Geometric Model	
	4.2.2	Fluid-Structure Interaction Solver	
	4.2.3	Aerodynamic Performance Analysis	
	4.2.4	Aeroelastic Response Analysis	
	4.3 H	Results	
	4.3.1	Wing folding increases aerodynamic performance by reducing press	ure drag 101

4.3.2 Wing flexibility increases aerodynamic performance more significantly in an		
extended wing	103	
4.3.3 Wing flexibility induces small-scale vortical structures that increase local		
vorticity and prevent boundary layer separation	106	
4.4 Discussion	109	
Chapter 5: Conclusion	126	
5.1 Discussion	126	
5.1.1 Coupling active and passive structures in a system for flow control	127	
5.1.2 Aerostructural responses for flow sensation	133	
5.1.3 Potential effects of variation wing structures within and among species	137	
5.1.4 Bio-inspired Applications	141	
5.2 Limitations and Future Directions	145	
5.3 Summary	148	
Bibliography150		

List of Tables

Table 2.1 Leave-One-Out Model Fits for PC1 and PC2 and the standard error
Table 2.2 Cohen's f^2 for PC1 and PC2 with standard deviations over 100 trees
Table 3.1 Storage modulus G' and loss modulus (G'')
Table 3.2 Percent change in loading and unloading stiffness, storage modulus and loss modulus
due to wing folding
Table 4.1 Geometric Parameters of Gmsh Models 94
Table 4.2 Fluid and Structural Properties 97
Table 4.3 Lift slope $\left(\frac{\partial C_L}{\partial \alpha}\right)$ and maximum lift-to-drag $\left(\frac{C_L}{C_D}\right)_{max}$ as a function of wing flexibility
(<i>E</i>) and wing shape
Table 4.4 Frequency and amplitude of the first two harmonics of wing tip displacement $\mathbf{z} *$ as a
function of wing flexibility (E) and wing shape
Table 4.5 Frequency and amplitude of the first two harmonics of wing pitch angle (θp) as a
function of wing flexibility (E) and wing shape

List of Figures

Figure 2.1 Feather rachis and vane shape were acquired and further modelled as a three panel
wing for XFLR5 analysis
Figure 2.2 Most of the feather variation is explained by the first two principal components axes
which correspond to aspect ratio and sweep, and feather type can be separated along the PC1
axis
Figure 2.3 The phylogenetic tree with all 23 species used in this study
Figure 2.4 Feather type, feather location, and $\frac{\partial c_L}{\partial \alpha}$ all contribute to explaining PC1 but $\frac{\partial c_L}{\partial \alpha}$
explains most of the variation while feather location on the wing and phylogenetic signal
explains relatively little of the variation
Figure 3.1 The experimental set up and treatments
Figure 3.2 Local force-position response to a cyclic load applied at the base of flight feathers in
pigeons indicates a strongly elastic viscoelastic response
Figure 3.3 Structures supporting distal feathers are stiffer than those supporting proximal
feathers but wing folding increases stiffness in the proximal wing
Figure 3.4 Work absorption varies locally over the wing yet damping remains constant
Figure 4.1 Geometric models for the solid structure and fluid volume
Figure 4.2 Wing folding decreases pressure drag by reducing the size of the separation bubble
caused by boundary layer separation
Figure 4.3 Flexible wings perform better than rigid wings
Figure 4.4 Wing flexibility reorients the low-pressure region upwards and towards the leading
edge which contributes to increasing lift and reducing drag

List of Supplemental Material

Video 4.1 C_p distribution around an extended F1 ($E = 10^6$) wing at $V_{\infty} = 10m/s$ and $\alpha = 10^\circ$ (3x slow)

Video 4.2 C_p distribution around an extended F2 ($E = 10^9$) wing at $V_{\infty} = 10m/s$ and $\alpha = 10^\circ$

(3x slow)

Video 4.3 C_p distribution around a folded F1 ($E = 10^6$) wing at $V_{\infty} = 10m/s$ and $\alpha = 10^\circ$ (3x slow)

Video 4.4 C_p distribution around a folded F1 ($E = 10^6$) wing at $V_{\infty} = 20m/s$ and $\alpha = 10^\circ$ (3x slow)

Video 4.5 C_p distribution around a folded F2 ($E = 10^9$) wing at $V_{\infty} = 10m/s$ and $\alpha = 10^\circ$ (3x slow)

Video 4.6 C_p distribution around a folded F2 ($E = 10^9$) wing at $V_{\infty} = 20m/s$ and $\alpha = 10^\circ$ (3x slow)

List of Symbols

Amplitude
Area (exact definition in text)
Aeroelastic number
Angle of attack
Angle of attack at which $(C_L/C_D)_{max}$ occurs
Speed of sound
Distal chord length
Drag coefficient
Lift coefficient
Lift (coefficient) to drag (coefficient) ratio
Maximum lift (coefficient) to drag (coefficient)
Moment coefficient
Mean aerodynamic chord
Damping ratio
Drag force
Loss tangent or phase angle
Young's modulus
Strain
Frequency
Force (exact definition in text)
Cohen's f^2
Shear modulus
Complex modulus
Storage modulus
Loss modulus
Circulation
Stiffness

l	Length (exact definition in text)
L	Lift force
λ	Pagel's lambda
λ_2	Lambda2 criterion
Μ	Moment
Ма	Mach number
μ	Fluid viscosity
ω	Angular velocity
Р	Pressure
$\partial C_L / \partial \alpha$	Lift slope
R^2	R squared value
Re	Reynolds number
ρ	Fluid density
σ	Stress
t	Time
t	Wing thickness
τ	Shear stress
$ heta_p$	Pitch angle
ν	Poisson's ratio
V_{∞}	Free-flow velocity
W	Distance between two feathers
W	Work
ξ	Vorticity
Ζ	Dorsal-ventral wing tip displacement

Acknowledgements

I would like to start by thanking my supervisor, Dr. Douglas Altshuler, for welcoming me into his lab and being supportive as my research veered off in an unplanned direction over the years. I am eternally grateful for the opportunity to work in such an interdisciplinary lab which has generated many fruitful collaborations. In particular, I'd like to acknowledge Dr. Vikram Baliga, Christina Harvey, and Jolan Theriault for all their help during experiments, always being down for some science talk over beers, and putting up with sudden text messages from me asking "Does this make sense?!". I must also thank my committee: Dr. Robert Shadwick, Dr. Philip Matthews, and Dr. Rajeev Jaiman for all their guidance over the years.

The experimental work was facilitated by Ildiko Szabo and the Beaty Biodiversity Museum who sourced all the specimens used, Ken Chatwin who built our pigeon coop and supplied us with live pigeons, and our veterinarian, Dr. Po-Yan Cheng, who trained me in many of the surgical techniques. The computational work was made possible by Dr. Jaiman, Dr. Vaibhav Joshi, and Shayan Heydari who provided the source code for the fluid-structure solver and taught me how to set up cases.

Finally, it would be remiss of me to not acknowledge all the friends and family that have supported me during my PhD. To my labmates and friends within and outside the department, thanks for all the lunchbreak banter, coffee runs, fancy cocktails, mountains climbed, and mountains skied. To my parents, Alex and Sally Wong, thank you for keeping me alive for decades and ensuring I have the freedom, capability, and opportunity to pursue my academic interests. To my grandma, aunts, uncles, and cousins here in Vancouver, thank you for making this city feel like home.

xvii

Dedicated to Franklin, Chewie, Mama, and Bonnie for brightening up my days working on this

PhD with excited tail wags and the occasional headbutt.

Chapter 1: Introduction

1.1 Form and Flight

Flight technology has become increasingly critical for human civilisation. Conventional aircraft use for passenger travel and freight has seen a steady rise with a 4.9% increase in passenger travel, with over 8 trillion total kilometres travelled, in 2019 (International Civil Aviation Organization, 2019). The use of unmanned air vehicles (UAVs) or drones has increased even more rapidly in recent years. Drone applications have expanded beyond the military into commercial and personal use with applications such as aerial photography, shipping and delivery, search and rescue, and geotechnical or weather surveying among many others (Insider Intelligence, 2021). UAVs have the potential to be useful for a large variety of functions while maintaining a low energy requirement (Stolaroff et al., 2018) so its popularity is likely to continue to increase in the near future. Therefore, it is imperative that advances in UAV technology can ensure efficient performance over a large range of environmental conditions and mission parameters. Flying animals are capable of precisely this adaptability and can modulate their flight behaviour for a variety of tasks such as locomotion, prey-capture, predator-evasion, and courtship display. Therefore, we will first present an overview of what is currently known about animal flight, and bird flight in particular, in Chapter 1. This will provide context and justification for the three studies exploring previously unstudied, but critical aspects of avian flight in Chapters 2-4. Finally, we will interpret the findings of this dissertation for both expanding our understanding of mechanisms for flight adaptability in a bird's wing and hypothesize on potential bio-inspired applications.

The evolution of flight While it took man until the 20th century to master the skies, powered flight, an energetically demanding form of locomotion per unit time (Norberg, 1996),

has evolved independently at least four times: in insects, pterosaurs, birds, and bats. How animals evolved flight is still a hotly debated topic. There are two commonly discussed competing theories for vertebrate flight: the arboreal hypothesis (trees down) and the cursorial hypothesis (ground up). Although a few more hypotheses have been proposed for insects including the floating hypothesis, which proposes that wings formed from dorsal extensions used in thermoregulation, and the surface-skimming hypothesis, which theorises that gill-like structures were appropriated for swimming then flight (Norberg, 2007). The arboreal hypothesis suggests that tree-dwelling animals used proto-wings to glide from tree to tree or to glide from steep slopes, improving locomotory efficiency. The cursorial hypothesis suggests that grounddwelling animals used proto-wings to enhance their jumping abilities (Norberg, 2007) or to enable running over steep and complex terrains as seen in chukars and other extant ground birds (Dial et al., 2006). Researchers have used fossil records to argue support for and against both hypotheses which has led to a third hypothesis combining aspects of both the arboreal and cursorial to be proposed. This 'pouncing proavis' theory proposes that ground-dwelling predators used their proto-wings to improve control during a descent as they ambushed prey from above. It has been argued that this model agrees with the evolutionary sequence of morphological characters observed in fossil records (Garner et al., 1999). However, this debate could be further complicated by the possibility of multiple origins of powered flight due to either different initial ecological or behavioural pressures (Pei et al., 2020) or environmental conditions. For example, the atmospheric conditions during the late Paleozoic, late Mesozoic, and Tertiary ages had higher air densities which would facilitate the generation of aerodynamic forces (Dudley, 2000).

Regardless of how flight evolved, one consensus is that many of the anatomical characteristics that promote flight, such as low wing loading, existed prior to the capability for

true powered flight. Other adaptations such as shoulder stability or asymmetrical feathers appeared much later in evolutionary time. Therefore, early ancestors to birds likely had the ability to glide inefficiently with little control and used their wings for other locomotory tasks (Pei et al., 2020). As proto-birds and then birds evolved the necessary adaptations for flight, their survival was enhanced. Flapping flight allowed for increased thrust production and manoeuvrability, allowing for longer distances travelled to increase foraging area and higher aerial manoeuvrability to avoid predators or capture prey. Despite being energetically expensive, flight allows animals to cover 10-20 times more distance compared to a similarly sized animal on the ground (Jenni-Eiermann & Srygley, 2017). Being able to fly far enough and long enough to cross the planet in search of food or favourable breeding grounds isn't enough if birds don't have the ability to adapt to difficult and abnormal weather conditions or avoid predators at stopover areas (Newton, 2006) which is why a bird that is capable of transitioning from an endurance flight mode to a manoeuvrable flight mode will be more successful. In fact, it has been shown that birds that escape from predators with a larger upwards component have a better chance of survival, and all birds, with their ability to escape in three-dimensions, have a higher reported survival rate compared to non-flying mammals of the same size (Møller, 2010). Further enhancements to flight control evolved after this through improvements to neuromuscular control and the development of specialized muscular systems and feathers. The development of flight-specialized controls and structures allowed for more complex behaviours like hovering (Norberg, 2007). Kestrels are one bird that can intermittently engage a windhovering mode where they remain in a fixed position relative to the ground to search for prey. This ability allows kestrels to increase prey capture success, averaging 2.82 prey per hour compared to 0.31 prey per hour with soaring flight or 0.21 prey per hour from a perch (Videler et al., 1983). It is clear that

the evolution of flight over millions of years has provided birds an assortment of tools that allows them to engage in very distinct flight behaviours over large variations in the external environment.

While all three extant flying animal groups could provide valuable insight and inspiration for adaptive flight mechanisms, birds are a valuable model for bio-inspired design of UAVs due to their capacity for active wing morphing, their operation under an intermediate Reynolds regime, and their morphological and ecological diversity. Insects were the first to evolve flight. However, they fly by actuating passive wing structures either exclusively at the root or indirectly using thoracic muscles and are incapable of actively changing wing shape. They also operate lower Reynolds numbers $(10 - 10^5)$ than birds, bats or UAVs and generate lift in a manner different from predictions set by conventional aircraft theory (Ellington et al., 1996; Dickinson et al., 1999). Bats, the last to evolve powered flight, fly using highly articulated wings capable of active wing morphing in both spanwise and chordwise directions as well as active stiffness tuning over the entire wing (Cheney et al., 2014). Therefore, insects and bats represent the opposite ends of wing morphing complexity. Both birds and bats operate at the same intermediate Reynolds range as UAVs ($Re \sim 10^5$) and would provide valuable inspiration for UAV advances (Tank et al., 2017). However, birds have less active control over their wing shape compared to bats as the majority of the avian wing is made up of passive feathers. In other words, all wing shape changes are dependent on the active musculoskeletal components along the leading edge. An active-passive control coupled system is valuable in that it could inspire engineered morphing wings that have simpler control system, reducing computational costs, while still achieving adaptable flight behaviours. Despite having less active control over their wing shape, birds are considered one of the most successful group of animals with over 10,000

species distributed across seven continents and featuring a wide range of ecological and morphological diversity (Brusatte et al., 2015).

1.1.1 Avian Flight

Avian adaptations for flight Birds have multiple unique characteristics that facilitate flight. Many of these characteristics are adaptations that help alleviate the high energetic cost of flight while still being strong enough to resist aerodynamic forces. The avian skeletal system has been modified to be simultaneously rigid and lightweight. Rigidity is attained by the fusion of certain bones like the finger bones, parts of the vertebral column, and the pelvic girdle, and the enlargement of other bones such as the pectoral bones and the keel on the sternum where flight muscles powering the wings are attached. Weight reduction is attained by the loss of nonessential bones such bones for a long tail and teeth, as well as pneumatization of bones, particularly in the wings. Pneumatized bones are hollow thin-walled bones filled with air instead of marrow from various parts of the respiratory system, reducing the density of the skeletal system. Pneumatization has been correlated to the ability to fly; flightless birds such as penguins do possess pneumatized bones at all, diving birds such as loons have limited pneumatization, and long-distance fliers such as albatrosses and frigatebirds have pneumatized bones from wing root to wing tip (Cornell Lab of Ornithology, 2004).

The respiratory-cardiovascular system The lungs and air sacs are another adaptation reduce the weight of birds compared to other vertebrates of similar size. Birds have small lungs connected to nine thin-walled air sacs ensuring that air is distributed throughout the body cavity, reducing the overall density of the bird. These structures also enable a one-way flow of air that ensures that oxygen and carbon dioxide exchange can occur during inspiration and expiration, increasing the efficiency of gas exchange to the cardiovascular system (Cornell Lab of

Ornithology, 2004). The avian circulatory system is particularly robust against hypoxia, capable of resisting changes in pH caused by a decrease in CO₂ partial pressure. This efficient gasexchange system can allow birds to operate at extreme altitudes, the pinnacle of which can be found in bar-headed geese capable of flying over mountain peaks in the Himalayas (> 8000 m) (Jenni-Eiermann & Srygley, 2017).

Metabolic rate The high energetic cost of flight is revealed by the birds' high field metabolic rate, a measurement of the free-living animal's total energy expenditure including all constituent costs. It takes energy to fly, involving a constant battle to generate lift against gravity. Yet birds have no trouble achieving flight as demonstrated by alpine swifts which can spend 200 days of the year continuously in the air (Jenni-Eiermann & Srygley, 2017). The average metabolic rate of all birds does not differ much from mammals, although both have a higher metabolic rate than reptiles, being endotherms (Hudson et al., 2013). What sets birds apart is that the field metabolic rate of birds has been found to vary significantly, either phenotypically with large differences in migrant birds compared to non-migratory birds (Jetz et al., 2008), or behaviourally with an increased rate during flapping compared to gliding. The flexibility in metabolic rate may be a key factor in allowing birds to allocate energy towards intensive activities such as flight or escape (Jenni-Eiermann & Srygley, 2017).

Sensory control It is not enough to simply have the anatomical and physiological capabilities to power flight if there is no mechanism for controlling these structures and adapting processes to behavioural needs. Birds have a sophistical neurological system that can coordinate even the most complex and acrobatic flight manoeuvres. For rapid adjustments during flight, birds likely rely on a mixture of somatosensation, vestibular reflexes, and visual guidance.

Somatosensation is used to detect mechanical forces acting on the bird's body with high temporal and spatial resolution. There is very little known about the relevant pathways, with only indirect evidence for the importance of somatosensation during flight. Mechanosensory organs such as the Herbst corpuscles, rapid response vibration receptors, are localised in the soft tissue near feather follicles in areas that experience flow indicative of overall flow and flight performance such as the leading edge. Behavioural experiments have found that radial nerves respond proportionally to local flow velocity, and complex manoeuvres like take off and landing are impossible when this nerve is severed. Vestibular reflexes are critical for head and gaze stabilization which is critical for flight control. Head stabilization is so important that pigeons are unable to fly if they are unable to engage this reflex due to experimental fixation of their necks (Altshuler et al., 2015). Other work has found that the vestibular reflexes contribute to dictating wing and tail behaviour for pitch and roll control during flight. Therefore, the vestibular system is essential even during regular forward flight. The visual system is particularly important for flight control as most birds heavily rely on optic flow, the movement of visual signals across the eye, to control their position relative to the world around them. On a larger temporal scale, some birds also make use of baroreception, the sensation of pressure, and magnetoreception, the sensation of magnetic fields, to orient themselves relative to the earth (Altshuler et al., 2015).

Wings Out of all adaptations necessary for flight, the wing is the most important and investigating this multi-component structure is the key focus of this thesis. The avian wing is the primary morphological feature that enables flight. Broadly speaking, bird wings and aircraft wings are very similar, both featuring a streamlined, cambered shape that is thicker at the leading edge and tapering to a thin trailing edge. But instead of aluminum and carbon fibre, bird wings are made up of nine bones (the humerus, the ulna, the radius, two wrist bones, the

carpometacarpus, and three digits), multiple pairs of striated muscles and their associated tendons, smooth muscle, ligaments, and other soft tissues, and most importantly, feathers (Cornell Lab of Ornithology, 2004). These wings generate a majority of the aerodynamic forces necessary for flight.

Aerodynamics Aerodynamics, from the Greek words *aero* meaning air and *dynamis* meaning power, is the branch of physics that describes air flow and how it may transfer forces or energy to other materials in contact with the flow. Aerodynamics can tell us how a dandelion disperses seeds, how the giant Quetzalcoatlus may have flown, and how atmospheric and ocean circulation moves thermal energy to sustain life. The behaviour of air particles (or the particles of any fluid) can be described mathematically by the Navier-Stokes equations, a set of partial differential equations that describe fluid motion in a continuum by considering conservation of mass, conservation of momentum, and conservation of energy within a system. These equations describe the relationship between fluid properties such as velocity, pressure, density, and viscosity at a given point and time (Anderson Jr., 2011).

Precursor knowledge of fluid properties can go towards simplifying the Navier-Stokes equations to the point where they can be solved analytically or using numerical methods. For example, while real fluid flows have variations in density (compressible flow) and experience friction between shearing fluid layers due to viscosity (viscous flow), there are many situations in which changes are relatively small throughout the fluid volume and thus can be assumed to be constant, allowing us to assume incompressible and inviscid flow. In practice, homogeneous fluids flowing at a Mach number,

$$Ma = \frac{V_{\infty}}{c}$$

where V_{∞} is the flow velocity and *c* is the speed of sound, is less than 0.3 can be considered incompressible. Flows in which inertial forces dominate over viscous forces can be considered inviscid except within a thin region of fluid around a body surface in contact with the fluid known as the *boundary layer*. The relative importance of inertial forces compared to viscous forces is quantified by the Reynolds number,

$$Re = \frac{\rho_{\infty}V_{\infty}l}{\mu}$$

where ρ_{∞} is the density, V_{∞} is the flow velocity, *l* is the characteristic length of the body, and μ is the viscosity (Anderson Jr, 2011). *Re* provides a guideline for classifying the boundary layer flow as laminar at low *Re* or turbulent flow at high *Re* (NASA, 2021). The behaviour of the boundary layer is important for determining the degree of momentum exchange between the fluid body and the surface of the wing (Anderson Jr, 2011). Generally, birds operate at *Ma* < 0.3 and *Re* = 10⁵, indicating that we can assume incompressible flow but both laminar and turbulent flow must be considered at this intermediate Reynolds number (Tank et al., 2017).

An object placed in a fluid volume will interact with the surrounding fluid particles. The fluid particles each impart some momentum to the solid upon collision, and a moving solid in turn will impart some momentum to the fluid particles. Fluid momentum is related to pressure and shear stress via the Navier-Stokes equations. Integrating the pressures and shear stresses over the entire object's surface gives us the aerodynamic forces: *lift*, the force vector perpendicular to the incoming flow, *drag*, the force vector parallel to the incoming flow direction, as well as the aerodynamic *moments*, the tendency to rotate under load. For airfoils, it is assumed that the forces act through the centre of pressure. In analysis, it is common to non-dimensionalize the forces and moments to generate aerodynamic and moment coefficients:

Lift coefficient:
$$C_L = \frac{L}{\frac{1}{2}\rho_{\infty}V_{\infty}^2 A}$$

Drag coefficient: $C_D = \frac{D}{\frac{1}{2}\rho_{\infty}V_{\infty}^2 A}$
Moment coefficient : $C_M = \frac{M}{\frac{1}{2}\rho_{\infty}V_{\infty}^2 A}$

where *L* is the lift force, *D* is the drag force, *M* is the moment, ρ_{∞} is density, V_{∞} is the free-flow velocity, and *A* is the planform area (Anderson Jr, 2011). Analytical and numerical methods allow us to calculate aerodynamic forces and force sensors allow us to experimentally measure them.

Despite the relative ease in computing lift, there is no single "correct" explanation for lift generation (but there are many incomplete or misleading theories) (NASA, 2021). To better understand lift, it is necessary to first define the concept of vorticity (ξ):

$$\xi = \nabla \times \vec{V}$$

where \vec{V} is the velocity of the fluid element. Fluid elements in a moving fluid can be translating, rotating, deforming, or a combination of the three. One way of imagining how a fluid element can experience a non-zero net angular velocity in the absence of a spinning fluid motion is to consider a fluid element in the velocity gradient of a viscous boundary layer. This fluid element is moving in the direction of the flow but also experiences relative velocities in the opposite direction due to the faster flowing fluid on one side and a slower flowing fluid on the other side due to the velocity gradient. This results in a net rotation. Integrating vorticity over the entire solid surface *S* will give the overall *circulation* (Γ) around the object:

$$\Gamma = \iint_{S} \xi \cdot ds$$

Lift can only occur if circulation is non-zero. This is a fundamental aerodynamics theorem known as the *Kutta-Joukowski Theorem*:

$$L = \rho_{\infty} V_{\infty} \Gamma$$

and forms the basis of the circulation theory of lift. In other words, lift is proportional to vorticity (Anderson Jr, 2011).

Drag is less difficult to explain but instead can occur through many different mechanisms. Drag is defined as any force that resists the motion of the object moving through the fluid. Any object moving through a fluid experiences *parasitic drag* which is drag owing to fluid-solid contact. Parasitic drag can be further divided into two types: *friction drag* and *pressure drag*. Friction drag is caused by friction between the fluid and the solid surface due to fluid viscosity (NASA, 2021). Pressure drag, sometimes known as form drag, is caused by a pressure differential across the object that results in a net force against the direction of movement. Streamlining objects reduces pressure drag. In addition to these two forms of drag, an object that generates lift also experiences *induced drag*. This form of drag can only occur in finite, 3D wings because air is free to flow around the wing tip due to the pressure differential between the upper and lower surfaces of the wing that generate lift. As flow circles around the wing tip, it forms wing tip vortices that create a downwash, or downward moving air, reducing the effective local angle of attack (α) and reducing C_L and angling the lift vector backwards (NASA, 2021).

The angle of attack (α) is the orientation of the airfoil relative to the flow and can dictate flow behaviour around the airfoil, thus, significantly affecting the aerodynamic coefficients. As α increases, the pressure differential between the upper and lower surfaces of the airfoil increases, and subsequently, lift increases as well. However, if inertial forces are significant,

further increase in α to a critical stall angle will cause the boundary layer to separate, causing lift to decrease rapidly.

Overall, the summation of aerodynamic forces will dictate the movement of the airfoil. The forward component of the net force is known as *thrust* and a non-zero value will result in translational movement. The summation of moments also results in rotational movement which can occur around an axis aligned with the body *(roll)*, around an axis from wing tip to wing tip *(pitch)*, and around an axis orthogonal to both pitch and roll axes *(yaw)*.

Gliding A bird wing during gliding flight operates like the airfoil (the shaped surface of an aircraft wing that produces aerodynamic forces). Gliding trajectory and time aloft depends on a balance between aerodynamic forces and gravity. No thrust is generated during gliding flight so drag will reduce flight speed which, in turn, reduces lift. Eventually, upwards forces due to lift cannot overcome the animal's weight and the bird will lose altitude. The angle of descent, therefore, depends on the lift-to-drag ratio (i.e., higher lift-to-drag allows a bird to stay aloft for longer). During an equilibrium glide, all forces cancel out resulting in a constant sinking speed (Cornell Lab of Ornithology, 2004; Rosén & Hedenström, 2001). As such, gliding behaviour can be modified by adjust the lift-to-drag ratio.

Modification to density, flight speed, surface area, and their respective aerodynamic coefficients can affect the aerodynamic forces. The aerodynamic coefficients are influenced by angle of attack and wing shape, defined by its planform area and cross-sectional area, the latter which can be further described by camber, thickness, and surface roughness (Altshuler et al., 2015). Wing shape can vary significantly within a species among sex-age groups (Stiles et al., 2005) and among species. Interspecific variation of wing planform area has been correlated with aerodynamic function – the shorter, more tapered wings of adult male hummingbirds could have

been selected for to enhance manoeuvrability during courtship displays (Stiles et al., 2005), the high aspect-ratio, pointed wings of long-distance migrants have been shown to reduce induced drag (Lookwood et al., 1998), and the surface roughness in swifts ensure laminar flow and, therefore, drag reduction (Lentink & de Kat, 2014). However, generalization of flight behaviour with the planform area of an extended wing fails to account for trade-offs in performance along all three axes of movement, the multi-functional requirement of wings in a bird's life (Stiles et al., 2005), or the influence of environmental factors.

Birds often make use of environmental flow behaviour to supplement the aerodynamic capabilities of its wings. Fulmar petrels don't glide as well as dedicated endurance gliders such as the wandering albatross. Instead, they have been observed to take advantage of updrafts forming off cliff faces to reduce sinking speed (Pennycuick, 1960). White-backed vultures, capable of soaring over a broad range of airspeeds from 5.4m/s to 39.1m/s, circle within thermals over land (Tucker, 1988). It has also been suggested that when no thermals are found, large groups of gulls vigorously flap to disturb the air during still or calm days to initiate thermals (Woodcock, 1975).

Flapping Flight A common method used by birds to maintain or gain altitude is flapping flight. During flapping flight, the distal and proximal wing experience different forces. The proximal wing, due to its proximity to the body, does not experience much movement and behaves like a gliding wing. The distal wing, on the other hand, experiences significant out of plane movement. During the downstroke, the distal wing moves down and backwards. This movement significantly increases the angle of attack which causes the resultant aerodynamic force to be angled upwards and forwards, counteracting weight and generating thrust respectively. Meanwhile, the wing tip feathers twist to prevent stall over the distal wing.

Upstroke kinematics can vary among species. Smaller birds tend to twist their wings to decrease the angle of attack, reducing the magnitude of the backwards pointing lift to near zero, as well as partially tucking their wings in to reduce air resistance. They use a faster flapping frequency so they can afford to produce little to no thrust during the upstroke (Cornell Lab of Ornithology, 2004; Dvořák, 2016). Larger birds tend towards lower flapping frequencies so they must produce thrust during the upstroke as well. They employ much less wing folding during the upstroke and twist their humerus causing the upper surface of the distal wing to push against the air for thrust generation (Cornell Lab of Ornithology, 2004). Other birds such as raptors simply reduce the upstroke duration to compensate for the reduction in lift and thrust during the upstroke (Rayner, 1988). Thrust generation can also be understood by analysing the wake behind a flapping bird. A heaving oscillatory movement will generate a wake characterised by a reverse Kármán vortex street. This vortex pattern imparts momentum backwards which, due to Newton's law of action and reaction, results in forward movement for the bird (Dvořák, 2016).

Flapping kinematics can also vary within an individual to meet force production requirements for a given flight behaviour (Rayner, 1988). Lift can be enhanced by increasing flow velocity over the wing through changes in amplitude or frequency. Many birds seem to preferentially prefer increasing flapping amplitude over frequency. It has been hypothesized that this is a side effect of limitations in muscle-tendon dynamics. There are exceptions such as pigeons which don't seem to modify either frequency or amplitude significantly. As such, they may rely on other behavioural alternations to adjust flight performance (Altshuler et al., 2015).

Hovering True hovering is a specialized subset of flapping flight that produces no net movement. Hummingbirds hover by flapping their wings in a figure-8 pattern, resulting in bilateral vortex loops underneath each wing during both upstroke and downstroke. This allows

hummingbirds to generate lift throughout the entire flapping cycle which it directs upwards to hold a fixed position relative to the ground (Pournazeri et al., 2012).

In conclusion, wing shape is a key factor affect aerodynamic performance in gliding flight and involved in flapping flight kinematics. There does not exist a single wing shape that can optimize performance for all flight behaviours due to not only the variety in behaviours but also evolutionary, energetic, and physiological limitations (Rayner, 1988). The next best thing is a morphing wing. An individual bird has the capacity to change wing shape to some degree, whether for small adjustments during gliding flight or large changes during flapping flight. It is this ability that enables birds to achieve a large variation in aerodynamic output.

1.1.2 Wing Morphing

Wing morphing allows birds to modulate the airflow and the aerodynamic forces acting on the wing to suit behavioural and locomotory needs. The wing can be moved relative to the body through its shoulder joint which can alter dihedral or sweep or moved by rearranging its component parts relative to each other through its elbow and wrist joints for wing extensionflexion or pronation-supination or both (Altshuler et al., 2015).

Wing extension and flexion is one of the most prominently studied shape changes used to adapt the wing planform to flight behaviour. Birds tend towards an extended wing when gliding at low speeds and a folded wing when gliding at high speeds (Pennycuick, 1968; Rosén & Hedenström, 2001; Tucker & Parrott, 1970; Tucker, 1987). Gliding at higher speeds increases induced drag, but this is far overshadowed by the decrease in wing profile drag caused by wing folding (Pennycuick, 1968). Overall, this results in an attenuation of the decrease in lift-to-drag ratio at higher airspeeds (Tucker & Parrott, 1968). Wing folding is often accompanied by an increase in sweep, which improves lift production. Together, this shows that wing extension and

flexion can be used to increase the aerodynamic performance envelope (Lentink et al., 2007). Apart from the benefits during gliding flight, wing flexion is also important during other flight behaviours such as flapping flight, take off and landing. The steppe eagle has been observed to adopt a flexed M-shaped wing when nearing a perch. This wing folding shifts the centre of pressure forward of the centre of mass, causing the body to pitch upwards and stall, essentially applying a sudden brake against forward movement (Carruthers et al., 2007). Wing folding during landing also increases the camber to ensure high lift at low speeds for better landing control (Carruthers et al., 2010).

The coupling between out of plane wing morphing, such as camber and wing twist, and in plane extension-flexion has been frequently observed but only recently thoroughly quantified and its aerodynamic consequences explored. Wing extension restricts bending and twisting (Baliga et al., 2019) due to skeletal anatomy (Vazquez, 1992). In gulls, this behaviour couples spanwise camber to elbow and wrist angle, with camber decreasing as the wing extends. Elbow extension causes a drop in maximum C_L and $\frac{C_L}{C_D}$, decreasing aerodynamic efficiency, and a drop in the (always negative) pitch stability derivative, increasing pitch stability. As a result, wing morphing allows the gull to go from a low efficiency, high pitch stability shape when extended to a high efficiency, low pitch stability shape when folded (Harvey et al., 2019). In fact, through variation in elbow and wrist angles, the wing can hold certain performance metrics constant while varying other parameters, allowing for both coupling and decoupling of force production and stability depending on the trajectory of wing extension (Harvey et al., 2021).

Interspecific variation in elbow and wrist joint range of motion (Baliga et al., 2019) as well as relative lengths of wing bones and flight feather morphology can influence the *in vivo* wing shapes of an individual during morphing, and as such, there may also be interspecific variation in performance trade-offs and couplings due to wing extension. This suggests that aerodynamic performance range is integrated to wing morphing. This is what a recent study by Baliga et al., (2019) found: elbow and wrist range of motion better predicted flight style than the commonly used wing shape.

Wing morphing is only possible due to the coupling and action of the wing structures. Morphing can be active, involving metabolic energy input to their intrinsic wing muscles, or passive, deformations influenced by structural and material properties of the flexible components (Altshuler et al., 2015).

Skeleton The skeletal elements form the frame of the wing and as such, they are moved relative to each other to generate a shape change. At the most proximal end of the wing is the humerus which articulates with the scapula of the pectoral girdle. Like the mammalian arm, the humerus articulates on its distal end with the *radius* and *ulna* bones to form the elbow joint. The ulna and radius articulate with two wrist bones, the cuneiform or *ulnare* and the scapholunar or radiale, respectively, which in turn articulate with the hand bone, the *carpometacarpus* (Vazquez, 1992) which is fused, unlike mammalian carpals. The digits have also been reduced to three: the first digit is the alular digit, analogous to the thumb, the second digit is the major digit that forms the distal portion of the skeletal component of the leading edge, and the third digit is the minor digit. The carpometacarpus and the three digits are often collectively referred to as the manus (Cornell Lab or Ornithology, 2004). The restriction to out-of-plane movements such as bending or twisting (Baliga et al., 2019) is attributed to the shape of the two wrist bones which prevent the hyperpronation of the manus during downstroke and the supination of the manus during gliding flight (Vazquez, 1992). The wrist bones are small but their role in guiding skeletal movements during wing extension-folding is significant. Six wing bones: the humerus, ulna,

radius, ulnare, radiale, and carpometacarpus are needed to accurately model *in vivo* wing extension and flexion during flapping flight, forming a six-bar mechanism. Without wrist bones, it is impossible to account for the out-of-plane bending of the carpometacarpus during wing flexion (Stowers, 2017).

Muscles While the skeletal elements are loosely held together by ligaments and cartilage, the muscles are what both constrain and actuate movement of the bones during morphing. Muscles are made up of contractile cells bound together as striated muscle fibres if they are skeletal muscles or spindle-shaped cells if they are smooth muscle. Since muscles are only capable of a pulling, they are often arranged as antagonistic muscle pairs, occasionally with tendons at their attachment points forming a muscle-tendon unit. By acting in pairs, they are capable of reciprocal actions as one pulls and the other relaxes (Cornell Lab of Ornithology, 2004).

Skeletal muscle is responsible for most of the active wing morphing behaviour. The *pectoralis major* and the *supracoracoideus* form the muscle pairs responsible for the up and down motion of flapping flight, with the large multipennate pectoralis initiating downstroke and the smaller supracoracoideus initiating the upstroke (Altshuler et al., 2015). Both muscles are anchored on the keel in the bird's torso. The pectoralis then terminates at the ventral side of the humeral head while the supracoracoideus has a long tendon that travels dorsally through the foramen triosseum before looping back to attach to the dorsal side of the humeral head. The pectoralis is the most well-studied muscle due to its importance in flapping flight but gliding-predominant birds such as frigate birds also use their pectoralis, which have a deep layer *M. pect. major profundus* thought to stabilise the wing against strong upwards aerodynamic forces during high-speed gliding flight (Kuroda, 1961).
Other active changes to wing shape including extension and flexion are controlled by the intrinsic wing muscles. These muscles play a role in steady forward flapping flight but are absolutely necessary for complex manoeuvres such as take-off and landing (Dial, 1992). The exact anatomy of these intrinsic wing muscles can vary among species, with different birds having different fibre lengths or fibre types (Rosser et al., 1994; Welch & Altshuler, 2009), muscle-tendon ratios, numbers of attachment points, tendon structures, or sometimes lacking certain muscles entirely (Ciocca, 2021). Many of these intrinsic muscles are active at different points during the flapping cycle with the magnitude of activation correlating with different flight behaviours. The function of many of these muscles have not been thoroughly examined, but in general, they can both actuate movement when the muscle is used as the agonist or stabilise against excess movement when the muscle is used as the antagonist (Dial, 1992). In situ experiments on one of these muscles, the humerotriceps, commonly associated with elbow extension, have found that this muscle can act as an actuator, brake, or strut depending on activation timing, duration, and contractile frequency (Theriault et al., 2019). The capability to alter muscular function likely plays a role in allowing birds to explore a large variety of wing movements and subsequently different flight behaviours, especially complex manoeuvres (Warrick & Dial, 1998; Berg Robertson & Biewener, 2012).

Wing also have smooth muscle but very little is known about its role during wing morphing. Smooth muscle operates on a much slower time scale than striated muscle and is generally responsible for autonomic, non-voluntary functions in other parts of the body (Cornell Lab of Ornithology, 2004). Hieronymus (2006) was the first to thoroughly identify and describe the smooth muscle anatomy in a pigeon wing. From their attachment points to the flight feather shafts, he hypothesized that they play a role in adjusting wing posture during gliding flight or

over several wingbeats during flapping flight. Smooth muscle may be critical for ensuring a coherent and streamlined wing over a large range of environmental factors and wing movements by increasing or decreasing the range of motion of both covert and flight feathers (Hieronymus, 2006; Chang, 2020).

Feathers The skeleton and the muscles play a key role in active wing morphing by adjusting the position of components in the leading edge of the wing but most of the wing area is made up of feathers, passive structures used for flight, insulation, camouflage, and courtship displays (McKittrick et al., 2012). Feathers are embedded in the soft tissue of the wing at sites called *follicles* along feather tracts separated by feather-less skin called *apteria*. Without feathers, there would be no wing and no lifting surface, and as such, the arrangement and behaviour of feathers during flight is a key factor in dictating wing shape. In general, all feathers consist of a central shaft, separated into a lower portion known as the *calamus* and an upper portion known as the *rachis* upon which the vane extends. The vane itself is made up of branches called *barbs* held together with *barbules* (Cornell Lab of Ornithology, 2004; Ennos et al., 1995).

A bird's wing is made up of different types of feathers. Some feather types are quite specialized, including the semiplumes and down for insulation, the filoplumes for flow sensation (Brown & Fedde, 1993), and powder downs which disintegrate into powder for waterproofing (Cornell Lab of Ornithology, 2004). But the majority of a bird's feathers are contour feathers that streamline the bird. Contour feathers include *coverts* that streamline the area between the active components of the leading edge of the wing and the *flight feathers*. Flight feathers or *remiges* are further divided into two categories: *primaries* and *secondaries*, both attached to bones via ligaments. Primaries are attached to the distal bones of the wing, the carpometacarpus and the major digit while secondaries are attached to bony protrusions along the ulna (Cornell Lab of

Ornithology, 2004). These feathers form the parts of the wing that generate lift and thrust during flight (Worchester, 1996). A special group of coverts known as the *alular feathers*, attached via ligaments to the alula digit, can prevent boundary layer separation at high angles of attack, thus delaying stall (Lee et al., 2015).

Despite having no active contractile ability of their own, feathers are far from static. Feathers are incredibly flexible structures and capable of experiencing large deformations when acted upon by aerodynamic forces. One of the most well-studied examples of this is seen in the slotted primaries of soaring raptors. This feather geometry allows distal primary feathers to be isolated from their neighbours near their tip, causing them to bend upwards due to the upwards lift forces acting on the wing and resulting in a reduction of induced drag (Försching & Hennings, 2012). The effect of wing flexibility on deformation and performance will be discussed further in Chapter 1.3.

1.2 Flexible Materials

Compared to most full-sized and even UAV structures, all the wing components are highly flexible. Avian wing structures are lightweight, strong, and versatile. Understanding the material properties of individual structures and how they work together during wing morphing when subjected to loads can help us understand how these seemingly delicate materials can enable such a wide variety of flight behaviours.

Elasticity The behaviour of a material under an external force depends on the arrangement of its component atoms or molecules and the strength of the bonds between these units. In a Hookean, or linear elastic, material, the atomic structure is well-ordered and tightly bound. When a tensile or compressive load is applied perpendicular to the cross-section of a

material sample, the atoms are pulled apart or pushed together resulting in a deformation that can be normalized to *strain* (ε):

$$\varepsilon = \Delta l / l_0$$

where Δl is the change in length and l_0 is the length of the undeformed material. This deformation alters the balance between the attraction and repulsion forces between them, generating a non-zero net force. Normalizing this force per unit area gives us *stress* (σ):

$$\sigma = F/A$$

where *F* is the applied load and *A* is the cross-sectional area of the undeformed material. For a linear elastic, or Hookean, material, the relationship between stress and strain is linear and when the load is removed, the interatomic forces will return the deformed material back to its original shape according to the same stress-strain relationship. Therefore, no energy is lost. Materials can also be deformed such as in shear when the applied load is acting in the direction parallel to the cross-section of a material. *Shear stress* (τ) is therefore defined as:

$$\tau = F/A$$

where *A* is the cross-sectional area parallel to the applied shear force. This causes *A* to slide relative to the other surfaces. Instead of length change, we define the deformation as *shear strain* (γ). The relationship between stress and strain quantifies the bond strength between atoms, and therefore, the material's ability to resist deformation. For tensile/compressive loads, this is known as *Young's Modulus* (*E*):

$$E = \sigma/\varepsilon$$

And for shear forces, this is known as the *shear modulus* (G):

$$G = \tau / \gamma$$

These material properties are related by:

$$G = \frac{E}{2(1+\nu)}$$

where ν is the Poisson ratio, a ratio between tensile deformations and lateral contractions, $\nu = -\frac{\varepsilon_y}{\varepsilon_x} = -\frac{\varepsilon_z}{\varepsilon_x}$. Other deformations such as bending involve a combination of tensile, compressive, and shear stresses (Vincent, 1982).

However, many biological materials do not exhibit this linear elastic behaviour, and if they do, it is generally only during small deformations. This is because many biological materials are made of long chains of polymers arranged in a certain configuration. As a polymer-based material is deformed, the chains are rearranged, often aligning with the direction of the load. This results in deformation but with very little change in stress as the interatomic equilibrium of the atoms and molecules making up individual units of the polymer remains mostly unaffected. The two components of internal reactions, one due to interatomic/molecular bond strength and the other due to chain arrangement, lead to a non-linear stress-strain response (Vincent, 1982).

Viscoelasticity Biomaterials often have not only non-linear responses, but viscoelastic responses where energy is lost due to material damping. Viscoelastic materials respond in a manner between that of an elastic solid and a viscous fluid. Viscosity (μ) in a fluid is defined as follows:

$$\mu = \frac{\tau}{d\nu/dy}$$

where dv/dy is the velocity gradient. In a Newtonian fluid, μ is a constant and independent of strain or shear rate.

There are various viscoelastic models used to analytically model viscoelastic behaviour, but in this chapter, we will focus on the molecular model which is best understood by considering the material's response to a dynamic test. When a sinusoidal force is applied to the material, a Hookean solid will experience a strain that varies proportionally to stress and the stress-strain response will be in phase. On the other hand, for a viscous fluid, stress will be proportional to the strain rate and the stress-strain response will be out of phase by 90 degrees. A viscoelastic material will have a stress-strain phase lag (δ) somewhere in between 0 and 90 degrees. The stress-strain response can therefore be described by:

$$\sigma_0 = \varepsilon_0 G^* \sin(\omega t + \delta)$$

where G^* is the dynamic modulus, σ_0 is the maximum stress, ε_0 is the maximum strain, ω is the angular velocity, t is time, and δ is the phase lag. This can be expanded into an elastic term and a viscous term:

$$\sigma_0 = \varepsilon_0 G' \sin\omega t + \varepsilon_0 G'' \sin\omega t$$

where G' is the elastic modulus representing energy stored in the deforming material, and G'' is the viscous modulus representing energy dissipated as heat due to viscosity. G' is the real component and G'' is the complex component of G^* and when plotted on a complex plane, the angle between G^* and G' is δ . In other words,

$$tan\delta = \frac{G''}{G'}$$

The degree of contribution from the elastic and viscous component is determined by the deformation of the polymer backbone from the applied stress relative to the molecular displacements within the polymer. The molecular movements in phase with the external dynamic load will approximately represent energy storage while the molecular movements out of phase with the external dynamic load will approximately represent energy lost. This explains why temperature or load frequency can affect the viscoelastic response as the first affects the

molecular displacements of the polymer while the second affects the deformation of the overall polymer (Vincent, 1982).

Yield and Fracture Elasticity quantifies how well a material can resist deformation under an external load, but no material can deform indefinitely. Materials can be permanently altered or catastrophically fail under extreme conditions which is undesirable for wing components critical for flight. Yield or plastic deformation can occur when the covalent bonds between polymer units are broken, and the polymer is rearranged with bonds forming in the new configuration. The material has deformed and even when the load is lifted, it does not return to its original state. Fracture is less well understood for viscoelastic polymers but involves crack formation and propagation before full separation of the material into multiple parts. The strength of a material is determined by the stress at which fracture occurs (Vincent, 1982).

All biomaterials can experience stress-strain responses, yield, and fracture to some degree. However, describing the material properties of biomaterials can be complicated. Many biological structures are anisotropic, meaning that their material properties can vary depending on the axis of measurement, composite, meaning they are made up of multiple different materials working together, and highly non-linear. To further complicate matters, the wing is made up of multiple biomaterials, each with their own material and structural properties determined by their molecular composition and arrangement. Yet it is these material properties that allow all the wing components to enable the multitude of functions a wing must perform so understanding how they individually and collectively contribute to wing shape and aerodynamic performance is incredibly valuable.

1.2.1 Mechanical Properties of the Wing

Bones. Perhaps one of the prime examples of how a structure can meet seemingly contradictory requirements are the avian bones which are simultaneously lightweight to reduce the energetic cost of overcoming gravity, and strong and stiff relative to their weight (Dumont, 2010) to prevent excessive deformation or structural failure under aerodynamic forces.

The primary mineral in bones is hydroxyapatite ($Ca_5(PO_4)_3(OH)$) which is embedded in a collagen-mucopolysaccharide matrix. These individual materials work together as a composite, with the hydroxyapatite sandwiching the collagen matrix in a series of layers. The material properties of the bone structure, therefore, vary with porosity, volume fraction of the mineral phase, and orientation of the fibres. However, the mechanical capabilities of wing bones are only in part dictated by the properties of these individual materials, they are also dependent on the morphological or structural arrangement of these materials. It is through structure that bones achieve their lightweight but strong capabilities.

Avian bones consist of cortical bone surrounding a less-dense medullary core. The cortical bone is surrounded by a periosteal and endiosteal sheath (Novitskaya et al., 2017). The cortical bone has a density of 2.15 g/cm³, the highest out of all animals with bats coming in at a close second. However, despite their dense bones, they are incredibly light. The lightweight bones are a product of the pneumatization of the bones, reducing the density of the medullary core by filling it with air instead of marrow, and reducing the thickness of the cortical layer. However, thin-walled structures are prone to buckling under loads. To prevent buckling, avian bones are reinforced with ridges arranged at a 45° angle on the interior walls of the cortical layer to resist torsional stresses (Sullivan et al., 2017) and struts that stretch across the hollow middle to prevent ovalization and ensure bending resistance (Novitskaya et al., 2017). The exact

morphology can vary among bones within an individual and among species in a way correlated with functional requirements. Birds that that dive or swim such as cormorants or penguins have thicker cortices compared to soaring birds like raptors or albatrosses (Habib & Ruff, 2008). This reduces buoyancy during swimming and strengthens the bones against the higher loads of underwater flapping or diving impact (Sullivan et al., 2017).

Muscles and Integument The contractile elements of muscles are actin and myosin which interact and slide past each other via myosin-actin cross-bridge formation and activation. The stiffness of the muscle contractile units will therefore be dependent on the behaviour of the cross-bridges. Muscle fibres without cytoskeletal support have been found to have a Young's modulus of 38kPa when relaxed (little cross-bridge formation), 71kPa when activated (more cross-bridges formed and activated) and 156kPa when in rigor (cross-bridges formed and permanently locked) in rat soleus muscles (Ogneva et al., 2010). The viscoelastic and dynamic nature of muscles and the variation in structure, fibre length, fibre type (Rosser et al., 1994; Welch & Altshuler, 2009), muscle-tendon length, and functional behaviour due to stimulation timing, stimulation duration, and activation length (Theriault et al., 2019; Rack & Westbury, 1974) make it difficult to characterise the mechanical properties of the wing muscles. The density of avian striated muscle has often been approximated as $\rho_m = 1060 kgm^{-3}$ (Pennycuick, 1998), but it is unlikely that this is consistent for every muscle in the wing. The functional variation in mechanical properties can be inferred from some in vivo measurements; pigeon supracoracoideus experience significantly larger stresses with relatively little change in strain during ascending flight compared to descending flight, whereas the pectoralis experiences consistently less stress for the same amount of strain (Tobalske & Biewener, 2008). As such, we can infer that variation among muscles in their forces of contraction and length changes during

contraction during different flight modes can alter the mechanical properties such as stiffness or work absorption/output (Biewener et al., 1998; Tobalske & Biewener, 2008, Theriault et al., 2019).

While the pectoralis, supracoracoideus and intrinsic wing muscles alter skeletal configuration, other muscles have attachment points to the integument and may modulate the mechanical properties of the integument similar to the *plagiopatagialis propria* wing membrane muscles in bats (Cheney et al., 2014). The outermost layer of the integument is the epidermis or *cutis*, which is usually thin and highly elastic. This allows for stretching during the large kinematic changes needed for flight. An elastic membrane, the *lamina elastica*, envelopes all dermal muscles and separates the *cutis* layer from the underlying *dermis*. The dermis is further separated into the *stratum superficiale*, densely made up of collagen fibres, and the *stratum profundum*, less densely packed with collagen fibres (Stettenham, 2000). Collagen is primarily made up of glycine, proline, and hydroxyproline amino acids which promotes a triple helix fibre shape. This structure has a non-linear J-shaped stress-strain response under tension, providing the opportunity to 'select' different mechanical responses of collagen through the pre-loading of collagen fibres (Vincent, 1982).

The epidermal and dermal layers, along with an array of muscles, connect the feathers to the rest of the bird. Both striated and smooth muscles with attachment points on feathers have been found. Erector and depressor feather striated muscles attach indirectly to feather follicles and the subcutaneous fascia. Based on anatomical arrangement, it has been theorized that these muscles activate to either engage feather movement or resist aerodynamic loads (Homberger & De Silva 2000). Smooth muscle has been identified in the bird's wing, but its *in vivo* functions remain unknown (Hieronymus, 2016). In body contour feathers, smooth muscle connects the

follicles of plumulose feathers (e.g., down or semiplumes) to the dermal layers in the feather tracts and highly elastic tendons. It has been proposed that these smooth muscles control the local elasticity of the integument by pulling on these elastic fibres (Homberger & De Silva, 2003). Like the shoulder and intrinsic wing muscles, both striated and smooth muscles could be differentially activated or deactivated to modify the anchoring stiffness of the feathers and change the feather range of motion (Hieronymus, 2016). While the role of flight feather muscles and other surrounding soft tissue is unclear, we can infer the importance of passive soft tissue elasticity and muscular activation in feather attachment strength. Dissection and removal of the dermal layers and muscles significantly reduces the ability of even the flight feathers to stay in place apart from the most distal primaries. Furthermore, inhibition of neural output from the brain reduces the amount of force necessary to pluck covert feathers from the skin while activation of neural activity via electrical stimulation can increase the anchoring force to the feathers (Ostmann et al., 1964). This preliminary evidence suggests that soft tissue components, in some combination or another, contribute to holding the feathers in their proper place and maintaining the mechanical properties of the wing as a whole.

Feathers The importance of integument muscles on modulating the stiffness of feather range of motion lies in the fact that flight feathers on the wing that make up most of the lifting surface and are fundamental to the bird's ability to fly. As such, how they move and deform under aerodynamic loads is critical for aerodynamic performance. Feathers are made of β -sheet keratin proteins and all feathers have been found to be mostly of the same molecular weight (MW=11 000) and amino acid composition. These animo acids of the β -sheets interact to form a slow helical twist configuration (Vincent, 1982). While keratin has a Young's modulus on the order of magnitude of Gigapascals (GPa, 10⁹), the exact arrangement of these β -sheet helices

can result in some variation within a feather (Wang & Meyers, 2017), among feathers, and among species. Additionally, like all viscoelastic materials, mechanical properties will also vary with strain rate, or the frequency of a dynamic load generated by flapping flight (Bonser, 1996). Therefore, the Young's modulus increases towards the feather tip (Bonser & Purslow, 1995) due to an increase in keratin fibre alignment (Cameron et al., 2003) and with loading frequency. Many of the past studies focused exclusively on the feather cortex, the fibre-reinforced composite of the rachis that surrounds an inner medullary foam. Despite both being made up of keratin, their material properties are dramatically different; cortex density has been reported to be 1.15g/cm³ and medullary foam density has been reported to be around 0.05-0.08g/cm³. The Young's Modulus of the medullary foam also varies dramatically within a feather, going from 0.005-0.065GPa at the base to 0.3-1.58 at the tip, whereas the cortex stays relatively consistent. Some studies have suggested that the medullary foam does not contribute much to the rachis' overall bending stiffness (Bonser, 1996), although it may have significant contributions in preventing buckling failure (Bonser, 2001; Wang & Meyers, 2016).

Young's modulus might not vary much beyond an order of magnitude but data has shown that flexural stiffness does vary on a greater scale with feather location (Purslow & Vincent, 1978), feather type, and between species (Pap et al. 2015). It is structural geometry that influences this variation. The stiffest parts of the rachis correspond to a more square-like cross sectional area which delays "ovalization" (Wang & Meyers, 2017), a deformation to a more oval cross-section under load which decreases the second moment of area and reduces stiffness. Larger birds tend to have stiffer feathers relative to smaller birds (Worcester, 1996). Migratory blackcaps have been found to have stiffer (bending) and narrower rachises compared to sedentary blackcaps living in the same area, and this difference was largely explained by changes

in structural properties like rachis width and mass (De la Hera et al., 2010). Feather porosity is also variable within a feather between inner and outer vane, although it is not agreed upon how this affects the aerodynamic forces (Aldheeb et al., 2016). Variations in the mechanical properties through structural changes in feathers as well as other wing components can provide support to high load regions. However, it is unknown whether or not the functional necessity of load support during flight actually drove this variation in structure.

Multi-component Wing. Avian wing morphing is only successfully achieved when these passive and flexible feathers are coordinated by the active musculoskeletal movements. The mechanical properties of the material holding feathers together are critical for coordinating feather movement during wing morphing in a pigeon-inspired bio-hybrid robot (Chang et al., 2020). Feather microstructure on the vane barbules allow feathers to lock with their neighbours through a Velcro-like effect in a direction-dependent manner – microstructures generate larger attachment forces during extension compared to flexion (Matloff et al., 2020). Overall, structures on the feathers and the elasticity of the soft tissue ensure the appropriate coupling between all wing components throughout wing morphing *in vivo* and the mechanical properties of interacting structures may differ from those of the individual components. As such, the interaction between components of a whole wing during wing morphing should be accounted for when considering how a flexible wing behaves under aerodynamic load.

1.3 Fluid-Structure Interactions

The interaction of a moving or deforming structure with fluid flow is a reciprocal effect where fluid forces act to deform the solid and solid deformation alters the fluid flow. Bird wings are much more flexible than modern aircraft structures and experience high strain deformations. As a result, flow can be significantly altered due to these deformations which will, in turn, have

large effects on the aerodynamic performance. Aeroelasticity is concerned with the interaction of the inertial, elastic, and aerodynamic forces of a flexible solid experiencing air flow. Understanding aeroelastic responses of a system is important for understanding flight stability, structural vibrations, and static deformations in aeronautical engineering, and it also has valuable contribution to civil, mechanical, and nuclear engineering as well (Dowell, 2015). Aeroelasticity can be further divided into two types: static and dynamic. The analytical models for various types and sub-types of aeroelasticity are many and will not be covered in detail. This thesis will only provide a qualitative overview of aeroelasticity. For more details, please consult Dowell (2015).

Static Aeroelasticity Static aeroelasticity deals with the interaction of steady flow aerodynamics and solid mechanics. As air moves over the wing, aerodynamic forces act over the entire surface of the wing. For any loaded point on this flexible wing that is not on the elastic axis, these aerodynamic loads will generate aerodynamic moments around this axis. Deformation of the wing will also result in elastic moments around the elastic axis as the atomic bonds seek to return to an equilibrium state. The wing will deform until these moments reach equilibrium, a phenomenon known as *divergence*. Divergence can occur over any of the structure's degrees of freedom, and for a wing, can be result in bending, twisting, or a combination of both, and sweep. Divergence can lead to consequences such as control reversal, where wing deformation generates aerodynamic forces and moments counteracting desired control output, or structural failure, where deformation exceeds the maximum strain or strain rate tolerable (Dowell, 2015).

Dynamic Aeroelasticity Dynamic aeroelasticity deals with the interaction of aerodynamic, elastic, and inertial forces as well. Dynamic aeroelasticity concerns itself with dynamic stability problems such as flutter or the response to external dynamic disturbances such

as gusts. Although there are also dynamic aeroelasticity problems that occur in special cases such as transonic flight (buffeting, transonic aeroelasticity) or propellers specifically (propeller whirl flutter), these phenomena are not relevant for avian flight and will not be discussed further (Dowell, 2015).

Flutter is a dynamic instability involving the positive feedback between structural deformations and the aerodynamic forces and is dependent on coupling between stiffnesses along different degrees of freedom. The most basic type of flutter is caused by a coupling of two structural modes along two degrees of freedom: bending or plunge and twisting or pitch. Aerodynamic forces cause the airfoil to pitch upwards. This pitch up increases the angle of attack, increasing the lift force. The wing will bend upwards due to the increase in lift while pitching down back due to the elastic moment caused by torsional stiffness. However, inertial forces can cause the wing to continue pitching down, now generating negative lift and causing the wing to bend downwards before it rotates upwards again. The exact plunge and pitch behaviour depends on the frequencies of plunge and pitch modes which, in turn, is dependent on flight speed. When the frequencies of both modes are the same, we have flutter resonance. Aeroelastic flutter can be modelled with the following equation of motion using the assumption of simple harmonic motion and linear structural behaviour:

$$\left[\boldsymbol{M}_{\boldsymbol{h}\boldsymbol{h}}p^{2} + \left(\boldsymbol{B}_{\boldsymbol{h}\boldsymbol{h}} - \frac{\rho c V \boldsymbol{Q}_{\boldsymbol{h}\boldsymbol{h}}^{I}}{4k}\right)p + \left(\boldsymbol{K}_{\boldsymbol{h}\boldsymbol{h}} - \frac{\rho V^{2} \boldsymbol{Q}_{\boldsymbol{h}\boldsymbol{h}}^{R}}{2}\right)\right] \{u_{h}\} = 0$$

where M_{hh} , B_{hh} , K_{hh} , Q_{hh}^{I} , Q_{hh}^{R} are the modal mass, modal damping, modal stiffness, generalized aerodynamic damping, and generalized aerodynamic stiffness matrices respectively, ρ is air density, c is the mean aerodynamic chord length, V is the airspeed, k is the reduced frequency, p is $i\omega$ where $= i = \sqrt{-1}$, and u_h are modal displacements. While this equation is complex and can only be iteratively solved, it reflects the fact that aeroelastic flutter displacement is dependent on structural properties such as stiffness, damping, and mass distribution, as well as air speed (Hebert et al., 2018). Resolving the aeroelastic response allows us to characterise the flutter response as a function of flight speed which is used to predict the maximum speed an aircraft can employ without risking aeroelastic instabilities. Stable flutter occurs if the deformation time series has an amplitude that decreases with time and unstable flutter occurs in the deformation time series has an amplitude that increases with time. Transition from stable to unstable flutter occurs at the critical flutter velocity. Flutter velocity can also be found by analysing aeroelastic responses in the frequency domain and locating the velocity at which the imaginary component of the complex frequency becomes negative (Dowell, 2015).

In aeronautical engineering, aeroelastic response is generally perceived unfavourably as excessive deformation can increase the energy requirements for flight (Patil, 2011), result in undesirable control responses (Dowell, 2015), or end in structural destruction. Aircraft design must account for the aeroelastic responses over the entirety of the aircraft's performance envelope to ensure no disastrous consequences (Bisplinghoff & Ashley, 2013). However, both static and dynamic aeroelasticity have been found to enhance locomotory performance in nature.

1.3.1 Structural Dynamics in Nature

Fluid-structure interactions affect propulsors throughout the animal kingdom (Lucas et al., 2014), and have been found to often provide an enhancement to performance or promote stability against static aerodynamic loads (Försching & Hennings, 2012) or sudden gusts (Gamble et al., 2020). During flapping flight, increases in camber during the upstroke promote lift-enhancing leading-edge vortices (Mountcastle & Combes, 2013) resulting in a lower power requirement for flight (Hamamoto et al., 2007). Studies on pectoral fin oscillation in swimming

fish models indicate, however, that performance does not continue to increase with flexibility indefinitely. Performance only increases at a particular stiffness value for a given oscillatory frequency, with lift and thrust efficiency decreasing for fins more flexible or more rigid than that optimal stiffness value (Esposito et al., 2012). It has been proposed that maximum locomotory performance occurs when structural movement frequency is near the resonant frequency. Passerine and goose-inspired wings capable of spanwise bending can achieve a flutter frequency near the resonant frequency resulting in a negative mean power, meaning that energy is extracted from the surrounding fluid to generate thrust (Kodali et al., 2017), however this has not been measured directly in actual birds.

Dynamic aeroelasticity is an important phenomenon to study in the context of bird wings. Birds, like many other animals, are incredibly resistant to environmental perturbations even though some of the gust velocities can be on the same order of magnitude as the bird's flight speed, which would dramatically change the local flow direction near the wing (Zhang et al., 2018). Feather flutter has also been observed in at least 27 species (Clark & Prum, 2015) although it has been best studied in the context of non-vocal communication. Flutter in the tail feathers (Clark et al., 2013) or primary flight feathers (Clark et al., 2016) have been observed during courtship displays. Flutter has also been observed during regular flight as well with flutter speed and frequency dependent on individual feather shape (Clark & Prum, 2015) and featherfeather interaction (Clark et al., 2016). Unlike aircraft wings which primarily experience bending and twisting modes, feather flutter can present in at least four categories of mode shape which can be localised to a specific location on the feather: bending, torsion, tip flutter, and trailing vane flutter (Clark et al., 2011). Interspecific variation in the mechanical properties result in functionally useful changes in flow control, further indicating the importance of fluid-structure

interactions in ensuring that the avian wing can meet the behavioural requirements of a bird throughout its life. One unique example can be found in owls, famed for their near-silent flight. Owl feathers have much higher damping capabilities than other tested bird feathers. This increase in energy dissipation through molecular friction damping rapidly eliminates structural responses and reduces likelihood that the wing will experience flutter close to the wing's resonant frequency. This could be a mechanism that contributes to preventing mechanical vibration responses in the shaft that may generate sounds during flight (Gao et al., 2014).

1.3.2 Aeroelastic Tuning

Aeroelastic response can be beneficial or detrimental depending on the desired task. The ability to tune structural responses to meet performance requirements over changing environmental conditions would be valuable in promoting behavioural adaptability. Static aeroelastic responses such as wing twist can be adjusted to reshape the spanwise lift distribution and reduce induced drag. This can be done entirely passively or aided by active control to reduce optimization time (Weisshaar & Duke, 2006). Tuning of dynamic aeroelastic responses to modify a wing's flutter frequency or resonant frequency has also been proposed to improve the efficiency of oscillating propulsors (Ahlborn et al., 2006).

Flutter is caused by the interaction between elastic, inertial and aerodynamic forces so modifying one or more of these forces will affect the flutter response. Aerodynamic forces are primarily dictated by wing shape and fluid properties. That is, for a given wing shape moving at some speed V_{∞} , flutter speed and, therefore, flutter stability will be determined by the elastic and inertial properties of the wing. Flutter can be beneficial or detrimental to performance and it has been proposed that this is determined by whether flutter or other oscillatory movement frequency coincides with the resonant frequencies of the structure (Kodali et al., 2017). Ahlborn et al.,

(2006) proposed that the resonant frequency of a structural system can be tuned by modifying the mass moment of inertia or vertical acceleration. Modifying the mass moment of inertia may occur during wing folding (Harvey et al., 2022 in press) and analytical studies have found that shifting an added weight towards the wing tip or towards the trailing edge can decrease flutter frequency (Fazelzadeh et al., 2009). Structural rearrangements could also change the location of the inertial or elastic axis which can affect the relationship of the natural frequency with airspeed and modify the wing's sensitivity to gusts (Zhang et al., 2018). Numerical analyses have found that increased damping also broadens the resonance curve (Ahlborn et al., 2006), creating a large range of resonant frequencies that could be matched by the movement frequency to ensure a stable, thrust-producing mode where energy is transferred from structural movement to the flow for thrust generation (Patil, 2001). Since polymers have non-linear mechanical properties, damping and stiffness properties could be modified for the tuning of one or more resonant frequencies by pre-loading or pre-stretching materials to change where on the stress-strain curve the structures are operating. Further modulation of the mechanical properties could occur with activation of muscles or restriction of movement via ligaments (Ahlborn et al., 2006).

1.4 Objectives

While the ability to tune aeroelastic response for a given flight mode can obviously provide a benefit, it is unknown whether avian wing structures can do so. It is possible that any structural changes during wing morphing do not provide any benefits to aerodynamic performance and are simply by-products of other functional needs or evolutionary constraints.

The goal of this thesis is to begin to explore how coupled structural changes during wing morphing and flight can affect aerodynamic performance by examining the importance of aerodynamics on feather morphology and the effect feather arrangement has on aeroelastic

response and performance during wing morphing. In general, this thesis will answer the question: <u>"How can avian wing components and their arrangement in a structural system affect</u> <u>aerostructural responses and flight performance?</u>" This will be achieved by answering the following sub-questions in their respective data chapters:

<u>Chapter 2:</u> How important is aerodynamic performance in explaining feather morphology variation?

<u>Chapter 3:</u> How does wing extension-flexion affect the local mechanical properties of the pigeon wing?

<u>Chapter 4:</u> How can changes to wing mechanical properties coupled to wing extension-flexion during gliding flight affect aerostructural responses and flight performance?

Chapter 2: Aerodynamic performance covaries strongly with the largest axis of variation in feather shape among species.

2.1 Synopsis

Flight has evolved at least four times, in pterosaurs, insects, birds, and bats. Birds have achieved flight with a unique lifting surface made predominantly of multiple passive elements – feathers. Feathers are one of the most complex integumentary appendages amongst vertebrates, capable of serving a wide variety of functions, including thermal insulation, water resistance, courtship display, camouflage, and most prominently, flight (McKittrick et al., 2012). Despite working together to generate a cohesive wing, each individual feather contributes to the bird's flight ability. During a moult, a natural process in which birds lose old feathers and regrow new ones, feather gaps are formed and aerodynamic performance metrics such as the lift slope $\left(\frac{\partial c_L}{\partial \alpha}\right)$, where C_L is the lift coefficient and α is the angle of attack, are reduced (Hedenström & Sunada, 1999).

Feathers each consist of a main shaft, the rachis, and branching barbs which make up the vane, but this basic feather morphology also varies within a wing, among individuals and among species. Many past studies have tried to elucidate the significance of this variation, often by characterizing variation in one or two specific structural parameters of feather morphology and relating these changes to flight style or ecology (Pap et al., 2015; Osváth et al., 2020). Feather length (Wang et al., 2011) and vane asymmetry (Wang et al., 2019; Garner et al., 1999) have featured prominently due to their relationship with the onset of the evolution of avian flight. Variation in vane asymmetry in particular can affect how a feather responds to an aerodynamic

load, and in general, these patterns seem to achieve a structural function meeting the local aerodynamic forces encountered by each feather. For example, distal feathers, which are more likely to bend or twist during flight, have a vane asymmetry that would allow them to better resist to out-of-plane loads compared to proximal feather vanes (Ennos et al., 1995) or prevent aeroelastic instabilities (Försching & Hennings, 2012). Although many of these morphological trends were broadly consistent in multiple species, the exact magnitude or scale of the variation can differ (Osváth et al., 2020; Dawson, 2005), suggesting that variation among species in wing morphology or behaviour may also influence feather morphology.

Wing shape and flight behaviour, such as flapping versus gliding flight kinematics, can influence the local flow and aerodynamic forces over the wing. Due to the variation in aerodynamic forces over the wing, different parts of the wing are associated with different aerodynamic functions for a given locomotory gait. For example, feathers in the distal and proximal portion of the wing primarily experience high aerodynamic forces perpendicular to the vane for lift production during gliding flight. But during flapping flight, the complex movements of the distal wing for thrust production can generate forces in other directions as the wing moves through the air (Worchester, 1996). Therefore, the primary flight feathers, located on the distal wing and fixed to the carpometacarpus, often experience more directional variation in aerodynamic forces during wing morphing compared to the secondary flight feathers, located on the proximal wing and fixed to the ulna. A third type of flight-relevant feathers are the alular feathers, attached to the first digit or thumb of the wing. These feathers, located on the leading edge of the distal wing, are associated with a unique aerodynamic function among many other uses. Alular feathers help birds perform steep descents by maintaining an attached boundary layer over the wing and preventing stall (Lee et al., 2015). The variation in aerodynamic forces

over a wing due to location and flight behaviour is paralleled by variation in feather morphology (Ennos et al., 1995) even though flight feathers are rarely exposed to the airflow in isolation and interact to form a coherent wing surface. The correlation between individual feather shape and aerodynamic performance as determined by a bird's wing shape and behaviour suggests that feather shape has likely been influenced by aerodynamic function throughout evolutionary history (Wang et al., 2011).

2.1.1 Objectives

Feathers are clearly an important wing structure for avian flight and show remarkable variation coinciding with aerodynamic performance, yet the link between the evolution of feather morphology and flight capabilities over time is still unclear. Further clouding the issue is that multiple morphological changes could be tied to the onset of flight in proto-birds (Wang et al., 2019), or that extant birds are capable of behavioural modifications to overcome morphological disadvantages and constraints (Hedenström & Sunada, 1999).

This study seeks to shed light on the relationship between aerodynamic function and feather shape using a phylogenetic model across multiple species without dictating a specific morphological parameter to analyse. Throughout this study, we will answer the following questions:

- What are the main characteristics of variation in feathers within a wing, within species, and between species?
- 2) How does two-dimensional feather shape affect aerodynamic performance?
- 3) Does aerodynamic performance best explain variation in feather shape compared to feather location, feather type, or phylogenetic covariance?

2.2 Methods

2.2.1 Collection of Feathers

We obtained flight feathers from 38 adult specimens spanning 23 species representing a broad coverage of avian phylogeny, mass range, and flight styles. These specimens were frozen cadavers acquired from the Cowan Tetrapod Collection at the University of British Columbia's Beaty Biodiversity Museum (Vancouver, BC). Once the specimens were defrosted, flight feathers and alula feathers were extracted from the wing by carefully cutting away the tissue around the base of the feather shaft. Each feather was labelled by feather type: primaries, secondaries, or alula, and by location within that group of feathers, with the count starting with the feather closest to the wrist. Feathers that were too damaged or not fully formed were eliminated from the data set.

2.2.2 Image Processing

The feathers were placed on a green screen and photographed. A custom Image J macro first traced the rachis using a curved line, then separated the feather from the background, and finally outlined the feather vane (Figure 2.1A). A 1cm scale bar on the green screen was used to ensure rachis and vane outlines were to scale. Feathers where the background could not be reliably separated were eliminated from the data set, leaving 989 feathers in total.

2.2.3 Geometric Morphometrics

Two-dimensional shape analysis was performed using the *Momocs* package in R (Bonhomme et al., 2014). Vane and rachis coordinates were converted into outline and open class objects respectively. The vane outlines were smoothed over 200 iterations using a simple moving average and then interpolated so that each outline had 500 coordinates. All the vanes and rachises from left wings were flipped longitudinally so that none of the variation was due to wing

choice. The coordinates were all re-ordered so they start at the feather tip. We then used a full generalized Procrustes function which translated the vanes to superimpose their centroids, scaled the vanes by centroid area, and rotated the vanes to align the feather tip and base. Consequentially, all remaining variation could be attributed to shape alone.

The *Momocs* R package is an open-source package that helps quantitatively describe shape and its variation. *Momocs* quantified the deviation of outline points from the first point for the x and y coordinates separately, and then fit a Fourier series to this curve. A *Momocs* function estimated that 9 harmonics of the Fourier series were able to capture 99% of the harmonic power. Therefore, we quantified feather vane shape using an elliptical Fourier transform that output a list of components for the 9 harmonic coefficients. A principal component analysis was used to find axes of variation in these coefficients (Figure 2.1.B, C). Since PC1 and PC2 accounted for just under 72% of the total variation, all subsequent analysis on feather shape variation refers solely to these first two axes of variation.

2.2.4 Aerodynamic Modelling

We used an open-source code, XFLR5 (http://www.xflr5.tech/xflr5.htm), to analyse the effect of vane shape as an airfoil on aerodynamics. XFLR5 uses potential methods, simplified models of fluid flow, to resolve the aerodynamic forces over a 3D airfoil. As a result, these equations are only valid for inviscid, irrotational, time-independent, and incompressible flow. XFLR5 also does not make use of an interactive boundary layer; it interpolates results from the local wing lift from 2D XFOIL airfoil analysis on the boundary layer but does not modify the geometry of the surfaces and disturb the inviscid potential flow. This adds the additional limitation that XFLR5 results are only valid at low angles of attack and high Reynolds numbers. Despite these limitations, this method allows us to evaluate the trends in aerodynamic

performance in due to vane shape for a large sample of feathers quicker than with experimental measurements.

We modified the thinnest airfoil in the NACA database, NACA-006, to represent the 2D airfoil. This airfoil had a thickness of 2%, a maximum thickness position of 29.64%, a maximum camber of 0.17%, and a maximum camber position of 100%. It was meshed with 100 panels. Batch analysis was used from Reynolds number of 50000 to 500000 in intervals of 50000 and an angle of attack of -5 to 20 in intervals of 1, although some angles of attack at higher Reynolds numbers did not converge after 500 iterations.

We modelled the normalized vane shape output from the geometric morphometrics analysis as a three-panel wing in XFLR5. The vane was split into three sections equally along its span: the root, the middle, and the tip of the feather. A line was fit to the rachis of the root section and the angle formed by that line and the y axis was used to rotate the feather so that the root section is parallel to the y axis. For each section, sweep was defined as the angle of a line fitted to the rachis and span was defined as the difference between the maximum and minimum y value. We subset the outline points corresponding to the root-most and tip-most 10% of each section and defined the root chord and tip chord for that section respectively as the difference between the maximum and minimum x value of the subset data. To prevent the possibility of a chord of zero at the root and tip of the feather, we first removed the root-most third of the root section and the tip-most fifth of the tip section before proceeding as previously described. We chose to subset or remove data to the described quantities through trial and error, ensuring enough subset points to accurately represent the width of the vane. The three-panel geometry was overlayed against the outline of the feather and visually inspected for accuracy (Figure 2.1A).

This geometry was built in XFLR5 as one of the two wings of a symmetrical 3D plane. A vortex panel method, fixed speed type analysis was used. Viscosity (μ) was set at 1.813 × $10^{-5} Pa \cdot s$ and density (ρ) was set at 1.225 kg/m^3 . The reference area was calculated using a *Momocs* function on the vane outline. The reference span was taken as the sum of the span of the three panels. The reference chord was calculated using a custom function to determine the mean aerodynamic chord based on an algorithm determined by Diehl (1942). The approximate vane shape modelled using 3 panels was iteratively divided into an increasing number of panels to a maximum of 100 panels and the mean aerodynamic chord found until it did not deviate by more than 5×10^{-5} units. The final value was used as the reference chord (c_{mac}). The reference velocity was then calculated using a Re = 100000:

$$v_{ref} = \frac{Re\mu}{\rho c_{max}}$$

where μ is the dynamic viscosity ($\mu = 1.813 \times 10^{-5} Pa \cdot s$) and ρ is the density ($\rho = 1.225 kg/m^3$).

Finally, the mass of the feather was taken from the measured specimen values. XFLR5 ran this analysis for angles of attack between -5 to 20 in intervals of 1 and output aerodynamic coefficients as a function of angle of attack. As drag values calculated by XFLR5 are not very reliable, we evaluated aerodynamic performance by looking at the slope of the lift coefficient as a function of the angle of attack $\left(\frac{\partial C_L}{\partial \alpha}\right)$.

2.2.5 Statistical Analysis

To analyse how feather shape covaries with aerodynamic performance, location of the feather on the wing, or feather type, we first must account for phylogenetic history. Phylogenetic relation was determined using the maximum clade credibility (MCC) tree from Baliga et al.

(2019) pruned to the 23 species used in this study (Figure 2.2A). We then used a Bayesian multilevel model provided by the *'brms'* package in R accounting for both phylogenetic history with a covariance matrix and individual variation within species with specimen identity as random effects (Bürkner, 2017). We used a normal distribution as a prior for the fixed effects and a half-student-t distribution as a prior for the random effects. The following models were fit for the fixed effects:

where *PC* is either PC1 or PC2. Two Markov chains with 8000 iterations each were used to converge upon a posterior probability distribution.

To select the best model, Leave-One-Out (LOO) cross validation was performed to evaluate model fits. We also built a 6th model with the same fixed effects as (a), but without including the effect of phylogenetic autocorrelation to evaluate the importance of including phylogeny in the error estimates of the model. This was further evaluated by taking species means and running a phylogenetic generalized least squares analysis on model (a) using the *nlme* package in R (Pinheiro et al., 2021) using Pagel's lambda correlation to quantify phylogenetic signal (λ). This model was rerun using 200 alternative trees generated from BirdTree.org (https://birdtree.org) with 100 trees from the Ericson All Species set and 100 trees from the Hackett All Species set. We then evaluated the effect sizes of the fixed effects in the best model using Cohen's f^2 which is defined as:

$$f^2 = \frac{R_{AB}^2 - R_A^2}{1 - R_{AB}^2}$$

where A is the variable of interest and B is all other fixed variables. R^2 is the coefficient of determination which measures the proportion of variation in the dependent variable that is explained by the independent variable (Selya et al., 2012). This procedure was run over the 100 trees generated from BirdTree.org as well as the MCC tree.

2.3 Results

2.3.1 Feathers vary mostly in aspect ratio and curvature with feather type groupings along the PC1 axis

Flight feathers display a great deal of variation in shape despite the shared function of enabling flight locomotion (Pap et al., 2015). Using geometric morphometrics methods, we found that the first principal component (PC1) described 58.5% of the feather shape variation in the wings of 23 bird species and the second principal component (PC2) described 13.7% of the feather shape variation (Figure 2.2A), combining to a total of just under 72% of the total variation (Figure 2.2B). The morphospace generated by the *Momocs* R package suggested that PC1 primarily corresponds to feather aspect ratio and PC2 primarily corresponded to feather curvature or sweep (Figure 2.2A). The other principal components make up the rest of the shape variation but each of these axes is responsible for a much smaller portion of the feather shape (Figure 2.2B).

Feather type grouped along the PC1 axis: alula feathers had the lowest aspect ratio, secondary flight feathers had intermediate aspect ratio as well as the largest variation across PC2,

and primary flight feathers had the highest aspect ratio (Figure 2.2C, D, E). This grouping along the PC1 axis led us to use feather type as an interaction term for all other explanatory variables in further statistical analysis. This pattern was also seen in the PC scores for individual birds (Figure 2.3). In 12 out of 23 species in this study, multiple individuals were sampled per species. We observed high repeatability in the [PC2, PC1] feather morphospace between individuals of many species (e.g., compare *Colaptes auratus* vs. *Aechmorphorus occidentalis* in Figure 2.3). However, there were noticeable exceptions, such as *Corvus corax*, where there was considerable variation observed in the morphospace between individuals.

2.3.2 Aerodynamic performance $\left(\frac{\partial C_L}{\partial \alpha}\right)$ accounts most of the shape variation along PC1

We used an inviscid model for computational efficiency in XFLR5 to estimate aerodynamic performance of these feather shapes. Due to the inviscid nature of these models, the viscous-based drag results were unreliable, so we used a lift-based aerodynamic parameter $\left(\frac{\partial C_L}{\partial \alpha}\right)$ to evaluate aerodynamic performance. Upon initial observation, there seemed to be a correlation between $\frac{\partial C_L}{\partial \alpha}$, feather type, and also the location of the feather on the wing along the span with the PC1 axis: high $\frac{\partial C_L}{\partial \alpha}$, primaries and a distal position are associated with high aspect ratios on the right hand side of the PC1 axis while low $\frac{\partial C_L}{\partial \alpha}$, alulas and a proximal position are associated with low aspect ratios on the left hand side of the PC1 axis (Figure 2.3).

We confirmed that $\frac{\partial C_L}{\partial \alpha}$, feather type, and feather location together best explained variation in PC1 using LOOIC scores. The lowest LOOIC score for PC2 corresponded to the model that only considered feather location interacting with feather type, but the standard errors on all LOOIC values for PC2 large enough to indicate that no one model fit better than others (Table 2.1). Note that a model with only individual bird as a random effect and discounting phylogenetic covariance, had a LOOIC similar in value to that of the full model, but phylogenetic signal scores were high enough that we chose not to discount the effect of phylogeny and performed all further statistical analysis on the full model. This model was able to predict 92.9% of the variation in PC1 ($R^2 = 0.9288$) (Figure 2.4A, B) but only 21.3% of the variation in PC2 ($R^2 = 0.2131$).

Fixed Terms	PC1	PC2
$\frac{\partial C_L}{\partial \alpha}$ *feather type,	-4590.6 ± 89.8	-3643.8 ± 128.4
feather location* feather type		
$\frac{\partial C_L}{\partial \alpha}$ *feather type	-4322.4 ± 89.6	-3618.4 ± 126.4
feather location*feather type	-3366.6 ± 91.1	-3644.3 ± 130
feather type	-2974.6 ± 87.5	-3620 ± 127.7
none	-2107.4 ± 69.8	-3568.5 ± 126.1

Table 2.1 Leave-One-Out Model Fits for PC1 and PC2 and the standard error

Feather shape varied mostly with aerodynamic performance and very little influence from phylogenetic signal. We used Pagel's λ to evaluate the contribution of phylogenetic signal in the residual error of our model. $\lambda_{mean} = 0.361$ for PC1 and $\lambda_{mean} = 0.177$ for PC2 when calculated over 200 different phylogenetic trees (Figure 2.4C). As such, feather shape does not strongly affect the relationships among feather shape, feather type, feather location, and lift slope. Local effect size determined by Cohen's f^2 (Table 2.2, Figure 2.4D). As predicted, feather type accounted for a good deal of the variation in PC1, but the aerodynamic performance metric

 $\frac{\partial c_L}{\partial \alpha}$ accounted for more of the variation in PC1 than feather type. Feather location accounted for the least variation in PC1 and was only made relevant when combined with $\frac{\partial c_L}{\partial \alpha}$. Because the model was already a poor fit for PC2, none of the fixed effects in this study contributed much to explaining the variation in PC2. Overall, this study suggests that the variation we see in feather shape may be closely related to aerodynamic performance.

Fixed Effect	PC1	PC2
$\partial C_{L_{\rm rel}}$	2.477 ± 0.002	0.008 ± 0.0005
$\frac{-2}{2}$ *feather type	2.477±0.002	0.000±0.0005
00		
feather location*feather type	0.332 ± 0.0006	0.036 ± 0.0005
reaction reaction type	0.332 ± 0.0000	0.030 ± 0.0003
feather type	1.101 ± 0.0009	0.073+0.0005
reather type	1.101±0.0007	0.075±0.0005
∂C_{I}	4 215+0 003	0.041 ± 0.0005
$\frac{1}{2}$ + feather location	4.215±0.005	0.041 ± 0.0003
σα		

Table 2.2 Cohen's f^2 for PC1 and PC2 with standard deviations over 100 trees

2.4 Discussion

Flight feather structure is critical for ensuring successful flight as well as many other functions in a bird's life. Despite this, whether the observed variation in flight feather morphology within a single individual and among species is related to the ability to fly or not has not been conclusively and quantifiably established. This study seeks to answer this question using a new approach: quantifying variation without pre-prescribing a morphological trait to study using the *Momocs* R package for geometric morphometric analysis and using phylogenetic statistical models to identify explanatory factors that best explain this variation. We found that feather shape primarily varies in aspect ratio (PC1) and then curvature (PC2), with groupings by feather type (i.e., primaries, secondaries, alulas) along the aspect ratio axis. We also found that the major axis of variation varies closely with aerodynamic performance, feather location, and feather type, with most of the variation explained by aerodynamic performance with minimal phylogenetical signal.

Most of the variation in feather morphology can be described by its first two principal components which correspond to aspect ratio (PC1) and curvature or feather sweep (PC2) (Figure 2.2A) in all species studied (Figure 2.3). Past studies on feather morphology have often neglected these parameters to focus instead on vane asymmetry or rachis thickness due to their relevance to aeroelastic response. However, one study found that the relationship between rachis width and flight style disappeared after controlling for span and aspect ratio, suggesting that rachis width variation was a by-product of variations in wing planform and not directly related to aerodynamic function (Pap et al., 2015). Aspect ratio and sweep, however, are prominent parameters dictating planform area. Aspect ratio significantly affects aerodynamic performance in subsonic flight by increasing lift slope and lift-to-drag ratio (Umer et al., 2020). This is seen in bird flight as well where birds with high aspect ratio wings have an increased lift generation which could contribute to helping them glide long distances. Sweep has been found to improve longitudinal static stability in subsonic flight and is a relevant geometric parameter for transonic and supersonic flight (Umer et al., 2020). If the need for efficient and adaptable flight capabilities has strongly influenced the evolution of feather shape, it would logically follow that critical planform parameters for aerodynamic performance such as aspect ratio and sweep would vary in individual feathers to ensure the desired performance over the entire wing in all birds. Despite this, our model performed poorly in explaining curvature variation (Figure 2.4D, Table 2.2). As a result, we are unable to comment further on why birds seem to exhibit so much variation along the second axis of variation.

Feather type played an important role in explain variation along the PC1 axis (Figure 2.2C, D, E) across all studied species. It is only within feather type groups that distal feathers tend towards higher aspect ratios relative to proximal feathers (Figure 2.3) with feather location only loosely correlated with PC1 (Figure 2.4B) and having a low effect size (Figure 2.4D, Table 2.2). This pattern supports the importance of aerodynamic function as a selective pressure for feather shape instead of simply load magnitude and direction variability. Primaries and alular feathers are both positioned on the distal portion of the wing and would experience higher aerodynamic loads during flapping flight or higher directional variability due to wing morphing during gliding flight. Despite this commonality between the two feather types, our study reveals that primaries and alular feathers are on opposite ends of the PC1 axis which would not be the case if feather shape variation was shaped by aerodynamic loads because of feather position. Primaries and the alula perform different tasks in how they manage airflow over the wing. One of the functions of primaries and secondaries is lift generation, with higher forces on distal feathers which can lead to wing tip bending (Usherwood, 2009). It has been theorised using analytical methods that higher aspect ratio flight feathers could experience an increase in lift and torsional divergence stability via the shifting of the aerodynamic centre relative to the elastic axis (Försching & Hennings, 2012). The alula induces feather tip vortices that prevent boundary layer separation and stall. This effect was more pronounced over the distal wing because these vortices also introduced additional spanwise flow towards the wing tip (Lee et al., 2015), further improving lift production in the distal wing. In this case, the alula would not benefit from increased lift production from an increase in aspect ratio which may also interfere with stall prevention over the distal wing.

The link between lift production and feather shape was further quantified by our phylogenetic statistical analyses. Whereas inclusion of all the examined parameters (i.e., feather type, feather location, and aerodynamic performance) best explained the variation along PC1, lift slope $\left(\frac{\partial C_L}{\partial \alpha}\right)$, which increased with aspect ratio, was found to explain most of the variation in PC1 (Figure 2.4D, Table 2.2). Furthermore, phylogenetic relatedness did not matter significantly in our model, as indicated by the low value and variation of Pagel's λ (Figure 2.4C) and low variation of Cohen's f^2 . The lack of phylogenetic signal relevance indicates that other factors were at play in the feather shape diversification, and perhaps is indicative of the ease in which birds have gained or lost flight-relevant feather morphologies over evolutionary history (Wang et al., 2019).

The increase in lift slope with aspect ratio is unsurprising (Umer et al., 2020), but the high local effect size caused by aerodynamic performance is noteworthy and suggests that it may be one of the external factors influencing variation in feather morphology. Past studies have proposed arguments both for and against the importance of aerodynamic function as a selective pressure on feather shape. On one hand, flight is clearly important as it is what has allowed birds to successfully inhabit every continent on the planet; their ability to efficiently travel long distances and cross oceans means they have an increased capacity to find better climates for foraging and reproduction (Hedenström, 2002). On the other hand, the incredibly good fit of our aerodynamic performance-based model to feather shape is surprising as birds use their feathers for a variety of other tasks and not all flight feathers are even necessary to achieve flight. Whereas feather loss has been found to cause a small reduction in lift, birds with feather gaps *in vivo* still fly without experiencing measurable levels of stress, albeit with higher reported

predation rates (Hedenström & Sunada, 1999). As a result of the strong statistical support for aerodynamic function as a selective pressure, we propose that while peak aerodynamic performance may not be crucial for day-to-day life, its importance is elevated when it comes to achieving high-demand escape manoeuvres necessary for survival.

Contributing to the uncertainty around the importance of each individual feather during flight is the complex and multi-functional nature of avian feathers meaning that a number of possible variables of influence were not tested in this study. Relevant aerodynamic metrics and feather configurations were not included due to the limitations of XFLR5. We chose to use the lift slope as a metric for aerodynamic performance, but other metrics such as $\frac{C_L}{C_D}$ are used in other studies on the aerodynamics of avian flight. XFLR5 is also ill-equipped at modelling a feather aligned with the oncoming airflow which would be more relevant for investigating aerodynamic performance of the secondaries, or feathers interacting together which would be more biologically relevant. Feather functional morphology has also been closely tied to aeroelastic stability which was not investigated in this study. However, subsequent chapters in this thesis will address certain aspects of feather-feather interaction and aeroelastic response.

Studying similarities in a structure among species was the foundation of 18th and 19th century studies of anatomy and natural history. Relationships in form and function can help explain how structural patterns are explained by extrinsic or intrinsic factors, which in turn can be a powerful tool to infer historical selective forces on a morphological change (Lauder, 1981). This study sought to examine variations and similarities in feather structure and quantify the impact aerodynamic function has had on feather shape variation. Although we have not accounted for all factors that could affect feather shape, this analysis provides evidence that one of the major sources of variation across multiple bird species has covaried tightly with
aerodynamic performance as dictated by the feather's aerodynamic function. We have provided statistical, quantifiable support on top of the existing body of literature that feather morphology is closely tied to the evolution of flight in birds and also provided a framework for studying shape variation in a phylogenetic context.



Figure 2.1 Feather rachis and vane shape were acquired and further modelled as a three panel wing for XFLR5 analysis. A) Each feather was placed on green screen (*left*). The rachis was traced with a curve (*middle*). The green background was eliminated, and the outline of the vane was automatically selected (*right*).
B) The vane outline was processed with the *Momocs* R package, converting it to an outline object, smoothing the outline and normalizing using a Procrustes method. C) The feather was approximated automatically using three panels which were used to build an XFLR5 3D wing model.



Figure 2.2 Most of the feather variation is explained by the first two principal components axes which correspond to aspect ratio and curvature or feather sweep, and feather type can be separated along the PC1 axis. A) Distribution of all feathers along PC1 and PC2. Points are coloured by feather type. PC1 accounts for 58.3% of the variation and corresponds to aspect ratio. PC2 accounts for 13.7% of the variation and corresponds to aspect ratio. PC2 accounts for 13.7% of the variation and corresponds to sweep or curvature. B) The scree plot of all PCA components. The first two components account for 71.9% of the feather shape variation. For comparison, adding the third component only accounts for an additional 6.9% of the variation, with subsequent components contributing even less. C) Alula feathers, D) secondaries, and E) primaries are highlighted on the PC1, PC2 morphospace to further illustrate how feather type groups along the PC1 axis.



Figure 2.3 The phylogenetic tree with all 23 species used in this study. Each box is a faceted plot of a single individual derived from the PCA plot in Figure 2.2. In all birds, PC1 represented aspect ratio and PC2 represented sweep. Feather type is represented by the point colour and the shade of that colour corresponds to its location within that feather type from proximal (lighter coloured points) to distal (darker coloured points). The size of the point represents the magnitude of $\frac{\partial C_L}{\partial \alpha}$.



Figure 2.4 Feather type, feather location, and $\frac{\partial C_L}{\partial \alpha}$ all contribute to explaining PC1 but $\frac{\partial C_L}{\partial \alpha}$ explains most of the variation while feather location on the wing and phylogenetic signal explains relatively little of the variation. A) The model fit for PC1 against $\frac{\partial C_L}{\partial \alpha}$ and B) the model fit for PC1 against feather location. The R-squared value of this model was 0.9288 and the LOOIC score was -4590.6 ± 89.8, the lowest among all tested models. C) Pagel's λ value for PC1 and PC2 for the tree in Figure 2.3 and 200 alternative trees. $\lambda_{mean} = 0.361$ for PC1 and $\lambda_{mean} = 0.177$ for PC2. D) Cohen's f^2 for each fixed effect in the model. $\frac{\partial C_L}{\partial \alpha}$ had the largest local effect size on PC1 variation on its own while feather location had the lowest. Our model fit poorly for PC2 and as a result, all local effect sizes were low.

Chapter 3: Wing morphing makes use of different available mechanisms to locally modify mechanical and structural properties.

3.1 Synopsis

The avian wing is a complex multi-component structure, capable of supporting a multitude of functions. One function is maintaining sufficient lift over a variety of environmental conditions, which is supported by wing morphing to meet locomotory goals. A well-known example of wing morphing can be seen in how birds typically adopt an extended wing at lower gliding speeds and a flexed wing at higher gliding speeds (Pennycuick, 1968).

Wing morphing is largely controlled by active components concentrated in the leading edge where striated muscle pairs pull on bones to actuate or prevent movement (Biewener, 2011). This morphing rearranges the flight feathers that make up most of the lifting surface of the wing. Flight feathers can be primarily divided into two main categories: primaries, tightly bound to the carpometacarpus and digits 2 and 3, and secondaries, attached to bony protrusions on the ulna. Feather stiffness is dictated by a combination of two properties: a material property, Young's modulus (*E*), and a geometrical property, the moment of inertia (*I*). The β -sheet keratin fibers that make up feather material are arranged in a disorderly manner at the base of the feather, then aligned with the feather axis for most of the vaned region of the feather shaft, and finally in a disorderly manner again right at the tip (Cameron et al., 2003) which result in some variation in *E*. Overall, it has been found that *E* does not vary much beyond an order of magnitude ($E \sim 10^9$, Gigapascals) within a feather (Wang & Meyers, 2017) or as a function of feather location, feather type, species, load frequency, or temperature (Bonser & Purslow, 1995).

Flexural stiffness (*EI*) does, however, vary with feather location (Purslow & Vincent, 1978), feather type, and between species (Pap et al. 2015) primarily due to variation in *I*. Regions of the feather shaft with higher flexural stiffness feature a more square-like cross sectional area that delays "ovalization" (Wang & Meyers, 2017) defined as a decrease in the second moment of area due to a change to a more oval cross-sectional area.

Flight feathers are embedded in the various soft tissues on the caudal-dorsal side of the wing bones and connected by ligaments to the bones themselves. The outermost layer of this anchoring material is the thin and highly elastic epidermis or *cutis* followed by an elastic membrane, the lamina elastica, which envelopes dermal muscles and separates the cutis from the dermis (Stettenham, 2000). Besides the intrinsic and extrinsic striated muscles that control wing morphing, there is also a network of striated and smooth muscle that may act to adjust feather position. There is very little known about the function of feather muscles, especially those affecting the primary and secondary flight feathers. Studies on body contour feathers have found erector and depressor striated muscles that are theorized to act in conjunction with fatty subcutaneous fascia to rotate the feathers from a flattened streamlined position to upright and vice versa (Homberger & De Silva, 2000). A recent study by Hieronymus (Hieronymus, 2006) described the smooth muscle arrangement in the pigeon wing which is thought to modify behaviour-relevant postures throughout several wingbeats. It has been suggested this complex system of striated muscles, smooth muscles, and elastic ligaments act together to increase or decrease the range of motion to alter washout effects and flow separation.

The flight feathers and the soft tissue anchoring them in place have been shown to be critical for maintaining a coherent wing under aerodynamic loads (Matloff et al., 2020) although the exact contribution of each component and the mechanisms behind how they work together

are still largely unknown. A recent study using a "biohybrid" flying robot has shown that both the artificial elastic material holding real flight feathers together (Chang et al., 2020) as well as the feather microstructures providing a Velcro-like effect between adjacent feathers are necessary to maintain a coherent wing shape under an aerodynamic load (Matloff et al., 2020). This suggests that both feather anchoring soft tissue and feather-feather interaction act to couple feather movement to musculoskeletal movement during active wing morphing, allowing the wing to operate as an underactuated system when it comes to shape changes (Chang et al., 2020).

As the feathers are rearranged and the soft tissue is stretched or compressed to achieve a new wing shape, there will be a new degree of interaction between components of this structural system. Therefore, coupling wing morphing to feather position may also result in coupling wing morphing to the mechanical properties which provide mechanical advantages such as energy storage (Pennyucuick & Lock, 1976) or damping against vibration energy (Gao et al., 2014) to meet locomotory and environmental challenges.

3.1.1 Objectives

Despite the multitude of studies on the mechanical properties of individual feathers and the mechanisms of wing morphing, there is a gap in our understanding of the mechanical properties of multiple feathers in the context of wing morphing induced structural rearrangements.

My study begins to address this gap by performing dynamic mechanical tests at the base of individual flight feathers *in situ* with or without the support of neighbouring feathers in an extended or folded wing. This will contribute to answering the following questions:

- 1) How does wing folding affect the local mechanical properties of the wing?
- 2) What are the mechanisms behind local changes in mechanical properties?

3) How does wing folding affect the structural response to dynamic loading

3.2 Methods

3.2.1 Animal Subjects

Male and female rock pigeons (*Columba livia*) were acquired from a local breeder (Aldergrove, B.C., Canada) (n = 7, mass ranged from 344g to 568g). Birds were housed in a $9" \times 6" \times 4"$ wood and plastic pigeon coop in the Biological Sciences Building at the University of British Columbia. The room lighting was on a 12h light:dark cycle and later birds also had a window that let in natural light. Pigeons were allowed to feed on pigeon seed mix for a half an hour period every day and had *ad libitum* access to water and mineral and iodine grit. They were also occasionally given leafy greens, shredded zucchini, or hard-boiled egg treats for environmental enrichment. Animal care procedures were approved by the University of British Columbia's Animal Care Committee (A15-0116, A19-0113-A007).

3.2.2 In Situ Set-Up

Pigeons were anaesthetised using an isoflurane/oxygen mixture delivered at 1L/min. A facemask was placed over the pigeon's face and anaesthesia was induced using 4% isoflurane. Once the pigeon entered the surgical plane, assessed by toe pinches and degree of wing retraction, it would be intubated using an oral/nasal intubation tube (outer diameter: 3.3mm, inner diameter: 2.5mm, length: 98mm) lubricated with Muko Lubricating Jelly (Cardinal Health Canada Ink, Missisauga, ON). The anaesthesia was reduced to and continuously adjusted between 0.8-1.5% isoflurane to maintain the surgical plane. To assess the bird's anaesthetic awareness during the procedure, a model 2500A VET heart rate monitor (Nonin Medical Inc., Plymouth, MN) was attached to the bird's foot, an EMMA capnograph (Masimo Corporation,

Irvine, CA) was connected between the intubation tube and the tube from the isoflurane dispenser, and a cloacal thermometer was used to monitory body temperature.

The pigeon was placed ventral side up on a stage covered in absorbable bench liner paper. The left wing was manipulated into either an extended position (elbow angle = 90° , wrist angle = 135°) or a folded position (elbow angle = 50° , wrist angle = 60°). The wing was held in place by connecting the leading primary feather to a steel bolt using non-compliant beading string that pulled the feather cranially while two other steel bolts provided counter pressure at the wrist and carpo-metacarpus by pushing the leading edge caudally. Two ledges on each bolt, one above and one below the leading edge, prevented excessive wing rotation. A non-compliant beading string was used to fix the base of either a proximal feather, the first primary (P1) at the wrist joint, or a distal feather, the ninth primary (P9) at the leading edge, to the arm of a dualmode lever system (Model 305C-LR, Aurora Scientific Inc., Aurora Ontario). The wing was first left intact, then subsequently had all neighbouring feathers of the tested feather clipped at the base where it meets skin (Figure 3.1A, C).

3.2.3 Force-Displacement Measurements

The dual-mode lever system acts as both a servomotor by generating and recording a prescribed motion and a force transducer by recording the tension force on the string. The protocol was written and deployed by Dynamic Muscle Control Version 5.3 (Aurora Scientific Inc., Aurora, Ontario) which initiated a 2mm dorsal pull over 1.5s, followed by 15 repeats of a sinusoidal motion with a 4mm amplitude at 5Hz for 10 cycles followed by a 30s pause between each repeat (Figure 3.1B). After the first three animals, the protocol was modified to only generate 7 repeats as a time-saving measure since there was not much force-displacement

variation within an individual for a given treatment (Figure 3.2B). The force measurements were sampled at 100Hz.

Force-displacement data was extracted from the Dynamic Muscle Control output files. Each repeat of 10 cycles is categorized as a "loop". The force-displacement data was further separated into "loading" and "unloading" data based on whether the position vector was increasing or decreasing, respectively. In the total 4mm amplitude displacement, there was some variation in the first 1mm due to experimental differences in the tightness of the double overhand knot. Consequently, stiffness was determined by fitting a line to a subset of the data spanning position change of 1.5mm to 4mm for each cycle to remove contributions from data acquired when the string had slack in it, and calculating the slope (k):

$$k_{l} = \frac{F_{l}}{d_{l}}$$
$$k_{u} = \frac{F_{u}}{d_{u}}$$

where F is the force and d is the displacement. The subscripts l and u represent loading and unloading respectively.

The force and displacement values were normalized as a shear stress and strain respectively. Shear stress (τ) is given by:

$$\tau = \frac{F}{A} = \frac{F}{tw}$$

where t is the thickness of the soft tissue (skin, connective tissue, fat, muscle...etc.) in the dorsal-ventral direction, and w is the distance between two neighbouring feathers. Strain (ε) is given by:

where *l* is the length of the feather embedded in the wing. These morphological values were measured from a couple of sample specimens and applied to all data: $t_{proximal} = 7.55$ mm is the wrist thickness, $t_{distal} = 4.2$ mm is the carpometacarpus thickness, $w_{distal} = 3.8$ mm is the width of P10 with no modification because leading primary feathers are more tightly bound to one another, $w_{proximal} = 2.6$ mm $\times 2 = 5.2$ mm is double the width of P1 due to the spacing between more proximal primary feathers and all secondary feathers, $l_{proximal} = 12$ mm is the embedded length of P1, and $l_{distal} = 16$ mm is the embedded length of P10. Once these values were normalized, the maximum stress σ_{max} and maximum strain γ_{max} was found for each cycle. For each loop, the stress and strain time series was processed using a Fast Fourier Transform (John & Watson, 2020). The phase lag δ was calculated as the phase lag of the dominant frequency. Subsequently, the storage (G') and loss (G'') modulus representing the elastic and viscous contribution, respectively, to viscoelastic behaviour can be found as follows:

$$G' = \frac{\sigma_{max}}{\varepsilon_{max}} \cos\delta$$
$$G'' = \frac{\sigma_{max}}{\varepsilon_{max}} \sin\delta$$

Maximum stored work (W_{max}) is calculated by taking the area under a straight line drawn from the original starting position to the maximum force-displacement point. Net work (W_{net}) is calculated by taking the area inside the force-displacement loop.

The loss tangent $(tan\delta)$ which gives information about the relative importance of G'' compared to G' in a dynamic system is given by:

$$tan\delta = \frac{G''}{G'}$$

and the damping ratio as defined by Zahrai (2015) is given:

$$D = \frac{W_{net}}{4\pi W_{max}}$$

The damping ratio is commonly used to quantify the damping properties of structures against dynamic loads in civil engineering, particularly the stability of building structures embedded in compliant soil during earthquakes (Zahrai, 2015). As the feather is similarly a rigid structure embedded in a compliant substrate, this damping ratio as defined above is a valid metric to quantify the feather's ability to damp external vibrations.

All the previously described metrics were normalized relative to the extended position as follows:

$$\Delta X = \frac{X_{folded} - X_{extended}}{X_{extended}} \times 100\%$$

where X can be any of the following variables: k_l , k_u , G', G'', W_{max} , W_{net} , $tan\delta$, D.

3.2.4 Statistical Analysis

To test the hypothesis that feather-feather interaction or tissue compliance affects the above measurements, I built the following linear mixed-effects models using the *lmerTest* package (Kuznetsova et al., 2017) in R:

- (a) X or ΔX is affected by the fixed effects of both feather-feather interaction and feather location, (and wing position if the variable is not a percent change) as well as the random effect of individual animal variation.
- (b) X or ΔX is only affected by the fixed effect of feather-feather interaction and the random effect of individual animal variation.

- (c) X is only affect by the fixed effect of wing position and the random effect of individual animal variation (not available if the output variable is a percent change from an extended wing going to a folded wing)
- (d) X or ΔX is only affected by the fixed effect of feather location and the random effect of individual animal variation.
- (e) Neither feather-feather interaction or tissue compliance have any effect on X or ΔX , and as such, is only affected by individual animal variation.

Akaike information criterion (AIC) weights were used to compare which model encapsulates the most information contained in the data set. P-values were used to determine whether the effect of each of the treatments is significantly different from the null hypothesis. Confidence intervals, calculated using the *lme4* package (Bates et al., 2015), were used to determine the significance of the difference in effects between treatments. R^2 values were used to determine how much of the variation is explained by the independent variables contained in the best fit model.

3.3 Results

3.3.1 Feathers are anchored against cyclic loads in a non-linear, and largely elastic fashion.

The material and structures holding a feather in place responded to a dynamic test in a typical viscoelastic manner (Figure 3.2). The viscoelastic response is primarily elastic (Figure 3.2A) because the position lags force by an average of 11.56°. Viscoelastic materials exhibit both elastic and viscous behaviour: a purely elastic material would deform instantaneously in response to a load, whereas a purely viscous material exhibits a phase lag of 90°. There was negligible

change as a function of time, as force displacement-responses were largely invariable between cycles or repeats. There was, however, a large variation in force response among individuals. This is likely due a mixture of biological and experimental differences in a bird's exact depth of anaesthesia or the tightness of the knot on the non-compliant string connecting the feather to the servomotor arm.

Due to the viscoelastic nature of the wing materials, the force-displacement response featured energy-absorbing hysteresis and a shape typical of a fibrous biomaterial (Vincent, 1982) (Figure 3.2B). This can be seen as an initially more compliant response by the lower slope followed by a stiffer response in the higher slope at large displacements. This is a normal response for polymer fibres which uncoil from resting configurations under an initial load but become more resistant to further deformation once the fibres are completely straight and intramolecular forces are responsible for holding the polymer chain together. The forcedisplacement response forms a clockwise loop indicating that energy is absorbed throughout a cycle. When the material is loaded, the area under the curve representing energy stored is larger than when the material is unloaded and the area under that curve representing energy released. Therefore, some energy is not returned and is dissipated, generally as heat.

3.3.2 Stiffness decreases with wing folding due to increasing tissue compliance and increases near joints due to increasing feather-feather interaction.

Approximate stiffnesses varied locally with wing morphing and the presence or absence of support from neighbouring feathers (p < 0.01 for both k_l , k_u , and G'' on the effect of feather location, wing position, and feather-feather interaction, as well as the interactions of these effects; p < 0.01 for G' on the effect of feather location, wing position, and feather-feather interaction, but only the interaction between feather location and wing position) (Figure 3.3A,

C). Loading structural stiffness, taken as the slope of a line of best fit to the loading forcedisplacement data, was consistently higher within an individual compared to the unloading structural stiffness, taken from the unloading force-displacement data. However, there is no difference between the mean loading and unloading stiffness when considering the overall means (Figure 3.3A). For both loading and unloading stiffness, a model that includes all fixed effects of feather location, wing position, and feather-feather interaction best fits the data and explains more of the variance in the data relative to individual variation ($R_{marg}^2 = 29\%$, $R_{cond}^2 = 57.7\%$ for k_l ; $R_{marg}^2 = 30.6\%$, $R_{cond}^2 = 58.8\%$ for k_u).

The structures near distal feathers have a greater ability to store energy compared to those near proximal feathers, and this difference is further enhanced if the wing is extended compared to folded. There is less difference between the structures holding feathers in place to dissipate energy regardless of wing position, feather location or feather-feather interaction (Table 3.1) (Figure 3.3C). The storage modulus is always greater than the loss modulus, a result consistent with the force-displacement data indicating net work absorption. Like stiffness, a model that includes all fixed effects of feather location, wing position, and feather-feather interaction best explains the variance in the data relative to the effect of individual variation ($R_{marg}^2 = 47.0\%$, $R_{cond}^2 = 69.1\%$ for G'; $R_{marg}^2 = 64.9\%$, $R_{cond}^2 = 76.2\%$ for G'').

Feather Position	Wing Position	Feather-Feather	G' (MPa)	<i>G</i> '' (MPa)
		Interaction		
Distal	Extended	With Feather (WF)	0.3122	0.054
		No Feather (NF)	0.261	0.041
	Folded	WF	0.220	0.036

Table 3.1 Storage modulus (G') and loss modulus (G'')

		NF	0.181	0.029
Proximal	Extended	WF	0.040	0.007
		NF	0.040	0.006
	Folded	WF	0.059	0.012
		NF	0.024	0.005

Due to individual variation, some of the trends for stiffness and dynamic modulus within individuals are lost when observing the overall mean. These trends are more apparent when considering the percent change due to wing morphing, revealing that feather-feather interaction can increase stiffness, especially near joints, whereas increase in tissue compliance decreases stiffness overall due to wing folding (p < 0.001 for Δk_l , Δk_u , $\Delta G'$ and $\Delta G''$ for both the effect of feather position and feather-feather interaction) (Figure 3.3B, C). Stiffness marginally decreased with wing folding at distal feathers and increased dramatically at proximal feathers when all feathers were present. This trend was maintained at distal feathers when the effect of featherfeather interaction was removed, but not at proximal feathers which saw the stiffness decrease to distal feather levels (Table 3.2). This result is due to the proximity of proximal feathers to the wrist joint which leads to a larger change in feather overlap with folding compared to distal feathers that are more tightly fixed to the digit bones. This pattern is also reflected in the geometry-normalized values of storage and loss moduli. Overall, there was negligible difference between percent change of loading and unloading stiffnesses and storage and loss moduli, indicating that changes affect both the loading and unloading loops equally. Variation in the data for loading and unloading data and storage modulus is best explained as being correlated to feather position and feather-feather interaction ($R_{marg}^2 = 40.7\%$, $R_{cond}^2 = 66.1\%$ for Δk_l ;

$$R_{marg}^2 = 41.9\%, R_{cond}^2 = 67.4\% \text{ for } \Delta k_u; R_{marg}^2 = 37.0\%, R_{cond}^2 = 59.2\% \text{ for } \Delta G'; R_{marg}^2 = 41.7\%, R_{cond}^2 = 57.3\% \text{ for } \Delta G'').$$

 Table 3.2 Percent change in loading and unloading stiffness, storage modulus and loss modulus due to wing folding

Feather	Feather-	$\Delta k_l (\%)$	Δk_u (%)	$\Delta G'(\%)$	$\Delta G^{\prime\prime}(\%)$
Position	Feather				
	Interaction				
Distal	WF	-26.83	-35.10	-37.51	-36.00
	NF	-12.75	-19.47	-22.57	-25.70
Proximal	WF	74.40	73.09	69.32	-83.31
	NF	-36.76	-38.58	-43.10	-27.92

3.3.3 Work absorption is greater in the distal portion of the wing but increases in work absorption in the proximal wing due to feather-feather interaction during wing folding result in uniform damping over the entire wing.

Structures holding distal feathers in place can store more work than those holding proximal feathers in place when the wing is extended. This effect is not as apparent in a folded wing because wing folding does not cause significant change in stored work in distal structures but does significantly affect stored work in proximal structures (Figure 3.4A, B). Net work is significantly correlated with feather-feather interaction, feather location, and wing position (p < 0.001 for W_{net} for all the treatments and their interaction). Maximum stored work is significantly correlated with feather-feather interaction and feather location (p < 0.001 for W_{max} for the effect of feather-feather interaction and feather location, as well as the interaction of all the treatments) (Figure 3.4A). The variation in the data for net work is best explained by considering all the treatment effects ($R_{marg}^2 = 46.8\%$, $R_{cond}^2 = 64.1\%$ for W_{net}), whereas the variation for maximum stored work is only partially explained by all the treatment effects ($R_{marg}^2 = 28.7\%$, $R_{cond}^2 = 57.2\%$ for W_{max}). As such, we cannot make any conclusive statements on how wing position, feather location, or feather-feather interaction influences W_{max} for a given strain amplitude.

Percent changes in net work and maximum stored work show similar trends to stiffness. There was no change between percent change in net work and maximum stored work due to wing folding, and these percent changes are significantly correlated with feather-feather interaction and feather location (p < 0.001 for all fixed effects for ΔW_{net} and ΔW_{max}) (Figure 3.4B). Variation in the data is mostly explained by all the treatment effects ($R_{marg}^2 = 44.5\%$, $R_{cond}^2 = 56.3\%$ for ΔW_{net} ; $R_{marg}^2 = 35\%$, $R_{cond}^2 = 55.3\%$ for ΔW_{max}).

Despite these local differences in structural and material properties caused by differences in the contribution of feather-feather interaction and tissue compliance mechanisms, damping remains constant throughout the wing (Figure 3.4C-E). The elastic component of the dynamic modulus consistently dominates over the viscous component throughout the wing as seen by the mean loss tangent ranging from 0.17 to 0.32 (as shown by the overlapping confidence intervals) (Figure 3.4C). A loss tangent less than 1 reflects the storage modulus being larger than the loss modulus, or the material's ability to store energy through its elastic component is greater than its ability to dissipate energy through its viscous component. The damping ratio remains, statistically, constant, with a mean of 0.51 to 0.78 and is correlated with feather-feather interaction, feather location, and wing position (p < 0.001 for *D* for the effects of feather-feather

interaction, feather location, wing position, and the interaction between feather location and wing position) (Figure 3.4E). Once again, a model that accounts for all the treatment effects explains most of the variation ($R_{marg}^2 = 29.5\%$, $R_{cond}^2 = 41.8\%$ for tan δ ; $R_{marg}^2 = 17.6\%$, $R_{cond}^2 = 34.3\%$ for *D*).

As a result, there was no change in the loss tangent and damping ratio for all treatments $(p < 0.001 \text{ for } \Delta tan\delta)$ for the effects of feather-feather interaction, feather location and the interaction between these effects, and for *D* for the effects of feather location and the interaction between that and feather-feather interaction) (Figure 3.4D, F). There is a slight increase in both damping metrics in the proximal feather with wing folding when neighbouring feathers are not present, although this is not statistically significant. This result suggests that feather-feather interaction may be critical to maintain uniform damping over the wing near the wrist joint. Modelling all treatment effects explained a greater amount of the variation in data than individual variation ($R_{marg}^2 = 20.1\%$, $R_{cond}^2 = 43.5\%$ for $\Delta tan\delta$; $R_{marg}^2 = 12.3\%$, $R_{cond}^2 = 41.1\%$ for ΔD).

3.4 Discussion

Bird wings are remarkably complex, made up of multiple structures that possess a wide variety of shapes, sizes, and material properties. Recent studies have suggested potential mechanisms to explain how these structures work together to maintain streamlined shapes under aerodynamic loads with wing morphing during flight (Matloff et al., 2020). However, these studies had substituted certain biological components with artificial ones (Chang et al., 2020) and did not directly measure how the rearrangement of wing structures would affect the mechanical properties that play a part in maintaining this structural integrity. This study performs dynamic mechanical analysis on *in situ* pigeon feathers to determine how the soft tissue anchoring feathers and neighbouring feathers affect the mechanical properties of the wing in different morphs (Figure 1 and 2). Our results suggest that all the components of this structural system work together to modulate stiffness and work absorption (Figure 3) or maintain damping properties (Figure 4) in a manner coupled to morphing-induced shape changes. This may provide a mechanism for the coupling of mechanical properties with the kinematic response to wing morphing.

There is a strong correlation between local structural variation and wing morphing induced changes to mechanical properties. The proximal feather, P1, and the distal feather, P9, have different anatomical attachments. P1 is attached to the carpometacarpus primarily through attachments to other soft tissues neighbouring feather follicles. P9, on the other hand, is attached much more firmly to digits 2 and 3 via caudal and ventral phalangoremigial ligaments that wrap around the base of individual feather shafts (Hieronymus, 2016). P1 being anchored to a more compliant substrate relative to P9 explains the lower stiffness and modulus in the proximal feather location of this study (Figure 3.3A, C). These differences in these feather-anchoring structures result in two behaviours during wing flexion: 1) Distal primaries experience very little movement relative to their neighbours (Hieronymus, 2016), and 2) Distal primaries are tightly coupled with the digit angle, meaning they will move proximally with the digit (Chang et al., 2020). This increases feather overlap starting in the proximal primaries within this reduced wing area, increasing, in turn, the effect of feather-feather interaction in adjusting mechanical properties in the proximal wing (Figure 3.3B, C and 3.4B, D, F). The avian wing makes use of its feathers as a system of movable and overlapping slats to generate large changes in wing shape while minimizing decreases in structural integrity e.g., as seen in bats whose wing membranes will wrinkle at low elbow and wrist angles (Pennycuick, 2008).

Our results show that these local differences in mechanical properties result in local differences, and surprisingly some consistencies, in their response to a dynamic load. The structures supporting distal flight feathers absorb more work than structures supporting proximal flight feathers given the same or greater strains, although wing folding can increase work absorption in the proximal wing (Figure 3.4A, B). Work absorption, in this scenario, is the energy transferred from the external load to the structure and converted to kinetic energy and heat instead of being recovered as mechanical work. Work absorption, on its own, can be beneficial or detrimental depending on how that stored energy is used. Pigeons fold their wings at higher glide speeds (Pennycuick, 1968) which suggests that more energy could be transferred to the distal wing at low speeds compared to the proximal wing, but at high speeds and, likely high aerodynamic forces, a folded wing has a more consistent elastic energy efficiency, or ability to recover stored elastic energy as useful aerodynamic work, across the wing.

We also found that despite modulating mechanical properties using different mechanisms, damping is constant in an intact wing regardless of location or wing posture (Figure 3.4.C, D, E, F). Damping is defined as energy dissipation in a vibrating system often due to heat resulting in loss of oscillatory amplitude, either internally by "material damping" or externally by "system damping". Understanding the damping mechanisms and behaviour is at the core of a number of engineering disciplines and is critical for ensuring performance and failure prevention of everything from rotating machines, aircraft components, and civil structures in earthquake zones (Al-habibi et al., 2020). The damping ratio for concrete is usually less than 5%, and earthquake-resistant designs involving shear panels braced between steep frames still only yielded values of 35.5-40.2% (Zahrai, 2015). In contrast, the pigeon wing had a much greater damping ratio of 51-78%. The pigeon wing also had a loss tangent of 0.17-0.32 which is

noticeably lower than reported values for individual pigeon feathers ($tan\delta = 0.896 \pm 0.082$) which were calculated in isolated feathers under a different load condition (tensile instead of bending) (Gao et al., 2014). The high damping ratio and low loss tangent suggests that the structures supporting a feather, both soft tissue and neighbouring feathers, confer a constant damping ability over the entire wing that is not due to viscosity of the material itself (Figure 3.2, 3.3C). Previous studies have also found that the individual feathers of pigeons and other nonsilent flyers have a more elastic dynamic response, whereas owls that fly silently, have a more viscous dynamic response (Gao et al., 2014). Because there is structural variation in how proximal and distal feathers are held in place, it is possible that there is also variation in damping mechanisms. For example, feather-feather interactions are largely responsible for holding the proximal feathers in place which suggests that friction damping from the relative movement of feather surfaces could be responsible for the observed damping response (Akay & Carcaterra, 2014). This study shows that adding, removing, or modifying certain structural interactions could modify damping capabilities to increase (Ahlborn et al., 2006) or restrain resonance (Gao et al., 2014). Although it is unknown if Columba livia would need to enhance or damp resonant frequencies during natural flight, the long, curved barbs on the inner vane of P10 have been found to produce tonal sounds due to aeroelastic flutter and may provide a non-vocal signal of alarm (Niese & Tobalske, 2016). Other birds have been observed to modify feather-feather interaction to modify aeroelastic response. Crested pigeons have a modified P8 (Murray et al. 2017), reducing feather-feather interaction at that location, while Smithornis broadbills increase the gaps between distal flight feathers (Clark et al., 2016), resulting in non-vocal communication sounds due to aeroelastic flutter. Additionally, studies on earthquake-resistant structures often involve systems made up of stiffer elastic elements linked by more compliant structures which

can allow vibration-induced fatigue to be localized to specific, easily replaced structures (Zahrai, 2015).

This study offers only a snapshot at the possible mechanisms of linking structures to achieve a coupled mechanical capability using the avian wing as a model. Further studies will be needed to explore the extent of this effect with different wing positions, load frequencies and species. Since all the components are made up of viscoelastic materials, the stress-strain response will vary with strain rate or load frequency (Bonser, 1996). Although previous studies on isolated feathers have found no significant relationship between frequency and temperature and elastic energy efficiency (Pennycuick & Lock, 1976), pigeon flapping frequency has been reported to span a range of 5-10Hz (Theriault, 2019). Interspecific variation in feather shaft geometry (Pap et al., 2015; Worcester, 1996; De la Hera et al., 2010) and vane shape (Chapter 2) could result in differences in feather-feather interaction and, thus, differences in the wing's mechanical properties. Most significantly, changes in the material properties of the soft tissue anchoring feathers due to muscular activation have not been accounted for as all experiments were done in anaesthetised pigeons. In particular, the bases of the secondary and proximal primary feathers are surrounded by a vast network of striated and smooth muscles which, when activated, may increase attachment strength of feathers against larger aerodynamic loads (Ostmann, 1964; Hieronymus, 2016). As a result, it is possible that work absorbed, and damping has been overestimated.

Despite these limitations, this study provides the first investigation of how wing morphing affects local mechanical properties in birds, considering the avian wing as a system of interacting structures instead of a single coherent structure with varying geometry. Mechanical properties such as stiffness and damping play a large part in the aeroelastic response of

structures. The discovery that such responses can be tuned with very little input to a complex system of moving parts may lead to bio-inspired applications in aerospace or structural engineering.



Figure 3.1 The experimental set up and treatments. A) A servomotor actuated movement via a non-compliant string to the base of the feather shaft and simultaneously recorded force. B) The servomotor's position changes in an oscillatory fashion, featuring an amplitude of 4mm at 5Hz for 10 cycles repeated 7 times, with each repeat separated by 30s. C) Treatments involve varying wing position between extended and folded wings, varying feather location between a distal P9 feather and a proximal P1 feather, and feather-feather interaction between with feathers ("wf") and no feathers ("nf").



Figure 3.2 Local force-position response to a cyclic load applied at the base of flight feathers in pigeons indicates a strongly elastic viscoelastic response. A) A representative cycle from position (dashed line) and force (solid line) time series data shows that force and position are largely in phase. Treatments include feather location ("distal" (P9), "proximal" (P1)), wing position ("extended", "folded), and feather-feather interaction ("wf" (with feathers), "nf" (no feathers). Individual birds are separated by colour. B) Force-position traces over all cycles and repeats give a response typical of viscoelastic fibres.



Figure 3.3 Structures supporting distal feathers are stiffer than those supporting proximal feathers but wing folding increases stiffness in the proximal wing. Individuals are indicated by colour. Coloured points without an outline correspond to the value calculated from one repeat. Coloured points with a black outline correspond to the mean from all repeats. Black points correspond to the overall mean with 95% confidence intervals. Square points correspond to either loading stiffness or the storage dynamic modulus, while triangle points correspond to either unloading stiffness or the loss dynamic modulus. Data for A) stiffness, B) the percent change in stiffness due to wing folding, C) storage and loss dynamic modulus calculated from

normalized stress-strain values, and D) the percent change in dynamic modulus due to wing folding indicate that feather-feather interaction is a critical mechanism for increasing stiffness in the proximal wing during wing folding (p<0.001 for all both percent change in stiffness and dynamic modulus due to feather location and feather-feather interaction).



Figure 3.4 Work absorption varies locally over the wing yet damping remains constant. Coloured points without an outline correspond to the value calculated from one repeat. Coloured points with a black outline correspond to the mean from all repeats. Black points correspond to the overall mean with 95% confidence intervals. A) Net work (square) and maximum stored work (triangle) indicate a greater capacity for work absorption in the distal wing (p<0.001 for net work and maximum stored work due to feather location) but B) the percent change in net work and maximum stored work during wing folding indicates that the proximal wing sees a significant increase in net work absorption due to wing folding with feather-feather interaction

(p<0.001 due to feather location and feather-feather interaction). C) Loss tangent and D) the percent change in loss tangent are statistically consistent in an intact wing but increases in the proximal wing without feather-feather interaction. E) Damping ratio and F) the percent change in damping ratio are also statistically consistent in an intact wing. The increase in the proximal wing without feather-feather interaction is not statistically significant (see confidence intervals). Chapter 4: Wing stiffness modulates aerodynamic performance according to wing posture through changes in aeroelastic response.

4.1 Synopsis

Aeroelasticity has played an important role in shaping aircraft design since the early 20th century. In flight engineering it is defined broadly as "phenomena which exhibit appreciable reciprocal interaction (static or dynamic) between aerodynamic forces and the deformations induced thereby in the structure of a flying vehicle, its control mechanisms, or its propulsion system" (Bisplinghoff & Ashley, 2013). Throughout the development of modern aircraft technology, wings have become longer and slimmer, materials lighter and more flexible, and flight speeds faster. These advances have significantly improved the performance range of manmade aircraft, but also result in structures that experience greater deformations and larger aerodynamic forces. As a result, aeroelastic responses become more apparent, and with the increase in aircraft usage, understanding the aeroelastic responses of an aircraft over its entire performance range becomes critical (Bisplinghoff & Ashley, 2013). This is because unwanted aeroelastic behaviour can result in an increased propulsive energy requirement (Patil, 2011) at best, and destructive and catastrophic consequences in the worst-case scenario. Therefore, aircraft design must account for avoiding unwanted aeroelastic responses or encouraging advantageous aeroelastic responses (Bisplinghoff & Ashley, 2013). Unmanned micro-air vehicles that operate at intermediate Reynolds numbers ($Re \sim 10^5$), where flows are dominated by both viscous and inertial forces, have increased in popularity. The local and instantaneous forces due to flows at this flow regime can vary significantly as a function of geometry,

boundary layer separation and reattachment points, making it a difficult problem to study (Tank et al., 2017). Birds, as it happens, also operate at similar *Re* values and have flexible wings that experience larger aeroelastic deformations without structural failure than any man-made aircraft. Therefore, they are a valuable model for studying aeroelastic effects on flight performance.

Studies on aeroelastic response in nature have viewed aeroelasticity in a more constructive light, often finding that the large deformations observed do not end in catastrophe but instead can improve performance during swimming or flight. When it comes to flight, aeroelasticity is perhaps most well studied in insects. Insect wings are passive structures actuated only at their base but flapping-induced fluid-structure interactions can generate wing shape changes due wing inertia that can alter the flow and improve flight performance. One such instance occurs during the transition from downstroke to upstroke, when the insect's wing experiences an increase in camber that promotes the formation of a leading-edge vortex on the upper surface of the wing (Mountcastle & Combes, 2013). Consequently, the flexible wing generates greater lift with a lower power requirement (Hamamoto et al., 2007).

Bird wings, consisting mostly of interacting flexible feather elements, exhibit welldocumented, and often localized, aeroelastic behaviour albeit in the context of communication instead of flight (Clark & Prum, 2015). An oscillatory aeroelastic instability, i.e., flutter, in tail feathers (Clark et al., 2013) or primary flight feathers (Clark et al., 2016) is used to produce sounds for courtship displays. However, flutter, appears to be intrinsic to flight feathers and has been observed in at least 27 species over nine orders as well, including instances during regular flight (Clark & Prum, 2015). The effect of aeroelasticity on avian flight performance is much less well understood, although recent studies have begun to explore how avian wing flexibility

can alleviate unwanted upwards loads through passive decambering (Gamble et al., 2020) or break up large upstream vortical disturbances (Murayama et al., 2021).

Wing morphing further complicates the study of aeroelastic behaviour during bird flight. Unlike insects, birds have skeletal and muscular structures that can initiate active wing morphing by rearranging the passive feather elements coupled to these actuators (Biewener, 2011). Active wing morphing has allowed birds to adapt their wing shape to a large variety of environmental conditions and behaviours during flight. One of the most well-studied morphing behaviours is wing extension-flexion; birds tend to extend their wings when gliding at slow speeds and flex their wings when gliding at high speeds. This wing shape change has been found to be effective for reducing profile drag during high-speed flight (Pennycuick, 1968) and, due to feather rearrangement, also causes local changes in wing stiffness (Chapter 3). Bats are also able to adjust wing stiffness, albeit actively, using plagiopatagiales proprii muscles embedded in their wing membrane in a manner that correlated to aerodynamic force and flight speed (Cheney et al., 2014). Although there has been no work yet thoroughly examining how stiffness tuning can affect the flight performance envelope in birds and bats, experimental studies on fish fin stiffness revealed a nonlinear relationship between locomotory performance and appendage stiffness for a given fin motion and frequency. In other words, there exists a theoretical optimal stiffness for a given oscillatory gait or a theoretical optimal frequency for a given stiffness that maximizes lift or thrust efficiency (Esposito et al., 2012). The nature of the avian wing is such that, unlike insects, it can actively modulate wing stiffness, but unlike bats, changes in stiffness are coupled with changes to wing shape which, in turn, are correlated with certain flight behaviours. We propose coupling wing stiffness to a wing shape and flight behaviour could provide a mechanism

for the automatic tuning of aeroelastic response and the enhancement of aerodynamic performance without additional actuators.

4.1.1 Objectives

The goal of this study is to use fluid-structure computational methods to explain the aeroelastic mechanisms underlying changes to the relationship between wing stiffness and aerodynamic performance due to wing morphing. In Chapter 3, we found that wing stiffness can be significantly increased through feather-feather interaction during wing folding. This study explores whether coupling mechanical properties to wing shape in this fashion enhances performance rather than limiting it. If avian wing structural arrangement is such that mechanical properties are coupled to functional wing morphing, we would expect to see improved aerodynamic performance in stiffer folded wings during high-speed flight or more flexible extended wings during low-speed flight. This study answers the following questions to test these predictions and fill in some of the gaps in our current knowledge on how variable stiffness due to avian wing morphing affects flight performances:

- 1) How does wing folding affect aerodynamic performance?
- 2) How does wing stiffness affect aerodynamic performance?
- 3) How does wing stiffness affect aeroelastic response and wake vorticity?
 - 4.2 Methods

4.2.1 Geometric Model

The bird wing is a complex structure, made up of multiple materials of varying density, stiffness, and porosity among many other characteristics, all contributing to an irregular geometry with variable thickness and camber. Many shape parameters are altered even when considering only one morphing movement: wing extension and folding. To simplify the problem
and reduce the challenges involved in fluid-structure interaction (FSI) computational modelling of a complex structure, we simplified the wing as an isotropic, polygonal flat plate of constant thickness (Figure 4.1A).

To acquire geometric information of an extended and folded wing, we used OptiTrack motion capture technology (Natural Point Inc., Corvalis, Oregon) to acquire the 3D wing shape throughout the bird's elbow and wrist range of motion. Using two pigeon specimens, one wing each was disarticulated at the shoulder. Four infrared markers were placed on the dorsal side of the wing at the humerus head, elbow, wrist, and carpometacarpus to track skeletal movement. Seven other markers in total were placed on the leading edge and trailing edge of the wing (three on the leading edge and four on the tips of S10, S1, P7, and P10) to track wing shape. For more details on the motion capture methods, please see Harvey et al., (Harvey et al., 2022 in press). Elbow and wrist angle were calculated using the four skeletal markers. For the extended wing, we selected data corresponding to an elbow angle of $90\pm3^{\circ}$ and a wrist angle of $135\pm3^{\circ}$ to match the joint angles of the extended wing in Chapter 3. For the folded wing, increase in wing camber and feather-feather overlap caused the loss of some markers during the motion capture process and we were unable to capture a wing shape matching the elbow and wrist angles of the folded wing in Chapter 3. Therefore, we selected data corresponding to an elbow angle of $47\pm3^{\circ}$ and a wrist angle of $78\pm3^{\circ}$ as the closest match instead.

The selected data was then used to generate coordinates for a 2D outline of the wing planform. Four key points were extracted: the humerus, the leading-edge of the carpometacarpus, the tip of P10 and the tip of S10. We first projected the S10 coordinates onto a plane formed by the humerus, the leading-edge of the carpometacarpus and the tip of p10 to ensure that all four points would lie on the same plane. To do this, we let $\vec{v_1}$ be the vector from the leading-edge of

the carpometacarpus to the humerus and $\overrightarrow{v_2}$ be the vector from the leading-edge of the carpometacarpus to P10. The unit normal to this plane was then defined as:

$$\hat{n} = \frac{\overrightarrow{v_1} \times \overrightarrow{v_2}}{\|\overrightarrow{v_1} \times \overrightarrow{v_2}\|} = \langle n_i, n_j, n_k \rangle$$

Then, we let $\overrightarrow{v_3}$ be the vector from the leading-edge of the carpometacarpus to S10 and calculated the projected coordinates of S10 as follows:

$$d = \overline{v_3} \cdot \hat{n}$$
$$S10 = \{x - dn_i, y - dn_j, z - dn_k\}$$

Next, we rotated the coordinates so that they all lay on the x-y plane. This was done by finding the axis of rotation:

$$\overrightarrow{n_{rot}} = \widehat{n} \times \widehat{k} = \langle n_{rot,i}, n_{rot,j}, n_{rot,k} \rangle$$

where $\hat{k} = \{0,0,1\}$. The sine of the angle of rotation was defined as $s = \|\overrightarrow{n_{rot}}\|$ and the cosine of the angle of rotation was defined as $c = \hat{n} \cdot \hat{k}$. Therefore, the rotation matrix was calculated as:

$$\boldsymbol{R} = \boldsymbol{I} + \boldsymbol{S}\boldsymbol{S} + \boldsymbol{S}\boldsymbol{S}^2 \frac{1}{1+c}$$

where **I** is the identity matrix defined as $I = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}$, and **SS** is the skew symmetric cross-

product of $\overrightarrow{n_{rot}}$ defined as $SS = \begin{bmatrix} 0 & -n_{rot,k} & n_{rot,j} \\ n_{rot,k} & 0 & -n_{rot,i} \\ -n_{rot,j} & n_{rot,i} & 0 \end{bmatrix}$. The rotated coordinates for each

point were then calculated by multiplying the original coordinates with the rotation matrix:

$$\{x_r, y_r, z_r\} = \boldsymbol{R} \begin{cases} x \\ y \\ z \end{cases}$$

where $\{x, y, z\}$ are the coordinates with the projected S10 point. We also rotated the coordinates around the z-axis so that the root of the wing was parallel to the x-axis. The new coordinates were then calculated as follows:

$$\{x_r, y_r, z_r\} = \boldsymbol{R}_{\boldsymbol{y}} \begin{cases} x \\ y \\ z \end{cases}$$

where $\mathbf{R}_{y} = \begin{bmatrix} cos\theta & -sin\theta \\ sin\theta & -cos\theta \end{bmatrix}$, θ is the angle between the root vector, and $\{x, y, z\}$ are now the coordinates after the first rotation. Finally, we translated all the coordinates so that the humerus position lay at the origin $\{0,0,0\}$ to ensure that all wings were positioned at the same location within the fluid volume. For the folded wing, there was an additional transformation where we scaled the coordinates so that the root chord (c_r) matched that of the extended wing by multiplying the original coordinates by the scaling factor:

$$s = \frac{c_r - c_{r,f}}{c_{r,f} + 1}$$

where $c_{r,f}$ is the original root chord of the folded wing and c_r is the root chord of the extended wing.

After these transformations, we used the resultant four coordinates to construct a model (Figure 4.1A, B; Table 4.1) in Gmsh (Version 2.13.0 for Linux), a 3D finite element mesh generator (Geuzaine & Remacle, 2009). The coordinates were duplicated and projected upwards by a certain wing thickness (t), which would slightly vary between cases to ensure solver success for different flow conditions. Aeroelastic similarity to a realistic pigeon wing with a stiffness parameter, the Young's modulus, of E and a thickness of $t_{real} = 0.0036m$ was ensured using the aeroelastic number (Æ) to adjust the Young's modulus used in the solver (E') according to t:

$$\mathcal{A} = \frac{Et_{real}}{\frac{1}{2}\rho_f V_{\infty}^2 c_{mac}}$$

Therefore,

$$Et_{real} = E't$$

The mean aerodynamic chord (c_{mac}) was calculated using a custom function based on an analytic method outlined by Diehl (1942) that iteratively divided the wing planform into increasing number of panels up to a maximum of 200 panels until c_{mac} did not deviate by more than 5×10^{-5} units.

Parameter	Extended Wing	Folded Wing			
Span (b)	0.3732 m	0.1874 m			
Mean Aerodynamic Chord	0.1597 m	0.1883 m			
(c_{mac})					
Root Chord (c_r)	0.1670 m	0.1670 m			
Distal Chord (c_d)	0.3003 m	0.2866 m			
Area (S)	0.0495 m ²	0.0311 m ²			
Aspect Ratio (AR)	11.2522	4.5128			
Model Thickness (t)	Varies between 0.007 m to 0.0036 m				

A fluid volume was constructed around the wing (Figure 2.1C). This fluid volume was made up of a 6m x 6m cube with the corner points x = [-3,3], y = [0,6], and z = [-3,3]. On the upstream surface of the fluid volume, we included a half cylindrical volume to create a curved inlet. This half cylinder had a radius spanning points x = [-6, -3]. Overall, this resulted

in two volumes: the solid volume representing the wing, and the fluid volume representing the space within the fluid volume and outside of the wing volume. The solid volume was defined by two surfaces: the wing root and the rest of the wing. The fluid volume was defined by six surfaces: the inlet, the outlet, the wing tip side, the wing root side, the top, and the bottom. Both volumes discretized using an unstructured mesh made up of tetrahedral elements that adapted better to larger deformations compared to a structured mesh. Because Gmsh was unable to easily create mixed element meshes and our study was primarily concerned with large scale deformations instead of turbulent boundary layer phenomenon, we chose to exclude the creation of a boundary layer mesh. The wing volume was meshed with either an element length of 0.0025m or 0.005m to ensure solver success. Element length then increased throughout the fluid volume up to an element length of 0.5m at the inlet and 0.1m at the outlet to ensure good spatial resolution near the wing to accurately capture local flow patterns.

To further examine the effect of aspect ratio changes due to wing folding on aerodynamic performance, we also created three rectangular plate geometries with aspect ratios of 1, 4, and 10 which were set in the fluid volume defined above in place of the pigeon wing model. These models also allowed us to benchmark our solved flow patterns against that of a previous study by Shademan & Naghib-Lahouti (2020) (Figure 4.1B). All rectangular plates had a chord (*c*) of 0.15, similar to that of our bird wings and a thickness of 0.02, and a span of *b* where b = AR * c.

4.2.2 Fluid-Structure Interaction Solver

The behaviour of a fluid-structure system with large deformations was simulated using in-house code to solve the governing incompressible Navier-Stokes equations coupled with nonlinear structural equations (Gurugubelli & Jaiman, 2019; Li et al., 2021). The governing equations were discretized using a Galerkin-stabilised finite element method in an arbitrary

Lagrangian-Eulerian (ALE) reference frame (Li et al., 2021). ALE-based finite element methods have been found to accurately handle complicated fluid structure interaction cases with large deformations and complex kinematics such as those found in nature (Hamamoto et al., 2007). A radial basis function was used to interpolate fluid forces and structural displacements along the fluid-solid interface (Li et al., 2021) which was simulated using a second order accurate combined field with explicit interface (CFEI) formulation (Liu et al., 2014). A more detailed description of fluid-structure interaction solver methods can be found in Gurugubelli & Jaiman (2019) and Li et al. (2021).

The flow patterns around the wing with an angle of attack (α) of -10°, 0°, 10°, 20°, 30° were solved for cases with the fluid and structural properties listed in Table 3.2. The rectangular plate cases were solved for an α of 0°, 30°, 60°,90° to match the conditions in Shademan & Naghib-Lahouti (2020). Inlet and bottom surfaces of the fluid volume were defined by Dirichlet boundary conditions given as:

$$V_{\infty} = (u, v, w)$$

where

$$u = V_{\infty} \cos\left(\alpha \frac{\pi}{180}\right)$$
$$v = 0$$
$$w = V_{\infty} \sin\left(\alpha \frac{\pi}{180}\right)$$

The outlet and top surfaces of the fluid volume had a pressure outlet boundary condition of zero. Both side surfaces (root and tip) of the fluid volume were defined using planar symmetric slip conditions. All fluid volume surfaces also had ALE boundary conditions of zero meaning that these surfaces did not move due to fluid forces. The wing root also had Dirichlet boundary conditions of u = 0, v = 0, w = 0 and ALE boundary conditions of zero since the wing root in an actual bird would not interact with the fluid.

Property	Extended Wing	Folded Wing
Fluid Density (ρ_f)	1.225 kg/m ³	1.225 kg/m ³
Solid Density (ρ_s)	1060 kg/m ³	1060 kg/m ³
Fluid Viscosity (μ)	1.813 Pa·s	1.813 Pa·s
Free-Flow Velocity (V_{∞})	10 m/s, 20 m/s	10 m/s, 20 m/s
Reynolds Number* $\left(Re = \frac{\rho_f V_{\infty} c_{mac}}{\mu}\right)$	107942, 215884	127224, 254448
Poisson's Ratio (v)	0.3	0.3
Young's Modulus (<i>E</i>)	10^{6} (F1), 10^{9} (F2), ∞ (R)	10^{6} (F1), 10^{9} (F2), ∞ (R)

*Re = 150000 for the rectangular plate models.

For rigid model cases (i.e., $E = \infty$ or R), $\Delta t = 0.01s$ for 10000 iterations, while for FSI cases (i.e., $E = 10^6$, 10^9 or F1, F2), $\Delta t = 0.0001s$ for 50000 iterations with mesh displacement data saved every 50 iterations (sample frequency = 200Hz). Output files for Tecplot post-processing were created every 1000 iterations. Cases were run on the University of British Columbia's Advance Research Computing (ARC) Sockeye platform. Each case used 160 processor nodes and 128 GB of memory.

4.2.3 Aerodynamic Performance Analysis

To quantify how stiffness affected aerodynamic performance in different wing postures at different flight speeds, we evaluated the lift slope $\left(\frac{\partial C_L}{\partial \alpha}\right)$ and the maximum lift to drag ratio

 $\left(\left(\frac{c_L}{c_D}\right)_{max}\right)$ (defined below). All analyses were done on data between a normalized time of 150-250 where normalized time (t^*), a commonly used metric in computational fluid-structure analyses, was defined as:

$$t^* = \frac{tV_{\infty}}{c_{mac}}$$

Forces along each of the global coordinate axes (F_x, F_y, F_z) were output by the Simflow solver. Lift (*L*) and drag (*D*) were, therefore, defined as:

$$L = F_z \cos\alpha - F_x \sin\alpha$$
$$D = F_x \cos\alpha + F_z \sin\alpha$$

Lift and drag were then normalised as lift (C_L) and drag (C_D) coefficient to allow for comparison between cases during analysis:

$$C_L = \frac{L}{\frac{1}{2}\rho V_{\infty}^2 S}$$
$$C_D = \frac{D}{\frac{1}{2}\rho V_{\infty}^2 S}$$

These aerodynamic coefficients were used to calculate the aerodynamic performance metrics, $\frac{\partial C_L}{\partial \alpha}$ and $\left(\frac{C_L}{C_D}\right)_{max}$. The lift slope was calculated using the linear portion of the $C_L = f(\alpha)$ curve which corresponded to $\alpha = [-10,10]$ for all cases. $\frac{\partial C_L}{\partial \alpha}$ was defined as the slope of a line fit to this data. The maximum lift-to-drag ratio was calculated by finding the mean lift-to-drag ratio for all α in each combination of E, V_{∞} , and wing posture and identifying the maximum value among all α . The angle of attack at which the maximum value occurred was defined as $\alpha \left[\left(\frac{C_L}{C_D}\right)_{max}\right]$.

Finally, we visualised the pressure differential above and below the wing using a slice positioned at the y-coordinate corresponding to c_{mac} to better understand the aerodynamic performance results. We normalized the pressure data by calculating the coefficient of pressure:

$$C_p = \frac{\Delta P}{\frac{1}{2}\rho_f V_\infty^2}$$

and visualized its distribution in Tecplot (version 2013) (Tecplot USA, Bellevue, Washington).

4.2.4 Aeroelastic Response Analysis

To understand how wing flexibility affected aeroelastic responses and subsequently the local fluid flow, we quantified the plunge and twist behaviour at the wing tip and visualised the vortex patterns in the wake for the flexible wing cases. Like the post-processing done for aerodynamic performance (Chapter 4.2.3), all analyses were done on data between a normalized time of 150-250.

The dynamic response of the plunge or twist response at the wing tip was characterised by the frequency and strength of its first two harmonics. Simflow had output the displacements (x, y, z) of all mesh nodes on the edges making up the leading edge, distal chord, and trailing edge along the global axes. The coordinates were rotated so that V_{∞} was parallel to the x-axis of the global coordinate frame. As a result, the plunge response was defined as:

$$z^* = z_{TE} cos \alpha - x_{TE} sin \alpha$$

where z_{TE} and x_{TE} are the *z* and *x* coordinate of the most distal point of the trailing edge. We then found the pitch angle:

$$\theta_p = \arcsin\left(\frac{z_{LE}^* - z_{TE}^*}{c_d}\right)$$

in degrees, where z_{LE}^* is the rotated *z* coordinate of the most distal point of the leading edge and z_{TE}^* is the rotated *z* coordinate of the most distal point of the trailing edge. A fast Fourier transform (FFT) function from the R *stats* package was used to convert the z^* and θ_p time series into a frequency domain, a series of complex numbers with components representing the frequency, amplitude, and phase shift of each cycle. We normalized the transformed values by dividing these complex numbers by the number of terms (*N*). If *X*[*k*] is the k-th complex number resenting the amount of frequency *f* in the signal, we obtained the frequency (*f*), amplitude (*A*), and phase shift (δ) by:

$$f = \frac{X[k] * sampling rate}{N}$$
$$A = \sqrt{X[k]_{Re}^{2} + X[k]_{Im}^{2}}$$
$$\delta = \arctan\left(\frac{X[k]_{Im}}{X[k]_{Re}}\right)$$

where the sampling rate was 200Hz. We filtered out frequencies above the Nyquist frequency (half of the sampling rate) to account for aliasing due to the symmetric nature of Fourier transforms. The first two harmonics were identified using the 'findpeaks' function in the *pracma* R package (Borchers, 2021) as the two local maxima of a frequency plot with the greatest amplitude.

The lambda2 criterion was used to visualize how these dynamic aeroelastic responses influenced the local vortex patterns near the surface of the wing. Tecplot calculated the velocity gradient tensor from the velocity values $\vec{u}(x, y, z, t) = \langle u, v, w \rangle$ of each element output from Simflow:

$$\nabla \vec{u} = \begin{bmatrix} \partial_x u & \partial_y u & \partial_z u \\ \partial_x v & \partial_y v & \partial_z b \\ \partial_x w & \partial_y w & \partial_z w \end{bmatrix}$$

which can be decomposed into a symmetric part, the rate of strain tensor which describes the rate of stretching and shearing:

$$\boldsymbol{S} = \frac{\nabla \vec{u} + \nabla \vec{u}^{T}}{2} = \begin{bmatrix} \partial_{x} u & \frac{1}{2} (\partial_{y} u + \partial_{x} v) & \frac{1}{2} (\partial_{z} u + \partial_{x} w) \\ \frac{1}{2} (\partial_{y} u + \partial_{x} v) & \partial_{y} v & \frac{1}{2} (\partial_{z} v + \partial_{y} w) \\ \frac{1}{2} (\partial_{z} u + \partial_{x} w) & \frac{1}{2} (\partial_{z} v + \partial_{y} w) & \partial_{z} w \end{bmatrix}$$

and an antisymmetric part, the vorticity tensor, which describes the rate of rotation:

$$\mathbf{\Omega} = \frac{\nabla \vec{u} - \nabla \vec{u}^T}{2} = \begin{bmatrix} 0 & \frac{1}{2} (\partial_y u - \partial_x v) & \frac{1}{2} (\partial_z u - \partial_x w) \\ -\frac{1}{2} (\partial_y u - \partial_x v) & 0 & \frac{1}{2} (\partial_z v - \partial_y w) \\ -\frac{1}{2} (\partial_z u - \partial_x w) & -\frac{1}{2} (\partial_z v - \partial_y w) & 0 \end{bmatrix}$$

The Lambda2 criterion specifies that when the second eigenvalue (λ_2) of $S^2 + \Omega^2$, where $\lambda_1 \ge \lambda_2 \ge \lambda_3$, is negative, there is a vortex core. We used of Tecplot's Tensor Eigensystem command to obtain λ_2 and plotted isosurfaces for $\lambda_2 = -0.5$ coloured by the normalized velocity $u^* = \frac{\sqrt{u^2 + v^2 + w^2}}{v_{\infty}}$ at that node.

4.3 Results

4.3.1 Wing folding increases aerodynamic performance by reducing pressure drag

During wing folding, the wing experiences a decrease in aspect ratio, so we first explored how wing folding induced shape changes alone affect aerodynamic performance and compared the results to a rectangular plates of varying aspect ratio. The rectangular plate models showed similar trends to those found in Shademan & Naghib-Lahouti (2020) and confirmed that a decrease in aspect ratio resulted in the loss of lift (Figure 4.2A) and a loss of drag which shifted the lift-to-drag polar leftwards (Figure 4.2B). Likewise, a decrease in drag was observed in the folded wing geometry at all tested flight speeds that shifted the aerodynamic polar leftwards compared to the extended wing (Figure 4.2B) but did not observe a noticeable loss in lift (Figure 4.2A). Most notably, the overall performance of the extended and folded wing was very similar compared to the rectangular plates of varying aspect ratio (Figure 4.2A, B) even though the folded wing model had an aspect ratio of 4.5, more than half that of the extended wing with an aspect ratio of 11.3 (Table 4.1). Moreover, both wing models had very similar $\frac{\partial C_L}{\partial \alpha}$ and aerodynamic polars to the rectangular plate with an aspect ratio of 4.

By visualizing the mean C_p distribution around the wing at a y-z slice located at the ycoordinate where the chord is equivalent to c_{mac} , we found that the decrease in drag observed at lower aspect ratios was due to a reduction in size of the low-pressure boundary layer separation bubble in both the rectangular plate models and the wing models (Figure 4.2C). As aspect ratio increases, the low-pressure area in the wake of the rectangular plates grew larger as the boundary layer separates closer to the leading edge. A similar pattern was observed in the wing models, but the pressure differential magnitude was not as high, which explains why the aerodynamic forces in the extended and folded wing are very close in value. There were no noticeable differences due to flight speed suggesting that the effect of wing folding on aerodynamic performance at intermediate *Re* in this intermediate regime was very not sensitive to changes in *Re* within the same order of magnitude.

4.3.2 Wing flexibility increases aerodynamic performance more significantly in an extended wing

Flexible wings improved aerodynamic performance by increasing lift and decreasing drag, with a greater effect in the extended wing compared to a folded wing and a negligible effect on performance due to glide speed (Figure 4.3). However, both lift slope $\left(\frac{\partial C_L}{\partial \alpha}\right)$ and maximum lift-to-drag $\left(\frac{C_L}{C_D}\right)_{max}$ had a different relationship with *E* depending on wing shape and flight speed V_{∞} .

Lift production, quantified by the lift slope, had different "optimal" stiffness values between the two wing shapes. In the extended wing, $\frac{\partial C_L}{\partial \alpha}$ increased with decreasing *E*. The flexible F1 wings had the highest $\frac{\partial C_L}{\partial \alpha}$ at both flight speeds. In the folded wing, the $\frac{\partial C_L}{\partial \alpha}$ peaked with the moderately stiff F2 wings. The F2 wings had the highest $\frac{\partial C_L}{\partial \alpha}$ at both flight speeds (Figure 4.3A, Table 4.3). Wing shape is closely associated with flight speed in *in vivo* studies (Pennycuick, 1968), and we found that for a given flight speed V_{∞} , the extended wing had the highest $\frac{\partial C_L}{\partial \alpha}$ at low speeds and the flexible wing had the highest $\frac{\partial C_L}{\partial \alpha}$ for in wings, while at $V_{\infty} = 20m/s$, wing folding decreased $\frac{\partial C_L}{\partial \alpha}$ in flexible wings and increased $\frac{\partial C_L}{\partial \alpha}$ for F1, F2, and R wings during wing folding (Table 4.3). Overall, lift slope was consistently a little lower at higher speeds, although this difference is negligibly small compared to other test conditions, indicating that *E* has a larger effect on aerodynamic performance than a change in flight speed of 10m/s. Drag was reduced with increasing wing flexibility for all our cases, which can be observed in the left-shift of the lift-to-drag polar (Figure 4.3B). Despite the non-linear relationship between lift slope and wing flexibility, we saw a consistent improvement in the maximum lift-to-drag ratio $\left(\frac{C_L}{C_D}\right)_{max}$ due to wing flexibility with F1 wings having the highest value for a given wing shape and V_{∞} (Table 4.3). This result indicates that despite the decrease in lift slope in the folded F1 wing compared to the folded F2 wing, the reduction in drag was great enough to ensure that the folded F1 wing had a higher $\left(\frac{C_L}{C_D}\right)_{max}$. Although flexibility improved aerodynamic performance in both wing shapes, the magnitude of the improvement was noticeably greater in the extended wing compared to the folded wing (Figure 4.3B). Once again, maximum lift-to-drag was reduced at higher flight speeds for a given wing shape and *E*, but this effect was negligibly small compared to the effect of wing flexibility (Table 4.3).

Table 4.3 Lift slope $\left(\frac{\partial C_L}{\partial \alpha}\right)$ and maximum lift-to-drag $\left(\frac{C_L}{C_D}\right)_{max}$ as a function of wing flexibility (*E*) and wing shape

Wing Shape	V_{∞}	E	$\frac{\partial C_L}{\partial \alpha}$	$\left(\frac{C_L}{C_D}\right)_{max}$	$\alpha_{\left[\left(\frac{C_L}{C_D}\right)_{max}\right]}$
Extended	10m/s	F1 (10 ⁶)	0.0597	4.0375	10
Extended	10m/s	F2 (10 ⁹)	0.0548	2.3702	10
Extended	10m/s	R (∞)	0.0226	1.3029	20
Extended	20m/s	F2 (10 ⁹)	0.0449	2.3390	20
Extended	20m/s	R (∞)	0.0191	1.2788	20
Folded	10m/s	F1 (10 ⁶)	0.0430	4.4276	10

Folded	10m/s	F2 (10 ⁹)	0.0473	2.9862	10
Folded	10m/s	R (∞)	0.0263	1.8562	10
Folded	20m/s	F1 (10 ⁶)	0.0405	4.4344	10
Folded	20m/s	F2 (10 ⁹)	0.0459	2.9316	10
Folded	20m/s	R (∞)	0.0212	1.5793	20

The mean C_p distributions around the wing reveal that the increased lift and decreased drag (Table 4.3) with increasing flexibility is due to the low-pressure area being smaller in size and positioned further forward, towards the leading edge of the wing instead of over the trailing edge in the wake (Figure 4.4). This oriented the resultant force vector upwards in the direction of lift and not drag. In the flexible folded wings, we also observe that the low-pressure area is concentrated at the leading edge, indicating that a high velocity boundary layer has reattached at the trailing edge likely due to the increased effect of wing tip vortices. The effect of *E* on the pressure distributions could not be easily discerned by the mean C_p so we looked at the instantaneous C_p distributions in the flexible wings at its $\alpha_{\left[\left(\frac{C_L}{C_p}\right)_{max}\right]}$. We found that the wing

shape-dependent effects of wing flexibility on aerodynamic performance were the result of aeroelastic responses promoting or dissipating local vortex structures attached to the upper surface of the wing. At $V_{\infty} = 10m/s$, the extended F1 wing pitched up and down and had a small low-pressure region that moved along its upper surface whereas the extended F2 wing had a small low-pressure region that both moved along and away from the upper surface towards the trailing edge and into the wake (Videos 4.1 and 4.2, respectively). This resulted in the F2 wing having less lift and more drag compared to the F1 wing. At $V_{\infty} = 20m/s$, the folded F1 wing

experienced a similar low-pressure region along its leading edge, but unlike the extended wing, the aeroelastic deformation had an irregular S-shape and the low-pressure region did not travel all the way to the trailing edge (Video 4.4). This resulted in a loss of the pressure differential that generates aerodynamic force over the entirety of the wing surface and, therefore, a decrease in lift and drag compared to the extended wing. The folded F2 wing displayed similar behaviour as its extended counterpart except that some of the low-pressure regions that were shed away from the upper surface at the trailing edge were absent, leaving only the ones travelling along the upper surface (Video 4.6). The instantaneous pressure distributions suggest that vortex structure differs between cases. As a result, we looked further into the oscillatory behaviour of the flexible wings to decipher the mechanisms that drive the observed improvements in performance.

4.3.3 Wing flexibility induces small-scale vortical structures that increase local vorticity and prevent boundary layer separation

Flexible wings produced smaller vortex structures over the wing and in the wake compared to a rigid wing (Figure 4.6). The negative lambda-2 isosurfaces of both the flexible cases, either extended or folded, were similar compared to the rigid cases. This trend is correlated with the similarities of the aerodynamic performance between both flexible wings compared to the rigid wing (Table 4.3). Additionally, the smaller vortex structures lay closer to the wing's upper surface compared to the large separation bubble vortex caused by boundary layer separation in the rigid wing. As a result, local vorticity over the wing surface was higher in flexible wings, increasing the circulation, and therefore, lift.

The differences in instantaneous C_p between the two flexible wing cases for a given wing shape and V_{∞} were indicative of a difference in how the aeroelastic responses modified local fluid flow. Most notably, F1 wings experienced wing tip plunge and twist deformations at lower

amplitudes than the F2 wings, although the effect of this on the vortex isosurfaces were not as apparent (Figure 4.5, Table 4.4, 4.5). At $V_{\infty} = 10m/s$, aeroelastic responses for the F1 wing decreased in amplitude with wing folding whereas the F2 wing increased in frequency with wing folding. The larger amplitudes of the extended F1 wing caused a pitching movement not present in the extended F2 wing. These deformations allowed the wing to move in synchrony with the small vortex forming near the leading edge ensuring that it remained attached along the entirety of the wing's upper surface (Video 4.1) instead of being shed away from the surface (Video 4.2), improving lift production in the extended F1 wing. At $V_{\infty} = 20m/s$, the F1 wing was structurally unstable when extended so no data could be obtained for this case, but wing folding resulted in stable low frequency and high amplitude deformations. Like the results at a slower speed, aeroelastic response for the F2 wing also showed an increase in frequency (Figure 4.5, Table 4.4, 4.6). At this higher speed, the high amplitudes and low frequencies experienced by the folded F1 wing corresponded to the second mode shape. This did not allow the aeroelastic response to synchronize with the small vortex formed near the leading edge. Instead, the vortex seems to be destroyed towards the trailing edge (Video 4.3), reducing the enhanced lift effect observed in the extended wing. Meanwhile, the folded F2 wing at $V_{\infty} = 20m/s$ did not experience much change in its local flow patterns (Video 4.6) compared to the extended F2 wing at the same speed, and as such, did not experience as dramatic of a loss in aerodynamic performance due to folding. Taken together, these results suggest that the large improvement in aerodynamic performance in the extended wing with wing flexibility is dependent aeroelastic responses interacting with boundary layer to promote attachment and increasing vorticity, thus reducing drag and enhancing lift respectively.

Table 4.4 Frequency and amplitude of the first two harmonics of wing tip displacement (z^*) as a function of wing flexibility (*E*) and wing shape

Wing	V_{∞}	Ε	f_1	<i>A</i> ₁	f_2	<i>A</i> ₂	$\alpha_{\left[\left(\frac{C_L}{C_D}\right)_{max}\right]}$
Shape							
Extended	10m/s	F1 (10 ⁶)	6.27	5.21e-03	1.88	2.55e-03	10
Extended	10m/s	F2 (10 ⁹)	16.30	1.82e-05	14.42	1.34e-05	10
Extended	20m/s	F2 (10 ⁹)	18.75	1.29e-04	15.00	7.82e-05	20
Folded	10m/s	F1 (10 ⁶)	4.77	2.22e-04	11.67	1.49e-04	10
Folded	10m/s	F2 (10 ⁹)	74.27	2.17e-05	73.21	4.56e-06	10
Folded	20m/s	F1 (10 ⁶)	22.34	5.20e-03	44.68	2.75e-03	10
Folded	20m/s	F2 (10 ⁹)	73.40	3.15e-05	76.60	5.40e-06	10

Table 4.5 Frequency and amplitude of the first two harmonics of wing pitch angle (θ_p) as a function of wing flexibility (E) and wing shape

Wing	V_{∞}	E	f_1	<i>A</i> ₁	f_2	<i>A</i> ₂	$\alpha_{\left[\left(\frac{C_L}{C_D}\right)_{max}\right]}$
Shape							
Extended	10m/s	F1 (10 ⁶)	6.27	1.59	1.88	3.59e-01	10
Extended	10m/s	F2 (10 ⁹)	16.30	2.77e-03	14.42	2.04e-03	10
Extended	20m/s	F2 (10 ⁹)	18.75	1.96e-02	15.00	1.94e-02	20
Folded	10m/s	F1 (10 ⁶)	11.67	5.18e-02	4.77	4.03e-02	10
Folded	10m/s	F2 (10 ⁹)	74.27	3.934e-03	73.21	8.26e-04	10
Folded	20m/s	F1 (10 ⁶)	44.68	8.28e-01	22.34	4.88e-01	10

Folded	20m/s	F2 (10 ⁹)	73.40	5.72e-03	76.60	9.79e-04	10

In conclusion, wing folding-induced changes in stiffness can alter the local flow and vorticity via modulation of its aeroelastic responses in a way that enhances aerodynamic performance during flight behaviour commonly associated with wing extension and folding. Thus, coupling structural properties to wing morphing for passive flow control increased the aerodynamic performance envelope.

4.4 Discussion

Advances in aircraft technologies and design have achieved remarkable feats of flight. However, while birds cannot fly at Mach speeds or take-off with a 640-tonne payload, they far out-class any human-made aircraft in terms of versatility and adaptability. The avian wing can morph to meet behavioural needs by actuating or restraining skeletal movement via striated muscles (Biewener, 2011) that, in turn, automatically rearranges the feathers that make up most of the lifting surface of the wing (Taylor et al., 2012). Thus, these flexible feathers must interact to enable flight as well as many other critical behaviours (McKittrick et al., 2012). But as these feathers interact during wing morphing, they cause not only a wing shape change but also a change in wing stiffness (Chapter 3). Since avian wing stiffness is relatively low, aeroelastic response, a fluid-structure phenomenon that engineers often aim to avoid (Kehoe, 1995) but animals have been observed to selectively employ (Clark & Prum, 2015; Clark et al., 2013; Clark et al., 2016; Liao et al., 200), is significant. We, therefore, employed fluid-structure numerical modelling to explore how coupling wing morphing to changes in stiffness could differentially affect aerodynamic performance by modulating aeroelastic response. We found that the deformation of a flexible wing interacted with local vortex structures, increasing vorticity, and

preventing boundary layer separation which improved aerodynamic performance. Our results also suggest that the stiffness at which the best aerodynamic performance can be achieved is dependent on the wing shape and flight speed. These findings indicate that there may be a mechanism inherent in the multi-component avian wing that modulates aerodynamic performance by coupling structural properties to wing morphing.

Wing morphing involves complex three-dimensional changes in the bird's wing geometry with the limits of morphing range of motion showing interspecific variation correlated to flight style (Baliga et al., 2019). One of the better-studied morphing behaviours is wing extension and flexion, and past studies have found that birds tend to extend their wings during low-speed gliding flight and fold their wings during high-speed gliding flight (Pennycuick, 1968). Our rigid model simulations successfully reproduced the drag reduction associated with wing folding (Figure 4.2B, D) that has been experimentally measured in past studies on birds (Pennycuick, 1968; Lentink et al., 2007). This reduction in drag is the consequence of a decrease in the size and magnitude of the low-pressure wake formed during boundary layer separation (Figure 4.2D) as wing-tip vortices interact with the detaching boundary layer (Shademan & Naghib-Lahouti, 2020), indicating that wing folding reduces profile and pressure drag in particular (Pennycuick, 1968; Lentink et al., 2007).

As the wing folds, it changes its aspect ratio, sweep and planform area. Low aspect ratio has been found to delay boundary layer separation and reduce pressure drag in other numerical studies (Shademan & Naghib-Lahouti, 2020). Therefore, we compared the aerodynamic forces generated by the wing models against three rectangular plates of differing aspect ratio to better understand the role that aspect ratio plays in decreasing drag during wing folding. Even though the extended wing and folded wing had very different aspect ratios, they did not experience as

large of a reduction in pressure drag compared to the rectangular plates of similar aspect ratios (Figure 4.2). We can assume that the change in both sweep and taper of the wing models due to wing folding play an equally important role in dictating aerodynamic forces and cannot be neglected. In fact, our results are in line with other numerical studies that have found that increasing wing taper reduces induced drag, which in turn, reduces the effect of aspect ratio on pressure (Chen & Katz, 2004). Therefore, we would expect that the effect of wing-tip vortices interacting with the boundary layer is not as great in our tapered bird wing models, which is reflected in the small change in aerodynamic performance due to wing folding (Figure 4.2B).

In general, our aerodynamic force coefficients were like those found in the *in vivo* flight of pigeons in a wind tunnel. Pennycuick (1968) found that pigeons flying at 10m/s had a lift coefficient of around 0.8 and pigeons flying at 20m/s had a lift coefficient of around 0.3, although the angles of attack used by the pigeon in flight were not reported. If we compare these data to our rigid models, the extended wing underestimated the mean lift coefficient at $V_{\infty} =$ 10m/s ($C_L \sim 0.64$), and the folded wing overestimated the mean lift coefficient at $V_{\infty} = 20m/s$ ($C_L \sim 0.54$). However, our flexible wing models achieved mean lift coefficients much closer to *in vivo* experimental values ($C_L \sim 0.83$ in the extended wing with $E = 10^6$ at $V_{\infty} = 10m/s$, and $C_L \sim 0.41$ in the folded wing with $E = 10^6$ at $V_{\infty} = 20m/s$). That the flexible models performed closer to actual birds in flight highlights the importance of accounting for wing flexibility when studying avian flight performance.

We found that wing flexibility can have large effects on aerodynamic performance, greater even than a 10m/s increase in glide speed. Overall, wing flexibility increased lift and reduced drag compared to the rigid model (Figure 4.3). Past work has often focused on the effect of propulsor flexibility during an oscillatory limb movement such as flapping flight. These studies have generally found that flexibility is associated with increased lift (Mountcastle & Combes, 2013; Hamamoto et al., 2007; Esposito et al., 2012) or thrust (Kodali et al., 2017; Lucas et al., 2013) as well. Similar trends have been found in bio-inspired flexible fixed wing micro air vehicles (DeLuca et al., 2012; Hu et al., 2008). In these bio-inspired models, performance improvement has been credited to a steady deformation in camber that balances pressure and prevents boundary layer separation, but performance deterioration has been associated with flutter in the trailing edge causing an increase in drag (Hu et al., 2008). Contrary to this finding, our results show that aeroelastic flutter is not necessarily characteristic of poor performance, as all our flexible cases exhibited steady oscillatory deformation behaviour (Figure 4.5) yet consistently performed better than rigid wings (Figure 4.3). In some cases, drag was lower in the rigid model but this was overshadowed by improvements to lift due to wing flexibility, resulting in an overall improvement to lift-to-drag ratio.

Flutter movements caused a flapping-like motion in flexible wings. This deformation causes the wing to interact with the boundary layer, generating additional small vortices over the wing and in the wake, thus increasing vorticity, circulation, and energy mixing into the near wall flow all of which result in lift enhancement (Figure 4.6). This injection of high energy flow into the shear layer resulted in a smaller low-pressure separated region and reducing drag (Figure 4.4). This mechanism for wake-dependent drag reduction has been reported in low Reynolds number flows (Rojratsirikul et al., 2011) or vibration-induced vortex structure interactions for lift enhancement (Khan et al., 2017; Kang et al., 2015). Our study confirms that a similar phenomenon may be possible at the intermediate Reynolds numbers experienced by birds in flight.

Wing flexibility can be a gift or a curse; in some circumstances it can enhance performance while in others it may reduce it. While the flexible wings had a higher $\frac{\partial C_L}{\partial \alpha}$ and $\left(\frac{C_L}{C_D}\right)_{max}$ than the rigid wings in all the cases in this study, the level of flexibility (E) that generated the highest C_L , C_D , $\frac{\partial C_L}{\partial \alpha}$ or $\left(\frac{C_L}{C_D}\right)_{max}$ varied for a given V_{∞} and wing shape. The nonlinear nature of the relationship between structure flexibility and the performance of a specific propulsor shape has been highlighted in some past work (DeLuca et al., 2012; Esposito et al., 2012). Based on the findings of this study, we propose that coupling changes to the structural properties with wing morphing (Chapter 3) allows for flexibility-based modulation of aerodynamic performance in a way that enhances the performance of flight behaviour associated with specific wing shape. An extended wing flying at a low speed of $V_{\infty} = 10m/s$ had the highest $\frac{\partial C_L}{\partial \alpha}$ of 0.06 with a wing stiffness of $E = 10^6$ (F1). However, a folded wing flying at a high speed of $V_{\infty} = 20m/s$ had the highest $\frac{\partial c_L}{\partial \alpha}$ of 0.046 with a wing stiffness of $E = 10^9$ (F2) (Figure 4.3A). We propose that two phenomena can explain these results: dynamic aeroelastic instabilities and frequency coupling between structural responses and local flow patterns.

The first explanation is that the aerostructural responses of an extended F1 wing are unstable. No simulation cases of an extended wing with a flexibility of $E = 10^6$ flying at a high speed of $V_{\infty} = 20m/s$ successfully ran to completion. This is likely due to extremely unstable flutter and divergence aeroelastic responses that the solver was not equipped to handle. Experimental work by Lentink et al. (2007) on freeze-dried swift wings in a wind tunnel found that extended wing specimens experienced violent vibrations at speeds of 15-20m/s leading to structural failure.

The second explanation is that the frequency and amplitude of the wing deformation dictates the behaviour of the vortices generated from the wing moving in and out of the shear layer which can enhance or mitigate vortex-induced lift. An extended F1 wing at $V_{\infty} = 10m/s$ pitched up and down at large amplitudes and low frequencies (Figure 4.5A, C) resulting in a vortex rolling from the leading edge to the trailing edge during the pitch up movement which is subsequently dissipated during the pitch down movement (Video 4.1). In contrast, the extended F2 wing at $V_{\infty} = 10m/s$ had some of the vortices shed away from the surface (Video 4.2). In the extended F1 wing, the vortices remained near the upper surface which increases the local vorticity (Kang et al., 2015) and significantly enhances C_L at low speeds with increasing flexibility. However, when the wing is folded, the flow pattern is changed such that F1 wings lose their vortex-induced lift enhancement. At both speeds, vortex structures seem to lose coherence and are "destroyed" before they meet the trailing edge due to either low deformation amplitudes at $V_{\infty} = 10m/s$ (Video 4.3) or a higher frequency chord-wise mode at $V_{\infty} = 20m/s$ (Video 4.4). The folded F2 wing at both flight speeds seemed to maintain a steady, albeit higher frequency, stream of vortices along the upper surface of the wing (Video 4.5, 4.6). Therefore, a bird gliding at low speeds may extend its wings to increase lift production by increasing lifting surface area and reducing induced drag through an increase in aspect ratio. Coupling a decrease in stiffness due to a reduction in feather-feather interaction (Chapter 3) could further enhance lift production. In the broadest sense, structural changes coupled to wing morphing can modulate the synchronicity of aerostructure behaviour to further increase flight performance.

The synchronization of aeroelastic behaviour to modify vortex patterns to either promote or mitigate load generation has been observed in flexible objects deforming in the wake of a cylinder. Flexible fins have been found to constructively or destructively interact with the von Kármán vortices shed in the cylinder's wake which enhance or mitigate forces (Banerjee et al., 2021). In some situations, constructive interaction with vortical disturbances may prove advantageous. Rainbow trout (Oncorhynchus mykiss) have been found to actively initiate thrust generation through oscillatory synchronization by altering their kinematics when encountering environmental vortices, a behaviour known as a Kármán gait. They increase the amplitudes of oscillatory body movements and synchronize the frequency of these body movements with the upstream vortices to generate enough propulsive thrust to hold position (Liao et al., 2003). On the other hand, flexible wings or wing structures have also been found to destructively interact with vortical disturbances which can aid in flight stability when encountering gusts or turbulence. Bio-inspired flexible flaps can significantly suppress aerodynamic fluctuations and reduce vorticity thereby improving flight stability but also reducing the lift-enhancement effect (Murayama et al., 2021). The implication is that the effects of flexibility come with a trade-off between the ability to efficiently enhance lift and the ability to efficiently stabilize against large disturbances. As a result, the observed increase in wing stiffness due to wing folding at higher speeds may lead to a trade-off in lift production for the ability to attenuate large fluctuations in aerodynamic forces due to self-excited oscillations or external disturbances.

This study provides the first investigation of how the observed coupling between wing morphing and wing flexibility can modulate flow behaviour near the wing through aerostructural deformations in a way that benefits locomotory behaviour associated with wing extension and flexion. However, this study involves a highly simplified wing geometry and future studies will have to be done with either a more realistic structural model with camber and varying thickness or bird wing specimens to confirm the mechanisms proposed here. One of the major limitations is that our model was isotropic in flexibility. The location of the flexion can also have an

important effect on force generation (Murayama et al., 2021; Lucas et al., 2014), and the wing is a complex multi-component structural system that experiences local changes to stiffness due to wing folding (Chapter 3). Additionally, this study only evaluates wing morphing and aerostructural responses during gliding flight. Flapping flight is a critical part of avian locomotion which must be investigated when evaluating whether local changes in stiffness during wing morphing might improve or impair to flight performance.

In conclusion, this study provides a preliminary investigation into how aerodynamic performance varies as a function of wing stiffness in the context of wing morphing and the associated behaviours. We first quantified aerodynamic performance and found that lift production was enhanced in highly flexible extended wings at low speeds whereas moderately flexible folded wings performed better at higher speeds. By visualizing vortex structures, we found that lift enhancement is a result of synchronized aeroelastic deformation with flow vortices enabling high vorticity over the upper surface of the wing and drag reduction is a result is a smaller low-pressure wake. These findings on how passive flow control can be modulated when coupled to wing morphing may provide inspiration for wing morphing technologies in micro air vehicles, which are seeing increased usage.



Figure 4.1 Geometric models for the solid structure and fluid volume. A) Extended (left) and folded (right) wings as seen here in a isometric (above) and overhead (below) views, and B) rectangular plates with varying

aspect ratio were created in Gmsh. C) The wing or rectangular plate was placed inside a fluid volume with a curved inlet.



Figure 4.2 Wing folding decreases pressure drag by reducing the size of the separation bubble caused by boundary layer separation. A) The lift coefficient increases dramatically with aspect ratio in the rectangular plates (blue points) but minutely with aspect ratio in the extended (triangles) or folded (squares) wing models at $Re = 1 \times 10^5$ (black) or $Re = 2 \times 10^5$ (red). B) Drag is increased with aspect ratio in the rectangular

plates (blue points) and in the extended (triangles) or folded (squares) wing models at $Re = 1 \times 10^5$ (black) or $Re = 2 \times 10^5$ (red). This causes the lift-to-drag polar to be right shifted. C) The pressure coefficients of a wing or rectangular plate with $\alpha = 30^\circ$ in a XZ slice positioned at the y-coordinate with a chord length equivalent to the mean aerodynamic chord show that the low-pressure separation bubble caused by boundary layer separation increases with aspect ratio. The effect is more pronounced in the rectangular plates (centre column) compared to the wing models (left and right columns). Low pressure is represented by dark bluepurple colours and high pressure is represented by a yellow colour.



Figure 4.3 Flexible wings perform better than rigid wings. Stiffness is represented by point and line colour. Free-flow velocity (V_{∞}) is represented by point shape. A) In the extended wing, lift slope increases with increasing flexibility (left), but in the folded wing, lift slope is highest at moderate flexibility (F2) $(E = 10^9)$ (right). B) Lift is increased and drag decreased with increasing flexibility, expanding the polar envelope. This effect is greater in the extended wing (left) than in the folded wing (right).



Figure 4.4 Wing flexibility reorients the low-pressure region upwards and towards the leading edge which contributes to increasing lift and reducing drag. This is shown via the pressure coefficient distribution in a XZ slice positioned at the y-coordinate with a chord length equivalent to the mean aerodynamic chord for the wing positioned at the

 $\alpha_{\left[\left(\frac{C_L}{C_D}\right)_{max}\right]}$. Low pressure is represented by dark blue-purple colours and high pressure is represented by a

yellow colour.



Figure 4.5 Wing folding decreases the amplitude of aeroelastic responses in the very flexible wing and increases frequency in the aeroelastic response of the moderately flexible wing. Wing stiffness is given by point and line colour, the first two harmonics are defined by line type, and amplitude is represented by point size. Each panel consists of data coloured that corresponds to the specified free-flow velocity V_{∞} with data greyed out for the other V_{∞} . At $V_{\infty} = 10m/s$, wing tip plunge displacement had A) low frequencies and high amplitudes in the F1 ($E = 10^6$) wing and low frequencies and low amplitudes in the F2 ($E = 10^9$) wing in the extended wing. With wing folding the amplitudes decreased in the $E = 10^6$ wing whereas frequencies

increased in the $E = 10^9$ wing. B) At $V_{\infty} = 20m/s$, the $E = 10^6$ extended wing case failed and the $E = 10^9$ extended wing had low frequencies and low amplitudes. With wing folding, the $E = 10^6$ folded wing had low amplitudes and high frequencies while the $E = 10^9$ wing once again experienced an increase in frequency. Similar trends were observed for wing twist at C) $V_{\infty} = 10m/s$ and D) $V_{\infty} = 20m/s$.



Figure 4.6 The aeroelastic responses due to wing flexibility allow the wing structure to move into the detached boundary layer increasing vorticity, reducing the wake size particularly in the extended wing. Lambda-2 isosurfaces are visualized with a value of $\lambda_2 = -0.5$ for the wing positioned at the $\alpha_{\left[\left(\frac{C_L}{C_D}\right)_{max}\right]}$. The isosurfaces

are coloured by normalized velocity at $v^* = 0.9$ (red) and 1.1(blue).

Chapter 5: Conclusion

5.1 Discussion

The ability to fly was likely a major contributing factor to the diversification and success of birds (Brusatte et al., 2015). Their morphing wings allow them to actively engage different flight modes (Carruthers et al., 2007; Carruthers et al., 2010) and eliminate unwanted aerodynamic behaviour due to environmental factors (Reynolds et al., 2014). Seamlessly changing wing shape during gliding flight involves the coordinated rearrangement of flight feathers via musculoskeletal action in the leading edge (Matloff et al., 2020). Despite feathers being critical structures for flight, there is still much we don't understand about how they contribute to aerodynamic performance over a variety of flight behaviours. We made use of a variety of methods, experimental, numerical, and statistical, to investigate how avian feathers and their arrangement in the context of the entire wing structural system during wing morphing affect aerostructural responses and flight performance. This was broken down into three questions and their findings can be summarized as follows:

How important is aerodynamic performance in explaining feather morphology variation?

Aerodynamic performance was a strong selective pressure driving feather shape variation among species, more so than feather location, feather type, or phylogeny.

How does wing extension-flexion affect the local mechanical properties of the pigeon wing?

Wing folding increases stiffness and work absorption in the proximal wing compared to the distal wing, while damping is maintained throughout wing folding through friction damping mechanisms in the proximal wing and internal viscosity in the distal wing.
How can changes to wing mechanical properties coupled to wing extension-flexion during gliding flight affect aerostructural responses and flight performance?

Increasing wing stiffness during wing folding or decreasing wing stiffness during wing extension can enhance lift production through fluid-structure frequency coupling. Taken together, we conclude that a feathered wing can be locally "tuned" for aerodynamic function through variation in its individual components and through variation in the interaction of multiple components to adjust mechanical properties and aerostructural responses.

5.1.1 Coupling active and passive structures in a system for flow control

Wing extension-flexion is achieved by coupling the position of flight feathers to muscleactuated skeletal movement (Matloff et al., 2020). This behaviour not only changes the wing shape to suit flight behaviour, providing drag reduction during high-speed flight (Pennycuick, 1968), but also locally changes the mechanical properties. Modifying stiffness alters aerostructural response differently depending on wing shape, affecting the synchronization between flutter frequency and flow vortex frequency, and subsequently influencing local vorticity and lift production. We suggest that while a feathered wing may not allow for active control over the entirety of the wing, variation in individual feather morphology and featherfeather interaction can still allow for a great degree of local flow control with minimal control complexity.

The complex 3D shape of the avian wing and the different kinematic gaits birds can choose from during flight result in variations in local aerodynamic forces which affect a bird's overall locomotory performance in life. Mechanisms for local flow control would allow a bird to modify these local aerodynamic forces to meet functional requirements. Perhaps one of the most well-known examples involves the alula. During gliding flight, wing twist results in an increase

in angle of attack near the distal wing (Cheney et al., 2021), putting that region at risk of stall. The alula, made up of small contour feathers attached to the minor digit, induces tip vortices that move spanwise distally and chordwise towards the trailing edge, adding vorticity to the boundary layer and preventing separation, thus delaying stall (Lee et al., 2015). Instead of adding a functionally specific structure such as the alula or leading-edge slats to modify flow patterns, we propose a mechanism in which morphing-induced changes to mechanical properties of the main wing structure influence how it interacts with the boundary layer to modify flow.

This thesis focuses on the aerostructural effects of avian wing extension-flexion in response to flight speed during fixed-wing gliding and had found indication that the mechanical properties associated with an extended or a folded wing during low or high-speed flight respectively improved lift production. Thus far, no studies have directly measured the force distribution over the wings of a gliding bird (Harvey & Inman, 2020). Flow visualization techniques found that downwash patterns of gliding birds with extended wings are indicative of a constant section lift coefficient distribution with wing tip vortices positioned just inboard of the wing tip (Usherwood et al., 2020). This vortex pattern agrees with a bell-shaped lift distribution proposed by Prandtl in 1933, which is characterised by a gradual reduction of loads from the wing root to the wing tip, a strong downwash near the wing root and a small upwash at the wing tip (Bowers et al., 2016). In this work, we found that the stiffness anchoring flight feathers in place was greater in the distal wing compared to the proximal wing in both the extended and folded wing. Broadly speaking, distal flight feathers are more tightly fixed in place and would require larger loads to displace near the base compared to proximal flight feathers. For static loads during steady gliding and assuming an unchanging bell-shaped lift distribution, it would seem the distal wing stiffness needlessly overcompensates.

The wing is a dynamic structure, capable of large-scale shape changes and passive aeroelastic effects. During gliding flight, the pigeons extend their wings at slow speeds (V_{∞} = 10m/s) and fold their wings at high speeds ($V_{\infty} = 20m/s$) (Pennycuick, 1968) which has the effect of increasing feather anchoring stiffness in the proximal wing during wing folding. Although we were unable to test identical mechanical properties in our computational model as the experimental values, we can make predictions based on the trends. At low speeds with an extended wing, the proximal wing where most of the lift is being produced (Bowers et al., 2016), was at its most flexible. Based on our computational results, a flexible extended wing at low speeds experienced large amplitude, low frequency structural vibrations that were synchronized with vortices in the leading-edge shear layer, increasing the strength of the lifting vortex. This behaviour would enhance the lifting capabilities of a slow flying pigeon. At high speeds with a folded wing, the proximal wing significantly increased in stiffness. If stiffness was not increased during flight at high speeds, our computational results found that the mode of the structural deformations was altered, and structural deformations were no longer synchronized with leadingedge vortices in a way that enhanced lift. Therefore, the ability to increase stiffness prevented some lift reduction during wing morphing in the proximal, lift-generating section of the wing.

The distal wing also produces lift during gliding flight, but we do not see much change in wing stiffness due to folding. We theorize that strictly coupling aerostructural modulation of lift production in the distal wing would not provide as much performance benefit for all the flight behaviours a bird might engage in. This may be because active morphing of the distal wing is critical for steering complex manoeuvres (Chang et al., 2020) as well as flapping flight (Cornell Lab of Ornithology, 2004). While the oscillatory behaviour in the low-stiffness proximal wing increased lift coefficient, this can come with trade-offs with stability and control (Curet et al.,

2013) as any slight deviation to the wing stiffness can result in large changes to deformation behaviour and uncouple the structural frequencies from the flow vortex frequencies. Increasing the risk is the low damping ratio of the entire wing independent of wing shape ($\delta = 0.17 - 0.32$). Higher damping ratios have been analytically found to broaden the resonance frequency range that can be used for frequency lock-in and improved performance efficiency (Ahlborn et al., 2006). Having a high stiffness in the distal wing may not result in the best lift production in that region, but it may come as a trade-off for improved control stability. While these predictions would need to be verified either computationally with a multi-material cambered wing or experimentally with wing specimens or live birds, the arrangement of the avian feathered wing is such that dynamic aerostructural effects on flow control are promoted in one section of the wing while restricted in another.

Non-flapping flight includes more than steady forward motion, as birds also encounter gusts and turbulence. These disturbances can change suddenly within a small geographical area (Emeis et al., 2007) and vary greatly in magnitude (Hewston & Dorling, 2011), so the ability to adapt quickly to a broad range of conditions is critical. Atmospheric disturbances tend to either be at small scales and high frequencies as in the case of turbulent eddies (Watkins et al., 2006) or large scales and lower frequencies as in the case of updrafts produced by surface topography, temperature gradients, internal waves, or gust fronts (Laurent et al., 2021). Studies in other birds have found that they alter their behaviour in response to turbulence parameters. Bee-eaters switch to soaring-gliding flight instead of flapping flight in environments with high turbulence kinematic energy such as updrafts (Sapir et al., 2011), while gulls prefer a folded and cambered wing shape while flying in air with higher maximum gust speeds (Harvey et al., 2019). The rock or common pigeon often flies in urban environments which feature larger wind profile slopes,

turbulence intensities and magnitudes (Emeis et al., 2007). Our study found consistent high damping capabilities (51-78%) throughout the wing under a 5Hz dynamic load and dynamic aeroelastic responses were present even if the bird was flying in calm air. It is possible that the high damping could rapidly eliminate external influences on the structural deformation and promote structural frequencies that enhance lift during flight. In bio-inspired models, flexible wings allowed for rapid stabilisation with less overshoot in response to gusts (Zhang et al., 2018). It may even be possible that structural deformations of the wing due to fluid-structure interactions could break up upstream vortical disturbances (Murayama et al., 2021), ensuring more regular flow over the wing. However, as we did not experimentally test realistic turbulent conditions in either our dynamic mechanical tests on a pigeon wing (turbulence intensity < 0.03%) or our computer simulations, further work is required to evaluate how mechanical properties coupled to wing morphing contribute to flight performance in gusty or turbulent environments.

Besides gliding flight, birds use their wings for flapping flight which involves different aerodynamic loads due to the movement of the wing and high angles of attack compared to gliding flight. The wing root of a bird has higher pressure coefficients due to a greater thickness and camber in the proximal wing. However, as the wing goes through a flapping cycle, higher velocities at the wing tip during downstroke will generate larger dorsal-ventral forces in the distal wing compared to the proximal wing (Usherwood, 2009; Usherwood et al., 2003). The forces experienced by the distal wing are further increased during costly manoeuvres such as take-off and landing (Usherwood et al., 2005) which is reflected in the high-strain deformations of the distal flight feathers (Corning & Biewener, 1998). The downstroke is typically done with an extended wing. The proximal wing does not move as much during flapping flight so we can

assume that mechanisms for flow control and lift enhancement are similar to the mechanisms during gliding flight as previously described. Our work found that the extended distal wing is stiffer than the proximal wing (Figure 3.3A, C, Figure 3.4A). A stiffer wing offers more load resistance during the increased forces of flapping flight. Our simulations found that high stiffness prevented high amplitude deformations (Figure 4.5). Restricting the deformations of the components anchoring flight feathers would prevent the bending point from occurring too close to the leading edge. The location of propulsor bending has been found to be consistent among animals of all shapes and sizes moving through different media and likely corresponds to some near-optimal location for propulsive efficiency (Lucas et al., 2014). During the upstroke, the wing is folded, and the distal wing experiences dorsal-ventral forces during the upstroke (Usherwood et al., 2003). The distal wing continues to have a higher stiffness than the proximal wing, reflecting the higher load resistance still required. However, the stiffness was slightly reduced which may allow for spatial separation of the flight feathers, giving them the space to twist and align with the flow during the upstroke and reducing air resistance and drag-based forces propelling the bird towards the ground (Cornell Lab of Ornithology, 2004).

Our studies have found that wing folding can vary mechanical properties and this selective modulation of properties coupled to a specific wing shape can alter the local flow through fluid-structure interactions in a way that increases aerodynamic performance over a range of flight behaviours. While our computational simulations were unable to match the experimental properties measured in a pigeon *in situ*, we took a broad view of the trends to propose ways the avian morphing structural system could be locally tailored for different flight behaviours and suggest that there is value in having local flow control through different structural mechanisms. Having the mechanical properties be dictated by feather-feather

interaction in the proximal wing and soft tissue compliance in the distal wing could allow frequency synchronization for lift enhancement in the proximal wing without compromising the aeroelastic behaviour of the distal feathers during flapping flight. In other words, the avian wing couples passive aeroelastic effects to simple active controls to alter local lift distribution over the wing with little controller input.

5.1.2 Aerostructural responses for flow sensation

Wing folding can alter the local mechanical properties of the wing through featherfeather interaction which has effects on their structural deformation under flow during flight. Currently, there has been no work quantifying the dynamic aeroelastic response of the flight feathers of pigeons, or any other bird, during gliding flight and linking these responses to mechanosensation of local flow. Despite this, it has been inferred that the deformation of select groups of feathers in response to specific flapping behaviours or gust disturbances encodes information about flow around the wing (Carruthers et al., 2007). Due to the prominence of the topic in recent flight research, we discuss how wing morphing induced changes to aerostructural response would impact flow sensation.

The avian wing has the necessary neural anatomy for mechanosensation which would provide relatively fast and localized signals for force stimuli during flight (Altshuler et al., 2015). In fact, birds have more touch corpuscles in their skin than mammals, reptiles or even non-volant birds, giving them high spatial sensitivity and signifying the importance of local mechanosensation for flight (Homberger & De Silva, 2000). Mechanoreceptors are localized around feather follicles and are stimulated by movement of the feather embedded in that follicle. Mechanoreceptors can be classified into two types: slow adapting receptors such as Merkel cells and Ruffini endings and fast responding cells such as the vibration sensitive Herbst corpuscles (Altshuler et al., 2015). Slow adapting receptors have been found near the propatagial covert feathers and the alula joint. During feather deflection or alula extension, these receptors discharge with a frequency dependent on the amplitude of deformation but independent of duration of deformation. The location of these mechanoreceptors and their response to static and passive deflections of the feathers suggest that they could be encoding information about flow separation and stall (Brown & Fedde, 1993), a phenomenon also found in bat hairs (Sterbing-D'Angelo et al., 2011). Vibration sensitive mechanoreceptors have been found at the base of both primary (Hörster, 1990) and secondary flight feathers (Brown & Fedde, 1993). These early studies noted that the vibration response varied with flow speed but did not report this relationship. Nevertheless, these fast receptors discharged with a frequency dependent on flow speed (Brown & Fedde, 1993), or more specifically, with frequency (Hörster, 1990) indicating that these receptors could be encoding flight speed.

Herbst corpuscles are generously and randomly spread throughout the wing, with over 1000 in the distal wing of the pigeon alone. The corpuscles tested in two studies by Hörster (1990; 1990) found that while they have a broad bandwidth, responding to frequencies from 50Hz to 1800Hz, they are most sensitive to only a narrow band of frequencies. At their preferred frequency, these mechanoreceptors respond to vibration signals with amplitudes as low as 0.1µm. Stimuli frequencies lower than the preferred frequency require greater amplitude to trigger a neural signal (Hörster, 1990). The neural signal measured in the radial nerve, the nerve that innervates all these Herbst corpuscles in the distal wing, showed that information on the stimulus frequency relative to the corpuscle's preferred frequency is encoded as well, occasionally generating a 1:3 or 1:4 stimulus-response for higher frequencies and a 2:1 stimulusresponse for lower frequencies. In our study, all scenarios resulted in the wing model fluttering at

frequencies much lower than any of the preferred frequencies of the Herbst corpuscles found in literature. We found that wing folding increased local stiffness in the proximal wing due to an increase in feather-feather interaction. Our subsequent computer models suggest that increasing stiffness can increase the wing tip plunge frequency and decrease the amplitude, going from a frequency of 6.27 Hz and an amplitude of 5.21 mm for a wing stiffness of $E = 10^6$ to a frequency of 73.40 Hz and an amplitude of 0.003 mm for a wing stiffness of $E = 10^9$. Hörster's measurements found that for a frequency of about 100 Hz, an amplitude of roughly 0.04 mm would be needed to trigger neural activity (Hörster, 1990). However, our wing model is highly simplified and does not account for a more realistic multi-material wing shape with surface roughness, covert deflections, and variable camber and thickness so exact frequency and amplitude values would not be representative of those experienced by a bird in flight. Our values were within range of feather vibration frequencies of a diving peregrine falcon (30-35 Hz) (Brücker et al., 2016) while feather flight sounds measured in members of the Columbidae family range from 0.39-2.89 kHz (Clark & Prum, 2015), possibly exceeding the reported upper limits of the measured Herbst corpsucles in Hörster's study. Therefore, it is also possible that not all vibration sensitive mechanoreceptors are tuned for such high frequencies (Hörster, 1990).

Regardless, we found that our wing morphing-mechanical properties coupled mechanism in the wing resulted in a larger difference in aeroelastic response in both frequency and amplitude as the bird flies at a higher speed due to the increase in local wing stiffness. To compare, if the pigeon could fold its wings when flying at higher speeds without changing its local wing stiffness, its wing tip would be oscillating with a frequency of 22.34 Hz and an amplitude of 5.2 mm, a much smaller change in frequency and amplitude compared to a folded wing with an increase in stiffness. Therefore, coupling stiffness changes to wing folding for

faster gliding speeds, provides a mechanism for more distinct mechanosensation neural signals. The ability to properly detect flow speed is particularly important in the proximal wing because lift forces are proportional to speed squared.

The structure of the avian wing involving a series of interacting passive feathers coupled to active morphing elements provides a mechanism that can improve local flow sensation. Morphing induced changes to stiffness to improve differentiation of flight speeds can be localized to the area of the wing where it is most needed without affecting the sensitivity of other parts of the wing. Overlapping feathers also result in high damping via mechanical friction between feathers. This means that energy from feather movement is mostly lost to heat instead of transferring to its neighbours. This likely contributes to the fact that vibrations have been found to be poorly transmitted between neighbouring feathers; mechanoreceptors at the feather follicle are not sensitive to vibrations from its neighbouring feathers (Brown & Fedde, 1993).

Flow sensing plays a valuable role in flight control. Not much is known on this topic in birds because their flow sensing components, the feathers, are also their lift-generating surfaces, making it difficult to separate one function from the other. Nevertheless, we can infer from the magnitude of anatomical resources in the form of mechanoreceptors in the wing (Hörster, 1990) as well as other work in bats, that birds likely depend on flow mechanosensation for speed and manoeuvrability control, especially near stall conditions (Sterbing-D'Angelo et al., 2011). While we were unable to test these topics in our study, our results allow us to predict how the mechanical properties and structural deformations of a morphing wing could improve local flow sensation.

5.1.3 Potential effects of variation wing structures within and among species

Modern birds (*Neornithes*) are a group of incredibly successful animals, with over 10,000 species spread over the globe. Following the K-Pg mass extinction event 66 MYA, birds rapidly diversified over the next 15 million years in both form and distribution. Today, birds can be found on every continent and in every ecological niche (Claramunt & Cracraft, 2015; Brusatte et al., 2015). Most birds are capable of remarkable feats of flight. The 2g bee hummingbird in the humid tropics (Brusatte et al., 2015) can maintain flight control and manoeuvrability despite its size relative to atmospheric disturbances. The 20kg great bustard from dry palaearctic regions can travel over 10,000 km in a single season to reach wintering grounds despite it being one of the heaviest flying birds in the world (Kessler et al., 2013). While a morphing wing can greatly expand the performance envelope and flight capabilities of an individual bird under variable conditions, our findings suggest that wing components such as individual feathers have been shaped by natural selection for aerodynamic function, further increasing the flight capabilities among bird species and contributing to the diversity and success of birds.

The change in stiffness due to feather-feather interaction is dependent on the number of feathers overlapping and the degree of overlap for a given change in wrist angle as well as the stiffness of individual feathers. It is intuitive to imagine that feather-feather interaction is dependent on feather shape, the number of feathers on the manus relative to the arm, and the wrist and elbow range of motion. But whether or not interspecific variation in any of these parameters affects morphing-induced stiffness changes and flight performance is unknown. Our study has found that while primary flight feathers always number ten in total, the number of secondary flight feathers on the proximal wing can vary significantly. In our data set, we had a maximum of 28 secondaries in the American white pelican and 7-8 secondaries in the northern

flicker. This was not solely due to bird size as the much larger common raven also only had 8 secondaries. Instead, we propose that feather count has more in common with the relative length of the hand bones (carpometacarpus and major digit) compared to the arm bones (ulna and radius). Other skeletal morphology parameters have been linked with flight style. Soaring birds tend to have longer hand lengths while passerine type flyers tend to have lower hand lengths (Wang et al., 2011). Flight kinematics, quantified as the magnitude of span reduction in the upstroke compared to the downstroke, had a non-linear relationship with the ratio between humerus length and ulna length (Nudds et al., 2007). Perhaps most telling is a study that found that the humerus, ulna, and manus all scaled with positive allometry against mass (>0.33) with the ulna possibly having a higher scaling exponent than the manus although the difference was not statistically significant (0.39-0.43 for the ulna and 0.39-0.4 for the manus). This indicates that larger birds would have a relatively longer ulna and manus compared to small birds (Nudds, 2007). The northern flicker and the common raven both have 8 secondaries, but the common raven has a body mass 7.46 times greater than that of the northern flicker. In agreement with the allometric relationship found by Nudds (2007), the common raven's ulna length of 114.4mm exceeds that of isometric scaling which would predict a length of 94.54mm. Since the ulna length scales positively with mass but the feather count was independent of mass, the secondaries on the common raven are spaced approximately 14.9mm apart whereas the secondaries on the northern flicker are scaled 5.9mm apart. As a result, greater wrist joint movement would be required to output the same degree of feather-feather interaction in the common raven.

Range of motion in the wrist joint would also dictate the degree of overlap of flight feathers; a bird incapable of moving to wrist angles lower than those seen in the pigeon would

likely experience less feather-feather interaction and increase in stiffness compared to our study, assuming that all other parameters such as feather count, feather shape, manus-to-ulna length ratio, and feather stiffness remain the same. For example, it has been found that a gull can attain a smaller wrist angle than a pigeon (Baliga et al., 2019). This suggests that all else being equal, the gull could stack more of its feathers on top of one another during wing folding to increase local stiffness. However, if we account for feather count and ulna length from our morphological measurements, we find that pigeons have a theoretical 6.8mm spacing between its secondaries whereas a gull has a 7.5mm spacing. Therefore, more wrist flexion would be required to involve more feathers in reinforcing local stiffness. Elbow and wrist joint range of motion has been found to vary with flight style with soaring or swimming birds having a tightly coupled elbowwrist range of motion compared to flapping birds. This means that flapping, passerine-like birds can more easily decouple wrist flexion from elbow flexion (Baliga et al., 2019), giving flapping birds a greater ability to locally modify feather-feather interaction and feather attachment stiffness independently of large reductions in span and planform area that come with elbow and wrist coupled wing folding. With these preliminary trends, we propose that smaller birds, more prone to the effects of turbulence or more likely to fly in cluttered environments, have a greater sensitivity when it comes to control of local wing stiffness via wing morphing. They could possibly effect larger changes in wing stiffness through feather-feather interaction with less degree of change in wrist angle independent of elbow angle, allowing for more rapid and reactive tuning during difficult conditions.

Flexural stiffness, a function of both the Young's modulus and the second moment of area, also displays some dramatic variation among feathers (Osváth et al., 2020) and among species (Osváth et al., 2020; Bachmann et al., 2012; Worcester, 1996) which may influence the

change in wing stiffness due to feather-feather interaction. Stacking five feathers all with high stiffness values would have a different result compared to stacking five feathers all with low stiffness values. Variations in flexural stiffness have been noted in several studies and has often been linked to flight style preferences. In a study by Osváth et al. (2020), soaring or gliding birds like the common buzzard or the white stork tended to have more compressed rachis cross-sectional areas in proximal feathers suitable for withstanding ventral-dorsal loads. Flapping birds like the house sparrow have moderately compressed rachises. Whereas diving birds that primarily swim with their legs like the pygmy cormorant have depressed rachises which are more flexible in the ventral-dorsal axis (Osváth et al., 2020). Therefore, more feather-feather interaction (i.e., greater flexion of the wrist joint) would be required in diving birds, and to some extent, the flapping house sparrow to increase the overall local stiffness. However, as we do not have range of motion or feather data on these species, we are unable to comment directly on how range of motion, feather counts, or feather shape could offset this variability in individual feather stiffness.

Flight feathers near the wing tip do not experience much change in mechanical properties due to wing folding but interspecific variation in individual feather stiffness and feather shape can allow for modulation of local structural behaviour during flight. Out of four species tested by Osváth et al. (2020), the common buzzard and the house sparrow had the greatest variation in rachis cross-sectional area within a feather, with the feather tip being more flexible than the base. Distal feather aeroelastic bending and twisting is a noted phenomenon during soaring flight and flapping flight. During soaring flight, the emarginated primaries of many soaring birds are individually exposed to the flow, causing them to bend upwards under aerodynamic forces and reduce induced drag in a manner like aircraft winglets. During flapping flight, primaries at the

wing tip twist during the upstroke to reduce the angle of attack to near-zero to prevent negative lift generation and reduce air resistance (Cornell Lab of Ornithology, 2004). We found that primaries consistently had a higher aspect ratio shape compared to secondaries and alular feathers. Long, thin feathers would have less surface for interaction with its neighbours and combined with a reduction in flexural stiffness near the wing tip, could facilitate separation of wing tip flight feathers during soaring flight or the upstroke during flapping flight. Overall, we suggest that modulation of feather shape as well as feather arrangement are both possible mechanisms for adjusting aerostructural behaviour during flight.

The structure of individual components as well as the arrangement of the components relative to each other as a function of wing morphing allow for the possibility of tuning local aerostructural responses and overall performance under various flight conditions. However, how important these mechanisms are for avian flight, fitness, and survival are unknown. Evolutionary selection has been thought to depend on actual ecological performance which may be constrained by, but is not equivalent to, maximum performance capacity (Husak, 2006). In other words, just because birds have the mechanism to modulate aerostructural responses to improve aerodynamic performance, it does not mean they rely on this mechanism. Further experimental work must be done to understand the biological significance of such mechanisms, but in the meantime, the findings of this study could provide valuable insight in the development of engineered flight technology.

5.1.4 **Bio-inspired Applications**

As UAV or drone use and applications increase (Insider Intelligence, 2021), research and development has focused on ensuring efficient performance of these UAVs over a large range of usages and environmental conditions. However, doing this requires a good understanding of the

flow behaviour over the drone's wings under varying conditions which is difficult to accomplish due to the size and speed of these drones. At the intermediate Reynolds regime at which UAVs and birds operate at ($Re \sim 10^5$), local and instantaneous aerodynamic forces can charge significantly as a function of wing geometry and boundary layer behaviour (Tank et al., 2017). Therefore, we applied a mixture of experimental and computational methods using avian models to generate hypotheses for possible mechanisms of adaptive flight technologies for future investigation.

Geometric changes to wings have a long history of improving flight performance, but it is only recently that interest has shifted to include the importance of mechanical properties in morphing UAV structures as well. UAVs have progressed a lot and can be as efficient as birds if they are acting within a narrow performance range, but birds with their morphing wings still have the control and aerodynamic mechanisms to operate over a larger operational range and, as a result, can provide valuable inspiration for future multi-functional UAV technologies (Harvey & Inman, 2021; Weishaar et al., 2006). Flow control does not require dynamically morphing wings and aircraft have long relied on geometric alterations to the wing to control flow. Controlling boundary layer transition and separation can provide significant improvements to performance, with a delay in boundary layer transition on the wing by 50% potentially saving 8% of commercial aircraft fuel. Conventional techniques involve microjet arrays (Kreth et al., 2010), vortex generators placed upstream of the separation point, slotted airfoils, trailing edge flaps, cavities on the upper wing surface, and increases to the surface roughness, all of which, in some way or another, promote boundary layer attachment (Genç et al., 2020). These methods all improve lift and reduce drag but require permanent structural changes that cannot be adjusted as needed. For example, a sudden gust might move the separation point upstream of vortex

generators, rendering them obsolete. Morphing wings, on the other hand, allows for nonpermanent shape changes without compromising the aerodynamic properties or flow control capabilities under alternate conditions. The avian wing has also achieved morphing capabilities without adding significant controller weight or complexity (Di Luca, 2017).

The coupling of passive flexible components to a simple active leading edge could inspire mechanisms for flow control that improves aerodynamic performance by delaying boundary layer separation. These mechanisms could be implemented to reduce control complexity in past morphing wing technologies such as piezoelectric morphing of chordwise camber (Ohanian et al., 2013) or wing-tip devices (Lee & Wissa, 2020). Performance in turbulent as well as calm conditions is a highly desirable trait in UAVs due to their small size and their operation in urban environments or near the ground where flow is easily disturbed (Emeis et al., 2007). Turbulent eddies can vary in size and magnitude (Watkins et al., 2006) and can be a major limiting factor in UAV performance, severely impacting altitude control in these environments (Mohamed et al., 2014). Our work shows that varying aerostructural response by morphing-induced changes in stiffness can constructively or destructively interfere with eddies over the wing's surface. As such, the flow control capabilities of an avian wing inspired multicomponent structure could be tuned for turbulent conditions as well.

Under the rapidly changing conditions of drone flight, wing morphing structural changes must be timed to have an effect exactly when they are needed which calls for rapid and accurate flow sensation built into the control algorithm (Patel & Kroo, 2006). Flow sensing is a relatively new field and sensors were historically simple and separate structures like pitot tubes or anemometers whose readings were localized to the location of the sensor (Fu et al., 2020). The flow field over a wing can vary to significantly affect aerodynamic performance at intermediate

Reynolds regimes (Tank et al., 2017) making distributed sensor arrays a valuable tool. In birds, the high spatial resolution of feathers and mechanosensors provides accurate sensing but is currently difficult to implement with artificial materials. Powering multiple independent panels would be energetically expensive and building sensors into a wing adds a great deal of manufacturing complexity. There is also the uncertainty around the performance of sensor arrays if one of the sensors were to fail (Mohamed et al., 2014). Birds clearly are capable of good flight performance even with the occasional feather loss, but it has been suggested that they compensate for this using other senses. Recent work using pressure sensor arrays over a wing have shown that strain and pressure data used by a closed-loop artificial neural network provides enough information for good estimation of angle of attack, flight speed, and aerodynamic forces and moments even during stall conditions or unsteady flow (Wood et al., 2019; Araujo-Estrada & Windsor, 2021). Therefore, despite the concerns around sensor arrays, they provide a clear advantage for flight control in small UAVs.

Vibration sensation and modification is a rich field of research outside of aircraft technology since vibrations are present in other mechanical equipment and building structures as well. Vibrations can be unwanted as they can disturb function, shorten service life, or cause catastrophic failure (Yan et al., 2020). But in other situations, vibrations may be encouraged, for example in the context of wind harvesters, flexible structures that convert the vibrations due to aerodynamic load to electrical energy (Abdelkefi, 2020). The mechanisms for aerostructural control using a coupled passive-active structural system proposed in this work could provide inspiration for vibration control in these fields as well. Semi-active vibration isolators with variable stiffness and damping have been found to provide the best and most adaptable functionality. Completely passive systems don't require energy input but only work well for high

frequency disturbances in the case of linear isolators or are too unstable in the case of nonlinear isolators (Yan et al., 2020). Active isolators react faster than passive isolators but the increase in control complexity increases costs, weight, and system size. Semi-active systems provide the best of both worlds with high reliability, performance, and adaptability (Zhao & Meng, 2020). Wind harvesters have been limited by the fact that dynamic structural behaviour is dependent on the vortex shedding frequency and the material's natural frequency. Therefore, combining intelligent systems with sensors to detect local airflow (Fu et al., 2020) and the ability to modify mechanical properties (Abdelkefi, 2016) like during avian wing morphing, could improve energy harvesting if the mechanical properties could be tuned to optimize oscillatory amplitude and frequency.

The avian wing, while by no means likely to be optimized for all its various functional requirements, nevertheless provides a source of inspiration for a structural system capable of tuning mechanical properties for flow control and sensing which has far-reaching applications in UAV flight, vibration isolation, energy harvesting, or perhaps all three (Anton & Inman, 2008) without much compromise to weight or control complexity (Bilgen et al., 2016).

5.2 Limitations and Future Directions

In this work, we propose that the avian wing structure enables local flow control via changes in mechanical properties and feather morphology for lift enhancement in a wing shape or gliding behaviour dependent manner. However, these findings are limited in scope as they are only valid for the specific tested conditions and aerodynamic parameters analysed, as well as by the assumptions made to simplify computational complexity.

Lift slope $\left(\frac{\partial C_L}{\partial \alpha}\right)$ and maximum lift-to-drag $\left(\frac{C_L}{C_D}\right)_{max}$ were used to evaluate aerodynamic performance, but aerodynamic performance is a vague and context-dependent concept and can be quantified with many other parameters such as thrust efficiency, drag at stall, and stability metrics. We used lift-based parameters under the assumption that in steady, forward gliding flight, lift production is generally preferable to extend time aloft and distance travelled. But we can make no conclusions on the flight performance in term of efficiency, accounting for muscular energetic input, or manoeuvrability. Lift-based parameters are commonly used in other flight research in animals and aircraft, so analysing our data with similar parameters facilitates comparison between our data and past studies. But to truly understand how avian wing structures affect flight performance in birds, further analysis would have to be done with other performance metrics. This would involve more computationally complex modelling. In Chapter 2, we used only lift slope as XFLR5 potential methods such as vortex lattice and panel methods assume inviscid flow to simplify the Navier-Stokes equations resulting in an underestimation of viscousbased drags. At low angles of attack, induced drag was also low due to the low value of lift leading to poor estimations of lift-to-drag. To analyse other performance metrics, either in-house numerical methods or commercial programs such as Ansys Fluent would be required.

Flapping flight and manoeuvrability are both major parts of bird flight and should be considered in discussions on avian flight performance. At the time of these experiments, Simflow was able to simulate flapping motion via a rotational motion around the wing root but was unable to model the more complex wing shape changes that occur during avian flapping flight. We also did not have measurements for inertial properties of individual feathers or the pigeon wing during morphing which are necessary for accurate analysis of flight

manoeuvrability. Recently, code for an analytical method to calculate inertial properties using geometric approximations has been made publicly available and could be used in the future to evaluate flight agility (Harvey et al., 2022 *in press*).

The bird's ability to use its wing structures adaptively in response to different environmental conditions is another aspect of performance to consider. In Chapter 3, we measured the mechanical properties of the wing in response to a 5Hz 4mm amplitude steady forced vibration, while in Chapter 4, the pigeon wing model was exposed to a steady flow at the low and high end of pigeon steady gliding speeds. However, birds are likely to encounter a wide variety of turbulence and gust amplitudes and frequencies. Therefore, we do not know how our active-passive structural system that couples changes in mechanical properties to wing shape would benefit flight under gust conditions. Expansion of Chapter 3 with a sweep of frequencies and amplitudes would allow us to properly characterize the dynamic response, which combined with *in vivo* measurements of feather vibration response of feathers at different air speeds and turbulence would define both the scope of variation in mechanical properties of the avian wing and the mechanical properties relevant to a free-flying bird. This information would be critical in determining if birds operate near their maximum capabilities or not and the necessity of their wing structural system.

The most important limitation that must be addressed before we explore other performance metrics is simplified wing shape used in our computational model. At intermediate Reynolds numbers ($Re \sim 10^4 - 10^6$), computational outputs may not agree with experimental results as flow in this Reynolds regime is highly sensitive to initial conditions and boundary layer behaviour (Tank et al., 2014). Our pigeon wing model was simplified to have constant thickness, no camber, and be isotropic. Avian wings are made up of multiple components such as

skeletal elements, striated and smooth muscle with active and dynamic behaviour, and feathers with varying shapes and mechanical properties within a feather and within a wing. To give strength to the conclusions in this thesis, a more realistic model or experimental validation will be needed. A more realistic computational model is currently being explored as an immediate follow-up to this work.

5.3 Summary

In conclusion, this thesis examined the relevance of individual feather morphology and their structural arrangement during wing morphing in controlling local flow patters via aerostructural responses and the effects on flight performance. We found that:

- Aerodynamic performance is a stronger selective pressure for 2D feather shape variation compared to the feather's location on the wing, the feather type, or phylogenetic relatedness.
- (2) Wing folding increases local stiffness and work absorption in the proximal wing compared to the distal wing, but damping is consistent in both the proximal and distal wing regardless of wing shape despite stemming from different mechanisms.
- (3) An extended wing at low speeds experiences structural deformations in sync with flow vortices shed from the leading edge, delaying boundary layer separation and enhancing lift.
- (4) An extended wing gliding at low speeds performs better with lower stiffness whereas a folded wing gliding at high speeds performs better with higher stiffness.
- (5) The avian wing is a complex system of interaction structures that allows for aerostructural tuning to modify lift and drag to suit flight behaviour.

These findings provide a useful starting point for future work on flow control and flow sensation through dynamic aerostructural responses in morphing wings in birds or UAVs.

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163

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166

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